# Review and Synthesis: Peatland and Wetland Models Simulating CH₄ Production, CH₄ Oxidation and CH₄ Transport Pathways

Amey S. Tilak[1], Alina Premrov[2,7], Ruchita Ingle[3], Nigel Roulet[4], Benjamin R.K. Runkle[5], Matthew Saunders[2], Avni Malhotra[6] and Kenneth A. Byrne[1]

[1] Department of Biological Sciences, University of Limerick, Limerick, Ireland (amey.tilak@ul.ie, ken.byrne@ul.ie)

[2] Botany School of Natural Sciences, Trinity College Dublin, Dublin, Ireland (apremrov@tcd.ie, saundem@tcd.ie)

[3] Department of Environmental Sciences, Wageningen University, Netherlands (ruchita.ingle@wur.nl).

[4] Department of Geography, McGill University, Montreal, Canada (nigel.roulet@mcgill.ca)

[5] Department of Biological and Agricultural Engineering, University of Arkansas, Fayetteville, AR, USA (brrunkle@uark.edu)

[6] Pacific Northwest National Laboratory, Richland, USA (avni.malhotra@pnnl.gov).

[7] Department of Environmental Science, Faculty of Science, Atlantic Technological University, Sligo, Ireland (alina.premrov@atu.ie)

*First author:* amey.tilak@ul.ie and *Corresponding authors:* Kenneth A. Byrne (ken.byrne@ul.ie) and Avni Malhotra (avni.malhotra@pnnl.gov)

**Abstract.** Peatlands play an important role in the global CH₄ cycle and models are key tools to assess global change effects on CH₄ processes. It remains unclear how well our existing wetland modelling frameworks are suited to peatland questions. Therefore, we reviewed 16 peatland or wetland models operating at different spatial (seconds-to-decadal) and temporal (soil core-to-global) scales, having different spin-up periods for carbon pool stabilization and various CH₄ production, oxidation and transport processes. Through a literature review, model specific advantages and limitations, common and specific driving inputs of all models and critical inputs of individual models impacting CH₄ plant-mediated transport, diffusion and ebullition were summarized. The 16 reviewed models were qualitatively ranked 0 to 4 (none-to-full process representations) with respect to CH₄ production, oxidation and transport. The most common temporal and spatial scale for 14 models was daily time-step and field scale respectively, while the spin-up stabilization periods of different carbon pools (peat, litter, roots, exudates, microbial, humus, slow, fast) of all models ranged 7 to 90102 years. With regards to CH₄ production and oxidation, 50% of reviewed models (Ecosys, CLM-Microbe, ELM-Spruce, Peatland-VU, Wetland-DNDC, TRIPLEX-GHG, TEM, CLM4Me) exhibited full to adequate process representation. Meanwhile 44, 44 and 25% models exhibited full to adequate process representation for plant mediated transport, diffusion and ebullition respectively. This meant there is ample scope to improve ebullition processes in the remaining 75% models. We conclude that existing models are adequate for site-level CH₄ flux assessments but may lack a predictive understanding of CH₄ production pathways.

## 1 Introduction

Northern peatlands contain partially decomposed plant derived organic matter that has accumulated over millennial time scales, due to the continuously water-logged conditions, acidic soils and low air temperatures (Nichols and Peteet, 2019; Hugelius et al., 2020; Loisel and Gallego-Sala, 2022). These waterlogged conditions drastically slow down the decomposition of organic matter, resulting in net accumulation of peat (Hugelius et al., 2020; Qiu et al., 2020; Qiu et al., 2021). Although peatlands cover 3% of the global land area they store twice as much carbon as the world's forest (Humpenöder et al., 2020; Loisel and Gallego-Sala, 2022). Globally, $600 \pm 100$ Pg C is stored in peatlands (Leifeld and Menichetti, 2018; Leifeld et al., 2019; Nichols and Peteet, 2019). However, during the last century, peatlands across the globe have been drained and degraded and converted into agricultural lands, grasslands and croplands, releasing stored carbon as $CO_2$ (Abdalla et al., 2016; Fluet-Chouinard et al., 2023). To mitigate $CO_2$ losses to the atmosphere, peatlands are being rewetted by raising the water levels closer to the soil surface to enable continuous anaerobic conditions for carbon

sequestration (Leifeld et al., 2019). Even though peatland rewetting most commonly decreases net $CO_2$ emissions, it simultaneously increases $CH_4$ emissions (Abdalla et al., 2016; Günter et al., 2020). This tradeoff is important since $CH_4$ is the
45 second most potent greenhouse gas (GHG), having 34 times stronger radiative forcing compared to $CO_2$, but a shorter lifetime (12 years) compared to $CO_2$ (300-1000 years) (Abdalla et al., 2016). Furthermore, $CH_4$ fluxes from rewetted peatlands are spatially and temporally variable and driven by peat depth, vegetation types, microbial compositions, peat and air temperatures, precipitation and resulting water table depths (Wilson et al., 2015; Abdalla et al., 2016; Vroom et al., 2022; Ge et al., 2024).
50
The two most common monitoring approaches that are utilized to measure $CH_4$ fluxes from peatlands and wetlands are the top-down and bottom-up approaches (Ma et al., 2021; Erland et al., 2022; Liu et al., 2023; McNicol et al., 2023; Forbich et al., 2024). Bottom-up measurement approaches typically quantify spatial and temporal trends in $CH_4$ fluxes via chamber measurements with known area and volume (Hutchinson and Livingston, 2002; Kutzbach et al., 2007; Hendriks et al., 2007;
55 Schrier-Uijl et al., 2010) and continuous eddy covariance (EC) measurements (Baldocchi et al., 2001a; Denmead, 2008; Oertel et al., 2012). Although chamber measurements quantify $CH_4$ fluxes from specific source areas, they require multiple replications to capture spatial and temporal variations and often do not provide continuous flux data, while the EC method provides continuous temporal $CH_4$ flux data, but these measurements are not easily attributable to a specific microsite type (Erland et al., 2022). Automated chambers of different designs (Courtois et al., 2019; Mander et al., 2022) also measure $CH_4$
60 fluxes at a sub-daily temporal resolution and are utilized to capture hot moments from a known source area, typically not captured by manual chamber and EC methods (Zhao et al., 2024). The top-down approach utilizes atmospheric observations of $CH_4$ concentrations combined with models that account for atmospheric transport from an emitting to an observation location (NASEM, 2018; Erland et al., 2022). The different top-down approaches that are generally utilized are remote observations, towers, aircraft, and satellites (Tedeschi et al., 2022). However, for predicting future wetland/peatland $CH_4$
65 fluxes under a range of climatic and environmental conditions, computer models are parametrized against measured $CH_4$ fluxes and in-situ environmental data to minimize the error between simulated and measured fluxes (Grant, 1998; Grant, 1999; Xu et al., 2016; Morin et al., 2022). Models are also utilized to enhance the understanding of various processes occurring in different peatlands and wetlands such as the $CH_4$ production, $CH_4$ oxidation and $CH_4$ transport (plant-mediated, diffusion and ebullition) (Tang et al., 2010; Riley et al., 2011; Zhang et al., 2022). The other important goal of developing
70 models is identifying the critical inputs that influence modelled outputs related to $CH_4$ production, $CH_4$ oxidation and $CH_4$ transport pathways to improve the process understanding (Xu et al., 2016; Mozafari et al., 2023).

The recent reviews of $CH_4$-revelant models by Xu et al. (2016) and Mozafari et al. (2023) highlighted and discussed the processes of methanogensis, methanotrophy and $CH_4$ transport pathways of different terrestrial models impacted by their
75 associated environmental conditions and differentiated 45 peatland and wetland models that simulated $CH_4$ production, $CH_4$ oxidation and $CH_4$ transport into four categories: 1) terrestrial ecosystem models simulating biogeochemical and vegetation dynamics, 2) hydrological models, 3) land surface models, 4) ecohydrological models simulating bogs and fens in the Northern hemisphere respectively. Meanwhile Forbich et al. (2024) provided an historical overview on inclusion of wetland $CH_4$ components in Earth system models (ESMs), discussed how $CH_4$ modelling approaches evolved over time and
80 highlighted the knowledge gaps and challenges faced in accurately estimating $CH_4$ fluxes. However, it remains unclear as to what extent these models could be used for peatland applications. Furthermore, it remains unclear whether these models represent peatland relevant processes and inputs for $CH_4$. Across peatland applications, future users of models require information on relevant spatial-temporal scales, key model inputs (to ensure that they have corresponding measurements) and on process representation. Therefore, the goals of this review are to synthesize the attributes, strengths and weaknesses
85 of existing models that could be applied to peatland $CH_4$ questions. Specifically, we: a) summarize the spatial and temporal operating scales and spin-up stabilization periods of different carbon pools; b) identify the model driving inputs that are common and separate to all reviewed models; c) summarize models simulating one or two or three $CH_4$ transport pathways i.e., plant mediation, diffusion and ebullition; d) qualitatively rank the process representations in each model for $CH_4$ production, $CH_4$ oxidation and $CH_4$ transport; e) summarize the advantages and limitations of each reviewed model;
90 e) synthesize the critical model inputs impacting individual plant-mediation, diffusion and ebullition. We hope this review enables new model users to decide which model suits their needs best, but also provide a synthesis of $CH_4$ process representation across reviewed models.

## 2 Materials and Methods

### 2.1 Identifying models simulating CH$_4$ processes

We identified models that simulated CH$_4$ production, CH$_4$ oxidation and CH$_4$ transport (plant-mediated, ebullition and diffusion) in peatland and wetland environments using "Google Scholar" and "Web of Science" having the following search key words: a) models simulating CH$_4$ fluxes peatlands and wetlands; b) models simulating CH$_4$ transport pathways peatlands and wetlands; c) process based CH$_4$ models peatlands and wetlands; d) mechanistic models simulating CH$_4$ fluxes peatlands and wetlands; d) microbial models simulating CH$_4$ fluxes peatlands and wetlands; e) biogeochemical models simulating CH$_4$ fluxes peatlands and wetlands and f) dynamic global vegetation models simulating CH$_4$ fluxes peatlands and wetlands. Each key word resulted in a plethora of published papers, technical reports, documentation, non-peer-reviewed papers, grey literature (reports, policy documents, technical notes) and inaccessible full text papers respectively. Non-peer reviewed papers, grey literature and inaccessible full-text papers were not considered in this review.

### 2.2 CH$_4$ model selection and review

From each key word or phrase, peer reviewed published papers associated with each model were identified i.e., model specific development papers, model application papers, model review papers and technical model documentation. Also, models were only chosen if they were written in English and published from 1997 to 2022. Model documents pertinent to the above-mentioned criteria were manually screened, identified and selected. Statistical or black box models simulating CH$_4$ fluxes in peatlands and wetlands were not considered in this review. This review specifically focused on identifying models that are process based, mechanistic and microbial, operating at the plot, field, regional, national and global scales that simulated all three CH$_4$ transport pathways (plant transport, ebullition, and diffusion), at least two CH$_4$ transport pathways or simulated total CH$_4$ flux. From these above-mentioned criteria, 16 models were selected (Table 1). Firstly, we distinguish the spatial and temporal operating scale of each model, quantify the spin-up period required to stabilize different carbon pools for each model, summarize models simulating one or two or three CH$_4$ transport pathways and qualitatively rank each model into five process representation categories from 0 to 4, with the rank 0 having no process representation, rank 1 minimal process representation, rank 2 intermediate process representation, rank 3 adequate process representation and rank 4 full process representation with respect to CH$_4$ production, CH$_4$ oxidation, CH$_4$ plant transport, CH$_4$ diffusion and CH$_4$ ebullition. The no process representation implies that the specific peatland or wetland model does not incorporate any processes or mechanisms simulating CH$_4$ production, oxidation and transport. In case of the minimal process representation, the specific peatland or wetland model exhibits simplified representation of CH$_4$ fluxes without quantifying in detail the different CH$_4$ production, and oxidation pathways, while the transport process are only described using rate coefficients. Models with intermediate process representation incorporate some degree of CH$_4$ production and oxidation, while CH$_4$ transport is described based on rate coefficients and CH$_4$ concentrations supporting bubbling, minimum and threshold CH$_4$ concentrations and vegetation specific CH$_4$ transport and oxidation factors. The adequate process representation quantifies different CH$_4$ production, oxidation and transport pathways (Zhuang et al., 2004; Zhu et al., 2014; Salmon et al., 2022), while full process representation quantifies detailed microbial CH$_4$ production and oxidation processes (Grant and Roulet, 2002; Xu et al., 2015; Wang et al., 2019; Ricciuto et al., 2021). A concise description of all the reviewed models is available in the Supplementary material.

140 **Table 1.** Selected peatland or wetland model and their references.

| Model name | Model references |
|---|---|
| CLM-Microbe | Xu et al. (2015) ; Wang et al. (2019) ; He et al. (2021) ; Zuo et al. (2022); He et al. (2024) |
| HIMMELI | Raivonen et al. (2017) |
| Peatland-VU | van Huissteden et al. (2006); van Huissteden et al. (2009); Petrescu et al. (2010); Budishchev et al. (2014); Mi et al. (2014); Lippmann et al. (2023) |
| Wetland-DNDC | Li et al. (1992a), Li et al. (1992b) ; Li (2000) ; Zhang et al. (2002) ; Gilhespy et al. (2014) ; Deng et al. (2015); Webster et al. (2013) ; Taft et al. (2019) |
| TRIPLEX-GHG | Zhu et al. (2014) ; Zhu et al. (2016); Zhu et al. (2017) |
| WETMETH | Nzotungicimpaye et al. (2021) |
| ORCHIDEE model (various versions) | Largeron et al. (2018) : high-latitude-ORC-HL-PEAT; Qiu et al. (2018) : revision 4596 ; Giumberteau et al. (2018) : MICT (v.8.4.1) ; Qiu et al. (2019) : PEAT land surface model (SVN r5488) ; Salmon et al. (2022): revision 7020-PCH$_4$, |
| BASGRA-BGC | Huang et al. (2021) |
| TEM | Zhuang et al. (2004) ; Zhuang et al. (2010) ; Tang et al. (2010) ; Li et al. (2020) |
| Ecosys | Grant and Roulet (2002) ; Grant et al. (2015a) ; Grant (2015b) ; Grant et al. (2017a); Grant et al. (2017b) ; Chang et al. (2019) |
| LPJWhyMe | Wania et al. (2009a) ; Wania et al. (2009b); Wania et al. (2010) |
| MEM | Lai (2009) |
| CH4MOD | Li et al. (2010) ; Li et al. (2012) ; Li et al. (2016) ; Li et al. (2017), Li et al. (2019); Li et al. (2020); Zhang et al. (2020); |
| PEPRMT | Oikawa et al. (2017) ; Fertitta-Roberts et al. (2019); Mack et al. (2023) |
| ELM-SPRUCE | Xu et al. (2015) ; Shi et al. (2015) ; Hanson et al. (2020) ; Yuan et al. (2021); Wang et al. (2019); Ricciuto et al. (2021) |
| CLM4Me | Oleson et al. (2010) ; Lawrence et al. (2011); Riley et al. (2011) |

## 3 Results

### 3.1 Model temporal and spatial scales

145    The reviewed peatland or wetland models operate at different temporal scales. For example, Ecosys (Grant and Roulet, 2002; Grant et al., 2012; Grant et al., 2017a, b) operates at seconds and hourly time scale, while HIMMELI (Raivonen et al., 2017) and ORCHIDEE-PCH4 (Salmon et al., 2022) operate at half-hourly time scale, PEPRMT (Oikawa et al., 2017) operate at daily time scale and CLM-Microbe (Xu et al., 2015 ; Wang et al., 2019), TEM (Zhuang et al., 2004), ELM-Spruce (Xu et al., 2015 ; He et al., 2020 ; Yuan et al., 2021 ; Wang et al., 2019) and Ecosys operate at hourly time scale (Table 2).

150    However, the most widely utilized temporal scale for 14 out of 16 models was the daily-time step. With regards to spatial operating scale, CLM-Microbe operates at lab, plot and field scale, while the most widely utilized spatial scale for 14 out of 16 models was field scale (Table 2).

### 3.2 Model spin-up times for stabilizing different carbon pools

155    The spin-up time required for stabilization of different carbon pools for all models ranged from 7 to 90102 years (Fig. 1). For example, HIMMELI, which is not embedded into any peatland carbon model requires seven-spin-up years to stabilize peat $CH_4$ concentrations (Raivonen et al., 2017). Peatland-VU (van Huissteden et al., 2006) requires 20-60 years for stabilizing different carbon pools such as peat, litter, roots, exudates, microbial and humus (personal communications, Tanya Lippmann, 2022). However, Wetland-DNDC (Zhang et al., 2002) requires 20-200 years of spin-up to stabilize soil organic

160    carbon (SOC), soil N pools and soil water filled pore spaces (WFPS) (Webster et al., 2013; Deng et al., 2015; Taft et al., 2019). The exact number of years for stabilizing different carbon pools in Peatland-VU and Wetland-DNDC depends upon

the site-specific climate, soils, vegetation and local environmental conditions. Models such as Ecosys (Grant and Roulet, 2002), ORCHIDEE (peat land surface, MICT, Peat-4596, PCH$_4$) (Largeron et al., 2018; Qiu et al., 2018; Giumberteau et al., 2019), TEM (Zhuang et al., 2010; Li et al., 2020) and TRIPLEX-GHG (Zhu et al., 2014) require 41-300 years spin-up to
165    stabilize hydrology, soil thermal regimes, soil moisture, C in dead plants and vegetation productivity (Fig. 1). However, the spin-up time of ORCHIDEE-PCH$_4$ varies depending on the site type i.e., bog vs. fen vs. marsh. For example, the spin-up period for carbon pool stabilization at Winous Point Marsh site, USA was 32 years, while it was 10060 years at a fen site in Germany (Salmon et al., 2022). Qiu et al. (2018) utilized ORCHIDEE-PEAT (revision 4596) at 30 peatland sites located in boreal, temperate, arctic and arctic permafrost and the spin-up time to stabilize carbon pools was 10100 years. Models like
170    CLM4Me (Riley et al., 2011), LPJWhyMe (Wania et al., 2010) and ELM-SPRUCE (Ricciuto et al., 2021) have spin-up times of 1500, 1000 and 1250 years respectively. Spin-up times in CLM4Me (Riley et al., 2011) consists of: 1) 500 years spin-up using atmospheric data and 2) 1000 years spin-up subject to land use, N and aerosol deposition. In LPJWhyMe (Wania et al., 2010), 1000 years spin-up implemented using climate data such as air temperature, cloud cover, monthly total precipitation and monthly number of wet days, while in ELM-SPRUCE (Ricciuto et al., 2021), four soil carbon pools and
175    three litter pools were stabilized for 1250 years. However, carbon pool stabilization in LPJWhyMe requires 90000 years spin-up +102 years of transient runs (Wania et al., 2009b). The carbon pool stabilization in CLM-Microbe varies for different biomes, e.g., tropical and temperate 1500 years spin-up, boreal and arctic 2000 years and wetlands 3000 years (Fig. 1; He et al., 2023). Meanwhile the stabilization in WETMETH consists of three phases: 1) 5000 years spin-up for climate state equilibrium; 2) 169 years transient runs of CO$_2$ concentrations and 3) site-specific runs based on measured data
180    (Nzotungicimpaye et al., 2021). However, no information on carbon pool stabilization is provided for MEM (Lai, 2009), CH4MOD (Li et al., 2010) and PEPRMT (Oikawa et al., 2017) as of October 22, 2024.

185

190

195

200

205

**Table 2.** Temporal and spatial operating scales of 16 peatland or wetland models.

| Spatial scales | Peatland or Wetland Models | Temporal scales | Peatland or Wetland Models |
|---|---|---|---|
| Seconds | | Lab | CLM-Microbe |
| Half hourly | HIMMELI, ORCHIDEE-PCH4 | Plot | CLM-Microbe, HIMMELI, Peatland-VU, Ecosys, ELM-SPRUCE |
| Hourly | CLM-Microbe, TEM, Ecosys, ELM-SPRUCE | Field | CLM-Microbe, Peatland-VU, TRIPLEX-GHG, TEM, LPJWhyMe, MEM, ELM-SPRUCE, HIMMELI, Wetland-DNDC, BASGRA-BGC, Ecosys, CH4MOD, PEPRMT, CLM4Me |
| Daily | CLM-Microbe, Peatland-VU, TRIPLEX-GHG, BASGRA-BGC, LPJWhyMe, PEPRMT, CLM4Me, HIMMELI, Wetland-DNDC, ORCHIDEE-PCH4, TEM, MEM, CH4MOD, ELM-SPRUCE | Regional | TRIPLEX-GHG, WETMETH, ORCHIDEE-PCH4, TEM, CLM4Me |
| Monthly | TRIPLEX-GHG, LPJWhyMe, CLM4Me | National | TRIPLEX-GHG, WETMETH, ORCHIDEE-PCH4, TEM, CLM4Me |
| Seasonal | WETMETH | Global | TRIPLEX-GHG, WETMETH, ORCHIDEE-PCH4, TEM, CLM4Me |
| Yearly | WETMETH, LPJWhyMe | | |
| Decadal | WETMETH | | |

210

215

220

6

**Figure 1.** Spin-up times in terms of stabilizing different carbon pools for all reviewed wetland or peatland models. Each model has its own unique color for easy identification. Also, a single model can possess different time scales, e.g., CLM-Microbe having different C stabilization periods for tropical, temperate, and arctic ecosystems.

225

230

235

### 3.3 Common model driving inputs

240     Each of the selected peatland or wetland models (Table 1) was manually screened to identify driving inputs common to all models with respect to climate, hydrology, peat physical and chemical and different vegetation species (Table 3). Generally, climate inputs are easily available from on-site measurements or global databases (NCAR climate data, Copernicus, Europe, NASA Climate data services, NOAA Climate data and local databases (Irish Metrological Service and United States

245 Environmental Protection Agency). The hydrological and peat physical and chemical data (Table 3) can be obtained from literature, laboratory and site-specific field measurements.

### 3.4 Model specific driving inputs

    The number of model inputs (Table 4) are generally proportional to how comprehensively each model simulates the

250 intricacies of processes like hydrology, soil physical, soil chemical, soil microbial processes and vegetation dynamics. For example, CLM-Microbe (Xu et al., 2015; Wang et al., 2019) and Ecosys (Grant and Roulet, 2002; Grant, 2015; Grant et al., 2015) and ELM-SPRUCE (Ricciuto et al., 2021; Yuan et al., 2021) require extensive microbial inputs (growth, death rates and temperature sensitivity of acetoclastic methanogens, aerobic methanotroph and growth rate $H_2$-$CO_2$-dependent methanogens) compared to MEM (Lai, 2009) which only requires acrotelm and catotelm depth, decomposition rates and

255 carbon to peat ratio. Models like Peatland-VU, Wetland-DNDC, TRIPLEX-GHG, BASGRA-BGC, ORCHIDEE-PCH4, LPJWhyMe and CH4MOD utilize different decomposition rates for different carbon pools (humus, peat, roots and litter, exudates, slow and fast carbon pools) which are rarely available from site-specific measured data, instead, they are fine-tuned during model parametrization (van Huissteden et al., 2006; Webester et al., 2013 ; Li et al., 2004a ; Zhang et al., 2002; Zhu et al., 2014 ; Zhu et al., 2016 ; Zhu et al., 2017; Salmon et al., 2022; Huang et al., 2021; Wania et al., 2010; Li et al.,

260 2010 ; 2016 ; 2020 ; Zhang et al., 2020). Also, inputs related to $CH_4$ transport such as plant-mediated transport, $CH_4$ oxidized during plant transport, ebullition and diffusion rate coefficients are not measured at all peatland and wetland sites but fine-tuned to minimize the error between simulated and measured $CH_4$ fluxes. The model specific driving inputs that are generally available from site-specific studies are specific leaf area, harvested above-ground biomass, maximum and minimum vegetation growth rates, rooting depth, peat thickness, initial peat carbon levels, growing degree days, standing

265 water above peat surface, WTDs, leaf and litter C and N, lignin concentration in litter and C:N ratio.

270

275

280

**Table 3.** Driving inputs common across peatland or wetland $CH_4$ models (for individual model references see Table 1).

| Climate inputs | Hydrological inputs | Physical & Chemical inputs | Vegetation inputs |
|---|---|---|---|
| Precipitation | Water table depths | No of peat layers & individual depths | Leaf area index, |
| Evapotranspiration | Peat moisture in different depths | Initial soil organic C all peat depths | Specific leaf area, |
| Air temperature | Surface flow inputs (runoff) | pH all peat depths | Max root depth, length, & tortuosity |
| Solar radiation | Hydraulic conductivity all peat layers | Bulk density all peat depths | Plant functional types (PFTs), |
| Short & long wave radiation | Porosity all peat layers | Peat temperature all peat depths | Above & below ground biomass, its C: N concentrations |
| Wind speed | Field capacity all peat layers | C:N ratios all peat depths | Litter C & N concentrations |
| Humidity | Wilting point all peat layers | Soil $CH_4$ concentrations each peat layer | Initial senescence rates/scalars and above & below ground biomass |
| Cloud cover | | Threshold $CH_4$ concentration for ebullition | |
| Vapor pressure | Volumetric water content | | |

285

290

295

300

**Table 4.** Model specific driving inputs for reviewed peatland or wetland models.

| | Model specific driving inputs | | | | |
|---|---|---|---|---|---|
| **CLM-Microbe** (Xu et al., 2015 ; Wang et al., 2019) | **HIMMELI** (Raivonen et al., 2017) | **Peatland VU** (van Huissteden et al., 2006 ; 2009) | **Wetland DNDC** (Webester et al., 2013 ; Li et al., 2004a ; Zhang et al., 2002) | **TRIPLEX GHG** (Zhu et al., 2014 ; Zhu et al., 2016 ; Zhu et al., 2017) | |
| 1) half-saturation coefficient of available carbon mineralization, 2) max rate of acetate production available carbon, 3) decomposition rate constant dissolved organic matter, 4) decomposition rate constant biomass of bacteria and fungi, 5) leaf N fraction Rubisco enzyme, 6) growth respiration parameter 7) methanogen growth & death rates 8) plant mediated, diffusion & ebullition rate constants | 1) aerobic & anaerobic respiration rate 2) $CH_4$ oxidation inputs (Michaelis-Menten) 3) methanogenesis sensitivity to $O_2$ inhibition, 4) root decay constant, 5) root tortuosity 6) ebullition & diffusion constants & specific leaf area | 1) SOM decomposition constants (peat, humus), 2) min & max primary production 3) carbon fraction each layer organic matter reservoir, 4) root and litter senescence 5) exudate factor 6) harvested biomass fraction 7) $CH_4$ oxidation & production 8) $CH_4$ transport (rate constants) | 1) Atmospheric $CO_2$, $NO_3$-N, $NH_4$-N in precipitation, 2) biomass & leaf C & C:N ratio in wood 3) growing degree days 4) vegetation growth respiration and dark respiration fraction, 5) humus fraction, 6) vegetation harvesting dates, 7) fertilization rates. 8) $CH_4$ production, oxidation & transport parameters | 1) diurnal temperature range 2) wet day frequency, 3) soil texture, 4) plant functional types, 5) topography (soils & veg) 6) decomposable, structural, and resistant carbon pool decomposition rates, protected slow pool, passive pool, and non-protected slow pool rates), 7) $CH_4$ production, oxidation, and transport parameters. | |

305

310

**Table 4.** continued.

| | Model specific driving inputs | | | |
|---|---|---|---|---|
| **WETMETH** (Nzotungicimpaye et al., 2021) | **ORCHIDEE-PCH4** (Salmon et al., 2022) | **BASGRA-BGC** (Huang et al., 2021) | **Terrestrial Ecosystem Model (TEM)** (Zhuang et al., 2004 ; 2010 ; Tang et al., 2010) | **Ecosys** (Chang et al., 2019 ; Grant and Roulet, 2002 ; Grant, 2015 ; Grant et al., 2015 ; Bouskill et al., 2020) |
| 1) thickness of oxic-anoxic zone<br>2) carbon content<br>3) topographic maps (spatial wetland distribution)<br>4) plant functional types<br>5) $CH_4$ production (temperature coefficient)<br>6) $CH_4$ oxidation scaling parameter. | 1) plant functional types,<br>2) $CH_4$ production & oxidation,<br>3) $CH_4$ transport (oxic: anoxic decomposition ratio, methanotrophy rate, root $CH_4$ oxidation, root depth, efficiency plant mediated $CH_4$ transport, moisture connectivity and $CH_4$ mixing ratio bubbles). | 1) C & N, root, leaf & stem<br>2) dissolved organic carbon,<br>3) harvest date, fertilizer<br>4) distance between two drainpipes, radius & depth<br>5) labile, very labile, and passive SOM constants,<br>6) grass maintenance and growth respiration rates,<br>7) oxidation & production rates<br>8) $CH_4$ rate constants plant transport, diffusion, ebullition. | 1) soil thermal conductivity<br>2) soil heat capacity,<br>3) soil C, N & soil texture,<br>4) vegetation (canopy water conductance, its max value & leaf water potential)<br>5) scalars: redox, pH, moisture, and soil temperature on $CH_4$ production and $CH_4$ oxidation<br>6) $CH_4$ pathways (rate constants ebullition, plant transport, diffusion, root area, plant aerenchyma factor) | 1) soil organic carbon, sand, silt content, field capacity, wilting point, hydraulic conductivity, grid cell slopes<br>2) Atmospheric concentrations ($O_2$, $CO_2$, $CH_4$, $N_2O$)<br>3) tillage, fertilization, irrigation & harvesting inputs,<br>4) plant & microbial functional type (PFTs & MFTs) inputs<br>5) nutrient cycling (C, N, P) |

315

320

325

330 **Table 4.** continued

| | | Model specific driving inputs | | | |
|---|---|---|---|---|---|
| **LPJWhyMe** (Wania et al., 2010) | **Methane Emission Model (MEM)** (Lai, 2009) | **CH4MOD** (Li et al., 2010 ; 2016 ; Zhang et al., 2020) | **PEPRMT** (Oikawa et al., 2017 ; Fertitta-Roberts et al., 2019) | **ELM-SPRUCE** (Xu et al., 2015 ; He et al., 2020 ; Yuan et al., 2021 ; Wang et al., 2019) | **CLM4Me** (Lawrence et al., 2011 ; Oleson et al., 2010 ; Riley et al., 2011) |
| 1) inundation stress non-flood tolerant PFTs<br>2) decomposition rates: fast & slow carbon pools<br>3) production & oxidation inputs<br>4) transport pathways inputs | 1) acrotelm and catotelm (depth, decomposition, mineralization rates)<br>2) carbon to peat ratio | 1) standing water depth;<br>2) sand fraction,<br>3) max above ground biomass<br>4) growing degree days<br>5) senescence degree day<br>6) non-structural component of plant litter,<br>7) SOM first order decay rate<br>8) initial N & lignin in litter<br>9) plant carbohydrates amount | 1) absorbed photosynthetically active radiation (APAR),<br>2) initial soil organic carbon<br>3) labile soil organic carbon. | 1) observed GPP, NPP, plant biomass,<br>2) DOC, acetate concentrations,<br>3) initial N concentrations,<br>4) bacterial and fungal turnover rates,<br>5) growth & death rates methanotrophs, methanogen,<br>6) minimum $CH_4$ solubility,<br>7) dissolved organic matter turnover rate.<br>8) maximum acetate production rate<br>9) half-saturation coefficient available carbon mineralization<br>10) dissolved organic matter turnover rate | 1) $CH_4$ production (Q10 & pH impact)<br>2) $CH_4$ oxidation (max oxidation rate)<br>3) $O_2$ & $CH_4$ half-saturation oxidation coefficients<br>4) $CH_4$ transport parameters (aerenchyma radius, porosity, $CH_4$ concentration threshold) |

335

### 3.5 Models simulating CH$_4$ transport pathways

Out of 16 reviewed models, 12 models simulate all three CH$_4$ transport pathways of plant-mediated, ebullition and diffusion (Fig. 2). MEM only simulates diffusion and ebullition but not plant-mediated transport (Lai, 2009) while CH4MOD only simulates plant-mediated transport and ebullition, but not diffusion (Li et al., 2010; 2016; 2017). The
340  PEPRMT (Oikawa et al., 2017) simulates plant-mediated transport and diffusion but not ebullition, while WETMETH does not simulate any CH$_4$ transport pathways, but rather simulates total CH$_4$ flux (Nzotungicimpaye et al., 2021).
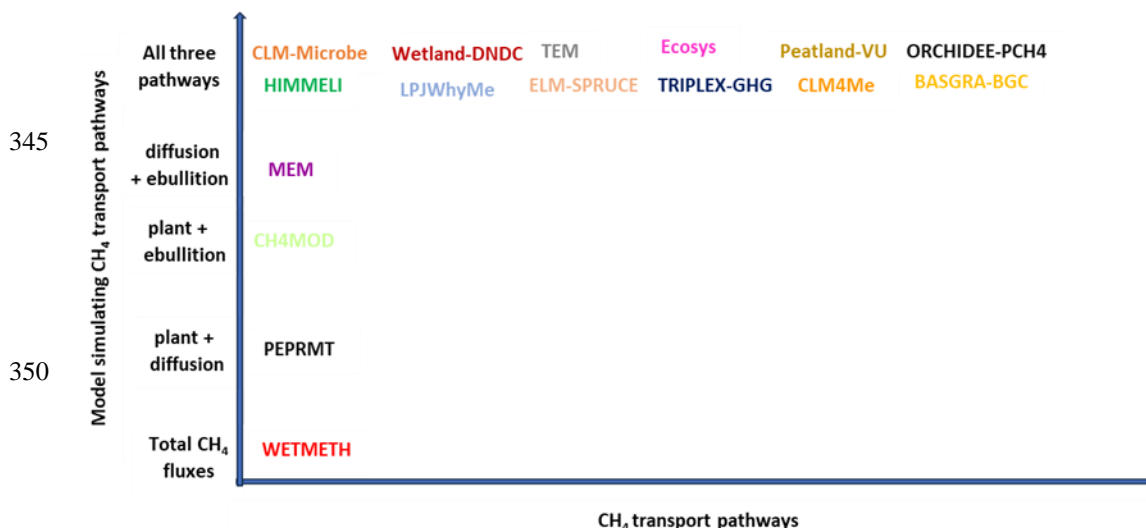


**Figure 2.** Reviewed peatland or wetlands models simulating CH$_4$ transport pathways. Each model has its own unique colour for easy identification. The + sign means model simulates both mentioned CH$_4$ transport pathways.

### 3.6 Model process-representations: Full (rank 4) and adequate (rank 3)

The 16 reviewed models were distinguished into five categories to qualitatively rank: CH$_4$ production, CH$_4$ oxidation and
360  CH$_4$ transport processes. The ranking was done using qualitative categories 0 to 4 (as explained in section 2.2). The following sections provides information on models categorized under rank 4 (full) and rank 3 (adequate) based on their model process-representations for production, oxidation and transport processes, whereas categorization of all 16 reviewed models into the five categories is presented in Figures 3 and 4.

### 3.6.1 Production and oxidation models

Models like CLM-Microbe, Ecosys and ELM-Spruce (Fig. 3) exhibited full CH$_4$ production and oxidation processes, since they comprehensively simulate microbial mediated processes of production (hydrogenotrophic methanogenesis, acetoclastic methanogenesis and H$_2$ production) and oxidation (aerobic methanotrophy and anaerobic methanotrophy) (Grant and Roulet, 2002; Xu et al., 2015; Riccuito et al., 2021). Meanwhile models like Peatland-VU, Wetland-DNDC, TRIPLEX-
370  GHG, TEM, CLM4Me exhibited adequate production and oxidation processes (Fig. 3). For example, in Peatland-VU, CH$_4$ production depends on C concentration in fresh soil organic matter reservoirs (root exudates, litter, manure, dead roots, microbes and humus), reference temperature, peat temperature and rate constant R$_o$ (site-tuning parameter depending upon organic matter quality and environmental factors), while the CH$_4$ oxidation is temperature sensitive and simulated using Michaelis-Menten constants i.e., K$_m$ (half saturation) and V$_{max}$ (max reaction rate) (van Huissteden et al., 2006; 2009). In
375  Wetland-DNDC, CH$_4$ production is simulated as a function of C substrates (electron donors: H$_2$ and DOC and electron acceptors: NO$_3$, Mn$^{4+}$, Fe$^{3+}$, SO$_4^{2-}$ and CO$_2$) resulting from soil organic matter decomposition and root exudates, available CH$_4$ concentrations in each layer and pH, soil temperature and redox scalars (Zhang et al., 2002; Deng et al., 2015; Gilhespy et al., 2014), while the CH$_4$ production and oxidation can simultaneously occur within a given peat volume having anaerobic

13

and aerobic portions based on soil redox (Zhang et al., 2002; Deng et al., 2015). Overall, 50% of the models exhibited full
380 and adequate CH$_4$ production and CH$_4$ oxidation process representation, while the remaining 50% exhibited intermediate to
no process representation (Fig. 3).

### 3.6.2 Plant mediated transport models

Models like Ecosys, HIMMELI, ORCHIDEE-PCH4, TEM, LPJWhyMe, CLM4Me, Peatland-VU exhibited full to
adequate process representation (Fig. 4). For example, in Ecosys, plant-mediated CH$_4$ transport is simulated using air-water
385 interfacial area in root, 1/2 distance between adjacent roots, root length, total cross-sectional area of root axes, detailed
mathematical equations in Grant and Roulet (2002). Meanwhile the plant-mediated transport in HIMMELI is simulated
using specific leaf area (SLA), leaf area index (LAI), root tortuosity and porosity (Raivonen et al., 2017) while the plant-
mediated transport in Peatland-VU is simulated using root factor, vegetation specific CH$_4$ factor, vegetation growth rate
proportional to primary production and fraction of CH$_4$ oxidized during plant transport (van Huissteden et al., 2006; 2009).
390 Finally, in ORCHIDEE-PCH4, plant-mediated transport is simulated using vegetation rate constant, efficiency of plants in
transporting CH$_4$, root fraction, vertical root distribution, LAI, CH$_4$ concentrations in soil and atmosphere and CH$_4$ oxidized
during plant transport, detailed equations in Salmon et al. (2022). Overall, 44% of the models exhibited full and adequate
CH$_4$ plant-mediated process representation, while the remaining 56% of models exhibited intermediate to no process
representation (Fig. 4).

### 3.6.3 Diffusion models

395 Models like Ecosys, TRIPLEX-GHG, CLM4Me, HIMMELI, ORCHIDEE-PCH4, TEM, LPJWHYMe, exhibited full to
adequate process representation (Fig. 4). For example, in Ecosys, diffusion is simulated using atmospheric CH$_4$
concentrations, constants for CH$_4$ oxidation, air filled porosity and diffusivity, extensive equation details, refer Grant and
Roulet (2002). Meanwhile, in TRIPLEX-GHG, diffusion is simulated using CH$_4$ molecular diffusion coefficients in air and
400 water, peat porosity, water filled pore spaces, peat tortuosity coefficient and relative volume of coarse pores based on soil
texture (Zhu et al., 2014), while diffusion in CLM4Me is simulated using air-filled and water-filled porosities, aqueous and
gaseous diffusion coefficients of CH$_4$ and O$_2$, peat temperature and water retention curve (Riley et al., 2011). Like plant-
mediated transport, 44% of models exhibited full and adequate CH$_4$ diffusion process representation, while the remaining
56% models exhibited intermediate to no process representation (Fig. 4).

### 3.6.4 Ebullition models

405 Ecosys, HIMMELI, ORCHIDEE-PCH4 and TEM (Fig. 4) exhibited full to adequate process representation. For example,
Ecosys simulates ebullition using temperature growth function related to fermentation & methanogenesis processes, Ostwald
gas solubility coefficient 30°C, atmospheric pressure, soil temperature and gas constant, details refer Grant and Roulet
(2002). Meanwhile in HIMMELI, (Raivonen et al., 2017) and TEM (Tang et al., 2010), concentrations of CH$_4$, CO$_2$, O$_2$ and
410 N$_2$ and sum of their partial pressures are utilized to simulate the occurrence of ebullition. However, it is assumed that N$_2$ is
always in equilibrium with its atmospheric concentration of 78% and solubilities of CH$_4$, CO$_2$, O$_2$ in water are computed
using Henry's law coefficient, so essentially, if sum of the partial pressures of the dissolved CH$_4$, CO$_2$, O$_2$ and N$_2$ exceed the
sum of atmospheric and hydrostatic pressure, ebullition occurs in HIMMELI (Raivonen et al., 2017). Tang et al. (2010)
modified the TEM into a multi-substance model (CH$_4$, O$_2$, CO$_2$ and N$_2$) to simulate CH$_4$ production, oxidation, and transport
415 using pressure-based ebullition algorithm, details, refer, Tang et al. (2010). Overall, only 25% of the models exhibited full
and adequate process representation, providing an ample scope to improve diffusion processes in 75% models exhibiting
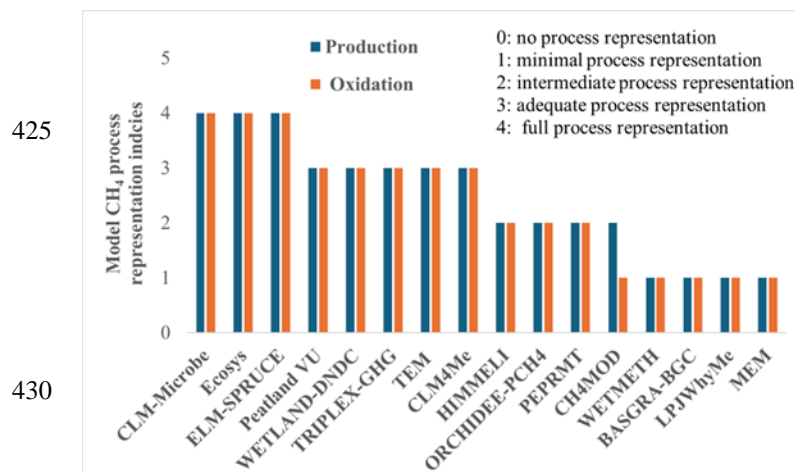intermediate to no process representation (Fig. 4).

420

**Figure 3.** CH$_4$ process representation indices of production and oxidation. Note: the definition of the process representation indices is described in detail in section 2.2.
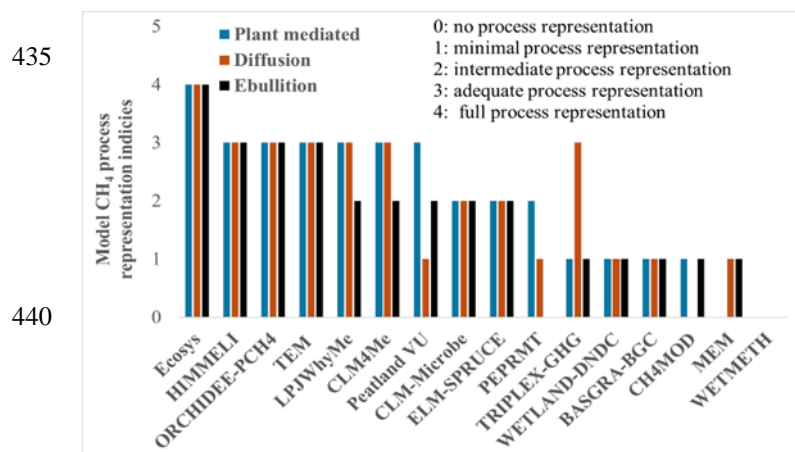


**Figure 4.** CH$_4$ process representation indices of plant-mediated transport, diffusion and ebullition. Note: the definition of the process representation indices is described in detail in section 2.2.

### 3.7 Advantages of reviewed models

All models were manually screened to identify the advantages of each model with respect to simulated CH$_4$ processes, robustness (tested in varied environments), global field testing, minimal inputs and simulation of specialized CH$_4$ transport processes (Table 5). For example, CLM-Microbe (Xu et al., 2015; Wang et al., 2019) comprehensively simulates CH$_4$ microbial processes, while BASGRA-BGC specifically simulates dual porosity nature of peat soils (Huang et al., 2021). The Ecosys (Grant and Roulet, 2002; Grant et al., 2015; 2017) comprehensively simulates WTDs, CH$_4$ production, CH$_4$ oxidation and three CH$_4$ transport pathways, while ELM-Spruce (Xu et al., 2015; He et al., 2020; Yuan et al., 2021; Wang et al., 2019) comprehensive simulates all CH$_4$ processes occurring in the forested peatlands. The PEPRMT (Oikawa et al., 2017) incorporates the lag effect of lowering water table on CH$_4$ production and quantifies CH$_4$ fluxes from restored wetlands and rice fields. With regards to robustness and global field testing, HIMMELI (Raivonen et al., 2017) has the ability to simulate varied peat environments, while Peatland-VU (van Huissteden et al., 2006; 2009; Budishchev et al., 2014; Mi et al., 2014), Wetland-DNDC (Li et al., 1992a, b; Li, 2000 ; Zhang et al., 2002; Gilhespy et al., 2014; Deng et al., 2015) and TRIPLEX-GHG (Zhu et al., 2014; Zhu et al., 2016; Zhu et al., 2017) were tested against field data from arctic, temperate, tundra and boreal peatlands and wetlands. BASGRA-BGC has been tested using field data from Finland, Sweden and Norway, but there is ample scope for further model testing from temperate and tropical sites (Huang et al., 2021).

15

LPJWhyMe (Wania et al., 2010) simulates $CH_4$ fluxes across regional, national, and global scales, while CH4MOD (Li et al., 2010; 2016; 2017) can be utilized to simulate $CH_4$ fluxes from wetlands, marshlands, peatlands and fens. ELM-Spruce (Xu et al., 2015; He et al., 2020; Yuan et al., 2021; Wang et al., 2019) is widely tested against field measured data from forested Minnesota peatlands, tropical and Amazonian peatlands, while Ecosys (Grant and Roulet, 2002; Grant et al., 2015; 2017) is
465    widely tested across the globe (100 or more publications). With regards to model inputs, WETMETH (Nzotungicimpaye et al., 2021), MEM (Lai, 2009) and PEPRMT (Oikawa et al., 2017) are less input intensive, but the modelled $CH_4$ fluxes simulated the measured $CH_4$ fluxes from different peatland and wetland sites located in pan-arctic, tropical, temperate and boreal regions (Lai, 2009; Oikawa et al., 2017; Fertitta-Roberts et al., 2019; Nzotungicimpaye et al., 2021). Finally, with respect to simulating specialized $CH_4$ transport processes, TEM incorporates a 4-substance ($CO_2$, $CH_4$, $O_2$ and $N_2$) pressure-
470    based algorithm, which resulted in modelled $CH_4$ fluxes accurately simulating measured $CH_4$ fluxes (two Michigan peatlands) via ebullition (Tang et al., 2010).

### 3.8 Limitations of reviewed models

Similar to model advantages, the limitations of each model were differentiated with respect to processes not simulated, highly input intensive, larger computational resources, not simulating different peatland types and $CH_4$ transport pathways
475    (Table 6). For example, HIMMELI (Raivonen et al., 2017) and BASGRA-BGC (Huang et al., 2021) do not simulate snow dynamics, while the HIMMELI does not simulate any electron acceptors, except $O_2$. Peatland-VU (van Huissteden et al., 2006; 2009; Budishchev et al., 2014; Mi et al., 2014) does not simulate particulate and dissolved organic carbon and peat subsidence, while Peatland-VU and ELM-Spruce (Xu et al., 2015; He et al., 2020; Yuan et al., 2021; Wang et al., 2019) do not simulate peat growth and changes in peatland microtopography. TRIPLEX-GHG (Zhu et al., 2014; Zhu et al., 2016; Zhu
480    et al., 2017) does not incorporate different plant functional types (PFTs) and does not simulate dynamic $O_2$ concentration changes. WETMETH (Nzotungicimpaye et al., 2021) lacks detailed process representation of $CH_4$ production and oxidation and does not simulate $CH_4$ storage underneath frozen soil and its release upon snow melt. ORCHIDEE versions (Peatland surface, MICT, Peat-4596, PCH4) (Largeron et al., 2018; Qiu et al., 2018; Giumberteau et al., 2019) simulate vertical peat growth, but lateral peat development is lacking in grid-based simulations. For ORCHIDEE to simulate tropical peatlands,
485    improvements in representation of tropical vegetation are required, for example, oxidation of deeper peat due to tropical tree pneumatophores (breather roots) (Qiu et al., 2019). ORCHIDEE versions also require improved representation of Holocene climate, distinguishing bogs vs. fens to parameterize water inflows and incorporating dissolved organic carbon (DOC) leaching to improve C budget and $CH_4$ emissions (Salmon et al., 2022). PEPRMT (Oikawa et al., 2017) ignores $CH_4$ production and $CH_4$ oxidation in multiple peat layers, while no carbon pools can be simulated at millennial to centennial
490    time scales. TEM (Zhuang et al., 2004) does not simulate $CH_4$ release during the non-growing season in frozen climates and does not simulate $CH_4$ fluxes from coastal wetlands. MEM (Lai, 2009) does not simulate any vegetation types, while improvements are required in processes related to peat mineralization and water table simulations. CLM4Me (Lawrence et al., 2011; Oleson et al., 2010; Riley et al., 2011) requires improvements in simulating surface and subsurface hydrology, pH and redox, while daily WTDs are not simulated in CH4MOD (Li et al., 2010; 2016; 2017).

495

500

**Table 5.** Advantages of reviewed peatland or wetland models.

| processes | Good model robustness and global field testing | Minimal inputs | Specialized CH$_4$ transport process |
|---|---|---|---|
| **CLM-Microbe, BASGRA-BGC, Ecosys, ELM-SPRUCE and PEPRMT:** simulate key CH$_4$ processes. | **HIMMELI, Peatland-VU, Wetland-DNDC, TRIPLEX-GHG, BASGRA-BGC, LPJWhyMe, CH4MOD, Ecosys and ELM-SPRUCE:** field tested in different biomes in varied environments (arctic, tundra, boreal, temperate and tropical) | **WETMETH, Methane Emission Model (MEM) and PEPRMT:** minimal inputs yet simulated fluxes followed the trends of measured fluxes adequately . | **TEM:** accurately mimicking measured CH$_4$ fluxes via ebullition |

**Table 6.** Limitations of reviewed peatland or wetland models.

| Model limitations due to unrepresented processes | Highly input intensive, larger computational cost & associated modelled uncertainties | Limited representation of wetland types |
|---|---|---|
| **HIMMELI, Peatland-VU, TRIPLEX-GHG, WETMETH, ORCHIDEE-PCH4 revision 7020, BASGRA-BGC, Terrestrial Ecosystem Model (TEM), Methane Emission Model (MEM), CH4MOD, PEPRMT, ELM-SPRUCE and CLM4Me:** model processes related to snowpack, electron acceptors, dissolved organic carbon, peat subsidence, peat growth, changes in peatland microtopography, incorporating more multiple plant functional types (PFTs), improving ebullition algorithm, improving process representation of CH$_4$ production and CH$_4$ oxidation, incorporating tropical peat vegetation, distinguishing peatlands vs. fens to better parameterize water inflows, improvements in simulating surface and subsurface hydrology, pH and redox, simulation of daily water table depths etc. | **CLM-Microbe:** highly microbial input intensive, site-specific microbial inputs not always available impacting modelled CO$_2$ and CH$_4$ fluxes. **TRIPLEX-GHG:** high computational resources. **ELM-SPRUCE:** extensive microbial inputs & high computational resources. **Peatland-VU:** field measured soil carbon reservoir (peat, roots, litter) data not available at all sites leading to higher uncertainties in model outputs. **BASGRA-BGC:** lack of drainage data, carbon (C), nitrogen (N) contents impact model results. **Ecosys:** lack of continuous spatial and temporal field data constrains calibration and validation. **Terrestrial Ecosystem Model (TEM):** not every peatland site has measured ebullition data. | **WETMETH:** does not distinguish and simulate different wetland types. **ORCHIDEE-PCH4:** does not distinguish ombrotrophic vs. minerotrophic peatlands. **CLM4Me:** grid cell approach does not capture differences in wetland types. |

17

## 3.9 Model inputs most impactful on simulating CH₄ fluxes

Published literature pertinent to individual models were manually screened, and it was identified that 5 out of 16 models tested their model-sensitivities on inputs for predicting total $CH_4$ fluxes, rather than individual $CH_4$ transport pathways (Fig. 5). Of the remaining 11 models, three models did not publish their sensitivity analysis, while eight models tested their sensitivities to model inputs for simulating individual $CH_4$ transport pathways (Fig. 7). Based on the reviewed published model-sensitivities, the model-inputs were categorized for each model into those that have a critical impact on the total $CH_4$ fluxes (Fig. 6) and individual $CH_4$ transport pathway predictions (Fig. 7).
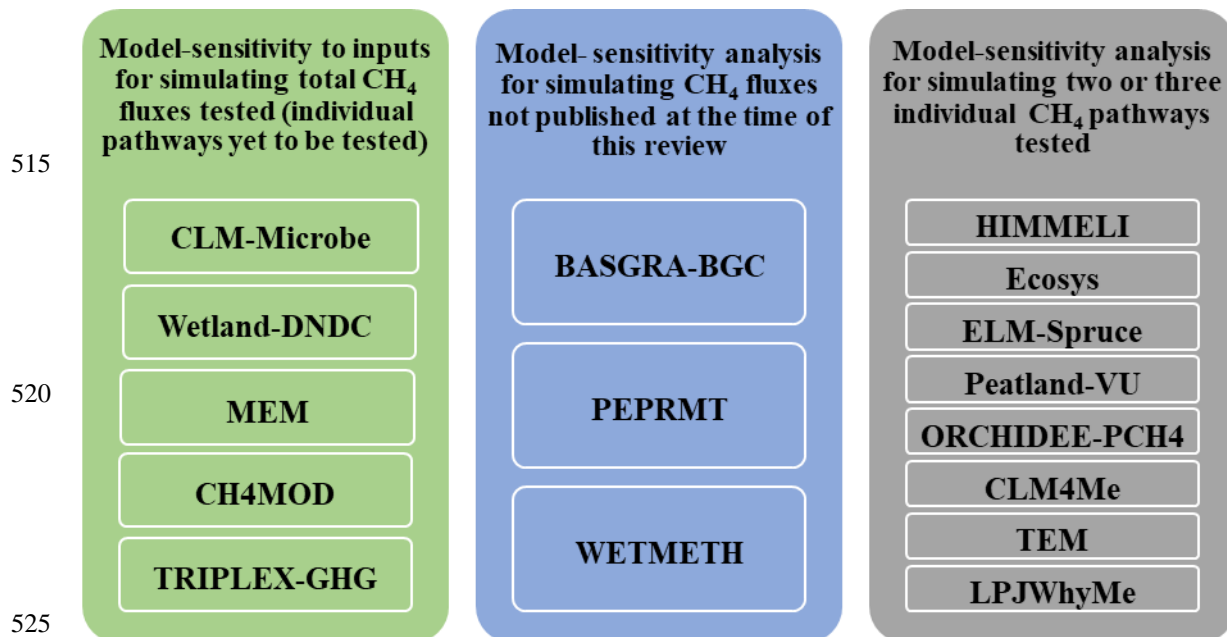


**Figure 5.** Reviewed peatland or wetland models distinguished into three categories shown above. Note: this figure reflects the information relevant to this review only and at the time when this review was conducted.

18

545

550
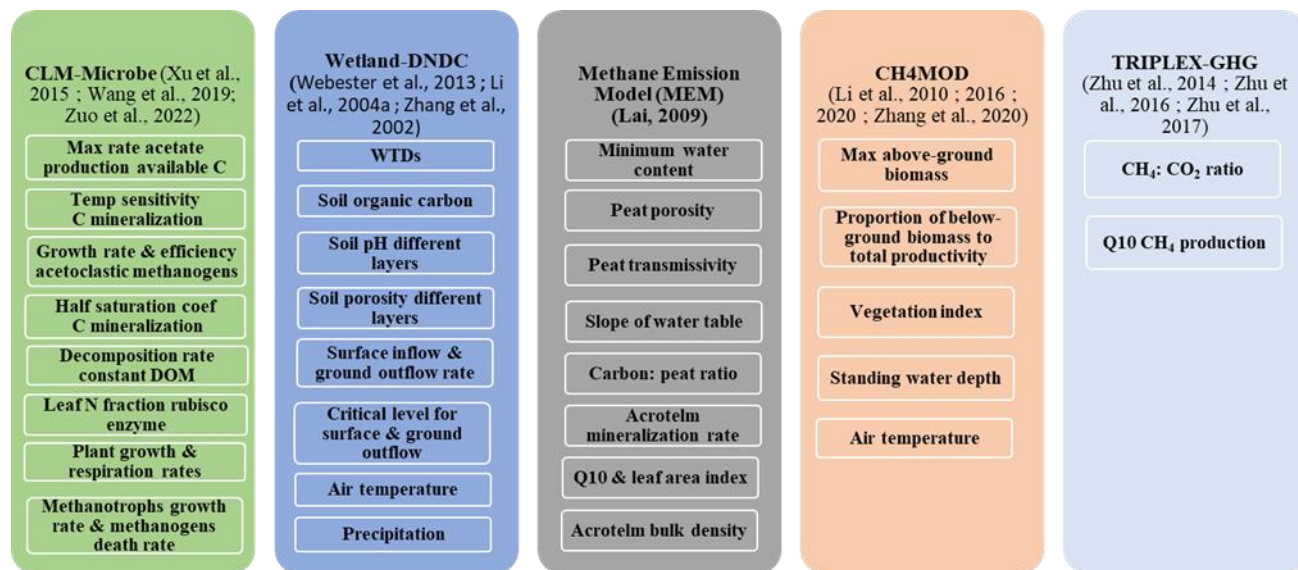


**Figure 6.** Critical inputs in each model impacting total CH₄ flux predictions.
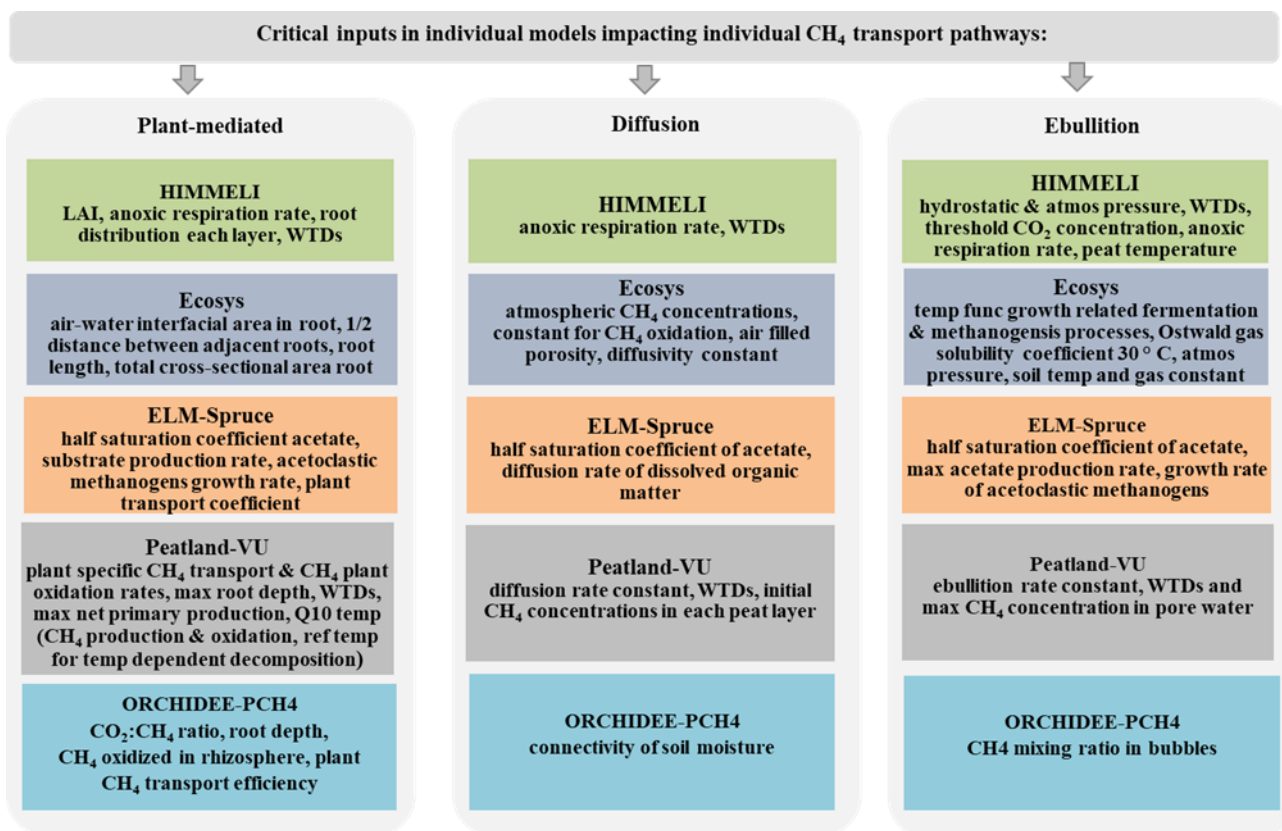
555

560

565

570

575



**Figure 7.** Critical inputs in each model impacting individual $CH_4$ transport pathway of plant-mediated transport, diffusion
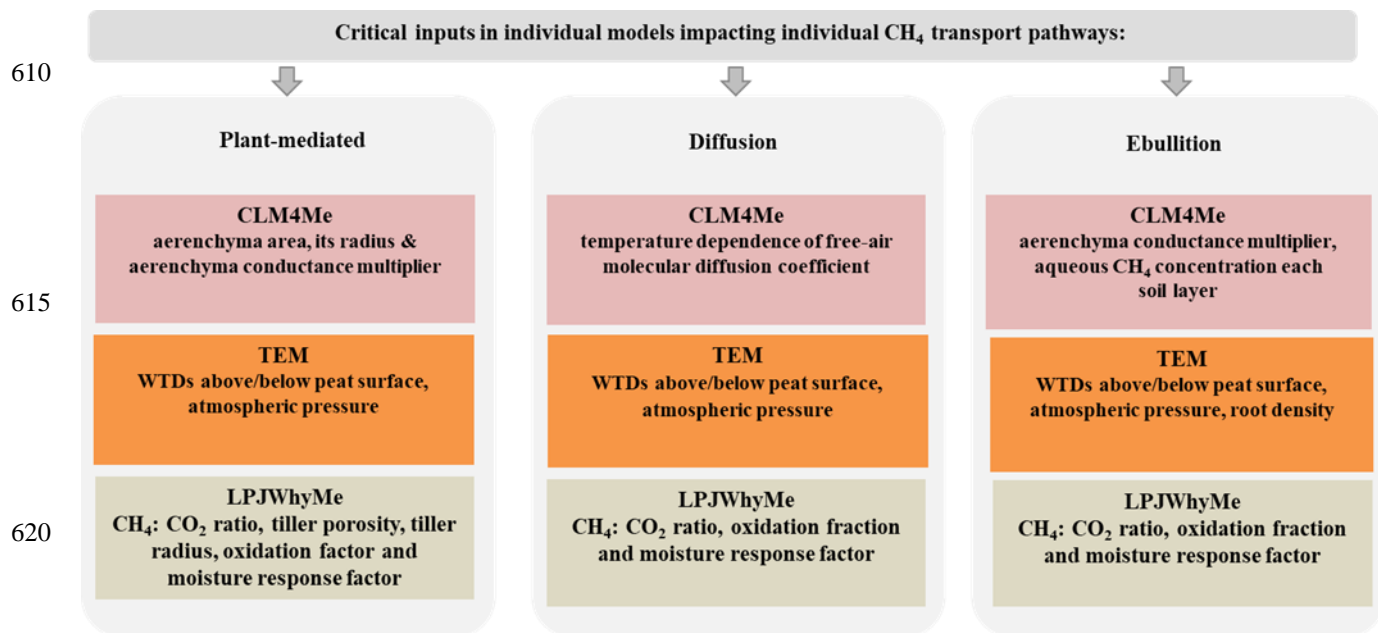595 and ebullition.

600

605

**Figure 7.** continued.

## 4 Discussion

### 4.1 Model parameterization for fine-tuning measured and simulated CH4 fluxes

The common driving variables required to parametrize any peatland or wetland models are climate, hydrology, physical and chemical properties, vegetation (Table 3) and measured $CO_2$ and $CH_4$ fluxes (Schrier-Uijl et al., 2010; Oertel et al.,
640 2012). These variables vary spatially and temporally within a single and different sites, thus strongly impacting $CH_4$ production, oxidation and transport (Zuo et al., 2022; He et al., 2024). Therefore, models are parametrization against measured fluxes and driving variables available for limited spatial and temporal periods. But different models operate at different spatial and temporal scales (Table 2), exhibit different time frames for stabilization of different carbon pools (Fig. 1) and exhibit varying degrees of process representations (Figs. 3 and 4). Model parameterization in this review does not
645 refer to the parameterization performed in the source-code, but it refers to the fine tuning of the model inputs (Table 4) to minimize the error between the simulated and measured $CH_4$ flux data. So, parametrization will depend upon how adequately each model simulates $CH_4$ production, $CH_4$ oxidation and $CH_4$ transport processes. For example, CLM-Microbe, Ecosys and ELM-Spruce exhibit full $CH_4$ production and oxidation process representation (Fig. 3) since they have larger microbial inputs such as growth and death rates of methanogens and methanotrophs etc., where such site-specific microbial
650 data is rarely available, but is fine-tuned to have good agreement between simulated and measured fluxes (Xu et al., 2015; Wang et al., 2019; Ricciuto et al., 2021). However, Zuo et al. (2024) parameterized CLM-Microbe using site-specific genomic data which improved the model's ability to accurately reproduce measured $CH_4$ fluxes. But such site-specific genomic data is not available at all sites, so simulated changes in methanogen biomass cannot be verified against measured data (Zuo et al., 2022). Models like Peatland-VU, Wetland-DNDC, BASGRA-BGC, HIMMELI, MEM, PEPRMT,
655 CH4MOD have lesser microbial inputs compared to CLM-Microbe, Ecosys and ELM-Spruce. However, the key parametrization inputs in less microbially intensive models are aerobic and anaerobic decomposition rates of different pools (peat, humus, roots, litter, exudates, fast, slow), vegetation (leaf area index, primary production), and $CH_4$ parameters (Michaelis-Menton oxidation, diffusion, ebullition and plant transport rate constants) (Table 4). However, the decomposition rates of different pools are rarely available from site-specific studies, but they are rather fine-tuned to reduce the error
660 between simulated and measured fluxes, as in Peatland-VU (Mi et al., 2014) and Wetland-DNDC (Deng et al., 2015; Taft et al., 2019). Models like TRIPLEX-GHG, CLM4Me, ORCHIDEE-PCH4, LPJWhyMe, TEM and WETMETH simulate fluxes at regional, national and global scale consisting of grid scale resolutions varying from 0.25-0.5° respectively. These key inputs are spatial distributions of soil texture, pH, carbon contents, topographical features, wetland distributions and satellite derived inundation and non-inundation data (Table 4). But these models are linked to earth system models, for example,
665 ORCHIDEE-PCH4 is embedded in ORCHIDEE-PEAT revision 4596 (Qiu et al., 2018) and ORCHDEE land surface model (Krinner et al., 2005) having their own inputs. However, generally regional, national and global scale models require larger time frames for carbon pool stabilizations (Fig. 1), exhibit larger flux uncertainties due to lack of detailed $CH_4$ production and oxidation processes (Nzotungicimpaye et al., 2021), do not distinguish bogs, fens, or marshes and lack incorporation of dissolved organic carbon (DOC) leaching to improve C budget and $CH_4$ fluxes (Salmon et al., 2022).

670 **4.2 Model performance of goodness of fit between measured and simulated CH4 fluxes**

All reviewed models evaluated the goodness of fit between simulated and measured data using R-squared ($R^2$, Coefficient of Determination (CD). However, a few models: BASGRA-BGC, and PEPRMT utilized normalized root mean square error and Nash Sutcliffe efficiency (NSE) (Nash and Sutcliffe, 1970) to compare simulated vs measured. Field testing of CLM-Microbe (Arctic tundra, freshwater marsh, mountain peatland and undisturbed Alaska fen), Ecosys (upland tundra, lowland
675 fen, poorly drained fen) and ELM-Spruce (ombrotrophic peatland) found simulated fluxes in agreement with measured $CH_4$ fluxes having an $R^2$ 0.41-0.91 (Grant and Roulet, 2002; Grant et al., 2015; Ricciuto et al., 2021; Yuan et al., 2021; Wang et al., 2019; Zuo et al., 2022). But discrepancies between simulated and measured $CH_4$ fluxes were observed, for example in CLM-Microbe, simulated $CH_4$ fluxes peaked earlier than measured $CH_4$ fluxes (Xu et al., 2015), while simulated $CH_4$ fluxes were under-estimated at daily and hourly scale by 20 and 25% compared to measured $CH_4$ fluxes (Wang et al., 2019).
680 Meanwhile, Peatland-VU was field tested at eutrophic and oligotrophic Dutch sites, Stordalen mire (discontinuous permafrost) and Northeast Siberia (continuous permafrost) (van Huissteden et al., 2009; Petrescu et al., 2008; Mi et al., 2014) and Wetland-DNDC at North American wetlands, boreal fens Ontario, Canada, Alaska, fen and intensively cultivated horticultural UK peat soils (Zhang et al., 2002; Webster et al., 2013; Deng et al., 2015; Taft et al., 2019). Peatland-VU simulated $CH_4$ fluxes agreed with measured $CH_4$ fluxes at seasonal and annual scale, but exhibited low $R^2$, since measured

685  peaks were not captured by simulated peaks, this under-estimation was some-what improved by incorporating net primary
     production (vegetation) and $CH_4$ oxidation parameters (van Huissteden et al., 2009). The $R^2$ in case of Wetland-DNDC
     varied from 0.37-0.66 (North American Wetlands), 0.37-0.85 (Alaska fen) and exhibited low $R^2$ in UK horticultural peat
     soils due to simulated moisture not in agreement with measured moisture. Field testing of BASGRA-BGC (Huang et al.,
     2021) in Finland, Denmark and Norway, MEM in Mer Bleue Bog, Canada (Lai, 2009), CH4MOD in marsh and mountain
690  peatlands, China (Li et al., 2010), PEPRMT in restored wetlands and rice paddies in Sacramento-San Joaquin River Delta,
     California (Oikawa et al., 2017) and HIMMELI in two Finland peat sites (Raivonen et al., 2017) revealed good agreement
     between simulated and measured $CH_4$ fluxes having $R^2$: 0.25-0.80 (BASGRA-BGC), 0.31-0.82 (CH4MOD), 0.46-0.81
     (PEPRMT), 0.63-0.70 (HIMMELI). While the field testing of TRIPLEX-GHG (Zhu et al., 2014), WETMETH
     (Nzotungicimpaye et al., 2021), LPJWhyMe (Wania et al., 2010), ORCHIDEE-PCH4 (Salmon et al., 2022), CLM4Me
695  (Riley et al., 2011) and TEM (Zhuang et al., 2004) across wetlands, fens, marshes and peatlands located in Temperate,
     Tropical, Boreal, Pan-arctic, Arctic, Sub-arctic, Tundra and Boreal forest generally revealed good agreement between
     measured and simulated $CH_4$ fluxes having $R^2$ 0.1-0.7 (TRIPLEX-GHG), simulated $CH_4$ fluxes (4.1 Tg yr$^{-1}$) in agreement
     with measured $CH_4$ fluxes (3.9 ± 1.3 Tg yr$^{-1}$) for West Siberian lowlands (WETMETH), normalized root mean square error
     (NRMSE 0.40-1.15) for LPJWhyMe at all peatland and wetland sites respectively.

700  **4.3 Model sensitivity analysis**
     Models like BASGRA-BGC, PEPRMT and WETMETH have ample scope for conducting sensitivity analysis to identify
     critical inputs impacting $CH_4$ production, oxidation and transport. Meanwhile, CLM-Microbe, Wetland-DNDC, MEM,
     CH4MOD and TRIPLEX-GHG have not yet identified critical inputs sensitive to individual $CH_4$ pathways (Fig. 6).
     However, HIMMELI, Ecosys, ELM-Spruce, Peatland-VU, ORCHIDEE-PCH4, CLM4Me, TEM and LPJWhyMe identified
705  critical inputs for individual $CH_4$ transport pathways (Fig. 7). However, all these models conducted local sensitivity analysis
     to identify the critical inputs, except Peatland-VU which conducted global sensitivity analysis (GLUE methodology) (van
     Huissteden et al., 2009). More effort should be directed to conduct global sensitivity analysis rather than local sensitivity
     analysis. For future model users, critical plant mediated inputs, common to all models, are root distribution in each layer,
     WTDs, LAI, max root depth, plant transport coefficient, $CH_4$ oxidized in rhizosphere, plant-specific $CH_4$ transport factor,
710  plant growth and respiration and Q10 production and Q10 oxidation. Common critical diffusion inputs are WTDs, air-filled
     porosity, soil porosity, $CH_4$ diffusion rate constant, $CH_4$ atmospheric concentration, $CH_4$ concentration in each soil layer, soil
     moisture connectivity and $CH_4$:$CO_2$, while common critical ebullition inputs are $CH_4$ concentrations in each soil layer,
     pore-water and threshold $CH_4$ concentrations, WTDs, $CH_4$:$CO_2$, $CH_4$ ebullition rate constant, soil temperature and $CH_4$
     atmospheric concentration.

715  **4.4 Modelling challenges**
     All reviewed models revealed common difficulties affecting their parametrizations due to non-availability of continuous
     flux and in-situ environmental data (Ueyama et al., 2022). So, models are often parametrized using discontinuous flux and
     in-situ environmental data. For example, Peatland-VU, Wetland-DNDC, BASGRA-BGC and CLM4Me were generally
     parametrized using discontinuous $CH_4$ flux and spatially and temporally limited environmental in-situ data, resulting in
720  simulated $CH_4$ peaks not adequately capturing the measured $CH_4$ peaks, while in case of CLM-Microbe, there were time-lag
     differences between simulated and measured $CH_4$ fluxes (Xu et al., 2015; Wang et al., 2019). Another challenge is the
     process complexity of $CH_4$ dynamics, since production and oxidation are characterized by complex interactions between
     microbial communities, hydrology, soil physical and chemical properties and vegetation (Zuo et al., 2024). However, many
     models simplify these interactions, by utilizing generic parameter values such as scaling parameters of $CH_4$ production and
725  $CH_4$ oxidation as in WETMETH (Nzotungicimpaye et al., 2021) and exclusion of critical processes in PEPRMT such as no
     $CH_4$ production and $CH_4$ oxidation in multiple peat layers and no carbon pool simulations at millennial to centennial time
     scales (Oikawa et al., 2017). However, CLM-Microbe, Ecosys, and ELM-Spruce, incorporate detail $CH_4$ production and
     $CH_4$ oxidation processes governed by growth and death rates of methanogens and methanotrophs, typically derived from
     lab incubation studies (Xu et al., 2015; Wang et al., 2019). Similar incubation studies are not widely available across
730  different peatland or wetland sites and across different ecoregions (tundra, arctic, tropical, boreal and temperate) limiting
     the applicability of these microbially-based models. Moreover, models struggle to capture the $CH_4$ fluxes during extreme
     weather events which is crucial for accurately predicting future $CH_4$ dynamics, where shifts in precipitation patterns and
     temperature could significantly alter $CH_4$ fluxes (Abdalla et al., 2016). Therefore, to adequately capture extreme weather

735 events, continuous weather, $CH_4$ fluxes and in-situ environmental data should be available for at-least 5 years, for models to have independent calibration and validation datasets, so that the future $CH_4$ fluxes can be accurately predicted under future climatic conditions (Xu et al., 2016).

### 4.5 Suggestions and recommendations on future research directions

a) **Need for continuous long-term field data**: For more accurate model-input parameterizations, it is recommended to have available continuous site-specific data on precipitation, evaporation, radiation, air temperatures and in-situ environmental
740 data (e.g. WTDs, peat temperature, peat moisture and leaf area index). A combination of manual chamber, EC tower, and automated chamber data be at-least available for 5 years, so that high quality spatial and temporal $CH_4$ fluxes are available for model parametrization, to accurately predict $CH_4$ fluxes under future climatic conditions including extreme events. To improve $CH_4$ predictions from different earth system models (ESMs) continuous flux and environmental in-situ data are required from data scarce regions namely Congo, Amazon and Southeast Asia rainforests, rice crop areas in India and
745 Bangladesh, Savanah, Africa, Central and South America (McNicol et al., 2023; Zhao et al., 2024).

b) **Online data repository**: There is a need to create an on-line repository containing genomic data related to methanotrophs, methanogens, bacteria and fungi from peatlands, marshes and fens of different nutrient gradients (rich, intermediate and poor) from different ecosystems such as arctic, subarctic, tundra, tropical, boreal and temperate to better parameterize microbial models like CLM-Microbe, Ecosys and ELM-Spruce.

750 c) **Development of new models**: Future modelling efforts should prioritize the mechanistic understanding of the microbial processes, possibly through the development of multi-species models that simultaneously simulate the interactions between different microbial communities and their influence on $CH_4$ fluxes. There is also a pressing need for an integrated model that considers the interplay between $CH_4$ dynamics and C and N cycling.

d) **Artificial intelligence (AI), Hybrid modelling and Machine learning**: Utilize continuous in-situ flux and environmental
755 data into different AI models which are computationally less intensive and faster than traditional models (US.DOE, 2024). More studies across the globe need to utilize the multi-model ensemble (MME) approach combining different machine learning models (decision tree (DT), random forest (RF), extreme gradient boosting (XGB), artificial neural network (ANN), Gated Recurrent Units (GRU) and Long Short-Term Memory (LSTM) using $CH_4$ chamber, EC tower, in-situ environmental data and current and future climate data to estimate current and future global peatland and wetland $CH_4$ emissions (Chen et
760 al., 2024; Chinta and Zu, 2024; Xiao et al., 2024).

e) **Sensitivity analysis**: Models like BASGRA-BGC, PEPRMT and WETMETH have ample scope for conducting local or global sensitivity analysis to identify critical inputs impacting $CH_4$ production, oxidation and transport, while CLM-Microbe, Wetland-DNDC, MEM, CH4MOD and TRIPLEX-GHG have ample scope to identify critical inputs impacting individual
765 $CH_4$ transport pathways. All the reviewed models need to conduct global sensitivity analysis rather than local sensitivity analysis.

f) **Remote sensing**: Utilize high-resolution remote sensing data alongside continuous data on $CH_4$ flux, peat moisture, peat temperature and WTDs, so that the earth system models can better capture wetland and peatland heterogeneous environments to accurately estimate $CH_4$ fluxes under different climatic and environmental conditions.

770 g) **Improvements in model process representation**: Models like HIMMELI and BASGRA-BGC may need to incorporate snow processes, while Peatland-VU may need to incorporate particulate and dissolved organic carbon processes and peat subsidence. TRIPLEX-GHG may benefit from incorporating different plant functional types, while WETMETH from detailed $CH_4$ production and $CH_4$ oxidation processes. Following improvements are suggested for ORCHIDEE-PCH4: incorporation of lateral peat growth, tropical vegetation growth processes, distinguishing between bogs and fens to
775 parameterize water inflows and incorporate dissolved organic carbon (DOC) leaching to improve C budget and $CH_4$ fluxes. Suggested improvements for CLM4Me include improving surface and subsurface hydrology, while suggestions for CH4MOD include incorporating groundwater processes to simulate daily WTDs.

## 5 Conclusions

This study reviewed 16 peatland and wetland models that simulated different temporal and spatial scales, exhibited
780 different spin-times for stabilization of different carbon pools, simulated two or three $CH_4$ transport pathways or total $CH_4$ fluxes and exhibited variable process representations of $CH_4$ production, $CH_4$ oxidation and $CH_4$ transport. To further improve the parameterization of microbial mediated models (Ecosys, ELM-Spruce and CLM-Microbe), we propose the development of online-data repository i.e., international databases incorporating genomic data related to methanogens and methanotrophs from different peatland and wetland types (bogs, fens, marshes, forested peatlands) located in arctic,
785 subarctic, tundra, tropical, boreal and temperate. In case of the ebullition, only 25% of the models exhibited full to adequate process representation. This essentially means that 75% of the models have scope to incorporate detailed processes or mechanisms related to ebullition. But direct measurements of ebullition from peat-water matrix are challenging and rarely measured in the field. More field studies need to measure ebullition using AI enabled platforms of edge computing and autonomous laboratories to capture ebullition hotspots and hot moments during extreme storm events, where $CH_4$ fluxes
790 rapidly occur within a shorter time frame. Also, along with incorporating high frequency field data, models also could improve their ebullition algorithms by incorporating different approaches ($CH_4$ pore water concentration (ECT), pressure (EPT) or free-phase gas volume (EBG) threshold), so that simulated $CH_4$ fluxes can capture the peaks of the measured $CH_4$ fluxes resulting in a better statistical agreement. In conclusion, we find that the existing $CH_4$ models could be adequate for site, plot and field scale $CH_4$ flux predictions, but that a mechanistic predictive understanding, particularly of $CH_4$ transport
795 pathways, is still lacking.

**Code and Data availability**. The authors confirm that the data supporting the findings of this study are available within the article and its Supplement.

**Competing interest**. The authors declare that they have no known competing financial interests or personal relationships
805 that could have appeared to influence the work reported in this paper.

## References

Abdalla, M., Hastings, A., Truu, J., Espenberg, M., Mander, Ü., and Smith, P.: Emissions of methane from northern
815 peatlands: a review of management impacts and implications for future management options, Ecology and Evolution., 6, 7080-7102, https://doi.org/10.1002/ece3.2469, 2016.

Acosta, M., Dušek, J., Sonia Chamizo, S., Serrano-Ortiz, P., and Pavelka, M.: Autumnal fluxes of $CH_4$ and $CO_2$ from Mediterranean reed wetland based on eddy covariance and chamber methods, Catena, 183, 104191, https://doi.org/10.1016/j.catena.2019.104191, 2019.

820 Avis, C.A., Weaver, A.J., and Meissner, K.J.: Reduction in areal extent of high-latitude wetlands in response to permafrost thaw, Nat, Geoscience, 4, 444-448, https://doi.org/10.1038/ngeo1160, 2011.

Baldocchi, D.D., Falge, E., and Wilson, K.W.: A spectral analysis of biosphere-atmosphere trace gas flux densities and meteorological variables across hour to multi-year time scales, Agric. For. Meteorol, 107(1), 1-27, https://doi.org/10.1016/S0168-1923(00)00228-8, 2001a.

825 Baldocchi, D.D.: Assessing the eddy covariance technique for evaluating carbon dioxide exchange rates of ecosystems: past, present and future, Global Change Biology, 9, 479-492, https://doi.org/10.1046/j.1365-2486.2003.00629.x, 2003.

Brunke, M.A., Broxton, P., Pelletier, J., Gochis, D., Hazenberg, P., Lawrence, D.M., Leung, L.R., Niu, G.Y., Troch, P.A., and Zeng, X.: Implementing and evaluating variable soil thickness in the Community Land Model, version 4.5 (CLM4.5), Journal of Climate, 29(9), 3441-3461, https://doi.org/10.1175/JCLI-D-15-0307.1, 2016.

830 Budishchev, A., Mi, Y., van Huissteden, J., Belelli-Marchesini, L., Schaepman-Strub, G., Parmentier, F.J.W., Fratini, G., Gallagher, A., Maximov, T.C., and Dolman, A.J.: Evaluation of a plot-scale methane emission model using eddy covariance observations and footprint modelling. Biogeosciences, 11, 4651-4664, https://doi.org/10.5194/bg-11-4651-2014, 2014.

Bouskill, N.J., Riley, W.J., Zhu, Q, Mekonnen, Z.A., and Grant, R.F.: Alaskan carbon-climate feedback will be weaker than inferred from short-term experiments, Nat Commun, 11, 5798, https://doi.org/10.1038/s41467-020-19574-3, 2020.

835 Chang, K-Y., Riley, W.J., Brodie, E.L., McCalley, C.K., Crill, P.M., and Grant, R.F.: Methane Production Pathway Regulated Proximally by Substrate Availability and Distally by Temperature in a High-Latitude Mire Complex, Journal of Geophysical Research: Biogeosciences, 124, 3057-3074, https://doi.org/10.1029/2019JG005355, 2019.

Chen,S., Liu, L., Ma,Y., Zhuang, Q., and Shurpali, N.J.: Quantifying global wetland methane emissions within situ methane flux data and machine learning approaches, Earth's Future, 12, e2023EF004330, https://doi.org/10.1029/2023EF004330, 840 2024.

Chinta, S., Gao, X., and Zhu, Q.: Machine learning driven sensitivity analysis of E3SM land model parameters for wetland methane emissions, Journal of Advances in Modeling Earth Systems, 16, e2023MS004115, https://doi.org/10.1029/2023MS004115, 2024.

Deng, J., Li, C., and Frolking, S.: Modelling impacts of changes in temperature and water table on C gas fluxes in an 845 Alaskan peatland, Journal of Geophysical Research: Biogeosciences, 120(7), 1279-1295, https://doi.org/10.1002/2014JG002880, 2015.

Denmead, O.T.: Approaches to measuring fluxes of methane and nitrous oxide between landscapes and the atmosphere, Plant Soil, 309, 5-24, https://doi.org/10.1007/s11104-008-9599-z, 2008.

Erland, B. M., Thorpe, A.K., and Gamon, J. A.: Recent Advances Toward Transparent Methane Emissions Monitoring: 850 A Review, Environmental Science & Technology, 56 (23), 16567-16581, https://doi.org/10.1021/acs.est.2c02136, 2022.

Fertitta-Roberts, C., Oikawa P.Y., Jenerette, G.D.: Evaluating the GHG mitigation-potential of alternate wetting and drying in rice through life cycle assessment, Science of Total Environment, 653, 1343-1353, https://doi.org/10.1016/j.scitotenv.2018.10.327, 2019.

Fluet-Chouinard, E., Stocker, B.D., Zhang, Z. Malhotra, A., Melton, J.R., Poulter, B., Kaplan, J.O., Goldewijk, K.K., Siebert, 855 S., Minayeva, T., Hugelius, G., Joosten, H., Barthelmes, A., Prigent, C., Aires, F., Hoyt, A.M., Davidson, N., Finlayson, C.M., Lehner, B., Jackson, R.B., McIntyre, P.B.: Extensive global wetland loss over the past three centuries, Nature, 614, 281-286, https://doi.org/10.1038/s41586-022-05572-6, 2023.

Forbrich, I., Yazbeck, T., Sulman, B., Morin, T.H., Tang, A-C-I., Bohrer, G.: Three Decades of Wetland Methane Surface Flux Modeling by Earth System Models-Advances, Applications, and Challenges, Journal of Geophysical Research: Biogeosciences, 129, e2023JG007915, https://doi.org/10.1029/2023JG007915, 2024.

Fumoto, T., Kobayashi, K., Li, C., Yagi, K., and Hasegawa, T.: Revising a process-based biogeochemistry model (DNDC) to simulate methane emission from rice paddy fields under various residue management and fertilizer regimes, Glob. Chang. Biol, 14 (2), 382-402, https://doi.org/10.1111/j.1365-2486.2007.01475.x, 2008.

Gedney, N., and Cox, P.M.: The sensitivity of global climate model simulations to the representation of soil moisture heterogeneity, J. Hydrometeorol, 4, 1265-1275, https://doi.org/10.1175/1525-7541(2003)004%3C1265:TSOGCM%3E2.0.CO;2, 2003.

Ge, M., Korrensalo, A., Laiho, R., Lohila, A., Makiranta, P., Pihlatie, M., Tuittila, E.-S., Kohl, L., Putkinen, A. and Koskinen, M.: Plant phenology and species-specific traits control plant $CH_4$ emissions in a northern boreal fen, New Phytol, 238, 1019-1032, https://doi.org/10.1111/nph.18798, 2023.

Gilhespy, S., Anthony, S., Chadwick, D., del Prado, A., Li, C., Misselbrook, T., Rees, R.M., Salas, W., Sanz-Cobena, A., Smith, P., Tilston, E., Topp, C-F.E., Vetter, S., and Yeluripati, J. B.: First 20 years of DNDC (DeNitrification DeComposition): Model evolution, Ecological Modelling, 292(24), 51-62, https://doi.org/10.1016/j.ecolmodel.2014.09.004, 2014.

Granberg, G., Grip, H., Ottosson Löfvenius, M., I. Sundh, I., Svensson, B.H., and Nilsson, M.: A simple model for simulation of water content, soil frost, and soil temperatures in boreal mixed mires, Water Resources Research, 35(12), 3591-3968, https://doi.org/10.1029/1999WR900216, 1999.

Grant, R.F.: Changes in Soil Organic Matter under Different Tillage and Rotation: Mathematical Modeling in ecosys, Soil Sci. Soc. Am. J, 61, 1159-1175, https://doi.org/10.2136/sssaj1997.03615995006100040023x, 1997.

Grant, R.F.: Simulation of methanogenesis in the mathematical model Ecosys, Soil Biol. Biochem, 30, 883-896, https://doi.org/10.1016/S0038-0717(97)00218-6, 1998.

Grant, R.F.: Simulation of methanotrophy in the mathematical model ecosys. Soil Biology and Biochemistry, 31(2), 287-297, https://doi.org/10.1016/S0038-0717(98)00119-9, 1999.

Grant, R., and Roulet, N.: Methane efflux from boreal wetlands: Theory and testing of the ecosystem model Ecosys with chamber and tower flux measurements, Global Biogeochem. Cycles, 16 (4), 1054, https://doi.org/10.1029/2001GB001702, 2002.

Grant, R.F., Baldocchi, D.D., and Ma, S.: Ecological controls on net ecosystem productivity of a seasonally dry annual grassland under current and future climates: Modelling with ecosys. Agricultural and Forest Metrology, 152,189-200, https://doi.org/10.1016/j.agrformet.2011.09.012, 2012.

Grant, R.F.: Modelling changes in nitrogen cycling to sustain increases in forest productivity under elevated atmospheric $CO_2$ and contrasting site conditions, Biogeosciences, 10, 7703-7721, https://doi.org/10.5194/bg-10-7703-2013, 2013.

Grant, R.F.: Nitrogen mineralization drives the response of forest productivity to soil warming: Modelling in ecosys vs. measurements from the Harvard soil heating experiment, Ecological Modelling, 288, 38-46, https://doi.org/10.1016/j.ecolmodel.2014.05.015, 2014.

Grant, R.F., Humphreys, E.R., and Lafleur, P.M.: Ecosystem $CO_2$ and $CH_4$ exchange in a mixed tundra and a fen within a
895    hydrologically diverse Arctic landscape: 1 Modeling versus measurements, J. Geophys. Res. Biogeosci, 120, 1366-1387,
https://doi.org/10.1002/2014JG002888, 2015a.

Grant, R.F.: Ecosystem $CO_2$ and $CH_4$ exchange in a mixed tundra and a fen within a hydrologically diverse Arctic landscape:
2. Modelling impacts of climate change, J. Geophys. Res. Biogeosci, 120, 1388-1406,
https://doi.org/10.1002/2014JG002889, 2015b.

900    Grant, R.F., Mekonnen, Z.A., Riley, W.J., Wainwright, H.M., Graham, D., and Torn, M.S.: Mathematical modelling of arctic
polygonal tundra with Ecosys: 1. Microtopography determines how active layer depths respond to changes in temperature
and precipitation, Journal of Geophysical Research: Biogeosciences, 122, 3161-3173, https://doi.org/10.1002/2017JG004035,
2017a.

Grant, R.F., Mekonnen, Z.A., Riley, W. J.,Arora, B., and Torn, M.S.: Mathematical modelling of arctic polygonal tundra
905    with Ecosys: 2. Microtopography determines how $CO_2$ and $CH_4$ exchange responds to changes in temperature and
precipitation, Journal of Geophysical Research: Biogeosciences, 122, 3174-3187, https://doi.org/10.1002/2017JG004037,
2017b.

Guimberteau, M., Zhu, D., Maignan, F., Huang, Y., Yue, C., Dantec-Nédélec, S., Ottlé, C., Jornet-Puig, A., Bastos, A.,
Laurent, P., Goll, D., Bowring, S., Chang, J., Guenet, B., Tifafi, M., Peng, S., Krinner, G., Ducharne, A., Wang, F., Wang, T.,
910    Wang, X., Wang, Y., Yin, Z., Lauerwald, R., Joetzjer, E., Qiu, C., Kim, H., and Ciais, P.: ORCHIDEE-MICT (v8.4.1),
a land surface model for the high latitudes: model description and validation, Geosci. Model Dev, 11, 121-163,
https://doi.org/10.5194/gmd-11-121-2018, 2018.

Günther, A., Barthelmes, A., Huth, V. Joosten, H., Jurasinski, G., Koebsch, F., Couwenberg, J.: Prompt rewetting of drained
peatlands reduces climate warming despite methane emissions, Nat Commun, 11, 1644, https://doi.org/10.1038/s41467-020-
915    15499-z, 2020.

Hanson, P.J., Griffiths, N.A., Iversen, C.M., Norby, R.J., Sebestyen, S.D., Phillips, J.R., Chanton, J.P., Kolka, R.K.,
Malhotra, A., Oleheiser, K.C., Warren, J.M., Shi, X., Yang, X., Mao, J., and Ricciuto, D.M.: Rapid net carbon loss from a
whole-ecosystem warmed Peatland, AGU Advances, 1, e2020AV000163, https://doi.org/10.1029/2020AV000163, 2020.

He, L., Lipson, D. A., Mazza Rodrigues, J. L., Mayes, M., Björk, R. G., Glaser, B., Thornton, P.E., and Xu, X.: Dynamics of
920    fungal and bacterial biomass carbon in natural ecosystems: Site-level applications of the CLM-Microbe model, Journal of
Advances in Modeling Earth Systems, 13, e2020MS002283, https://doi.org/10.1029/2020MS002283, 2021.

He, L., Rodrigues, J.L.M., Mayes, M.A., Lai, C.-T., Lipson, D.A., and Xu, X.: Modeling microbial carbon fluxes and stocks
in global soils from 1901 to 2016, Biogeosciences. 21, 2313-2333, https://doi.org/10.5194/bg-21-2313-2024, 2024.

Hermoso de Mendoza, I., Beltrami, H., MacDougall, A.H., and Mareschal, J.-C.: Lower boundary conditions in land surface
925    models- effects on the permafrost and the carbon pools: a case study with CLM4.5, Geosci. Model Dev, 13, 1663-1683,
https://doi.org/10.5194/gmd-13-1663-2020, 2020.

Höglind, M., Van Oijen, M., Cameron, D., Persson, T.: Process-based simulation of growth and overwintering of grassland
using the BASGRA model, Ecol. Model, 335, 1-15, https://doi.org/10.1016/j.ecolmodel.2016.04.024, 2016.

Höglind, M., Cameron, D., Persson, T., Huang, X., and van Oijen, M.: BASGRA_N: a model for grassland productivity,
930    quality, and greenhouse gas balance, Ecol. Model, 417, 108925, https://doi.org/10.1016/j.ecolmodel.2019.108925, 2020.

Huang, X., Silvennoinen, H., Kløve, B., Regina, K., Kandel, T.P., Piayda, A., Karki, S., Lærke, P.E., and Höglind, M.: Modelling $CO_2$ and $CH_4$ emissions from drained peatlands with grass cultivation by the BASGRA-BGC model, Science of the Total Environment, 765, 144385, https://doi.org/10.1016/j.scitotenv.2020.144385, 2021.

Huang, Y., Ciais, P., Luo, Y., Zhu, D., Wang, Y., Qiu, C., Goll, D.S., Guenet, B., Makowski, D., De Graaf, I., Leifeld, J.,
935 Kwon, M.J., Hu, J., and Qu, L.: Tradeoff of $CO_2$ and $CH_4$ emissions from global peatlands under water-table drawdown, Nat. Clim. Chang, 11, 618-622, https://doi.org/10.1038/s41558-021-01059-w, 2021.

Hugelius, G., Loisel, J., Chadburn, S., Jackson, R.B., Jones, M., MacDonald, G., Marushchak, M., Olefeldt, D., Packalen, M., Siewert, M.B., Treat, C., Turetsky, M., Voigt, C., and Yu, Z: Large stocks of peatland carbon and nitrogen are vulnerable to permafrost thaw, Proceedings of the National Academy of Sciences, 117 (34), 20438-20446,
940 https://doi.org/10.1073/pnas.1916387117, 2020.

Humpenöder, F., Karstens, K., Lotze-Campen, H., Leifeld, J., Menichetti, L., Barthelmes, A., and Popp, A.: Peatland protection and restoration are key for climate change mitigation, Environmental Research Letters, 15(10), 104093, https://doi.org/10.1088/1748-9326/abae2a, 2020.

Hendriks, D.M.D., van Huissteden, J., Dolman, A.J., and van der Molen, M.K.: The full greenhouse gas balance of an
945 abandoned peat meadow. Biogeosciences. 4, 411-424. https://doi.org/10.5194/bg-4-411-2007, 2007.

Hutchinson, G.L., and Livingston, G.P.: Soil-atmosphere gas exchange, in Methods of Soil Analysis, part 4, Physical Methods, edited by J. H. Dane, and G. C. Topp, pp. 1159-1182, Soil Sci. Soc. of Am., Madison, Wisconsin, 2002.

Krinner, G., Viovy, N., de Noblet-Ducoudré, N., Ogée, J., Polcher, J., Friedlingstein, P., Ciais, P.,Sitch, S., and Prentice, I.C.: A dynamic global vegetation model for studies of the coupled atmosphere-biosphere system, Global Biogeochem.
950 Cycles, 19, GB1015, https://doi.org/10.1029/2003GB002199, 2005.

Kutzbach, L., Schneider, J., Sachs, T., Giebels, M., Nykänen, H., Shurpali, N. J., Martikainen, P. J., Alm, J., Wilmking, M.: $CO_2$ flux determination by closed-chamber methods can be seriously biased by inappropriate application of linear regression, Biogeosciences, 4(6), 1005-1025, https://doi.org/10.5194/bg-4-1005-2007, 2007.

Lai, D.Y.F.: Modelling the effects of climate change on methane emission from a northern ombrotrophic bog in Canada.
955 Environ Geology, 58, 1197-1206, https://doi.org/10.1007/s00254-008-1613-5, 2009.

Largeron, C., Krinner, G., Ciais, P., and Brutel-Vuilmet, C.: Implementing northern peatlands in a global land surface model: description and evaluation in the ORCHIDEE high-latitude version model (ORC-HL-PEAT), Geosci. Model Dev, 11, 3279-3297, https://doi.org/10.5194/gmd-11-3279-2018, 2018.

Lawrence, D.M., Oleson, K.W., Flanner, M.G., Thornton, P.E., Swenson, S.C., Lawrence, P.J., Zeng, X., Yang, Z.L., Levis,
960 S., Sakaguchi, K., Bonan, G.B., Slater, A.G.: Parameterization Improvements and Functional and Structural Advances in Version 4 of the Community Land Model, Journal of Advances in Modeling Earth Systems, 3, M03001, https://doi.org/10.1029/2011ms000045, 2011.

Leifeld, J., and Menichetti, L.: The underappreciated potential of peatlands in global climate change mitigation strategies, Nat Commun, 9, 1071, https://doi.org/10.1038/s41467-018-03406-6, 2018.

965 Leifeld, J., Wüst-Galley, C., and Page, S.: Intact and managed peatland soils as a source and sink of GHGs from 1850 to 2100, Nat. Clim. Chang, 9, 945-947, https://doi.org/10.1038/s41558-019-0615-5, 2019.

Li, C., Frolking, and S., Frolking, T.A.: A model of nitrous oxide evolution from soil driven by rainfall events: 1. Model structure and sensitivity, Journal of Geophysical Research: Atmosphere, https://doi.org/10.1029/92JD00509, 1992.

970 Li, C., Frolking, and S., Frolking, T.A.: A model of nitrous oxide evolution from soil driven by rainfall events: 2. Model applications, Journal of Geophysical Research: Atmosphere, https://doi.org/10.1029/92JD00510, 1992.

Li, C.S.: Modeling trace gas emissions from agricultural ecosystems. In: Wassmann, R., Lantin, R.S., Neue, HU. (eds) Methane Emissions from Major Rice Ecosystems in Asia, Developments in Plant and Soil Sciences, vol 91. Springer, Dordrecht, https://doi.org/10.1007/978-94-010-0898-3_20, 2000.

975 Li, T., Huang, Y., Zhang, W., and Song, C.: CH4MOD$_{wetland}$: A biogeophysical model for simulating methane emissions from natural wetlands, Ecological Modelling, 221 (4), 666-680, https://doi.org/10.1016/j.ecolmodel.2009.05.017, 2010.

Li, T., Huang, Y., Zhang, W., Yu, and Y.-Q.: Methane emissions associated with the conversion of marshland to cropland and climate change on the Sanjiang Plain of northeast China from 1950 to 2100, Biogeosciences, 9, 5199-5215, https://doi.org/10.5194/bg-9-5199-2012, 2012.

Li, T., Xie, B., Wang, G., Zhang, W., Zhang, Q., Vesala, T., and Raivonen, M.: Field-scale simulation of methane emissions 980 from coastal wetlands in China using an improved version of CH4MOD$_{wetland}$, Science of Total Environment, 559, 256-267, https://doi.org/10.1016/j.scitotenv.2016.03.186, 2016.

Li, T., Zhang, Q., Cheng, Z., Wang, G., Yu, L., and Zhang, W.: Performance of CH4MODwetland for the case study of different regions of natural Chinese wetland, Journal of Environmental Sciences, 57, 356-369, https://doi.org/10.1016/j.jes.2017.01.001, 2017.

985 Li, T., Li, H., Zhang, Q., Ma, Z., Yu, L., Lu, Y., Niu, Z., Sun, W., and Liu, J.: Prediction of $CH_4$ emissions from potential natural wetlands on the Tibetan Plateau during the 21st century, Science of Total Environment, 657, 498-508, https://doi.org/10.1016/j.scitotenv.2018.11.275, 2019.

Li, T., Lu, Y., Yu, L., Sun, W., Zhang, Q., Zhang, W., Wang, G., Qin, Z., Yu, L., Li, H., and Zhang, R.: Evaluation of CH4MOD$_{wetland}$ and Terrestrial Ecosystem Model (TEM) used to estimate global $CH_4$ emissions from natural wetlands, 990 Geosci. Model Dev, 13, 3769-3788, https://doi.org/10.5194/gmd-13-3769-2020, 2020.

Lippmann, T.J.R., van der Velde, Y., Heijmans, M.M.P.D., Dolman, H., Hendriks, D.M.D., and van Huissteden, K. (2023). Peatland-VU-NUCOM (PVN 1.0): using dynamic plant functional types to model peatland vegetation, $CH_4$, and $CO_2$ emissions, Geosci. Model Dev, 16, 6773-6804, https://doi.org/10.5194/gmd-16-6773-2023, 2023.

Liu, Y., Paris, J-D., Vrekoussis, M., Quéhé, P-Y., Desservettaz, M., Kushta, J., Dubart, F., Demetriou, D., Bousquet, P., and 995 Sciare, J.: Reconciling a national methane emission inventory with in-situ measurements, Science of the Total Environment, 901, 165896, https://doi.org/10.1016/j.scitotenv.2023.165896, 2023.

Loisel, J., and Gallego-Sala, A.: Ecological resilience of restored peatlands to climate change, Commun Earth Environ, 3, 208, https://doi.org/10.1038/s43247-022-00547-x, 2022.

Lu, X., and Zhuang, Q.: Evaluating climate impacts on carbon balance of the terrestrial ecosystems in the Midwest of the 1000 United States with a process-based ecosystem model, Mitig Adapt Strateg Glob Change, 15, 467-487, https://doi.org/10.1007/s11027-010-9228-z, 2010.

Ma, S., Worden, J.R., Bloom, A-A., Zhang, Y., Poulter, B., Cusworth, D.H., Yin, Y., Pandey, S., Maasakkers, J.D., Lu, X., Shen, L., Sheng, J., Frankenberg, C., Miller, C.E., and Jacob, D.J.: Satellite Constraints on the Latitudinal Distribution and Temperature Sensitivity of Wetland Methane Emissions. AGU Advances.
1005 2, e2021AV000408, https://doi.org/10.1029/2021AV000408, 2021.

Ma, S., Jiang, L., Wilson, R. M., Chanton, J. P., Bridgham, S., Niu, S., Iversen, C. M., Malhotra, A., Jiang, J., Lu, X., Huang, Y., Keller, J., Xu, X., Ricciuto, D. M., Hanson, P. J., and Luo, Y. Evaluating alternative ebullition models for predicting peatland methane emission and its pathways via data-model fusion, Biogeosciences, 19, 2245-2262, https://doi.org/10.5194/bg-19-2245-2022, 2022.

1010 Mack, S.K., Lane, R.R., Deng, J., Morris, J.T., and Bauer, J.J.: Wetland carbon models: Applications for wetland carbon commercialization, Ecological Modelling, 476, 110228, https://doi.org/10.1016/j.ecolmodel.2022.110228, 2023.

Maier, M., Weber, T.K.D., Fiedler, J., Fuß, R., Glatzel, S., Huth, V., Jordan, S., Jurasinski, G., Kutzbach, L., Schäfer, K., Weymann, D., and Hagemann, U.: Introduction of a guideline for measurements of greenhouse gas fluxes from soils using non-steady-state chambers, Journal of Plant Nutrition and Soil Science, 185, 447-461,
1015 https://doi.org/10.1002/jpln.202200199, 2022.

McNicol, G., Fluet-Chouinard, E., Ouyang, Z., Knox, S., Zhang, Z., Aalto, T., Bansal, S., Chang, K-Y., Chen, M., Delwiche, K., Feron, S., Goeckede, M., Liu, J., Malhotra, A., Melton, J.R., Riley, W., Vargas, R., Yuan, K., Ying, Q., Zhu, Q., Alekseychik, P., Aurela, M., Billesbach, D.P. Campbell, D.I., Chen, J., Chu, H., Desai, A.R., Euskirchen, E., Goodrich, J., Griffis, T., Helbig, M., Hirano, T., Iwata, H., Jurasinski, G., King, J., Koebsch, F., Kolka, R., Krauss, K., Lohila, A.,
1020 Mammarella, I., Nilson, M., Noormets, A., Oechel, W., Peichl, M., Sachs, M.T., Sakabe, A., Schulze, C., Sonnentag, O., Sullivan, R.C., Tuittila, E-C., Ueyama, M., Vesala, T., Ward, E., Wille, C., Wong, G, X., Zona, D., Windham-Myers, L., Poulter, B., and Jackson, R.B.: Upscaling wetland methane emissions from the FLUXNET-CH4 eddy covariance network (UpCH4 v1.0): Model development, network assessment, and budget comparison, AGU Advances, 4, e2023AV000956, https://doi.org/10.1029/2023AV000956, 2023.

1025 Meissner, K.J., Weaver, A.J., Matthews, H.D. and Cox, P.M.: The role of land surface dynamics in glacial inception: A study with the UVic Earth System Model, Clim. Dyn, 21, 515-537, https://doi.org/10.1007/s00382-003-0352-2, 2003.

Mi, Y., van Huissteden, J., Parmentier, F.J.W., Gallagher, A., Budishchev, A., Berridge, C.T., and Dolman, A.J.: Improving a plot-scale methane emission model and its performance at a northeastern Siberian tundra site, Biogeosciences,
1030 11, 3985-3999, https://doi.org/10.5194/bg-11-3985-2014, 2014.

Mozafari, B., Bruen, M., Donohue, S., Renou-Wilson, F., and O'Loughlin, F.: Peatland dynamics: A review of process-based models and approaches, Science of The Total Environment, 877, 162890, https://doi.org/10.1016/j.scitotenv.2023.162890, 2023.

Morin, T.H., Riley, W.J., Grant, R.F., Mekonnen, Z., Stefanik, K.C., Sanchez, A-C-R., Mulhare, M.A., Villa, J., Wrighton,
1035 K., and Bohrer, G.: Water level changes in Lake Erie drive 21st century $CO_2$ and $CH_4$ fluxes from a coastal temperate wetland, Science of The Total Environment, 821, 153087, https://doi.org/10.1016/j.scitotenv.2022.153087, 2022.

Morin, T.H., Bohrer, G., Stefanik, K.C., Rey-Sanchez, A.C., Matheny, A.M., and Mitsch, W.J.: Combining eddy-covariance and chamber measurements to determine the methane budget from a small, heterogeneous urban floodplain wetland park, Agricultural and Forest Metrology, 237-238 (1), 160-170, https://doi.org/10.1016/j.agrformet.2017.01.022, 2017.

1040 Nash, J.E., and Sutcliffe, J.V.: River flow forecasting through conceptual models' part I-A discussion of principles, Journal of Hydrology, 10(3), 282-290, https://doi.org/10.1016/0022-1694(70)90255-6, 1970.

Nichols, J.E., and Peteet, D.M.: Rapid expansion of northern peatlands and doubled estimate of carbon storage, Nat. Geosci. 12, 917-921. https://doi.org/10.1038/s41561-019-0454-z, 2019.

Nzotungicimpaye, C.-M., Zickfeld, K., MacDougall, A.H., Melton, J.R., Treat, C.C., Eby, M., and Lesack, L.F.W.
1045 WETMETH 1.0: a new wetland methane model for implementation in Earth system models,
Geosci. Model Dev, 14, 6215-6240, https://doi.org/10.5194/gmd-14-6215-2021, 2021.

Oertel, C., Herklotz, K., Matschullat, J., and Zimmerman, F.: Nitric oxide emissions from soils: a case study with temperate
soils from Saxony, Germany, Enviro Earth Sci, 66, 2343-2351, https://doi.org/10.1007/s12665-011-1456-3, 2012.

Oikawa, P.Y., Jenerette, G.D., Knox, S.H., Sturtevant, C., Verfaillie, J., Dronova, I., Poindexter, C.M., Eichelmann, E., and
1050 Baldocchi, D.D.: Evaluation of a hierarchy of models reveals the importance of substrate limitation for predicting carbon
dioxide and methane exchange in restored wetlands, J. Geophys. Res. Biogeosci, 122, 145-167,
https://doi.org/10.1002/2016JG003438, 2017.

Oleson, K.W., Bonan, G.B., Feddema, J.J., Vertenstein, M., and Kluzek, E.: Technical description of urban parameterization
for the Community Land Model (CLMU), NCAR Technical Note NCAR/TN-480+STR, 169 pp, 2010.

1055 Papale, D., Reichstein, M., Aubinet, M., Canfora, E., Bernhofer, C., Kutsch, W., Longdoz, B., Rambal, S., Valentini, R.,
Vesala, T., and Yakir, D.: Towards a standardized processing of Net Ecosystem Exchange measured with eddy covariance
technique: algorithms and uncertainty estimation, Biogeosciences, 3, 571-583, https://doi.org/10.5194/bg-3-571-2006, 2006.

Peltola, O., Raivonen, M., Li, X., and Vesala, T.: Technical note: Comparison of methane ebullition modelling approaches
used in terrestrial wetland models, Biogeosciences, 15, 937-951, https://doi.org/10.5194/bg-15-937-2018 , 2018.

1060 Petrescu, A.M.R., van Huissteden, J., Jackowicz-Korczynski, M., Yurova, A., Christensen, T.R., Crill, P.M., Bäckstrand, K.,
and Maximov, T.C.: Modelling $CH_4$ emissions from arctic wetlands: effects of hydrological parameterization.
Biogeosciences, 5, 111-121, https://doi.org/10.5194/bg-5-111-2008, 2008.

Petrescu, A.M.R., van Beek, L.P.H., van Huissteden, J., Prigent, C., Sachs, T., Corradi, C.A.R., Parmentier, F.J.W., and
Dolman, A.J.: Modelling regional to global $CH_4$ emissions of boreal and arctic wetlands, Global Biogeochem, Cycles,
1065 24, GB4009, https://doi.org/10.1029/2009GB003610, 2010.

Qiu, C., Zhu, D., Ciais, P., Guenet, B., Krinner, G., Peng, S., Aurela, M., Bernhofer, C., Brümmer, C., Bret-Harte, S., Chu,
H., Chen, J., Desai, A. R., Dušek, J., Euskirchen, E. S., Fortuniak, K., Flanagan, L. B., Friborg, T., Grygoruk, M., Gogo, S.,
Grünwald, T., Hansen, B. U., Holl, D., Humphreys, E., Hurkuck, M., Kiely, G., Klatt, J., Kutzbach, L., Largeron, C.,
Laggoun-Défarge, F., Lund, M., Lafleur, P. M., Li, X., Mammarella, I., Merbold, L., Nilsson, M. B., Olejnik, J., Ottosson-
1070 Löfvenius, M., Oechel, W., Parmentier, F.-J. W., Peichl, M., Pirk, N., Peltola, O., Pawlak, W., Rasse, D., Rinne, J., Shaver,
G., Schmid, H. P., Sottocornola, M., Steinbrecher, R., Sachs, T., Urbaniak, M., Zona, D., and Ziemblinska, K.: ORCHIDEE-
PEAT (revision 4596), a model for northern peatland $CO_2$, water, and energy fluxes on daily to annual scales,
Geosci. Model Dev, 11, 497-519, https://doi.org/10.5194/gmd-11-497-2018, 2018.

Qiu, C., Zhu, D., Ciais, P., Guenet, B., Peng, S., Krinner, G., Tootchi, A., Ducharne, A., and Hastie, A.: Modelling northern
1075 peatland area and carbon dynamics since the Holocene with the ORCHIDEE-PEAT land surface model (SVN r5488),
Geosci. Model Dev, 12, 2961-2982, https://doi.org/10.5194/gmd-12-2961-2019, 2019.

Qiu C, Zhu D, Ciais P, Guenet B, and Peng S.: The role of northern peatlands in the global carbon cycle for the 21st
century, Global Ecol Biogeogr, 29, 956-973, https://doi.org/10.1111/geb.13081, 2020.

Qiu, C., Ciais, P., Zhu, D., Guenet, B., Peng, S., Petrescu, A-M-R., Lauerwald, R., Makowski, D., Gallego-Sala, A.V.,
1080 Charman, D.J., and Brewer, S.C.: Large historical carbon emissions from cultivated northern peatlands. Sciences Advances,
7 (23), 1-10, https://www.science.org/doi/epdf/10.1126/sciadv.abf1332, 2021.

Raivonen, M., Smolander, S., Backman, L., Susiluoto, J., Aalto, T., Markkanen, T., Mäkelä, J., Rinne, J., Peltola, O., Aurela, M., Lohila, A., Tomasic, M., Li, X., Larmola, T., Juutinen, S., Tuittila, E.-S., Heimann, M., Sevanto, S., Kleinen, T., Brovkin, V., and Vesala, T.: HIMMELI v1.0: HelsinkI Model of Methane build-up and emission for peatlands, Geosci.

1085    Model Dev, 10, 4665-4691, https://doi.org/10.5194/gmd-10-4665-2017, 2017.

Ricciuto, D. M., Xu, X., Shi, X., Wang, Y., Song, X., Schadt, C. W., Griffiths, N.A., Mao, J., Warren, J.M., Thorton, P.E., Chanton, J., Keller, J.K., Bridgham, S.C., Gutknecht, J., Sebestyen, S.D., Finzi, A., Kolka, R., and Hanson, P.J.: An integrative model for soil biogeochemistry and methane processes: I. Model structure and sensitivity analysis, Journal of Geophysical Research: Biogeosciences, 126, e2019JG005468, https://doi.org/10.1029/2019JG005468, 2021.

1090    Riley, W.J., Subin, Z.M., Lawrence, D.M., Swenson, S.C., Torn, M.S., Meng, L., Mahowald, N.M., and Hess, P.: Barriers to predicting changes in global terrestrial methane fluxes: analyses using CLM4Me, a methane biogeochemistry model integrated in CESM, Biogeosciences, 8, 1925-1953, https://doi.org/10.5194/bg-8-1925-2011, 2011.

Sabbatini, S., Mammarella, I., Arriga, N., Fratini, G., Graf, A., Hörtnagl, L., Ibrom, A., Longdoz, B., Mauder, M., Merbold, L., Metzger, S., Montagnani, L., Pitacco, A., Rebmann, C., Sedlák, P., Šigut, L., Vitale, D., and Papale, D.: Eddy covariance

1095    raw data processing for $CO_2$ and energy fluxes calculation at ICOS ecosystem stations, Int. Agrophys, 32(4), 495-515, https://doi.org/10.1515/intag-2017-0043, 2018.

Salmon, E., Jégou, F., Guenet, B., Jourdain, L., Qiu, C., Bastrikov, V., Guimbaud, C., Zhu, D., Ciais, P., Peylin, P., Gogo, S., Laggoun-Défarge, F., Aurela, M., Bret-Harte, M. S., Chen, J., Chojnicki, B. H., Chu, H., Edgar, C. W., Euskirchen, E. S., Flanagan, L. B., Fortuniak, K., Holl, D., Klatt, J., Kolle, O., Kowalska, N., Kutzbach, L., Lohila, A., Merbold, L., Pawlak,

1100    W., Sachs, T., and Ziemblińska, K.: Assessing methane emissions for northern peatlands in ORCHIDEE-PEAT revision 7020, Geosci. Model Dev, 15, 2813-2838, https://doi.org/10.5194/gmd-15-2813-2022, 2022.

Shahan, J., Chu, H., Windham-Myers, L., Matsumura, M., Carlin, J., Eichelmann, E., Stuart-Haentjens, E., Bergamaschi, B., Nakatsuka, K., Sturtevant, C., and Oikawa, P.: Combining eddy covariance and chamber methods to better constrain $CO_2$ and $CH_4$ fluxes across a heterogeneous restored tidal wetland, Journal of Geophysical Research: Biogeosciences, 127,

1105    e2022JG007112, https://doi.org/10.1029/2022JG007112, 2022.

Shi, X., Thornton, P.E., Ricciuto, D.M., Hanson, P.J., Mao, J., Sebestyen, S.D., Griffiths, N.A., and Bisht, G.: Representing northern peatland microtopography and hydrology within the Community Land Model, Biogeosciences, 12, 6463-6477, https://doi.org/10.5194/bg-12-6463-2015, 2015.

Schrier-Uijla, A.P., Kroon, P.S., Hensen, A., Leffelaar, P.A., Berendsea, F., Veenendaala, E.M.: Comparison of chamber and

1110    eddy covariance-based $CO_2$ and $CH_4$ emission estimates in a heterogeneous grass ecosystem on peat, Agricultural and forest metrology, 150(6), 825-831, https://doi.org/10.1016/j.agrformet.2009.11.007, 2010.

Stocker, B.D., Spahni, R., and Joos, F.: DYPTOP: a cost-efficient TOPMODEL implementation to simulate sub-grid spatio-temporal dynamics of global wetlands and peatlands, Geosci. Model Dev, 7, 3089-3110, https://doi.org/10.5194/gmd-7-3089-2014, 2014.

1115    Susiluoto, J., Raivonen, M., Backman, L., Laine, M., Makela, J., Peltola, O., Vesala, T., and Aalto, T.: Calibrating the sqHIMMELI v1.0 wetland methane emission model with hierarchical modeling and adaptive MCMC, Geosci. Model Dev, 11, 1199-1228, https://doi.org/10.5194/gmd-11-1199-2018, 2018.

Taft, H.E., Cross, P.A., Hastings, A., Yeluripati, J., and Jones, D.L.: Estimating greenhouse gases emissions from horticultural peat soils using a DNDC modelling approach, Journal of Environmental Management,

1120    233, 681-694, https://doi.org/10.1016/j.jenvman.2018.11.113, 2019.

Tan, L., Ge, Z., Zhou, X., Li, S., Li, X., Tang, J.: Conversion of coastal wetlands, riparian wetlands, and peatlands increases greenhouse gas emissions: A global meta-analysis, Global Change Biol, 26, 1638-1653, https://doi.org/10.1111/gcb.14933, 2020.

Tang, J., Zhuang, Q., Shannon, R.D., and White, J.R.: Quantifying wetland methane emissions with process-based models of different complexities, Biogeosciences, 7, 3817-3837, https://doi.org/10.5194/bg-7-3817-2010, 2010.

Ueyama, M., Knox, S.H., Delwiche, K.B., Bansal, S., Riley, W.J., Baldocchi, D., Hirano, T., McNicol, G., Schafer, K., Windham-Myers, L., Poulter, B., Jackson, R.B., Chang, K.-Y., Chen, J., Chu, H., Desai, A.R., Gogo, S., Iwata, H., Kang, M. Mammarella, I., Peichl, M., Sonnentag, O., Tuittila, E-S., Ryu, Y., Euskirchen, E.S., Göckede, M., Jacotot, A., Nilsson, M.B., and Sachs, T.: Modeled production, oxidation, and transport processes of wetland methane emissions in temperate, boreal, and Arctic regions. Global Change Biology, 29, 2313-2334, https://doi.org/10.1111/gcb.16594, 2023.

U.S. DOE.: Artificial Intelligence for the Methane Cycle, DOE/SC-0213, U.S. Department of Energy Office of Science, https://doi.org/10.2172/2204972, 2024.

van Huissteden, J., van den Bos, R., and Alvarez, I.M.: Modelling the effect of water-table management on $CO_2$ and $CH_4$ fluxes from peat soils, Neth. J. Geosci, 85(1), 3-18, https://doi.org/10.1017/S0016774600021399, 2006.

van Huissteden, J., Petrescu, A.M.R., Hendriks, D.M.D., and Rebel, K.T.: Sensitivity analysis of a wetland methane emission model based on temperate and arctic wetland sites, Biogeosciences, 6, 3035-3051, https://doi.org/10.5194/bg-6-3035-2009, 2009.

Vroom, R.J.E., Geurts, J.J.M., Nouta, R., Borst, A.C.W., Lamers, L.P.M., and Fritz, C.: Paludiculture crops and nitrogen kick-start ecosystem service provisioning in rewetted peat soils, Plant Soil, 474, 337-354, https://doi.org/10.1007/s11104-022-05339-y, 2022.

Walter, B.P., and M. Heimann: A process-based, climate-sensitive model to derive methane emissions from natural wetlands: Application to five wetland sites, sensitivity to model parameters, and climate, Glob. Biogeochem. Cycles, 14 (3), 745-765, https://doi.org/10.1029/1999GB001204, 2000.

Weaver, A.J., Eby, M., Wiebe, E.C., Bitz, C.M., Duffy, P.B., Ewen, T.L., Fanning, A.F., Holland, M.M., MacFayden, A., Matthews, H.D., Meissner, K.J., Saenko, O., Schmittner, A., Wang, H., and Yoshimori, M.: The UVic Earth System Climate Model: Model description, climatology, and applications to past, present and future climates, Atmosphere-Ocean, 39, 361-428, https://doi.org/10.1080/07055900.2001.9649686, 2001.

Wang, Y., Yuan, F., Yuan, F., Gu, B., Hahn, M.S., Torn, M.S., Ricciuto, D.M., Kumar, J., He, L., Zona, D., Lipson, D.A., Wagner, R., Oechel, W.C., Wullschleger, S.D., Thornton, P.E., and Xu, F.: Mechanistic Modeling of Microtopographic Impacts on $CO_2$ and $CH_4$ Fluxes in an Alaskan Tundra Ecosystem using CLM-Microbe Model, Journal of Advances in Modeling Earth Systems, 11, 4288-4304, https://doi.org/10.1029/2019MS001771, 2019.

Wang, J.M., Murphy, J.G., Geddes, J.A., Winsborough, C.L., Basiliko, N., and Thomas, S.C.: Methane fluxes measured by eddy covariance and static chamber techniques at a temperate forest in central Ontario, Canada, Biogeosciences, 10, 4371-4382, https://doi.org/10.5194/bg-10-4371-2013, 2013.

Wania, R., Ross, I., and Prentice, I.C.: Integrating peatlands and permafrost into a dynamic global vegetation model: 1, Evaluation and sensitivity of physical land surface processes, Global Biogeochemical Cycles, 23, GB3014, https://doi.org/10.1029/2008GB003412, 2009a.

Wania, R., Ross, I., and Prentice, I.C.: Integrating peatlands and permafrost into a dynamic global vegetation model: 2, Evaluation and sensitivity of vegetation and carbon cycle processes, Global Biogeochemical Cycles, 23, GB3015,
1160   https://doi.org/10.1029/2008GB003413, 2009b.

Wania, R., Ross, I., and Prentice, I.C.: Implementation and evaluation of a new methane model within a dynamic global vegetation model: LPJ-WHyMe v1.3.1, Geosci. Model Dev, 3, 565-584, https://doi.org/10.5194/gmd-3-565-2010, 2010.

Webster, K.L., McLaughlin, J.W., Kim, Y., Packalen, M.S., and Li, C.: Modelling carbon dynamics and response to environmental change along a boreal fen nutrient gradient, Ecological Modelling, 248(10), 148-164,
1165   https://doi.org/10.1016/j.ecolmodel.2012.10.004, 2013.

Wilson, D., Dixon, S.D., Artz, R.R.E., Smith, T.E.L., Evans, C.D., Owen, H.J.F., Archer, E., and Renou-Wilson, F.: Derivation of greenhouse gas emission factors for peatlands managed for extraction in the Republic of Ireland and the United Kingdom, Biogeosciences, 12, 5291-5308, https://doi.org/10.5194/bg-12-5291-2015, 2015.

Xiaofeng, X., Schimel, J.P., Thornton, P.E., Xia, S., Fengming, Y., and Goswami. S.: Substrate and Environmental Controls
1170   on Microbial Assimilation of Soil Organic Carbon: A Framework for Earth System Models, Ecology Letters, 17 (5), 547-555, https://doi.org/10.1111/ele.12254, 2014.

Xiaofeng, X., Elias, D.A., Graham, D.E., Phelps, T.J., Carroll, S.L., Wullschleger, S.D., and Thornton. P.E.: A Microbial Functional group-based Module for Simulating Methane Production and Consumption: Application to an Incubated Permafrost Soil, Journal of Geophysical Research Biogeosciences, 120 (7), 1315-1333,
1175   https://doi.org/10.1002/2015JG002935, 2015.

Xiao, H., Song, C., Li, S., Lu, X., Liang, M., Xia, X., and Yuan, W.: Global wetland methane emissions from 2001 to 2020: Magnitude, dynamics and controls, Earth's Future, 12, e2024EF004794, https://doi.org/10.1029/2024EF004794, 2024.

Xu, X., Elias, D.A., Graham, D.E., Phelps, T.J., Carroll, S.L., Wullschleger, S.D., and Thornton, P.E.: A microbial functional group-based module for simulating methane production and consumption: Application to an incubated permafrost
1180   soil, Journal of Geophysical Research: Biogeosciences, 120, 1315-1333, https://doi.org/10.1002/2015JG002935, 2015.

Xu, X., Yuan, F., Hanson, P. J., Wullschleger, S.D., Thornton, P.E., Riley, W.J., Song, X., Graham, D.E., Song, C., and Tian, H.: Reviews and syntheses: Four decades of modeling methane cycling in terrestrial ecosystems, Biogeosciences, 13, 3735-3755, https://doi.org/10.5194/bg-13-3735-2016, 2016.

Yang, W.H., McNicol, G., Teh, Y.A., Estera-Molina, K., Wood, T.E., and Silver, W.L.: Evaluating the classical versus an
1185   emerging conceptual model of peatland methane dynamics, Global Biogeochemical Cycles, 31, 1435-1453, https://doi.org/10.1002/2017GB005622, 2017.

Yuan, F., Wang, Y., Ricciuto, D.M., Shi, X., Yuan, F., Brehme, T., Bridgham, S., Keller, J., Warren, J.M., Griffiths, N.A., Sebestyen, S.D., Hanson, P.J., Thornton, P.E., and Xu, X.: Hydrological feedback on peatland $CH_4$ emission under warming and elevated $CO_2$: A modeling study, Journal of Hydrology, 603 part D, 127137.
1190   https://doi.org/10.1016/j.jhydrol.2021.127137, 2021.

Zhao, J., Weldon, S., Barthelmes, A. Swails, E., Hergoualc'h, K., Mander, U., Qiu, C., Connolly, J., Silver, W.L., and Campbell, D.I.: Global observation gaps of peatland greenhouse gas balances needs and obstacles, Biogeochemistry, 167, 427-442, https://doi.org/10.1007/s10533-023-01091-2, 2024.

Zhang, Y., C. Li, C. C. Trettin, H. Li, and G. Sun.: An integrated model of soil, hydrology, and vegetation for carbon
1195   dynamics in wetland ecosystems, Global Biogeochem. Cycles, 16 (4), 1061, https://doi.org/10.1029/2001GB001838, 2002.

Zhang, Q., Li, T-T., Zhang, Q., Wang, G-C., Yu, L-J., Guo, B., and Han, P-F.: Accuracy analysis in CH4MOD$_{wetland}$ in the simulation of $CH_4$ emissions from Chinese wetlands, Advances in Climate Change Research, 11 (1), 52-59, https://doi.org/10.1016/j.accre.2020.06.003, 2020.

1200    Zhang, Z., Chatterjee, A., Ott, L., Reichle, R., Feldman, A.F., and Poulter, B.: Effect of Assimilating SMAP Soil Moisture on $CO_2$ and $CH_4$ Fluxes through Direct Insertion in a Land Surface Model, Remote Sensing, 14 (10), 2405, https://doi.org/10.3390/rs14102405, 2022.

Zhu, Q., Liu, J., Peng, C., Chen, H., Fang, X., Jiang, H., Yang, G., Zhu, D., Wang, W., and Zhou, X.: Modelling methane emissions from natural wetlands by development and application of the TRIPLEX-GHG model, Geosci. Model Dev, 7, 981-999, https://doi.org/10.5194/gmd-7-981-2014, 2014.

1205    Zhu, Q., Peng, C., Liu, J. Jiang, H., Fang, X., Chen, H., Niu, Z., Gong, P., Lin, G., Wang, M., Wang, H., Yang, Y., Chang, J., Ge, Y., Xiang, W., Deng, X., and He, J-S.: Climate-driven increase of natural wetland methane emissions offset by human-induced wetland reduction in China over the past three decades, Sci Rep 6, 38020, https://doi.org/10.1038/srep38020, 2016.

Zhu, Q., Peng, C., Ciais, P., Jiang, H., Liu, J., Bousquet, P., Li, S., Chang, J., Fang, X., Zhou, X., Chen, H., Liu, S., Lin, G., Gong, P., Wang, M., Wang, H., Xiang, W., and Chen, J.: Interannual variation in methane emissions from 1210    tropical wetlands triggered by repeated El Niño Southern Oscillation, Global Change Biology, 23, 4706-4716, https://doi.org/10.1111/gcb.13726, 2017.

Zhuang, Q., Melillo, J.M., Kicklighter, D.W., Prinn, R.G., McGuire, A.D., Steudler, P.A., Felzer, B.S., and Hu, S.: Methane fluxes between terrestrial ecosystems and the atmosphere at northern high latitudes during the past century: A retrospective analysis with a process-based biogeochemistry model, Global Biogeochemical Cycles, 18, GB3010, 1215    https://doi.org/10.1029/2004GB002239, 2004.

Zhuang, Q., He, J., Lu, Y., Ji, L., Xiao, J., and Luo, T.: Carbon dynamics of terrestrial ecosystems on the Tibetan Plateau during the 20th century: an analysis with a process-based biogeochemical model, Global Ecology and Biogeography, 19, 649-662, https://doi.org/10.1111/j.1466-8238.2010.00559.x, 2010.

Zuo, Y., Wang, Y., He., L., Wang, N., Liu, J., Yuan, F., Li, K., Guo, Z., Sun, Y., Zhu, X., Zhang, L., Song, C., Sun, Li., and 1220    Xu, X.: Modelling methane dynamics in three wetlands in Northeastern China by using the CLM-Microbe model, Ecosystem Health and Sustainability, 8(1), 2074895, https://doi.org/10.1080/20964129.2022.2074895, 2022.

Zuo, Y., He, L., Wang, Y., Liu, J., Wang, N., Li, K., Guo, Z., Zhang, L., Chen, N., Song, C., Yuan, F., Sun, Li., and Xu, X.: Genome-enabled parameterization enhances model simulation of $CH_4$ cycling in four natural wetlands, Journal of Advances in Modeling Earth Systems, 16, e2023MS004139, https://doi.org/10.1029/2023MS004139, 2024.

1225

1230