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Importance of vegetation classes in modeling CH₄ emissions from boreal and subarctic wetlands in Finland



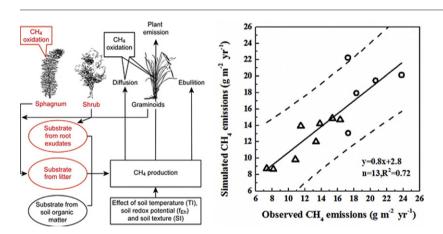
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HIGHLIGHT

- CH₄ emission from Finnish wetlands was simulated by CH4MOD_{wetland}.
- We recalibrated the vegetation parameters of graminoids, shrubs and Sphagnum
- Simulated CH₄ variations agreed well with the eddy-covariance observations.
- Annual CH₄ emissions were reasonably simulated in different years and sites.
- Parameterization of different vegetation process was essential in long-term CH₄ estimates.

GRAPHICAL ABSTRACT



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ABSTRACT

Boreal/arctic wetlands are dominated by diverse plant species, which vary in their contribution to CH₄ production, oxidation and transport processes. Earlier studies have often lumped the processes all together, which may induce large uncertainties into the results. We present a novel model, which includes three vegetation classes and can be used to simulate CH_4 emissions from boreal and arctic treeless wetlands. The model is based on an earlier biogeophysical model, $\text{CH}_4\text{MOD}_{\text{wetland}}$. We grouped the vegetation as graminoids, shrubs and Sphagnum and recalibrated the vegetation parameters according to their different CH_4 production, oxidation and transport capacities. Then, we used eddy-covariance-based CH_4 flux observations from a boreal (Siikaneva) and a subarctic fen (Lompolojänkkä) in Finland to validate the model. The results showed that the recalibrated model could generally simulate the seasonal patterns of the Finnish wetlands with different plant communities. The comparison between the simulated and measured daily CH_4 fluxes resulted in a correlation coefficient (R^2) of 0.82 with a slope of 1.0 and

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Vegetation community Boreal and subarctic wetlands Parameterization an intercept of $-0.1~\rm mg~m^{-2}~h^{-1}$ for the Siikaneva site (n = 2249, p < 0.001) and an R² of 0.82 with a slope of 1.0 and an intercept of 0.0 mg m⁻² h⁻¹ for the Lompolojänkkä site (n = 1826, p < 0.001). Compared with the original model, the recalibrated model in this study significantly improved the model efficiency (EF), from -5.5 to 0.8 at the Siikaneva site and from -0.4 to 0.8 at the Lompolojänkkä site. The simulated annual CH₄ emissions ranged from 7 to 24 g m⁻² yr⁻¹, which was consistent with the observations (7–22 g m⁻² yr⁻¹). However, there are some discrepancies between the simulated and observed daily CH₄ fluxes for the Siikaneva site (*RMSE* = 50.0%) and the Lompolojänkkä site (*RMSE* = 47.9%). Model sensitivity analysis showed that increasing the proportion of the graminoids would significantly increase the CH₄ emission levels. Our study demonstrated that the parameterization of the different vegetation processes was important in estimating long-term wetland CH₄ emissions.

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1. Introduction

Methane (CH₄) is among the most important greenhouse gases (GHG) with 100-year global warming potential (GWP) 50 times greater than that of $\rm CO_2$ when considering the emission of $\rm CH_4$ leads to ozone production, aerosols, stratospheric water vapour, and importantly increasing its own lifetime (Myhre et al., 2013; Shindell et al., 2009). The trend of atmospheric $\rm CH_4$ concentration is characterized by a decreasing growth rate from the early 1980s until 1998, a stabilization period from 1999 to 2006, and a renewed growth after 2006 (Dlugokencky et al., 2009; Nisbet et al., 2014; Rigby et al., 2008). A rise in the natural wetland emissions and fossil fuel emissions probably accounts for the renewed increase in global methane levels after 2006 (Kirschke et al., 2013).

Natural wetlands are the single largest natural source of CH_4 (Denman et al., 2007; Wuebbles and Hayhoe, 2002) and have the largest absolute uncertainty of any of the emission categories (Kirschke et al., 2013). The boreal and arctic wetlands are of particular concern because they comprise up to 50% of the total global wetland area (Lehner and Döll, 2004). Moreover, while the boreal and arctic peatlands constitute <3% of the world's total land area, they contain approximately one-third of the global soil carbon. Furthermore, they release 46 Tg CH_4 -C into the atmosphere annually (Gorham, 1991), which is equivalent to 12.2% of the total global emission (Wuebbles and Hayhoe, 2002).

Boreal and arctic wetlands are dominated by diverse vegetation, consisting of graminoids (i.e., grassy plants, which are mostly sedges), shrubs and Sphagnum mosses (Crum and Planisek, 1992). Plants serve as the major control of CH₄ emissions from wetlands (Bhullar et al., 2013; Joabsson and Christensen, 2001; Shannon et al., 1996). The different vegetation species effectively influence CH₄ production, oxidation and emissions. Previous ¹⁴C-labeling experiments have suggested that CH₄ production is fueled by recent plant photosynthesis through root exudates (Dorodnikov et al., 2011; King et al., 2002; Megonigal et al., 1999). However, the amount of root exudates differs between plant species (Bridgham et al., 2013) and accounts for only 0.1%-10% of the net fixed carbon (Farrar et al., 2003; Jones et al., 2004; Phillips et al., 2008). Previous studies (Busch and Lösch, 1999; Verville et al., 1998) have also shown the importance of plant aerenchymous tissues in CH₄ transport. However, considerable differences were reported in CH₄ oxidation through the vascular transport between vegetation species (Popp et al., 2000; Ström et al., 2005). Recently, cooperation between methanotrophic bacteria and water-submerged Sphagnum was shown to reduce methane emissions (Bridgham et al., 2013; Kip et al., 2012; Larmola et al., 2010; Liebner et al., 2011; Parmentier et al., 2011). The rates of potential oxidation ranged from 0 to 80 μ mol g dw⁻¹ day⁻¹ (Kip et al., 2012; Larmola et al., 2010; Raghoebarsing et al., 2005).

The above variations have been ascribed to differences in the CH₄ substrate, plant transport and oxidation of CH₄ and can be reproduced by plot-scale models if the vegetation parameters of the model are correctly specified (Berrittella and Huissteden, 2011; Huissteden et al., 2009; Parmentier et al., 2011). The present regional or global scale

model simulations of CH_4 fluxes often lumped the effects of all vegetation together, which may induce large uncertainties in the estimates (Melton et al., 2013; Meng et al., 2015; Petrescu et al., 2010; Zhu et al., 2015). In addition, most previous process-based models have concentrated on a single vegetation type (e.g., graminoids) and only a few considered the complex vegetation composition for model validation (Li et al., 2010; Meng et al., 2012; Walter and Heimann, 2000; Walter et al., 1996; Xu and Tian, 2012; Zhang et al., 2002; Zhu et al., 2014).

Finland has the highest coverage of mires in the world, with its typical boreal and subarctic wetland plant communities consisting of graminoids, shrubs and *Sphagnum* (Tomppo, 2000). Climate change and long-term drainage may have changed the plant community in the past and may alter it again in the future (Laine et al., 1995). In this study, we studied CH₄ fluxes at two Finnish wetland sites dominated by different vegetation proportions utilizing two flux data sets of eight and five years. The main objective of this study is to present a novel model based on the earlier model by Li et al. (2010), now including three vegetation classes that can be used generically for the future study of boreal and arctic treeless wetlands.

2. Materials and methods

2.1. Study sites

The study was carried out in two wetlands located in Southern and Northern Finland. The Siikaneva site is an oligotrophic fen located in Southern Finland, in an area close to the border of the southern and middle boreal zones (61°49.961′N, 24°11.567′E, 160 m a.s.l.). The long-term (1971–2000) annual mean temperature of this region is 3.3 °C. The annual precipitation is 713 mm, of which approximately one-third falls as snow (Aurela et al., 2007). The Siikaneva site consists of relatively homogenous lawn vegetation dominated by sedges (*Carex* spp., *Eriophorum* spp.), *Scheuchzeria palustris* L., and *Sphagnum mosses*. Hollows are covered by *Sphagnum* species adapted to the wettest conditions, while somewhat higher hummocks are covered in dwarf shrub vegetation occurring among the lawn-level vegetation. The peat depth is a maximum 5.5 m (Mathijssen et al., 2016). More detailed site descriptions were presented in earlier work (Aurela et al., 2007; Rinne et al., 2007).

The Lompolojänkkä site $(67^{\circ}59.835'N, 24^{\circ}12.546'E, 269 \text{ m a.s.l.})$ is an open, pristine and nutrient-rich sedge fen located in northwestern Finland, 160 km north of the Arctic Circle. The long-term (1971-2000) annual temperature and precipitation in the area are -1.4 °C and 484 mm, respectively. The peat depth at this site is up to 2.5 m at the center of the fen (Mathijssen et al., 2014). The site is surrounded by forest. The relatively dense vegetation layer is dominated by *Betula nana*, *Menyanthes trifoliata*, *Salix lapponum*, *Carex lasiocarpa* and *C. rostrata*, patchy *Sphagnum* mosses and brown mosses. A small stream flows through the site, and the stream zone is dominated by willow bushes (*S. lapponum*). For more detailed site description see Aurela et al. (2009) and Lohila et al. (2010).

2.2. Field measurements

The methane fluxes were measured at the Siikaneva and Lompolojänkkä sites using the eddy covariance (EC) method, in which the vertical flux between atmosphere and ecosystem is obtained as a covariance of high-frequency (10 Hz) observations of vertical wind and CH₄ concentration (Baldocchi, 2003). The measurements at the eastern end of the Siikaneva fen were collected from 2005 to 2012. A three-dimensional acoustic anemometer (USA-1, METEK, Germany) was used with two different CH₄ analyzers (years 2005-2008: TDL, TGA-100, Campbell Scientific Inc., USA; years 2008-2012: RMT-200, Los Gatos Research, USA). At Lompolojänkkä, the data period covered years 2006– 2010 with a USA-1 anemometer and RMT-200 (Los Gatos Research, USA) CH₄ analyzer. The acoustic anemometer was placed 3 m above the peat surface (2.75 m at Siikaneva), and the air intake of the CH₄ analyzer was located at both sites 15-20 cm below the measurement path of the anemometer. Post-field processing of the EC-data was accomplished using commonly used methods as follows: the fluxes were calculated as half-hourly block averages, and the high-frequency losses were corrected for using an empirically determined transfer function (Mammarella et al., 2009). The Webb-Pearman-Leuning (WPL) correction (Webb et al., 1980) was applied when applicable (Laurila et al., 2005). More details of the measurement systems and data post-processing are given in previous studies (Aurela et al., 2009; Laurila et al., 2005; Lohila et al., 2016; Peltola et al., 2013; Rinne et al., 2007). For this study, the half-hourly averages were further averaged to daily fluxes to match the time resolution of the model. We made a summation of daily CH₄ fluxes to calculate the observed total amount of annual CH4 emissions from the Siikaneva and Lompolojänkkä sites. The short gaps of CH₄ flux measurements between the two back-to-back days of observation at the Siikaneva site were linearly interpolated.

A set of meteorological and soil parameters were recorded continuously at both sites. These included the air temperature and humidity, precipitation, photosynthetical photon flux density, net radiation, peat temperature at different depths and water table depth. The daily averages of the air temperature, peat temperature (at a depth of 5–7 cm) and water table depth were used to drive the CH4MOD $_{\rm wetland}$.

The maximum above-ground biomass (W_{max}) for each plant species was determined at Siikaneva in August 2006 (Laine et al., 2011). In 2005 and between 2007–2012, we inferred the maximum above-ground biomass according to the annual maximum leaf area index (LAI) from 2005–2012, which was simulated based on 2006 data (Raivonen et al., 2015). For the Lompolojänkkä site, biomass sampling was conducted in July–August of 2006–2009. The biomass was separated into graminoids, shrubs and Sphagnums but was pooled together to generate the total maximum above-ground biomass as well as the fraction of each vegetation type. This was obtained to support the model simulation. Data were not collected in 2010, so we used the same method as for Siikaneva to infer biomass data for 2010.

2.3. Model description and modification

In the previous study, we developed a process-based biogeophysical CH4MOD_{wetland}, which was used to simulate CH₄ production, oxidation and emission from the natural wetland ecosystem (Li et al., 2010). The original CH4MOD_{wetland} was developed based on the CH4MOD model, which is used to simulate CH₄ emissions from rice paddies (Huang et al., 1998; Huang et al., 2004; Huang et al., 1997). Its main modifications are related to the supply of methanogenic substrates in natural wetlands that differ significantly from those in rice paddies. The hypothesis of the original CH4MOD_{wetland} is that methanogenic substrates are the carbohydrates derived from plants via root exudates and from the decomposition of plant litter and the soil organic matter, CH₄ production rates are thus determined by the availability of methanogenic substrates and by the influence of environmental factors, such as soil temperature, soil redox potential and soil texture. In the latest version of

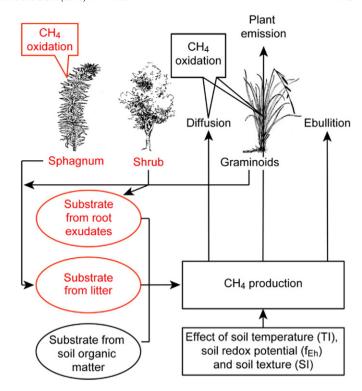


Fig. 1. Conceptual explanation of the CH4MOD_{wetland} model. The red frame shows the novel features of the present model.

CH4MOD_{wetland} (Li et al., 2016), plant-mediated transport, ebullition and diffusion are mechanisms of CH₄ transport. CH₄ oxidation happens during plant-mediated transport and diffusion. The model inputs include daily peat temperature and daily water table depth. Its outputs are the daily CH₄ atmospheric emissions. For more details about this model, please see previous studies (Li et al., 2010; Li et al., 2012; Li et al., 2016; Li et al., 2015).

In previous studies, the CH4MOD_{wetland} was usually used in Chinese wetlands (Li et al., 2012, 2015, 2016) that were covered by graminoids with aerenchymous tissue. All of the parameters related to the vegetation were for the graminoids. However, the original model may not be appropriate to the boreal and subarctic wetlands, which are covered by a complex plant community with graminoids, shrubs and Sphagnum. In this study, we distinguished three main classes of wetland vegetation with respect to their functionality in CH₄ production, oxidation and emission: graminoids, with aerenchymous tissues, shrubs and Sphagnum mosses. Fig. 1 shows the conceptual explanation of the present model. The classification was based on the different capability of the vegetation in CH₄ production and oxidation. The graminoids provide root exudates and litter for methanogenic substrates. When they transport CH₄ to the atmosphere through the aerenchymous tissues, part of the CH₄ is oxidized. Shrubs can also contribute to CH₄ production through the root exudates and litter. However, they are assumed not to be capable of transporting gases (Walter et al., 2001). The Sphagnum does not have roots, so it is assumed that they only provide litter for CH₄ production. They can contribute to CH₄ oxidation through a symbiotic relationship between methanotrophs and Sphagnum mosses, especially in flooded environments (Kip et al., 2012; Larmola et al., 2014; Parmentier et al., 2011; Raghoebarsing et al., 2005).

As shown in Fig. 1, CH₄ production rates are determined by the availability of methanogenic substrates and the influence of environmental factors. For wetlands with only graminoids, the root exudates and plant litters are only from the graminoids. For the Finnish wetlands, the substrates are derived from graminoids, shrubs and *Sphagnum*.

CH₄ production is calculated by:

$$P = m \times SI \times F_{EH} \times (C_{PG} + C_{PS} + C_{LG} + C_{LS} + C_{LM} + C_{SOM})$$
 (1)

$$C_{PG} = \alpha \times TI \times VI_G \times W_G^{\beta 1} \tag{2}$$

$$C_{PS} = \alpha \times TI \times VI_S \times W_S^{\beta 1} \tag{3}$$

where P is the CH₄ production (g m⁻² d⁻¹), and C_P , C_L and C_{SOM} are the carbohydrates derived from the plant root exudates, plant litter and soil organic matter, respectively (g m $^{-2}$ d $^{-1}$). The subscripts G, S and M represent graminoids, shrubs and Sphagnum mosses, respectively. As shown in Fig. 1, the root exudates are derived from graminoids (C_{PC}) and shrubs (C_{PS}). SI, TI, and F_{EH} denote the influence of the soil texture, soil temperature and soil redox potential, respectively, on CH₄ production (dimensionless); m is a factor (molar weight basis) that is used to convert carbohydrates into methane. The carbohydrates derived from plant root exudates are related to the daily aboveground biomass (W, g $m^{-2} d^{-1}$) and calculated by Eqs. (2) and (3). The vegetation indexes VI_G (Eq. 2) and VI_S (Eq. 3) are dimensionless parameters, which were used to quantify the different capacities for producing root exudates of the various plant species. In this study, we used VI_G and VI_S to represent the vegetation index for the graminoids and shrubs. α and β 1 are the empirical constants. The carbohydrates derived from the decomposition of litters of graminoids (C_{LG}) , shrubs (C_{LS}) , sphagnum (C_{LM}) and from soil organic matter (C_{SOM}) are simulated by first order kinetic equations. In the plant growth module, the logistic equation (Eqs. (S5)–(S6)) (Li et al., 2010) was used for simulating the plant growth. W_{max} is a parameter of the logistic equation to calculate the daily biomass and the root substrate (Eqs. 2–3). We also listed the equations used for calculating C_{LG} , C_{LS} , C_{LM} and C_{SOM} in Eqs. (S1)–(S4) in Supplementary material S1. All equations of this model are provided in a previous work (Li et al., 2010).

In the original model, CH_4 emissions are the summation of plant transport (E_P) (g m⁻² d⁻¹), ebullition (E_B) (g m⁻² d⁻¹) and diffusion (E_D) (g m⁻² d⁻¹). CH_4 oxidation happens through plant-mediated transport as well as diffusion processes. During plant transport, a portion of CH_4 is oxidized. We used P_{ox} for this portion. However, the original model did not consider the oxidation related to Sphagnums in the anaerobic environment. In boreal and subarctic wetlands, the cooperation between methanotrophic bacteria and Sphagnum was shown to reduce methane emissions (Kip et al., 2012; Larmola et al., 2014; Parmentier et al., 2011; Raghoebarsing et al., 2005). The oxidation rate is higher when the Sphagnum is water-submerged, but it is reduced to 10% of that rate when the Sphagnum was exposed to the air (Larmola et al., 2010). In the present study, we modified the original model by adding Eq. (4) to calculate the CH_4 oxidation associated with the endophytic methane-oxidizing bacteria in Sphagnum:

$$O_i = W_{si} \times OR \times n \times (F + 0.1 \times (1 - F))$$
(4)

where O_i (g m⁻² day⁻¹) is the daily rate of CH₄ oxidized by the endophytic methane-oxidizing bacteria in the *Sphagnum*. W_{si} (g m⁻²) is the daily biomass of *Sphagnum*. F is the submerged fraction of

Table 1Description of the model parameters used in this study.

Parameters	Description (Unit)	Value	Reference	
		Siikaneva	Lompolojänkkä	
W _{max}	Maximum above-ground biomass of the total vegetation species (g $m^{-2})$	253 ^a ,253 ^b ,298 ^c ,334 ^d ,334 ^e ,334 ^f ,362 ^g ,362 ^h	331 ^b ,310 ^c , 336 ^d ,372 ^e ,337 ^f	Laine et al. (2011); This study ⁱ
FW_G	Fraction of graminoids to the total above-ground biomass (%)	25	36	Laine et al. (2011); This study ⁱ
FWs	Fraction of shrubs to the total above-ground biomass (%)	11	46	Laine et al. (2011); This study ⁱ
FW_M	Fraction of <i>Sphagnum</i> to the total above-ground biomass (%)	64	18	Laine et al. (2011); This study ⁱ
P _{root-G}	Proportion of below-ground to the total production for graminoids (%)	50		Gill and Jackson (2000)
P _{root} _S	Proportion of below-ground to the total production for shrubs (%)	23		Gill and Jackson (2000)
VI_G	Vegetation index for graminoids (dimensionless)	2.4		Li et al. (2010)
VIs	Vegetation index for shrubs (dimensionless)	0.8		This study ^j
P _{ox}	The fraction of CH ₄ oxidized during graminoids-mediated transport (dimensionless)	0.4		This study ^j
OR	Oxidation rates by the endophytic methane-oxidizing bacteria in Sphagnum (umol CH ₄ g dw ⁻¹ day ⁻¹)	42		This study ^j
SOM	Concentration of soil organic matter (%)	98	90	Lohila et al. (2010);
				Putkinen et al. (2009)
)	Soil bulk density (g cm ⁻³)	0.3	0.1	Laiho et al. (2004);
				Lohila et al. (2010)
k1	First order decay rate for nonstructural litter of graminoid sand shrubs	0.027		Li et al. (2010)
k2	First order decay rate for structural litter of graminoids and shrubs	0.003		Li et al. (2010)
k3	First order decay rate for the Sphagnum litter	0.004		Waddington et al. (2003)
k4	First order decay rate for the soil organic matter	8×10^{-6}		Scanlon and Moore (2000)
m	factor (mole weight basis) to convert carbohydrates into methane	0.27		Huang et al. (1998)
α	Empirical constant	1.8×10^{-3}		Huang et al. (1998)
31	Empirical constant	1.25		Huang et al. (1998)
n	Conversion factor from µmol to gram	16×10^{-6}		This study

a For 2005

^b For 2006.

^c For 2007.

^d For 2008.

e For 2009.

^f For 2010.

g For 2011.h For 2012.

ⁱ Measured by this study at the Lompolojänkkä site.

j Newly calibrated parameter in this study.

Sphagnum, and (1-F) is the Sphagnum exposed in the air. *OR* (μ mol CH₄ g dw⁻¹ day⁻¹) represents the CH₄ oxidation per gram of dry mass *Sphagnum* per day, which should be calibrated. n is the μ mol to gram conversion factor.

2.4. Model parameterization

Table 1 shows the description and the values of the parameters in this study. Three parameters related to the plant species have been recalibrated in this study. The parameters include VI_S , P_{ox} and OR (Table 1). We used observed data from the year 2005 from the Siikaneva site to for the calibrations. For the vegetation indices, the VI_G for the graminoids has been calibrated in a previous study (Li et al., 2010). We therefore only need to calibrate VI_S in this study. We assumed that the root exudates represented 2.7% of the net primary productivity. This was the average value reported previously by (Farrar et al., 2003), who reported that the proportion of root exudates to the net primary productivity was 0.5%–5%. We first set VI_S as 1.0 and then ran the model to obtain the output of the root exudates, C_{PS} (Eq. 3). Then, VI_S was calculated by $VI_S = (NPP_S \times 2.7\%) / C_{PS}$. The NPP_S is the net primary productivity of shrubs in 2005 in the Siikaneva wetlands.

Graminoids and *Sphagnum* contribute to plant oxidation. For graminoids, a proportion of 0–90% of the produced CH₄ is oxidized when transporting through the aerenchyma (Popp et al., 2000; Ström et al., 2005). The unitless parameter P_{ox} represents this fraction. The OR (Eq. 4) is within a range of 0–62 μ mol CH₄ g dw⁻¹ day⁻¹ in Finland (Larmola et al., 2010). The minimum RMSE method (Zhuang et al., 2004) was used to calibrate the P_{ox} and OR. By setting an increment of 0.01 for P_{ox} and 0.1 for OR, the model was run for all combinations of P_{ox} within the range 0.0–0.9 and the OR within the range 0.1–62 until the root-mean-square error (RMSE) between the simulated and observed CH₄ fluxes was minimized.

2.5. Statistics used for model validation

The independent observations for 2006–2012 at the Siikaneva site and for 2006–2010 at the Lompolojänkkä site were used to validate the model. To show the improvement of the model performance, we modeled CH₄ emissions using a new model with improved vegetation effect parameterization in this study (hereafter called the new model). We also used the original model with the old parameters (Li et al., 2010) (hereafter called the old model). The differences between the new and old model are as follows: 1. the old model did not consider the oxidation related to the Sphagnum; 2. the old parameters were only for the graminoids, which means that all of the vegetation types were regarded as graminoids with aerenchymous tissues. A set of statistical methods (Smith et al., 1997) was used to evaluate the improvements of the model. We used the root mean-square error (RMSE), the mean deviation (RMD), the coefficient of determination (CD) and the model efficiency (EF) to quantify the model performance on the Finnish wetland sites. The implications and the equations of the above statistical elements are described in Supplementary Material S2.

2.6. Model sensitivity analysis

We conducted a sensitivity analysis to better understand the response of CH4MOD_{wetland} to the parameters of the Finnish wetlands.

Table 2Range and baseline of the factors used in the model sensitivity analysis.

Factors	Maximum	Baseline	Minimum	Reference
VI_G	3.0	2.4	0.1	This study, Li et al. (2010, 2015)
VI_S	3.0	0.8	0.1	This study, Li et al. (2010, 2015)
P_{ox}	1.0	0.9	0.0	Ström et al. (2005); Popp et al. (2000)
OR	62.0	42	0.1	Larmola et al., 2010

In the process of the sensitivity analysis, the average daily soil temperature and water table depth of different years of the two sites were used to drive the model. In previous studies, we tested the sensitivity of a subset of the parameters (Li et al., 2010, 2016). In this study, the parameters related to the vegetation species (e.g., VI_G , VI_S , P_{ox} and OR (Table 1)) were tested. To determine the model sensitivity, we ran CH4MOD_{wetland} by changing the value of one factor while holding the remaining factors constant. For example, the response of the simulated CH₄ fluxes to P_{ox} was iteratively simulated within a P_{ox} range of 0.0–0.9 (Table 2), while the other factors were set to a baseline value (Table 1). The baseline values of VI_G , VI_S , P_{ox} and OR were obtained from Table 1. The average vegetation fraction of the two sites ($FW_G = 31\%$, $FW_S = 28\%$ and $FW_M = 41\%$) was used when testing the model sensitivity to the above parameters.

Moreover, we also tested the effect of the vegetation composition on the $\mathrm{CH_4}$ flux. We changed the fraction of one plant within the range of 5% to 99% and maintained the ratio of the other two plant species the same. The fraction changed by 1% every time. For example, if the fraction of graminoids (FW_G) was 5%, FW_S and FW_M were 39% and 56%, which were calculated by a fixed ratio of 28:41. When the FW_G was 99%, FW_S and FW_M were 0.4% and 0.6%, respectively. There are 95 groups of the vegetation composition (Fig. S1). We ran the model with each group of vegetation fraction for a total of 95 times and estimated the response of the $\mathrm{CH_4}$ flux to the vegetation composition.

3. Results

3.1. Model validation

3.1.1. Validation of seasonal CH₄ variations

Fig. 2 and Fig. 3 show the seasonal patterns of the simulated and observed CH₄ emission from the Siikaneva site from January 2005 to December 2012 as well as from the Lompolojänkkä site from January 2006 to December 2010. We also compared the simulated and observed CH₄ fluxes in different years and across the whole observation period from the Siikaneva site (Fig. 4) and the Lompolojänkkä site (Fig. 5). Using the new model in this study, the pattern of the simulated variations (blue lines) generally matches the observed variations (Fig. 2a and Fig. 3a). The linear regression lines (black lines) between the simulated and observed CH₄ fluxes are close to the 1:1 lines (Figs. 4 and 5).

However, the old model significantly overestimated (red lines) the measured CH₄ emissions for both of the sites, especially for the Siikaneva site (Fig. 2a). The linear regression lines (red lines) between the simulated CH₄ against the observed values are always above the 1:1 lines, which also indicated a significant overestimation. The overestimation by the old model was likely caused by the fact that all vegetation types were considered to be graminoids. Compared with the shrubs and *Sphagnum*, the graminoids contribute more CH₄ emissions in the wetlands.

There are still some model biases introduced in the new model. For example, for the Siikaneva site, the new model did not capture some summer peak CH₄ fluxes in 2007, 2008, 2009 and 2010 (Fig. 2a). It also overestimated the peak CH₄ fluxes in 2006 as well as the observed CH₄ fluxes from August to September of 2011 (Fig. 2a). The regression of simulated and observed CH₄ fluxes by the new model resulted in slopes of 1.5 (Fig. 4b) and 1.3 (Fig. 4g), which also confirmed this overestimation. For the Lompolojänkkä site, the new model overestimated the summer peak of the CH₄ flux in 2006 and did not catch the summer peak of the CH₄ flux in 2007, 2008 and 2009 (Fig. 3a). The slope values of 1.2 in 2006 (Fig. 5a), 0.8 (Fig. 5b) and 0.9 (Fig. 5d) also indicated these discrepancies. In addition, the model did not catch some high values of the winter fluxes for both sites (Fig. 2a and Fig. 3a).

In general, the comparison between the simulated and measured daily CH₄ fluxes (Fig. 4i) produced a correlation coefficient (R^2) of 0.82 with a slope of 1.0 and an intercept of -0.1 mg m⁻² h⁻¹ at the Siikaneva site (n = 2249, p < 0.001) and resulted in an R^2 value of

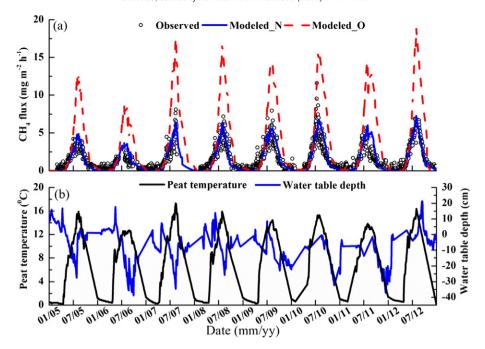


Fig. 2. Simulated and observed seasonal variations in the daily CH₄ fluxes (a) and environmental factors (b) from the Siikaneva site. The observed CH₄ fluxes of 2005 were used to calibrate the model. The blue solid line and red dashed line denote the simulated CH₄ fluxes from the updated and the old model, respectively.

0.82, with a slope of 1.0 and an intercept of 0.0 mg m $^{-2}$ h $^{-1}$ at the Lompolojänkkä site (n = 1826, p < 0.001) (Fig. 5f).

The statistical analysis suggested that the new model could generally simulate the seasonal patterns in the CH₄ fluxes, with a model efficiency of 0.76 at the Siikaneva site and 0.80 at the Lompolojänkkä site (Table 3). However, some discrepancies still existed (*RMSE* = 50.0% and 47.9% in Table 3). The minus values of the indicator *RMD* (Table 3) for both sites showed a slight negative bias between the simulated and observed CH₄ fluxes. In addition, another indicator *CD*, which is <1.0 for the two sites, suggested that the model described the trend in

the measured data to be worse than the mean of the observations (Table 3).

3.1.2. Comparison of the simulated and observed total annual CH_4 emissions

The new model significantly improved the simulations in the annual CH₄ emissions, compared with the old model (compared with Fig. 6a and Fig. 6b). The observed annual CH₄ emissions from the Siikaneva site (the triangles in Fig. 6a) ranged from 7.4 to 16.3 g m⁻², with an average value of 12.1 g m⁻², those from the Lompolojänkkä wetlands

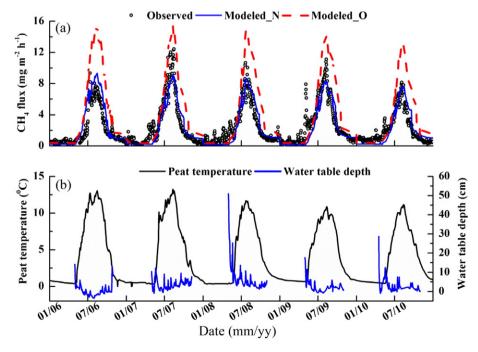


Fig. 3. Simulated and observed seasonal variations of the daily CH₄ fluxes (a) and environmental factors (b) from the Lompolojänkkä site. The blue solid line and red dashed line denote the simulated CH₄ fluxes from the updated and the old model, respectively.

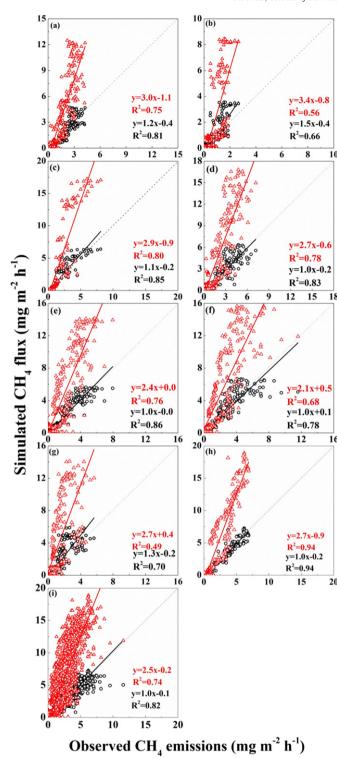


Fig. 4. Comparison of the simulated and the measured daily CH_4 emissions from the Siikaneva site in (a) 2005, (b) 2006, (c) 2007, (d) 2008, (e) 2009, (f) 2010, (g) 2011, (h) (2012) and (i) from 2006 to 2012. Black and red solid lines represent the correlation results from the updated and the old model, respectively. Black dashed lines represent 1:1 lines.

were in the range of 17.3 to 23.8 g m⁻² (circles in Fig. 6a), with an average of 19.5 g m⁻². The simulated annual CH₄ emissions from the Siikaneva site by the new model ranged from 7.1 to 14.8 g m⁻², with an average of 12.1 g m⁻², which corresponds to the observed values (Fig. 6a). However, the new model underestimated the CH₄ emissions

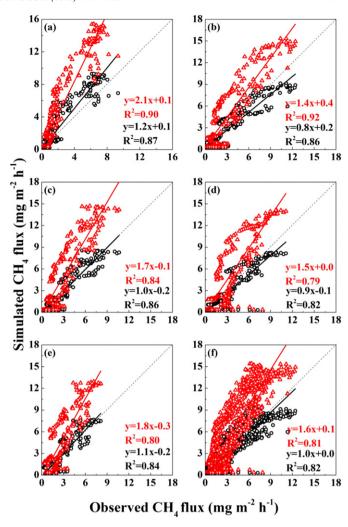


Fig. 5. Comparison of the simulated and measured daily CH_4 emissions from the Lompolojänkkä site in (a) 2006, (b) 2007, (c) 2008, (d) 2009, (e) 2010, and (f) from 2006 to 2010. Black and red solid lines represent the correlation results from the updated and the old model, respectively. Black dashed lines represent the 1:1 lines.

from the Lompolojänkkä site. The simulated values at the Lompolojänkkä site were in the range of 13.1 to 22.2 g m $^{-2}$, with an average of 18.6 g m $^{-2}$ (Fig. 6a). The comparison between the simulated and measured annual or seasonal CH₄ emissions (Fig. 6a) results in a correlation coefficient (R^2) of 0.72, with a slope of 0.8 and an intercept of 2.8 g m $^{-2}$ (n = 13, p < 0.001).

The model efficiency of 0.81 for both sites (Table 3) indicated that the differences in CH₄ emissions between the sites and in different years can, in general, be simulated. However, some discrepancies (RMSE=10.9% and 17.4%) between the simulated and observed annual or seasonal CH₄ emissions still existed in both sites. A negative systematic bias (RMD=-4.6%) was observed for the Lompolojänkkä site. The indicator CD higher than 1.0 indicated that the new model described the trend in the measured seasonal CH₄ emissions better than the mean of the observations from the Finnish wetland sites (Table 3). The model's efficiency was greatly improved by the new model (Table 3).

3.2. Model sensitivity analysis

The results of the sensitivity analysis are shown in Fig. 7. The model sensitivity analysis suggested that the CH₄ emissions increased linearly with VI_G (Fig. 7a) and VI_S (Fig. 7b). This linear response can be observed from Eq. (2) and Eq. (3). As VI_G and VI_S increased from 0.1 to 3.0, the CH₄

Table 3Statistical analysis of model performance on daily and annual CH₄ emissions for the different sites.

Criteria	Siikaneva				Lompolojänkkä			
	New model		Old model		New model		Old model	
	Daily	Seasonal	Daily	Seasonal	Daily	Seasonal	Daily	Seasonal
RMSE	50.0%	10.9%	259.0%	162.8%	47.9%	17.4%	124.1%	77.3%
RMD	-2.8%	0.1%	139.3%	160.0%	-2.5%	-4.6%	66.2%	75.6%
CD	0.76	1.45	0.09	0.02	0.89	1.18	0.28	0.12
EF	0.76	0.81	-5.48	-41.4	0.80	0.81	-0.38	-2.7
n ^a	2249	8	2249	8	1826	5	1826	5

RMSE is the root mean square error, RMD is the root mean deviation, CD is the coefficient of determination, EF is the model efficiency. See Supplementary S2 for the detailed definitions.

a n is the sampling number.

emissions increased by 6.0 g m⁻² (Fig. 7a) and 5.3 g m⁻² (Fig. 7b), respectively. The CH₄ emissions decreased with an increasing P_{ox} (Fig. 7c) and OR (Fig. 7d). P_{ox} is more sensitive than OR.

The CH₄ emissions increased exponentially with the increasing FW_G (Fig. 7e) but decreased exponentially with the increasing FW_S (Fig. 7f) and FW_M (Fig. 7g). Among these three factors, the CH₄ emissions were the most sensitive to the FW_G . An increase in the graminoid fraction from 5% to 99% (FW_G) would increase the CH₄ emissions by 70% (Fig. 7e). However, as the fraction of shrubs (FW_S) and Shagnum (FW_M) increased from 5% to 99%, the CH₄ emissions would decrease by 40% (Fig. 7f) and 41% (Fig. 7g), respectively.

4. Discussion

4.1. Effects of water table depth and peat temperature on CH₄ emissions

The soil or peat temperature and water table depth are regarded as the key environmental factors that influence CH₄ emissions from natural wetlands (Ballantyne et al., 2014; Daulat and Clymo, 1998; Schulz et al., 1997). The water table depth divides the anaerobic and aerobic zone and regulates the soil redox potential (Yu et al., 2001). The temperature controls activities of methanogenesis and methanotrophs (Whalen, 2005). A higher temperature will enhance the rate of microbial CH₄ production. The temperature is less sensitive for CH₄ oxidation relative to methanogenesis (Dunfield et al., 1993; Segers, 1998).

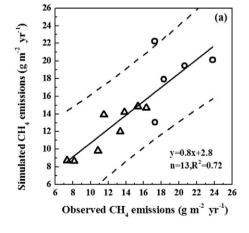
Previous studies reported remarkable differences in the impacts by the environmental factors on the CH₄ emissions among different wetlands. The measurements in the northeast China showed a significant relationship between CH₄ flux and water table level, but the relationship between CH₄ flux and soil temperature was not significant (Ding et al., 2003, Sun et al., 2013). A three year experiments reported that the CH₄ flux was not strongly correlated with the either the temperature or the water table depth in the first year, but did in the next two

years (Updegraff et al., 2001). Long-term effects of water table depth on CH_4 emissions have been reported by Huttunen et al. (2003). However, Hargreaves et al. (2001) have reported independence of the methane emission on the water table depth.

In this study, the CH₄ emission has the same seasonal patterns with the peat temperature from the Siikaneva site (Fig. 2) and the Lompolojänkkä site (Fig. 3), respectively. But it seems that the water table depth didn't control the CH₄ seasonal variations (Fig. 2 and Fig. 3). Similar result was found by Rinne et al. (2007) from the Siikaneva peatland, which showed that the daily measured CH₄ fluxes were dependent on the peat temperature, but not obviously related to the water table depth. There was thick moss layer (~30 cm) on the ground of the Finnish peatland. Although the water table depth was below the surface of the moss layer (minus value in Fig. 2b and Fig. 3b), it was still above the soil surface. According to Saarinen (1996), almost 90% of the root biomass is located in the uppermost 30 cm of the peat. So most of the methanogenic substrate, e.g., root substrate and root litter exists in the anaerobic zone. In addition, the aerenchyma of the sedges could effectively transport CH₄ from the peat to the atmosphere even during the lowest water table depths, and the aerobic peat surface layer would be bypassed (Rinne et al., 2007).

4.2. Different capacities in CH₄ emissions between plant species

CH₄ emission is the balance of the CH₄ production and oxidation. The correlation between net ecosystem productivity and CH₄ emission (Greenup et al., 2000; Waddington and Roulet, 1996; Whiting and Chanton, 1993) as well as the radiocarbon (Chanton et al., 1995) or ¹⁴C-label (Dorodnikov et al., 2011; King and Reeburgh, 2002) proved the contribution of plant photosynthates in CH₄ production. However, there is a great difference in the contribution of recent photosynthates to CH₄ production (Dorodnikov et al., 2011). Previous studies have reported a wide range of 0.5%–15% of the net assimilated C that converts



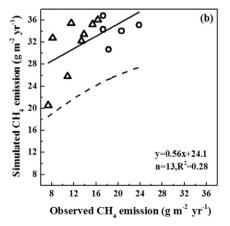


Fig. 6. Comparison of simulated and observed total seasonal/annual CH₄ emissions. (a) Simulated by the new model, (b) simulated by the old model. Black solid lines represent the correlation results. Black dashed lines represent the 95% prediction bands. The triangles and circles denote the Siikaneva site and the Lompolojänkkä site, respectively.

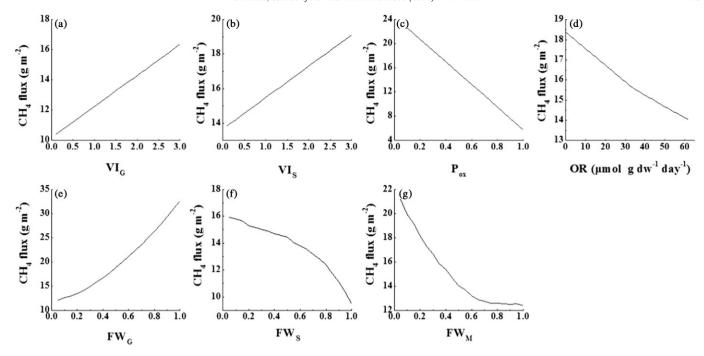


Fig. 7. Model sensitivity to model parameters. CH₄ sensitivity to the (a): Vegetation index for graminoids (VI_G) ; (b): vegetation index for shrubs (VI_S) ; (c): The fraction of CH₄ oxidized during graminoid-mediated transport (P_{ox}) ; (d): Oxidation rates of the endophytic methane-oxidizing bacteria in *Sphagnum* (OR); (e): Fraction of graminoids to the total above-ground biomass (FW_G) ; (f): Fraction of shrubs to the total above-ground biomass (FW_G) ; and (g): Fraction of *Sphagnum* to the total above-ground biomass (FW_M) ;

to the root exudates (Farrar et al., 2003; Gregory, 2006; Jones et al., 2004; Phillips et al., 2008). In a summary, of the 95 whole plant ¹⁴C labeling studies performed in the soil on a broad range of plant species, Jones et al. (2004) estimated that approx. 5–10% of the net fixed C is lost by root exudation, while experiments performed in hydroponics show that typically only 0.5-1.5% of the fixed C is lost (Farrar et al., 2003). This proportion was reported to be 1%-2% for forest (Phillips et al., 2008) and 7%-15% for crops (Gregory, 2006). According to our simulation for 13 years at two Finnish wetlands, the root exudates account for 4.0-8.0% and 2.1%-3.4% of the net assimilated C for the graminoids and the shrubs, respectively. These proportions are between the trees and the crops. The pulse-labeling experiment showed that the root exudates quickly transformed to CH₄ (King et al., 2002; King and Reeburgh, 2002). The fraction of photosynthesized C to CH₄ emissions was measured to be 0.03%-5% for vascular plant species in boreal wetland and arctic tundra systems (Dorodnikov et al., 2011; King et al., 2002; King and Reeburgh, 2002). Our simulated results for the graminoids fell in this range, which was 2.0%-3.4% in Siikaneva and 2.1%-3.1% in Lompolojänkkä.

There is also a great difference in the transportation and oxidation capacity of different plant species. There is no evidence indicating that shrubs or the Sphagnum are capable of transporting gas (Walter et al., 2001). Arenchymous graminoids provide gas conduits to CH₄ transportation (Joabsson et al., 1999). However, the contribution of plant-mediated CH₄ flux varies dramatically from 30%-100% of the total CH₄ flux (Bridgham et al., 2013). In this study, the plant-mediated CH₄ fluxes account for 63%-72%, which falls within the above range. The CH₄ oxidation occurred during the plant transport through the conduits, but the fraction is reported from 0-90% (Popp et al., 2000; Ström et al., 2005). For example, it is reported that Juncus effuses and Eriophorum vaginatum showed a higher oxidation rate (>90%) than Carex rostrata (20%-40%) (Ström et al., 2005). In our study, this fraction was 40%, which was similar to the observed fraction for Carex rostrata. The Sphagnum mosses play a role in controlling the CH₄ oxidation because methanotrophs can live in symbiosis with submerged Sphagnum species (Basiliko et al., 2004; Kip et al., 2010; Larmola et al., 2010; Raghoebarsing et al., 2005). Our simulation showed that in Siikaneva, 20% and 18% of the produced CH₄ was oxidized through the graminoids and *Sphagnum*, respectively. In Lompolojänkkä, these proportions were 28% and 10% because more graminoids and fewer *Sphagnum* existed in this wetland. However, to the best of our knowledge, no field observation related to the comparison of oxidation through different plant species was conducted to support the results of this model.

4.3. Importance of plant community composition in CH₄ simulations

In this study, we improved the model mainly by grouping the vegetation types and recalibrating the vegetation parameters according to the different capability of CH₄ emissions between plant species. This is an important function for process-based models for simulating CH₄ emissions from wetlands with varying vegetation compositions. The high spatial variability of CH₄ emissions is often observed in boreal and arctic wetlands dominated by complex plant communities (Budishchev et al., 2014; Kutzbach et al., 2004; Morrissey and Livingston, 1992; Sebacher et al., 1986). Previous observations have shown that the CH₄ fluxes were lower at the moss site than the Carex site in the arctic tundra (Christensen, 1993). In this study, a higher CH₄ emission was observed at the Lompolojänkkä site with a higher fraction of graminoids and a lower fraction of Sphagnum (Table 1). According to the sensitivity analysis (Fig. 7e and g), this community would induce a higher CH₄ emission in the Lompolojänkkä site compared to the Siikaneva site. To prove this, we also used the vegetation composition of the Siikaneva site to replace that of the Lompolojänkkä site, while maintaining the other parameters unchanged to make simulations. This replacement resulted in a simulated annual CH₄ emission ranges of 13.2–17.3 g m^{-2} yr⁻¹, which was approximately 25% lower than the observations and 22% lower than the simulations based on the actual vegetation composition.

At present time, a lot of process-based models e.g., CH4MOD_{wetland} (Li et al., 2010), Walter model (Walter and Heimann, 2000), CLM4Me (Riley et al., 2011), LPJWhyMe (Wania et al., 2010), DLEM (Xu and Tian, 2012), ORCHIDEE (Krinner et al., 2005), and TRIPLEX-GHG (Zhu et al., 2014), have been used in simulating methane emissions from wetlands. Most of the models calculated CH₄ production as a proportion

of heterotrophic respiration (HR), net primary productivity (NPP) or dissolved organic carbon (DOC) along with soil environmental modification factors. The models usually used an adjustable parameter (e.g., r in TRIPLEX-GHG, R_0 in Walter model, maximum rate of CH4 production in DLEM) in the CH₄ production equation to yield the best agreement for each site between simulation and observations. It is hard to distinguish the vegetation types in these models, thus all vegetation types were considered the same as graminoids. This inevitably induced uncertainties in the model simulation. For example, Zhu et al. (2014) significantly overestimated the CH₄ emissions from the Siikaneva site in 2005 using the TRIPLEX-GHG model, presumably because they considered all of the plant species to be graminoids. This is also the similar case in the previous version of CH4MOD_{wetland} model. However, in CH4MOD_{wetland} model, the methanogenic substrates were calculated separately, according to root substrate, plant litters and soil organic carbon. It is, therefore, easily to group the vegetation type by recalibrating the vegetation parameters (e.g., VI and P_{ox}), making it being applicable in the boreal and subarctic peatlands.

According to our sensitivity analysis results, the composition of the wetland plant community is also important in historical and future regional CH₄ estimations. Previous simulations have usually focused on the effects of climate change and CO2 fertilization on CH₄ emissions (Jin et al., 2015; Li et al., 2012; Shindell et al., 2004; Xu and Tian, 2012; Zhu et al., 2013; Zhuang et al., 2006). It should be noted that climate change and human activity can drive a shift in the wetland ecosystem plant community (Dieleman et al., 2015), which may affect the CH₄ emissions. These changes will be of significant importance concerning a nation's obligation to the United Nations Framework Convention on Climate Change (UNFCCC). For example, in Finland more than half the natural peatlands have been drained (Christensen et al., 2004). Laiho et al. (2003) reported that drainage in Finland causes a shift in the physiognomy of the vegetation, from sedges and grasses to arboreal species (trees and dwarf shrubs). CH₄ emission from drained peatlands is subject to the UNFCCC (Hiraishi et al., 2014). According to the sensitivity simulation by the new $CH4MOD_{wetland}$, this change would decrease the CH₄ emissions (Fig. 7e-g). The calibrated community-specific parameters of the CH4MOD_{wetland} facilitates the simulation of CH₄ emissions associated with the land cover changes in peatlands and helps to reduce the uncertainty in the national inventory of CH₄ emissions compared against the CH₄ emission factors from IPCC (Hiraishi et al., 2014). In future, the European government, and may be the governments of other parts of the world, will continue to support the wetland restoration projects (Christensen et al., 2004). When addressing the issue of wetland restoration, one important consideration should be how GHG fluxes are affected. Fenner et al. (2007) proposed that warmer climates and CO₂ fertilization will increase the level of vascular plant growth, leading in turn to a decrease in the Sphagnum cover. This may increase CH₄ emissions according to the sensitivity analysis conducted in this study (Fig. 7 e, f and g). The new CH4MODwetland can give a more reliable longterm projection of the CH₄ emissions from the restored wetland, which may help the government to evaluate the comprehensive consequences of wetland restoration in relation to GHG budget and the environment.

4.4. Uncertainties and future needs

The bias between the observed and simulated CH₄ fluxes (Fig. 3 and Fig. 4) indicates that uncertainties still exists in the simulation. These uncertainties may partly result from the incompleteness of the model structure. For example, CH₄ production and oxidation associated with the *Sphagnum* were not clear. It has been reported that the recent *Sphagnum subnitens* photosynthate carbon contributes to the dissolved organic carbon of peatlands, which may also act as the substrate of methanogenesis (Fenner et al., 2004). However, this was neglected in

the new model. In addition, Kip et al. (2010) demonstrated that potential oxidation rates in *Sphagnum* were the highest at 20 °C, much lower at 10 °C and undetectable at 4 °C with one exception. Although temperature control has been suggested to be less important for CH₄ oxidation than for CH₄ production (Dunfield et al., 1993; Segers, 1998), it should still be involved in the process-based model. Another example is that the model underestimated the CH₄ fluxes in winter for the Siikaneva site (Fig. 2a) and during March to April for the Lompolojänkkä site (Fig. 3a). This may be because the CH₄ produced in the peat over winter may be trapped by the snow and ice cover and then released as ice thawed in the following spring (Hargreaves et al., 2001). These processes should be considered in future work.

Uncertainties due to these limited observations should also induce uncertainties into the simulations. The biases between the modeled and observed CH_4 fluxes are not consistent in different years for the same site, e.g., they overestimate the CH_4 fluxes in 2006 (Fig. 4a) but underestimate the CH_4 emissions in 2007 (Fig. 4b) and 2009 (Fig. 4d). This may because we used the constant fraction of the plant species (Table 1). More detailed observations on the variations of the plant community composition are therefore important for CH_4 simulation, especially over long time scales.

5. Conclusion

This study successfully introduced three vegetation classes into a process-based biogeophysical model, e.g., CH4MOD_{wetland}, according to their differing abilities to supply methanogenic exudates, CH₄ oxidation and transport. The improved model can reasonably describe the observed seasonal CH₄ variations as well as the annual amount of total CH₄ emissions from the boreal and subarctic wetlands in Finland. It significantly increased the model efficiency and decreased the RMSE and RMD for the daily and annual CH₄ emissions compared to the original model with old parameters. The simulated seasonal and/or annual amounts of CH₄ emissions for the different sites and years agreed with the observed results and yielded an R^2 of 0.72 (n = 13, p < 0.001). However, there are still discrepancies between the observed and simulated CH₄ emissions, which may be induced by the incompleteness of the model structure as well as inaccurate input values such as the plant composition. Our study indicated that the shift in the wetland plant community compositions would significantly change the CH₄ emissions. The new CH4MOD_{wetland} will be linked to a precise vegetation map to reduce uncertainties of regional, national, continental or global wetland CH₄ emission estimates. This also help the government to make national report of CH₄ emissions from wetland and evaluate the comprehensive consequences of wetland restoration in relation to GHG budget.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.scitotenv.2016.08.020.

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