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Emissions of methane and other biogenic volatile organic compounds from boreal peatlands

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Academic dissertation

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ABSTRACT

This study aims to 1) quantify the spatial and temporal variation in diffusive and ebullitive methane fluxes, and to 2) assess the quantity and quality of BVOC emissions and how they are controlled by vegetation composition and environmental factors in boreal peatlands.

Methane fluxes were measured with static chambers and bubble traps from a boreal ombrotrophic bog and compared to eddy covariance measurements on the ecosystem level. BVOC emissions were measured with dynamic chambers from the same boreal bog and a nearby boreal fen. Vegetation removal treatments were applied to differentiate BVOC emissions from intact vegetation, mosses, and peat.

Both methane and BVOC emissions showed strong seasonality linked to temperature and vegetation phenology. While diffusive methane fluxes did not differ between three years or different plant community types, methane ebullition was highest during the wettest of the three years studied and varied spatially being greater from open water pools than from wet bare peat surfaces. Decrease in water table led to higher ebullition, but so did also increase in air pressure. In total, ebullition contributed only 2 % – 8 % to the methane emission on the ecosystem level, which supports the general paradigm that diffusion through peat and aerenchymatous plants are the main pathways for methane from peat to the atmosphere.

Isoprene was the most emitted BVOC from both peatlands. Isoprene emission was strongly linked to sedges, and thus isoprene and total BVOC emission rates were higher in the sedge-dominated fen than the shrub-dominated bog. Moreover, total BVOC and isoprene emissions were highest from intact vegetation. However, organic halide emissions had stronger link with water level as they were absent during exceptional drought in the summer 2018. Therefore, warming climate and associated drougths and shrubification are likely to alter the quality and quantity of BVOCs emitted from boreal peatlands.

Keywords: shrub, ebullition, moss, peat, sedge, vegetation composition

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Joensuu, 8th November 2022
Elisa Männistö

LIST OF ORIGINAL PUBLICATIONS

This thesis is based on data presented in the following articles, referred to by the Roman Numerals I-III. The articles I and II are reprinted with the permission of the publisher. The article III is a submitted version of the manuscript.

I Korrensalo A, Männistö E, Alekseychik P, Mammarella I, Rinne J, Vesala T, Tuittila E-S (2018) Small spatial variability in methane emission measured from a wet patterned boreal bog. Biogeosciences 15: 1749–1761. https://doi.org/10.5194/bg-15-1749-2018.

II Männistö E, Korrensalo A, Alekseychik P, Mammarella I, Peltola O, Vesala T, Tuittila E-S (2019) Multi-year methane ebullition measurements from water and bare peat surfaces of a patterned boreal bog. Biogeosciences 16: 2409–2421. https://doi.org/10.5194/bg-16-2409-2019.

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The above publications have been included at the end of this thesis with their copyright holders' permission.

AUTHOR’S CONTRIBUTION

Elisa Männistö is fully responsible for the summary of this doctoral thesis.

I) E. Männistö participated in conducting the data analysis. In the writing she shared the main authorship with A. Korrensalo while all other authors contributed.

II) E. Männistö participated in conducting the ebullition measurements and the data analysis. In the writing she acted as the main author with contribution of all other authors.

III) E. Männistö participated in planning of the study and the data analysis. She conducted the BVOC measurements and served as the main author of the manuscript with contributions from other authors.

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ABBREVIATIONS

BP	bare peat surface
BVOC	biogenic volatile organic compounds
C	carbon
CH_4	methane
CLR	*Carex lasiocarpa*/*rostrata* lawn
CO_2	carbon dioxide
EC	eddy covariance technique
E-DMNT	(E)-4,8-dimethyl-1,3,7-nonatriene
EW	water's edge
GLV	green leaf volatiles
HHU	high hummock
HL	high lawn
HO	hollow
HU	hummock
L	lawn
LAI	leaf area index
MP	study plot with Moss + bare Peat
OW	open water
P	study plot with bare Peat
PAR	photosynthetically active radiation
SOA	secondary organic aerosols
VMP	study plot with Vascular plants + Moss + bare Peat
W	water pool
WT	water table

1. INTRODUCTION

1.1. Peatlands and their greenhouse gas dynamics

Peatlands are wetland ecosystems that have important dynamic interaction with the atmosphere through gaseous carbon exchange of carbon dioxide (CO_2), methane (CH_4) and biogenic volatile organic compounds (BVOC). Peatland ecosystems are defined by their high water table and the consequent accumulation of organic material as peat. Because of the anaerobic conditions under water table, organic material is decomposed only partially and thus part of the carbon taken up as CO_2 from the atmosphere by plants during photosynthesis is stored in forming peat layers that can be several meters deep (Rydin and Jeglum, 2013). Therefore, peatlands are globally important carbon sinks with net carbon accumulation rate of 76 Tg C per year (Gorham, 1991) and have a major role in climate regulation. As peatland formation is contributed by cool and wet climate, around 87 % of the world's peatlands, c. 3.5×10^6 km^2, are located in boreal and sub-arctic regions in Fennoscandia, Russia and North America (Joosten and Clarke, 2002). The carbon storage of boreal and sub-arctic peatlands is estimated to be up to 450 Pg C, which is 1/3 of global soil carbon pool and equivalent of 75 % atmospheric carbon (Strack, 2008).

While high water table enables carbon storage through peat formation, it also creates favourable environment for production of methane that is a potent climate warming greenhouse gas in the atmosphere (IPCC, 2014). In the anoxic conditions below water table methanogenic microbes (Archaea) take part in decomposing organic matter without oxygen and generate methane as a metabolite in their energy production (Whalen, 2005). Consequently, peatlands are the largest natural source of methane with annual release of 20 – 45 Tg CH_4-C to the atmosphere (Gorham, 1991; Mikaloff Fletcher et al., 2004). Currently, boreal peatlands act as net sinks for atmospheric carbon (Yu, 2012), but due to methane emissions they can potentially have a climate warming impact as methane is 25 times more efficient than CO_2 in trapping heat in the atmosphere on a time scale of 100 years (Lelieveld et al., 1998). After several stable years, the global atmospheric methane concentration started rising rapidly in 2007 and it was further accelerated in 2014 (Nisbet et al., 2016; Nisbet et al., 2019). Although the causes for this continuing increase are poorly understood, the carbon isotope ratio of atmospheric methane has been changing at the same time, which suggests that at least part of the additional methane is emitted from microbial sources, such as wetlands (Nisbet et al., 2016; Nisbet et al., 2019).

A large part of produced methane is oxidized in the aerobic peat layer above water table by methanotrophic bacteria before entering the atmosphere (Hanson and Hanson, 1996; LeMer and Roger, 2001; Larmola et al., 2010) but the proportion oxidized depends on the transportation mode of methane from the peat to the atmosphere. There are three routes via which methane is emitted from the peatland: by diffusion through peat, diffusion through aerenchymatous vascular plants and by episodic bubble release, i.e., ebullition (LeMer and Roger, 2001; Raghoebarsing et al., 2005). Part of diffusive methane is oxidized when moving through aerated peat matrix and *Sphagnum* mosses to the atmosphere unless the surface of peatland is saturated with water (Hanson and Hanson, 1996; LeMer and Roger, 2001; Larmola et al., 2010), but the circumstances are different for the plant and bubble mediated methane fluxes. Hollow aerenchymatous tissue characteristic to sedges and other peatland plants growing in wet conditions enables transportation of oxygen from the atmosphere to the roots under water table (Wießner et al., 2002). At the same time, it also offers methane a pathway that bypasses the microbial consumption in the upper peat layer (Bhullar et al., 2013). Similarly, ebullition that can occur everywhere in a peatland but is more frequent from wet surfaces, such as open water pools and bare peat surfaces, releases methane directly to the atmosphere (LeMer and Roger, 2001). Thus, these two transportation routes have potential to lead to high methane emissions. The processes of methane production, consumption, and transport themselves are affected by water table that determines the thickness of aerobic and anaerobic peat layers (Dise et al., 1993) and regulates the hydrostatic pressure on peat (Chen and Slater, 2015), temperature that influences microbial activity as well as diffusion rate and solubility of methane (Dunfield et al., 1993; Strack et al., 2005), pH (Dunfield et al., 1993; Dedysh, 2002), quality and quantity of available substrate (Ström et al., 2003), and the type and productivity of vegetation (Bubier, 1995; Waddington et al., 1996; Joabsson et al., 1999). Additionally, atmospheric pressure and incoming energy flux can impact methane ebullition rate (Tokida et al., 2005; Comas et al., 2011; Chen and Slater, 2015).

In addition to methane, peatlands are also sources of other BVOCs, a versatile group of reactive hydrocarbons that in the atmosphere take part in climate regulation. Because of their reactivity, BVOCs impact the atmospheric chemistry in various ways, which can have both cooling and warming effect on the climate. In the lower atmosphere, troposphere, BVOCs contribute to the formation of secondary organic aerosols (SOA) (Hoffman, 1997; Virtanen et al., 2010; Kulmala et al., 2014) that play an important role in cloud formation having thus in total a negative radiative forcing effect that can mitigate the climate warming (Paasonen et al., 2013). However, BVOCs contribute also to the formation of tropospheric ozone (O_3) that acts as a climate warming greenhouse gas (Atkinson, 2000) and they prolong the lifetime of methane in the atmosphere by competing for the hydroxyl (OH) radicals that oxidize the compounds (Kaplan et al., 2006). While volatile organic compounds are generally released from both anthropogenic and natural processes, the dominant source of the total global emission is terrestrial vegetation with annual BVOC emission rate of 700-1000 Tg C (Guenther et al., 1995; Laothawornkitkul et al., 2009). Plants release BVOCs for complex reasons, as it is their way to communicate with other plants and organisms, attract pollinators, and defend themselves against biotic and abiotic stress factors, such as herbivory, pathogens, and severe environmental conditions (Bouwmeester et al., 2019). Hence, BVOCs are emitted from many different parts of plants, for example flowers, stems, roots, and leaf litter, but most of the BVOC emissions are from leaves (Guenther et al., 2012). Production and emission of BVOCs are controlled by temperature and/or light depending on the compound (Guenther et al., 1995; Hantson et al., 2017). Global BVOC emissions from vegetation are dominated by isoprene (2-methyl-1,3-butadiene; C_5H_8) that is the most emitted compound also from boreal and sub-arctic peatlands (e.g., Janson and De Serves, 1998; Haapanala et al., 2006; Tiiva et al., 2007a). However, BVOC studies in boreal ecosystems have mainly concentrated on forests that are major sources of other globally significant BVOCs, monoterpenes (C_{10}), and emit less isoprene (e.g., Cleveland & Yavitt, 1998; Aaltonen et al., 2013; Mäki et al., 2017; Hellén et al., 2018 and the references therein). While forests have been found to have important BVOC-mediated cooling impact for both boreal and arctic regions (Sporre et al. 2019; Yli-Juuti et al., 2021), the BVOC dynamics of peatlands are not yet well known.

Besides vascular plants, also mosses and soil are known to release BVOCs (Hanson et al. 1999; Hellen et al., 2006; Tiiva et al., 2009; Ekberg et al. 2011; Faubert et al., 2010b; Guenther et al., 2012; Aaltonen et al., 2013; Ramirez et al., 2010; Kramshøj et al., 2018). *Sphagnum* mosses that are key element in peatland vegetation have been shown to emit isoprene (Hanson et al. 1999; Hellen et al., 2006; Tiiva et al., 2009; Ekberg et al. 2011) as well as monoterpenes, sesquiterpenes (C_{15}) and other BVOCs (Faubert et al., 2010b). Soil and decaying litter are known to release BVOCs in boreal forests and arctic tundra (Guenther et al., 2012; Aaltonen et al., 2013; Ramirez et al., 2010; Kramshøj et al., 2018), and soil emissions can make up a significant proportion of the ecosystem scale BVOC emissions in treeless ecosystems (Kramshøj et al., 2016; Kramshøj et al., 2018; Li et al., 2020). However, the roles of vegetation and peat in peatland BVOC emissions have not been extensively partitioned in the field so far. Based on sedge removal from one plot and removal of all vegetation from another plot Hellén et al. (2006) suggested *Sphagnum* mosses to be the main isoprene source in a boreal fen. Otherwise BVOC emissions from intact vegetation, moss and peat have been measured in laboratory incubation studies of bog microcosms, which showed that peat contributed less than 10% to total isoprene emission from dry hummocks and wet hollows (Tiiva et al., 2009), and that peat released different mixture of BVOCs than vegetation (Faubert et al., 2010b). These studies show that vegetation composition and peat have important effects on peatland BVOC emissions and more research in the field and different peatland types is needed to fully understand the roles of vascular plants, mosses, and soil in peatland BVOC emissions.

1.2. Variation in the boreal peatland vegetation

Boreal peatlands are divided into two main types, fen and bog, based on their water and nutrient availability. Fens are minerotrophic peatlands that receive water and nutrients from the surrounding mineral soil, whereas bogs are ombrotrophic receiving water and nutrients only through atmospheric deposition (Vitt, 2006). Therefore, bogs are nutrient poor, while fen ecosystems can vary in their nutrient status from poor oligotrophic to rich eutrophic fens (Vitt, 2006). Due to these differences in their water and nutrient conditions, fen and bog ecosystems differ also in their vegetation composition (Vitt, 2006). Generally, bog vegetation is dominated by *Sphagnum* mosses and dwarf-shrubs, whereas different sedges are the most typical feature of fen vegetation.

Spatial variation of vegetation along the water table gradient is characteristic to boreal peatlands. This results in varying surface topography of hummocks rising above the mean water table, intermediate lawns, wet hollows, and open water pools (Rydin and Jeglum, 2013). The ground layer of nutrient poor boreal peatlands is dominated by *Sphagnum* mosses with different species adapted to different moisture and nutrient conditions, which drives the formation of varying surface types. *Sphagnum* mosses growing on hummocks can better retain water and have higher productivity in nutrient poor conditions, which allows them to grow above the mean water table relative to the average moss surface (Hayward and Clymo, 1982; Van Breemen, 1995). Species growing on intermediate lawns can utilize CO_2 from decomposition below and thus rise above and won the competition against hollow *Sphagna* (Smolders et al., 2001) that are limited to grow in wet surfaces due to their low drought tolerance (Van Breemen,1995; Väliranta et al., 2007). These differences between *Sphagnum* species create varying habitats among the water table favouring different vascular plants. Higher and drier hummocks have thicker layer of aerated peat enabling the growth of dwarf-shrubs that are better adapted to drought conditions than other peatland plants, but whose roots require aerobic soil conditions (Small 1972a and 1972b). In contrast, sedges do not tolerate drought as well but can grow in wet surfaces, such as hollows, because their aerenchymatous tissue allows oxygen transportation to roots (Wießner et al., 2002). The result of these compositional differences in vegetation is a mosaic of different plant community types within a boreal peatland ecosystem.

1.3. Variation in the boreal peatland methane and BVOC fluxes

Spatial variation of vegetation and water table can potentially affect the methane flux rates of boreal peatlands. As the position of water table determines the thickness of aerobic and anaerobic peat layers, the higher the water table position, the thinner is the aerobic peat layer for methane consumption, while the anaerobic conditions for methane production are also situated closer to the peatland surface. Additionally, wet surfaces have typically more aerenchymatous vegetation and suitable conditions for ebullition, both of which can transport methane directly to the atmosphere. In contrast, plant community types with deeper water table such as hummocks can have the anaerobic methane production layer relatively deep under tens of centimeters of aerated peat and very little aerenchymatous vegetation. Therefore, lawns and hollows are generally considered to have higher methane emissions than hummocks (e.g., Bubier et al., 2005; Waddington and Roulet, 1996; Saarnio et al., 1997; MacDonald et al., 1998; Frenzel and Karofeld, 2000; Laine et al., 2007). However, in a compilation study the maximum methane fluxes were found to originate from surfaces with intermediate water table instead of the wettest surfaces (Turetsky et al., 2014). So far, most studies quantifying the diffusive methane fluxes have been conducted in fens that have more nutrients and aerenchymatous vegetation (Turetsky et al., 2014), while studies of spatial variation in methane fluxes in boreal bogs with more pronounced microtopography are scarce (see however, Waddington and Roulet, 1996; Frenzel and Karofeld, 2000; Laine et al., 2007). Moreover, only one of these studies considered methane ebullition (Frenzel and Karofeld, 2000), which spatial variation and contribution to the total ecosystem methane emission are still poorly known. Only few studies have directly quantified methane ebullition from waterlogged surfaces in boreal peatlands with gas traps (Hamilton et al. 1994; Strack et al., 2005; Strack and Waddington, 2008; Stamp et al., 2013) or estimated ebullition rates from steady chamber measurements (Riutta et al., 2007; Tokida et al., 2007; Goodrich et al., 2011). Furthermore, studies of the contribution of ebullition to the total methane emission have shown contrasting results, as the role of ebullition has been found to be either small (Riutta et al., 2007; Green and Baird, 2013) or even up to 50 % of the total emission (Christensen et al., 2003; Tokida, 2007).

Vegetation composition has been linked also to peatland BVOC emissions, although this link is still weakly established. Different plant species are known to release different composition of BVOCs (Helmig et al., 1999; Kesselmeier and Staudt, 1999; Duhl et al., 2008), and the main plant functional types of boreal peatlands, dwarf shrubs, sedges, and grasses, have been found to differ in their BVOC emissions (Klinger et al., 2002; Rinnan et al., 2005; Tiiva et al., 2007; Tiiva et al., 2009; Faubert et al., 2010b). Thus, the quality and quantity of BVOC emissions can be expected to be different between fen and bog ecosystems. This was indicated by the results of Klinger et al. (1994) from Hudson Bay lowland suggesting that peatland isoprene and terpene emissions increase along the successional gradient from fens to bogs. However, most of the following BVOC studies have concentrated on fens (Janson and de Serves, 1998; Janson et al., 1999; Rinnan et al., 2005; Hellén et al., 2006; Faubert et al., 2010a; Holst et al., 2010; Lindwall et al., 2016; Seco et al., 2020; Hellén et al., 2020), while the only studies regarding bog ecosystems have been conducted as laboratory incubations (Tiiva et al., 2009; Faubert et al., 2010b; Faubert et al., 2011). No studies so far have compared the BVOC emissions of the two peatland types.

In addition to quantifying the BVOC emissions from different peatland ecosystems, it is important to partition the role of vascular plants, mosses, and soil to understand how these different ecosystem components contribute to the total peatland BVOC emission. Besides vascular plants, both mosses and soil can release a diversity of BVOCs (Tiiva et al., 2009; Faubert et al., 2010b). *Sphagnum* mosses have been found to emit isoprene (Hanson et al. 1999; Hellén et al., 2006; Tiiva et al., 2009; Ekberg et al. 2011) as well as monoterpenes, sesquiterpenes and other BVOCs (Faubert et al., 2010b). Also peat has been shown in laboratory incubations to be a source of isoprene (Tiiva et al., 2009) and various other BVOCs that can be released from peat in different mixtures than from vegetation (Faubert et al., 2010b). Studies identifying the BVOC emissions from these different ecosystem components in the field are still lacking and needed to understand the BVOC dynamics of different peatland ecosystems under the changing climate.

1.4. Boreal peatlands under climate change

The ongoing global warming has been estimated to increase temperature and change the length and intensity of fluctuations in moisture conditions in the boreal region (IPCC, 2014). This has been predicted to decrease the water table of boreal peatlands, which alters their vegetation composition towards more dwarf-shrub dominated communities (Breeuwer et al., 2009; Kokkonen et al., 2019). Especially fens have been shown to undergo fast species turnover (Kokkonen et al., 2019), but also the dwarf-shrub cover of bog vegetation that is more resilient to change can increase (Breeuwer et al., 2009; Kokkonen et al., 2019). Decreasing water table and changes in vegetation have potential to lower the methane emissions from boreal bogs but predictions of these effects require understanding of contributions of different plant community types and ebullition to the total methane flux of the whole ecosystem. However, the quantity of methane emitted from peatlands, and especially the magnitude of ebullition, form the largest uncertainty in current models of the global methane budget that are needed to predict the effect of climate change on different ecosystems and their feedback to climate regulation (Riley et al., 2011; Melton et al., 2013; Peltola et al., 2018). Additionally, changing vegetation composition can also significantly affect the BVOC dynamics of peatland ecosystems, which may have further impact on climate regulation. As these connections are still poorly known, more knowledge of quality and quantity of BVOCs emitted from different ecosystem components and peatland types are needed to build even more elaborate climate models.

1.5. Aims of the study

This study aims to link the variation of methane and BVOC fluxes in a boreal peatland ecosystem to variation in vegetation. This supports the prediction of these fluxes under the vegetation change that is driven by changing climate and land use. I expected plant species composition to regulate methane and BVOC emissions together with seasonally varying environmental conditions. The study was carried out in a fen and a bog sites of a single boreal peatland complex as three sub-studies that aim to quantify I) diffusive methane emissions in different plant community types and II) methane emitted as ebullition from water and bare peat surfaces of a boreal bog, and to III) define the chemical composition of BVOCs emitted from fen and bog as well as quantify the rate of BVOC emissions from vascular plants, mosses, and peat. Finally, I discuss the implications of my results in connection to climate change.

2. MATERIALS AND METHODS

2.1. Site description

Data collection was conducted on two study sites that represent the main boreal peatland types, a sedge-dominated minerotrophic fen, and a *Sphagnum* moss -dominated ombrotrophic bog. The study sites are located in a large oligotrophic peatland complex, Siikaneva, in Ruovesi, Southern Finland (61°50’N, 24°12’E), 160 m a.s.l., which is situated within the southern boreal vegetation zone (Fig. 1, Ahti et al., 1968). The study sites are located c. 6 km west from the Juupajoki-Hyytiälä weather station, and the bog site is located 1.3 km northwest form the fen site. According to the 30-year averages from the weather station, annual rainfall is 707 mm, the annual temperature sum (base temperature of 5 °C) is 1318 degree days, and the average annual, January and July temperatures are 4.2 °C, -7.2 °C and 17.1 °C, respectively.

Imagery ©2022 CNES / Airbus, Landsat / Copernicus, Maxar Technologies, Map data ©2022 1 km

Figure 1. The locations of the two study sites, sedge-dominated minerotrophic fen and *Sphagnum* moss -dominated ombrotrophic bog, in Siikaneva peatland complex in Southern Finland (Map: Google Maps).

Both study sites have spatial variation of vegetation in relation to water table that is characteristic to boreal peatlands. This variation is more pronounced in the bog site where microtopography varies from open water pools and bare peat surfaces to hollows, lawns and hummocks that are covered by *Sphagnum* mosses. *Rhynchospora alba* (L.) Vahl. is the only species growing in bare peat surfaces, while in wet hollows the vegetation consists of *Sphagnum cuspidatum* Ehrh. ex Hoffm., *Sphagnum majus* (Russow) C.E.O. Jensen, *Carex limosa* L., *R. alba* and *Scheuchzeria palustris* L. In intermediate lawns moss carpet is formed by *Sphagnum magellanicum* Brid. (recently divided into two separate species *Sphagnum divinum* Flatberg & K. Hassel and *Sphagnum medium* Limpr.), *Sphagnum papillosum* Lindb. and *Sphagnum rubellum* Wils. and the dominating vascular species are *Eriophorum vaginatum* L., *Andromeda polifolia* L. and *Vaccinium oxycoccos* L.. Moss carpet in dry hummocks is dominated by *Sphagnum fuscum* (Schimp.) H. Klinggr., *Sphagnum angustifolium* (C.E.O. Jensen ex Russow) C.E.O. Jensen and *S. rubellum*, and dwarf-shrubs *Betula nana* L., *Calluna vulgaris* (L.) Hull, *Empetrum nigrum* L. and *V. oxycoccos*.

In the fen site microtopography varies from wet hollows to dry hummocks with different sedges dominated lawns being the most prominent part of the landscape. The most common species in hollows are *S. majus*, *S. papillosum*, *C. limosa* and *S. palustris*. In lawns, mosses *S. papillosum*, *Sphagnum fallax* (Klinggr.) Klinggr. and *S. angustifolium* form carpets while vascular vegetation is dominated by *E. vaginatum*, *Carex lasiocarpa* Ehrh., *Carex rostrata* Stokes, *Carex pauciflora* Lightf. and *A. polifolia*. Hummocks also have moss carpets of *S. papillosum*, *S. angustifolium* and S. *fallax*, and dwarf-shrubs *A. polifolia*, *B. nana*, *Rubus chamaemorus* L. and *V. oxycoccos* cover majority of the vascular plant layer.

Methane flux measurements for the sub-studies I and II were conducted in the bog site, while the BVOC fluxes in the sub-study III were measured from both the fen and the bog sites. Data for the sub-study I was collected during the growing seasons 2012 – 2014, for the sub-study II during the growing seasons 2014 – 2016, and for the sub-study III in 2017 – 2018, respectively.

An eddy covariance (EC) tower for measuring CO_2, methane and water fluxes on the ecosystem level was placed in the middle of the study site in the bog during 2012 – 2016. The study area was located within a radius of 30 m around the EC tower, where majority of the fluxes measured by the tower was estimated to originate.

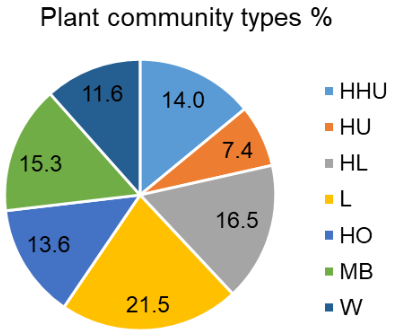

Figure 2. Proportions (percentage cover) of different plant community types in Siikaneva bog. High hummock (HHU), hummock (HU), high lawn (HL), lawn (L), hollow (HO), bare peat surfaces (BP) and open water pools (W).

For the sub-study I, 18 permanent measurement plots were established in the bog study area around the EC tower in three groups. Each group consisted of six plots that covered the spatial variation of different plant community types characteristic to the site: high hummock (HHU), hummock (HU), high lawn (HL), lawn (L), hollow (HO) and bare peat surface (BP) (Fig. 2). Boardwalks were built around all the measurement plots and the EC tower to allow measurements with minimum disturbance to the vegetation and peat.

For the sub-study II, gas traps were placed outside the measurement plots in bare peat surfaces and open water pools next to the boardwalks in the bog site.

Additionally, five new permanent measurement plot clusters with vegetation removal treatment were established next to already existing boardwalks in 2016 in both sites (altogether 10 clusters) to separate vascular plants, mosses and peat for the sub-study III. These measurement plots represented the most characteristic vegetation type of each site, lawn dominated by sedges *C. lasiocarpa* and *C. rostrata* (CLR) in the fen site, and hummock (HU) dominated by dwarf-shrubs in the bog site. Each plot cluster consisted of three plots, one of which had intact vegetation (Vascular+Moss+Peat=VMP), one had mosses and peat as vascular plants were removed (Moss+Peat=MP), and one had bare peat surface (Peat=P) were both vascular plants and mosses were removed (Fig. 3).

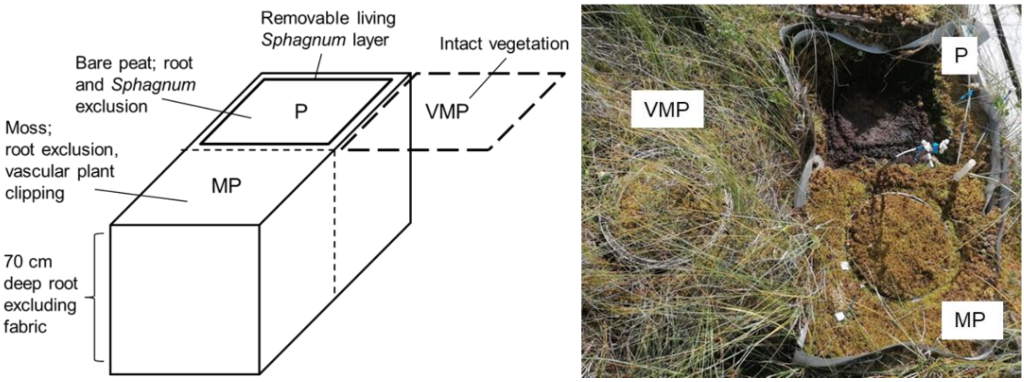

Figure 3. Experimental design of the study plot clusters to separate the ecosystem components of intact vegetation (Vascular+Moss+Peat=VMP), moss and peat (Moss+Peat=MP), and peat (Peat=P). Five replicate plot clusters were established in both Siikaneva fen and bog sites in 2016 for the sub-study III.

2.2. Vegetation measurements

To link methane fluxes and BVOC emissions to temporal and spatial variation in vegetation, leaf area of each vascular plant species was measured biweekly over the growing seasons for the 18 permanent sample plots in 2012 – 2014 (sub-study I) and for the ten VMP plots in 2017 – 2018 (sub-study III) following Wilson et al. (2007) and as presented in detail in I and III. Total LAI of all species (LAI_{TOT}) and LAI of aerenchymatous species (LAI_{AER}) were calculated for the statistical analyses in sub-study I. LAI_{AER} consisted of the leaf area of the five aerenchymatous species growing in the bog site, *C. limosa*, *E. vaginatum*, *R. alba*, *S. palustris* and *Trichophorum cespitosum* (L.) Hartm. Similarly, LAI_{TOT} of all species was calculated for the statistical analyzes in the sub-study III.

To describe the vegetation composition in the ten new plot clusters, area covered (%) by each vascular and moss species was estimated visually for all the VMP plots during the growing season maximum in August 2016. The species cover estimation was conducted again during the peak season in August 2018.

2.3. Methane measurements and data analysis

2.3.1. Diffusive methane flux measurements with chambers (I)

Diffusive methane fluxes between the six different plant community types and the atmosphere were measured with the static chamber method (Alm et al., 2007) in Siikaneva bog over the growing seasons of 2012–2014 as presented in detail in I. Temperature inside the chamber, peat temperature and water table (WT) at each plot was measured at the same time with the measurements. Methane flux (mg m^{-2} d^{-1}) during each measurement was then calculated as the linear change in methane concentration in relation to time and regarding the volume of and temperature in the chamber. Any nonlinear changes in concentration were excluded from the dataset (10.4 % of the measurements) as they were considered to result from ebullition or leak in the chamber. Spatial variation between the six plant community types as well as temporal variation within and between years of methane fluxes and environmental variables were tested with linear mixed-effects models using the function lme of the package *nlme* of R software (version 3.3.2).

2.3.2. Ebullition measurements from waterlogged surfaces (II)

Methane emissions released as bubbles from center and edge of open water pools (‘open water’, OW and ‘water’s edge’, EW) and bare peat surfaces (BP) of Siikaneva bog to the atmosphere were measured with floating gas traps over the growing seasons 2014–2016 (Fig. 4). A total of 16–20 gas traps were used depending on the year. More detailed description of the measurement is given in II.

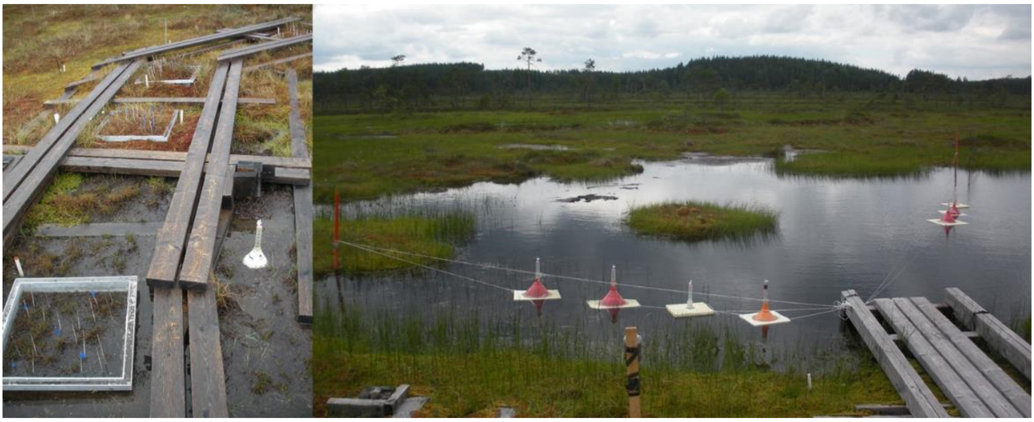

Figure 4. Study design for diffusive methane and ebullition measurements in Siikaneva bog. Study plots with square collars for static chamber measurements represented different vegetation community types from bare peat surfaces to high hummocks. Gas traps were used to measure methane ebullition from bare peat surfaces, as well as from edge and center of open water pools.

Average methane emission by ebullition was calculated separately for OW, EW and BP based on the area of the gas trap, number of days and volume of gas collected in each measurement period, and the average methane concentration of each measurement period. Finally, emissions were converted to mg m^{-2} d^{-1} by calculating methane density in each measurement period based on the average air temperature of the measurement period in degrees Celsius and the standard atmospheric air pressure, 101 325 Pa.

To link variation in ebullition to environmental variables, water table, water temperature, peat temperature and photosynthetically active radiation (PAR) were measured with data loggers at the site. Air temperature and pressure data for 2014–2016 were received from the Juupajoki-Hyytiälä weather station. Spatial and temporal variation in ebullition and the effect of the environmental variables on log-transformed ebullition flux rates were analysed with linear mixed-effects models using the function lme of the package *nlme* of the R software (version 3.3.2).

2.3.3. Upscaling the chamber and ebullition measurements to the ecosystem level (I-II)

To estimate the total amount of methane emitted from Siikaneva bog, methane fluxes measured with the static chambers and the gas traps were upscaled to the ecosystem level during the warmest months July and August in I and June, July, and August in II. Diffusive methane fluxes measured with the chambers were found to be similar among the six different plant community types (I), and therefore methane flux was interpolated to the ecosystem level as a mean of all the 18 sample plots. The upscaled flux was further weighted by the aerial cover of the six community types of the study area (88.4 %) (Fig. 2), which was based on vegetation inventories conducted over the 30 m radius study area in July 2012 and 2013 (Korrensalo, 2017). For upscaling the ebullition fluxes, total average ebullition flux was first calculated as a sum of average ebullition fluxes from open water pools and bare peat surfaces that were weighted with their relative surface area (11.6 % and 15.3 %) (Fig. 2). Total average ebullition flux was then interpolated linearly to the ecosystem level similarly to the chamber fluxes for June, July, and August each year.

2.3.4. Ecosystem level methane flux measurements with eddy covariance (I-II)

Continuous micrometeorological eddy covariance measurements were conducted in the center of the bog study site in 2012–2016 providing an independent ecosystem-scale estimate of methane fluxes that were compared with the upscaled chamber and ebullition fluxes. The eddy covariance measurement setup at the height of 2.4 m consisted of an ultrasonic anemometer (USA-1, Metek GmbH, Germany) and an open path methane concentration analyzer (LI-7700, LI-COR Biosciences, USA). The raw data was processed with EddyUH software that was also used to produce the 30 min average fluxes of latent heat, sensible heat, and methane (Mammarella et al., 2016). Standard EC data quality control (e.g., Aubinet et al., 2012) was performed using the software or manually, and the EC flux data during calm periods (friction velocity $u^* < 0.1$ ms^{-1}) were excluded from the analysis. Because of technical problems, flux quality filtering, or periods with insufficient turbulence, a large fraction of data (65 %) was missing from the EC flux series requiring gap-filling. This was done by first fitting a function to all three years of data,

$$F_{CH_4 mod} = a \cdot \exp\,(b \cdot T_{p20}) \qquad \text{Eq. (1)}$$

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 Siikaneva fen station, that also has an EC tower, or using linear interpolation, and spline-smoothed to eliminate diurnal-scale variability. This gave a general fit, based on which it was established that b=0.167 (95% CI [0.163, 0.170]). After that, *a* was determined for each year individually by fitting Eq. 1, 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.

2.3.5. Biogenic volatile organic compounds measurements

Biogenic volatile organic compounds (BVOC) emitted from intact vegetation (VMP), moss and peat (MP), and bare peat (P) were measured with dynamic chamber method from the plot clusters representing sedge dominated lawns (CLR) in the fen site (Fig. 5) and dwarf-shrub dominated hummocks (HU) in the bog site. Measurements were carried out over four campaigns, one in July 2017, and in three campaigns over the growing season 2018 as described in detail in III.

Figure 5. Biogenic volatile organic compounds (BVOC) measurement with dynamic chamber method from sedge dominated lawn in Siikaneva fen in 2018.

BVOC samples collected in 2017 were analysed with a thermodesorption instrument connected to a gas chromatograph in Finnish Meteorological Institute in Helsinki as described by Mäki et al. (2017). The samples collected in 2018 were analysed in University of Eastern Finland in Kuopio campus using a Perkin-Elmer ATD400 Automatic Thermal Desorption system (USA) that was connected to a Hewlett-Packard GC 6890 (Germany) gas chromatograph with a HP-5MS (60 m, 0.25 mm, 0.25 µm) column and a mass selective detector (Hewlett-Packard MSD 5973, USA). The 2018 samples were calibrated using isoprene, terpenoid, green leaf volatiles (GLV) and HC48 indoor air standards in methanol solution that were injected into sample tubes, methanol being then flushed away from the tubes with nitrogen (N_2) flow of 100 ml/min for 1 min. The flux rates (E, $\mu g\ m^{-2}\ h^{-1}$) of the different compounds were calculated for soil area (area inside the collar, m^2) and time (h) using Equation 2.

$$E = (C_{out} - C_{in})\ F_{chamber} \times 60 / A \qquad \text{Eq. (2)}$$

where C_{in} is the concentration of ingoing air sample ($\mu g\ m^{-3}$), C_{out} is the concentration of outgoing air sample ($\mu g\ m^{-3}$), $F_{chamber}$ ($m^3\ min^{-1}$) is the flow rate of air pumped into the chamber, and A (m^2) is the soil surface area inside the collar.

Based on the chemistry and function, detected BVOCs were classified into nine groups: hemiterpenes (isoprene), monoterpenoids (including both monoterpenes and oxygenated monoterpenes), sesquiterpenes, homoterpenes, alkanes, oxygenated alkanes, organic halides, benzenoids and green leaf volatiles (GLV) following Guenther et al. (2012). Only isoprene, monoterpenoids and sesquiterpenes were quantitated from the 2017 samples because of the standards used in their analyses. For the analyses, positive BVOC fluxes were transformed using the logarithmic transformation by Anderson et al. (2006), and compounds that were detected only once or twice (eight compounds) were excluded from the data. Negative fluxes indicating BVOC uptake were also excluded from the emission data and analysed separately. The data was statistically analysed in R (version 4.0.2) by fitting multivariate generalized linear models with negative binomial distribution using package *mvabund* (v4.1.9), linear mixed models using package *nlme* (v3.1-148) and principal component analyses (PCA) using package *FactoMineR* (v2.4) and visualized with the package *ggplot2* (v 3.3.3).

3. RESULTS

3.1. Spatial and temporal variation of methane fluxes

Methane emissions did not commonly differ between the six plant community types (Fig. 2 in I), although the plant community types were found to differ in their water table and vegetation (Fig. 1 in I). Only small spatial variability of methane fluxes was found as HU and HL had higher fluxes than HHU and BP in 2013, while methane fluxes from BP were higher than from HHU in 2014. Diffusive methane fluxes increased together with increasing peat temperature, $\mathrm{LAI_{TOT}}$ and $\mathrm{LAI_{AER}}$ (Fig. 4 in I) but they were not affected by water table. There were also no common differences in methane emissions between the three studied growing seasons (Fig. 2 and 3 in I), although the environmental variables differed between the years (Fig. 1 and Table 1 in I) with 2012 being the coolest and wettest year, while 2013 was the warmest and 2014 the driest. Methane emissions followed the same seasonal variation with vegetation and peat temperature increasing in spring until peaking in the middle of summer and starting to decrease towards autumn (Fig. 6). Additionally, negative net fluxes that indicate higher methane oxidation than production were detected occasionally every year, and from both dry and wet plant community types (Fig. 2 in I). In general, measured methane fluxes ranged from -309 to 1254 mg m^{-2} d^{-1}.

Higher methane ebullition was found from open water pools than from bare peat surfaces (Fig. 3 in II). There was further variation in ebullition rates within the pools as more bubbles were released from open water than from the water's edge (Fig. 3 in II). Ebullition was linked to the variation of several environmental factors. Primarily, ebullition increased with increasing peat temperature and decreasing water table (Fig. 4 in II). In addition, higher ebullition rates were connected to increasing atmospheric pressure during the weekly measurement period (Fig. 5 in II) and the weekly effective temperature sum denoting incoming energy flux. Similarly to the diffusive methane fluxes, ebullition followed the seasonal pattern of peat temperature (Fig. 5). There was also temporal variation in ebullition between the three studied years as the average ebullition flux rates were highest in the wettest year 2016, while the warmest and driest year 2014 and the coolest year 2015 did not differ from each other. Measured methane ebullition fluxes ranged 0–253, 0–147 and 0–186 mg m^{-2} d^{-1} with medians 2, 3 and 28 mg m^{-2} d^{-1} in 2014, 2015 and 2016, respectively.

3.2. Ecosystem-level methane fluxes

Diffusive methane fluxes upscaled to the ecosystem level were found to agree well with the ecosystem-level methane fluxes measured with the EC technique. The upscaled fluxes were the same order of magnitude as EC fluxes, and they both had the similar seasonal pattern following water table and peat temperature where the fluxes increased in the spring and had the highest peak in the middle of the summer before decreasing towards the autumn (Fig. 5). Even though the upscaled methane fluxes do not include ebullition as EC fluxes do, the upscaled fluxes were often higher than the EC fluxes, especially during the peak season (Fig. 5 in I). Ecosystem-level methane emissions upscaled from the chamber measurements for 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. The corresponding methane emissions measured with the EC were 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.

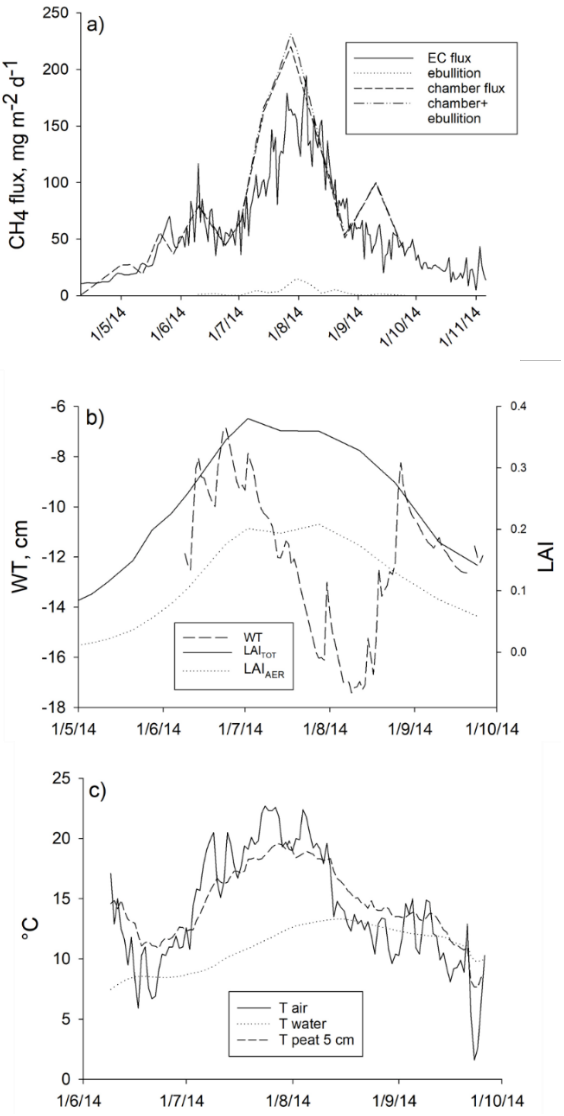

Figure 6. Ecosystem level methane (CH_4) fluxes (mg m^{-2} d^{-1}) and environmental conditions in Siikaneva bog during the growing season 2014. a) Diffusive methane fluxes measured with manual chambers (chamber flux) and methane released as bubbles from wet surfaces (ebullition) are upscaled to the ecosystem level and compared to the total methane flux measured with the eddy covariance technique (EC flux). Methane fluxes follow the seasonal trends of b) water table (WT), total leaf area index (LAI_{TOT}) and leaf area index of aerenchymatous vascular plants (LAI_{AER}), as well as c) temperatures of air (T air), water (T water), and peat in the depth of five centimeters (T peat 5 cm).

The amount of methane released from the bog site to the atmosphere as ebullition was found to be small when upscaled to the ecosystem level and compared to the EC and to the upscaled chamber measurements (Fig. 5). The upscaled ebullition fluxes were an order of magnitude lower than the EC fluxes each year (Fig. 6 and Table 3 in II) contributing 2–8 % to the EC flux. The total ecosystem methane flux combined from upscaled chamber and ebullition fluxes in 2014, thus considering all three emission routes of methane from peat to the atmosphere, was higher than the ecosystem-level EC flux, but both estimates followed the same seasonal pattern (Fig. 6 in II). The contribution of ebullition to the total upscaled methane flux during the peak season was found to be only 2–5 %.

3.3. Chemical composition and variation of BVOC fluxes

Both Siikaneva fen and bog sites were found to be sources of various BVOCs (III). Altogether 59 different compounds from nine different chemical groups (hemiterpenes, monoterpenoids, sesquiterpenes, homoterpenes, alkanes, oxygenated alkanes, organic halides, benzenoids, and GLV) were identified (Table 3 in III). Isoprene was the only detected hemiterpene and (E)-4,8-dimethyl-1,3,7-nonatriene (E-DMNT) was the only homoterpene. Additionally, we detected 25 compounds that were abundant in the samples but were not able to identify and quantify them with the used standards. These compounds included many sesquiterpenes that often had relatively high concentrations in the samples compared to majority of the identified compounds. As expected, isoprene was the most abundant compound emitted from both study sites and it had generally an order of magnitude higher emission rates than other BVOCs (Fig. 1 in III). Isoprene emission rate from intact vegetation (VMP) ranged from 0 to 717.5 $\mu g\ m^{-2}\ h^{-1}$ with mean 85.1 $\mu g\ m^{-2}\ h^{-1}$. VMP emitted most BVOCs with 56 detected compounds, while 46 compounds were found from moss and peat (MP) and 41 compounds from bare peat (P). However, there were four compounds that were found from surfaces were vascular plants were removed (MP and P) but not from VMP.

BVOCs were found to have strong variation within the growing season, as emissions peaked together with temperature and total leaf area of vascular plants. For all the BVOC groups, except for organic halides, higher emission rates were associated with the June/July campaign of 2018 when leaf area, temperature, and photosynthetically active radiation (PAR) were highest (Fig. 2 in III). All the same BVOC groups had lowest emission rates during the late autumn campaign conducted in October 2018, which further indicates the seasonality of the BVOC emissions (Fig. 2 and S3 in III).

The fen site was found to emit generally more BVOCs from intact vegetation than the bog site. This was mainly due to the emissions of isoprene and alkanes that were higher in the fen than in the bog site (Fig. S3 in III). Additionally, alkanes n-nonane, n-dodecane, n-tridecane and n-tetradecane were more abundant in the fen site but otherwise there were no differences between the sites in the emissions or abundance of the other BVOC groups.

Vegetation proved to be the key driver of BVOC emissions. Emissions of isoprene, monoterpenoids, sesquiterpenes, homoterpenes, and GLV correlated positively with total leaf area (Fig. 3 in III). Furthermore, isoprene and sesquiterpene emissions had a strong positive correlation with the leaf area of sedges, whereas higher monoterpenoid and homoterpene emissions were linked to higher leaf area of dwarf-shrubs (Fig. 3 in III).

The vegetation removal treatments revealed that BVOC emission mixtures differ between VMP, MP and P. BVOC emission rates were generally higher from VMP than from MP and P during the summer but no differences in the emissions between VMP, MP and P were found anymore in the autumn campaign when BVOC emission rates were generally low (Fig. 2 and S3 in III). Emissions of some BVOC groups differed between the treatments but not all.

Isoprene, sesquiterpene and homoterpene (E-DMNT) emissions were highest from VMP, except during the autumn when isoprene was emitted from P but not from vegetation. GLV were only found from vegetation and mainly from VMP as there were no emissions from P, and only one compound, 1-hexanol, was detected from MP in the fen site. VMP had also higher monoterpenoid emissions than P but they did not differ from monoterpenoid emissions from MP. Alkane emission from P was higher than from MP in the 10/2018 campaign, but generally there were no common differences in alkane emissions between the treatments. Finally, vegetation did not affect the emissions of oxygenated alkanes, organic halides and benzenoids (Fig. 3 and S3 in III).

Coincidentally, the growing season 2018 turned out to be exceptionally warm and dry in Northwestern Europe (Rinne et al., 2020). While temperature and vegetation regulated the BVOC emissions of most of the compound groups, organic halide fluxes were linked to water table (Fig. 2 and 3 in III). Organic halide emissions had a positive correlation with water table and were absent during the August campaign of 2018 when water table on both study sites was very low (Fig. 1, 3 and S3 in III).

4. DISCUSSION

4.1. Methane fluxes and their controls

Spatial variation of vegetation within peatland ecosystems has been linked to the variation in their methane fluxes (Bubier et al., 1993; Waddington and Roulet, 1996; Saarnio et al., 1997; MacDonald et al., 1998; Frenzel and Karofeld, 2000; Laine et al., 2007). In this study, diffusive methane emissions were found to be similar between highly varying plant community types over three consecutive growing seasons (I). This contradicts the hypothesis that methane emissions would be higher from wet plant community types that have thin aerobic peat layer for methane consumption and more aerenchymatous vegetation to transport methane from peat straight to the atmosphere, as found earlier in different peatland ecosystems (Bubier et al., 1993; Waddington and Roulet, 1996; Saarnio et al., 1997; MacDonald et al., 1998; Frenzel and Karofeld, 2000; Laine et al., 2007). However, the result of this study (I) is in line with the previous study that found the biomass production and net ecosystem exchange rates in the same bog site to also be similar between the plant community types, except for the bare peat surfaces that were small carbon sources (Korrensalo, 2017). Therefore, the evenness of carbon dynamics between different plant community types seems to be characteristic to the site. Unlike the diffusive methane fluxes, methane ebullition was found to vary spatially, as mean ebullition fluxes were higher from open water pools than from bare peat surfaces (II). Additionally, more methane bubbles were released from open water in the middle of the pools than from the water’s edge, which further indicates that wet conditions are stronger prerequisite for ebullition than the availability of fresh substrates for methanogenesis provided by vegetation (II).

Although no common differences in the diffusive methane fluxes between the different plant community types were found in this study, vegetation composition still influenced the flux rates as methane emissions increased together with both higher total leaf area and leaf area of aerenchymatous species (I). Aerenchymatous vascular plants are important conduits for methane from peat to the atmosphere allowing methane to bypass the aerobic consumption in the upper peat layer (Frenzel and Karofeld, 2000). While part of methane is known to be oxidized also in some plant species, such as rice (Bosse and Frenzel, 1997), significant methane oxidation in bog plants has not been detected (Frenzel and Rudolph, 1998). Instead, transport of methane through aerenchymatous plants has been shown to have a major contribution to the methane flux rate in boreal peatlands (Waddington et al., 1996; Frenzel and Karofeld, 2000; Korrensalo et al., 2021). In addition to the aerenchymatous leaf area, total leaf area further increase methane emissions in Siikaneva bog (I), which indicates the importance of substrate availability for methane production. Even though peatlands have organic soil, peat is often for a large part old and recalcitrant at the depths where methane is produced (Hogg, 1993; Christensen et al., 1999), and thus fresh organic material is needed as good quality substrate for methanogenesis. The found influence of both total and aerenchymatous leaf area may be one factor evening out the methane fluxes between the plant community types, because the dry types have high total leaf area despite their low aerenchymatous leaf area (I). Moreover, methane fluxes were shown to have strong seasonal pattern that follows the development of vegetation and temperature over the growing season (I). Because climate change will prolong the growing season in boreal regions due to rising mean temperature (IPCC, 2014), it can potentially increase methane emissions from peatlands.

Main explanation for the similar methane fluxes among different plant community types is likely found in the underlying processes of methane production and consumption that together control methane emissions rates. These processes are regulated by microbial communities in the peat that can strongly vary depending on the site in boreal bogs (Juottonen et al., 2015). Additionally, plant community type can affect the activity of microbial communities, but this effect is not consistent, and it can vary among bogs as well (Juottonen et al., 2015). Studying the microbial communities and their methane production and oxidation potentials in Siikaneva bog would add a missing piece to the puzzle of the methane dynamics of the site and further help revealing the controls of peatland methane fluxes.

Methane is consumed in the peat and *Sphagnum* mosses by methanotrophic bacteria that require aerobic conditions for methane oxidation (Hanson and Hanson, 1996; LeMer and Roger, 2001; Larmola et al., 2010). Plant community types adapted to drier conditions such as hummocks that rise high above the average water table have thick layer of aerated peat providing favorable habitat for methane oxidation, and thus hummocks can even serve as a sink for atmospheric methane (I; Frenzel and Karofeld, 2000). The activity of methane oxidation is usually highest near the average water table, where methanotrophs have an optimal availability of both methane and oxygen (Sundh et al., 1995; Dedysh, 2002). Therefore, negative net fluxes denoting methane consumption can be found also in plant community types adapted to wet conditions that have water table close to the soil surface when they are not waterlogged, as observed in this study (I). However, it is possible that part of the methane oxidation has been anaerobic (Smemo and Yavitt, 2007), which would also explain the two occasions of negative net fluxes taking place on waterlogged surface in this study (I). Microbial anaerobic methane oxidation has been regarded as the primary sink for methane in marine systems (Hoehler et al., 1994; Valentine 2002) and it has been shown to occur also in peatland ecosystems (Smemo and Yavitt, 2007; Gupta et al., 2013). While anaerobic oxidation is suggested to potentially have an important role in controlling methane fluxes of peatland ecosystems, its processes in peatlands are poorly known and require further studies (Smemo and Yavitt, 2007; Gupta et al., 2013; Miller et al., 2019). Without quantified knowledge of the underlying processes of methane production and consumption in the Siikaneva bog, it is not known how much of the negative net fluxes are explained by microbial aerobic and anaerobic methane oxidation.

Temperature is one of the most essential controls of peatland methane fluxes and methane emissions mainly increase together with increasing temperature. Rise in temperature increases the activity of both methanogenic and methanotrophic microbes, and while optimum temperature for both processes is around 20–30 °C, methane production has been found to be more temperature-dependent than methane consumption (Dunfield et al., 1993). Additionally, increasing temperature accelerates the rate of diffusive methane transport from peat to the atmosphere (Große, 1996), as well as decreases the solubility of methane, which increases bubble formation by transferring methane from aqueous to gaseous phase leading thus potentially to higher ebullition rate (Strack et al., 2005). This well documented effect of temperature on methane fluxes was also supported by this study, as increasing peat temperature was found to increase diffusive methane emissions (I) as well as ebullition (II). Moreover, higher incoming energy flux calculated as effective temperature sum also increased methane ebullition (II; Wik et al., 2014). These results indicate that rising mean temperature due to climate change will have a positive effect on the production and the transport rates controlling methane fluxes, and therefore potentially increase methane emissions from boreal peatlands.

The positive effect of rising temperature on methane emissions may be compensated by the changes in water table. Climate change has been predicted to lower water table in peatlands (Gorham, 1991; Roulet et al., 1992; Gong et al., 2012), which increases the thickness of aerated peat layer and can lead to higher methane consumption rate (Yrjälä et al., 2011). Although water table did not affect the methane fluxes from different plant community types in this study (I), one high hummock was found to occasionally serve as a methane sink in each three studied growing seasons. If mean water table in Siikaneva bog will get lower in the future due to climate warming, hummocks may turn from methane source to methane sink more regularly during the growing season. Lowering water table will also affect the ebullition rate, but its impact is different in the short term than in the long term. Generally, decreasing water table lowers the hydrostatic pressure in peat, which increases ebullition by increasing the volume of the gas phase of methane in peat (II; Tokida et al., 2007). This way the fluctuation of water table regulates ebullition rates on a seasonal level (II). However, bubble formation requires wet conditions, which is why ebullition is more frequent in waterlogged surfaces such as open water pools and bare peat surfaces. In this study, mean ebullitive methane flux rates were found to be higher during the wettest (2016) of the three studied growing seasons, especially from bare peat surfaces (II). While there was a peak in ebullition in the middle of the growing season in the warmest study year (2014), it was also the driest year and the mean ebullition level of bare peat surfaces remained low, respectively (II). These results indicate that sustained lowering of the water table can decrease peatland methane ebullition. Open water pools and bare peat surfaces cover together currently around 1/4 of the bog site, but drier conditions are likely to decrease their proportions in the future, which can further affect the methane emissions of the site. The found differences in ebullition rates between the growing seasons highlight the importance of multi-year studies in catching the inter-annual variation in ebullition fluxes that needs to be included in methane models.

This study supports the general paradigm that regards diffusion through peat and aerenchymatous vascular plants to be the dominant pathways of methane emissions from peat to the atmosphere (I, II; Bubier et al., 2005; Ström et al., 2005; Turetsky et al., 2014). The micrometeorological EC technique provides valuable information about the methane fluxes of the studied ecosystem, but it cannot differentiate the roles of different methane transportation routes or plant community types in the total flux. In this study, all these aspects were covered in the sampling in 2014, as diffusive methane fluxes from different plant community types were measured with the chamber technique (I) at the same time that methane ebullition was measured from waterlogged surfaces with the gas traps (II) and the eddy covariance tower was measuring the ecosystem-level methane flux (I, II). When the upscaled chamber and ebullition fluxes were combined for a total ecosystem methane flux of the bog site and compared to the eddy covariance measurements, the magnitude and seasonal pattern of both total fluxes were found to be similar (II). However, the contribution of ebullition to the upscaled total flux as well as to the eddy covariance flux were small, only 2–5 % during the peak season from June to August, whereas the upscaled chamber flux alone agreed well with the eddy covariance flux (II). These results were validated separately for both upscaled ebullition flux (II) and upscaled methane flux (I) that were compared to the eddy covariance flux with the same outcomes also in two other growing seasons. Bubbles are released from all plant community types beside the waterlogged surfaces, but their contribution to the total flux is negligible (II; Riutta et al., 2007), and thus ebullition from other plant communities than open water pools and bare peat surfaces were excluded from this study (II).

4.2. BVOCs and their controls

In addition to their features as important sinks for atmospheric carbon and sources of methane, the role of boreal peatlands in climate regulation is further complicated by them being sources of various BVOCs, which is the least known component. In this study, both minerotrophic fen and ombrotrophic bog were shown to be significant sources of isoprene as expected (III; Hellén et al., 2020.), and they emitted also numerous other BVOCs, some of which have not been reported before from boreal peatlands (III; Rinnan et al., 2005; Haapanala et al., 2006; Hellén et al., 2006; Faubert et al., 2010b), and some that could not yet be identified and quantified (III). These unidentified compounds included many sesquiterpenes that had often the next highest concentrations after isoprene in the samples (III). Recently, sesquiterpenes were newly found to dominate monoterpenes in BVOC emissions of a northern peatland (Hellén et al., 2020), which sides with this study. As there was also abundance of other compounds that remained unidentified for now, further studies with even more versatile standard compounds for reference would certainly still increase the understanding of the quality and quantity of BVOCs emitted from Siikaneva.

Similarly to the methane emissions, boreal peatland BVOC emissions have strong variation within growing season following the development of vegetation and temperature (III). Besides vegetation composition, temperature and light are important factors controlling the BVOC production and emissions (Guenther et al., 1993; Kesselmeier and Staudt, 1999; Peñuelas and Llusià, 2001; Duhl et al., 2008). Isoprene emission rate is directly dependent on temperature and light (Guenther et al., 1993), and emissions of other BVOCs are usually also regulated by one or both of these factors (Guenther et al., 1993; Kesselmeier and Staudt, 1999; Peñuelas and Llusià, 2001; Duhl et al., 2008). Accordingly, BVOC emissions of all groups except organic halides were found to be highest during the peak of the growing season, when leaf area was in its maximum and mean temperature was high (III). This seasonality of the emissions was further indicated by the lowest emission rates of almost all BVOC groups during the late autumn campaign when the temperature was low, and most vegetation had senesced (III). Therefore, warming climate and prolonging growing season in the boreal zone can lead to increased BVOC emissions from peatlands.

Our study was the first one to concurrently measure BVOC emissions from boreal fen and bog ecosystems, and it was found that total BVOC emission was higher in the fen than in the bog site from the plots with intact vegetation due to higher isoprene and alkane emissions in the fen site (III). Apart from few individual compounds, we did not find emissions of other BVOC groups to otherwise differ between the fen and the bog. The differences in BVOC emissions between the sites are likely linked to their different vegetation composition. Sedges that commonly dominate fen vegetation are known isoprene emitters (Ekberg et al., 2009), whereas dwarf-shrubs that are more abundant in bogs have been shown to emit more monoterpenes (Isebrands et al., 1999; Rinnan et al., 2005). This is in agreement with strong positive correlation between isoprene and sedge leaf area as well as between monoterpenoids and shrub leaf area that were found in this study and explains the higher isoprene emission from the sedge-dominated fen (III). As lowering water table can change vegetation composition of boreal fens from sedge-dominated towards higher cover of woody species (Kokkonen et al., 2019), climate change can lead to changes in quality and quantity of BVOCs emitted from fen ecosystems.

In this study, BVOC emissions from different ecosystem components of boreal peatlands – intact vegetation, mosses and peat, and bare peat – were systematically partitioned for the first time in the field with vegetation removal treatments (III). Intact vegetation, mosses, and peat each emit numerous BVOCs, and they can have different mixture of compounds (III; Tiiva et al., 2009; Faubert et al., 2010b). Vegetation removal affects the fluxes of some

BVOC groups but not all. Both vascular plants and *Sphagnum* mosses are known to emit isoprene (Ekberg et al., 2009; Ekberg et al., 2011) and its emissions add up accordingly with the highest flux rates found from intact vegetation and the lowest from peat (III; Tiiva et al., 2009). However, this is not the case with other BVOCs. Intact vegetation emits more monoterpenoids than peat but neither differ from monoterpenoid emission rate of mosses (III; Faubert et al. 2010b). Sesquiterpene emissions have also been found to be higher from vegetation than from peat (III; Faubert et al., 2010b). True to their name, green leaf volatiles are almost exclusively emitted from vascular plants, as only one compound was detected from moss and none from peat (III). Additionally, more homoterpenes were emitted from vascular plants than form mosses (III). Consequently, total BVOC emission is generally higher from intact vegetation than from mosses and peat, and from bare peat (III).

However, emissions of the remaining BVOC groups (alkanes, oxygenated alkanes, organic halides and benzenoids) did not have any common differences between the vegetation removal treatments, and since there were also a number of compounds that were found from moss and/or peat but not from intact vegetation, this study suggests that BVOCs can be trapped or consumed on their way to the atmosphere. Soils and litter have been shown to be substantial source of BVOCs and soil microbes have been found to be able to consume significant amount of their BVOC release (Ramirez et al., 2010; Kramshøj et al., 2018). In the arctic, majority of BVOCs released from thawing permafrost can be taken up in the active layer by microbial organisms, which regulates the BVOC emissions to the atmosphere (Kramshøj et al., 2018). It is possible that similar microbial consumption of BVOCs takes place in the aerobic layer of peatland soils, but so far it has not been studied.

Furthermore, low water table during periodic drought strongly reduced the emissions of organic halides from all treatments (III). Due to this effect, lowering water level and more frequently occurring drought events in the future can also directly change the quality and quantity of BVOC emissions from boreal peatlands.

4.3. Conclusions and future perspectives

Climate is undeniably warming having global impact on all ecosystems, but the warming and the ecological changes related to it are fastest in the boreal and arctic regions (IPCC, 2014). Dynamic process-based models, such as LJP Guess (Smith et al., 2001; Sitch et al., 2003) are valuable tools to understand and predict the effects of climate change on different ecosystems and their feedbacks to the climate, but they still lack important knowledge about how boreal peatland methane and BVOC dynamics are controlled by abiotic environmental factors and vegetation. This study bridges some of these knowledge gaps and shows that climate warming has both direct and indirect effects on boreal peatlands methane and BVOC emissions, which again may affect their feedback in climate regulation.

Temperature is major controller of both methane and BVOC emissions as it regulates microbial activity (Dunfield et al., 1993; Cleveland and Yavitt, 1998), methane diffusion rate (Große, 1996), methane solubility (Strack et al., 2005), and BVOC production rates in plants (Guenther et al., 1993; Kesselmeier and Staudt, 1999; Peñuelas and Llusià, 2001; Tarvainen et al., 2005; Duhl et al., 2008). Thus, climate warming can directly increase their emissions from boreal peatland ecosystems and this effect is further enhanced by the accompanying lengthening of the growing season. However, climate warming will also increase evapotranspiration (Helbig 2020) which is predicted to lower water table in boreal peatlands (Gorham, 1991; Roulet et al., 1992; Gong et al., 2012) leading to drier conditions that in turn reduce methane emissions. Lower water table also directly changes the quality of emitted BVOCs, because periodic drought events suppress the emissions of some volatiles.

Climate warming impacts the methane and BVOC emissions of boreal peatlands also indirectly by driving changes in their vegetation. Higher emission rates of both methane and BVOC associate to total leaf area that can be resilient to warming and/or drying despite changes in plant functional types composing the vegetation (Mäkiranta et al., 2018). Although there can be very little spatial variation in methane emissions between different plant community types, vegetation composition is a key driver of BVOC emissions. The most abundantly emitted BVOC in peatlands, isoprene, has a strong link with sedges, whereas dwarf shrubs emit more monoterpenoids. As water table drawdown changes plant species composition of boreal peatlands from sedge-dominated towards higher dwarf shrub cover, especially in fen ecosystems (Strack et al., 2006; Berg et al., 2007; Mäkiranta et al., 2018; Kokkonen et al., 2019), it can reduce their total BVOC emission by reducing isoprene emissions and change the peatland BVOC emission profile.

These climate warming -induced changes in boreal peatland ecosystems affect their feedbacks to the climate. Although warming can increase methane emissions, the simultaneous drying reduces them, and progressive cover of dry hummocks may potentially lead to increased methane uptake. This would have a climate cooling impact as long as drying is not so severe that it increases organic matter decomposition hindering peat accumulation and turning boreal peatlands from carbons sinks to sources. BVOCs have a net cooling impact on climate because their oxidation processes in the atmosphere lead to yields of secondary organic aerosols (SOA) that have an important role in cloud formation (Hoffmann et al., 1997; Atkinson et al., 2000; Virtanen et al., 2010; Paasonen et al., 2013). Thus, the total amount of BVOCs emitted from boreal peatland ecosystems can directly affect SOA formation and climate forcing. Additionally, the quality of the emitted BVOCs have also a direct impact, because different BVOCs result in different SOA yields (Faiola et al., 2019; McFiggans et al., 2019). As this study demonstrates the responsivity of BVOC emission rates and profile of boreal peatlands to vegetation structure and weather, further studies quantifying these effects in controlled set ups in the field are needed to fully understand boreal peatland BVOC emissions and their feedback under the warming climate.

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