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# Reviews and syntheses: Four decades of modeling methane cycling in terrestrial ecosystems

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**Abstract.** Over the past 4 decades, a number of numerical models have been developed to quantify the magnitude, investigate the spatial and temporal variations, and understand the underlying mechanisms and environmental controls of methane (CH<sub>4</sub>) fluxes within terrestrial ecosystems. These CH<sub>4</sub> models are also used for integrating multi-scale CH<sub>4</sub> data, such as laboratory-based incubation and molecular analysis, field observational experiments, remote sensing, and aircraft-based measurements across a variety of terrestrial ecosystems. Here we summarize 40 terrestrial CH<sub>4</sub> models to characterize their strengths and weaknesses and to suggest a roadmap for future model improvement and application. Our key findings are that (1) the focus of CH<sub>4</sub> models has shifted from theoretical to site- and regional-level applications over the past 4 decades, (2) large discrepancies exist among models in terms of representing CH<sub>4</sub> processes and their environmental controls, and (3) significant data–model and model–model mismatches are partially attributed to different representations of landscape characterization and inundation dynamics. Three areas for future improvements and applications of terrestrial CH<sub>4</sub> models are that (1) CH<sub>4</sub> models should more explicitly represent the mechanisms underlying land–atmosphere CH<sub>4</sub> exchange, with an emphasis on improving and validating individual CH<sub>4</sub> processes over

depth and horizontal space, (2) models should be developed that are capable of simulating CH<sub>4</sub> emissions across highly heterogeneous spatial and temporal scales, particularly hot moments and hotspots, and (3) efforts should be invested to develop model benchmarking frameworks that can easily be used for model improvement, evaluation, and integration with data from molecular to global scales. These improvements in CH<sub>4</sub> models would be beneficial for the Earth system models and further simulation of climate–carbon cycle feedbacks.

## 1 Introduction

Methane (CH<sub>4</sub>) is the second-most important anthropogenic greenhouse gas, accounting for ~15% of anthropogenic forcing to climate change (Forster et al., 2007; IPCC, 2013; Rodhe, 1990). Therefore, an accurate estimate of CH<sub>4</sub> exchange between land and the atmosphere is fundamental for understanding climate change (Bridgman et al., 2013; Nazaries et al., 2013; Spahni et al., 2011). The ecosystem modeling approach has been one of the most broadly used integrative tools for examining mechanistic processes, quantifying the budget of CH<sub>4</sub> flux across spatial and temporal

scales (Arah and Stephen, 1998; Riley et al., 2011; Walter et al., 1996; Zhuang et al., 2004) and predicting future flux (Anisimov, 2007). Specifically, many CH<sub>4</sub> models have been developed to integrate data, improve process understanding, quantify budgets, and project exchange with the atmosphere under a changing climate (Cao et al., 1995; Grant, 1998; Huang et al., 1998a; Potter, 1997). In addition, model sensitivity analyses help to design field and laboratory experiments by identifying the most uncertain processes and parameters in the models (Massman et al., 1997; Xu, 2010).

Based on the complexity of the CH<sub>4</sub> processes represented, CH<sub>4</sub> models fall into two broad categories: (1) empirical models that are used to estimate and extrapolate measured methanogenesis, methanotrophy, or CH<sub>4</sub> emission at plot, country, or continental scales (Christensen et al., 1996; Eliseev et al., 2008; Mokhov et al., 2007; Wania et al., 2009, 2010); and (2) process-based models that are used for prognostic understanding of individual CH<sub>4</sub> processes in response to multiple environmental drivers and budget quantification (reviewed below). This separation emphasizes the high-level model structure rather than the specific processes represented; therefore, models with many processes represented with empirical functions are still classified as process-based models if they represent many key processes of CH<sub>4</sub> production, oxidation, and transport. Although this separation is rather arbitrary, it helps one to understand the characteristics and purpose of models in a systems perspective.

Over the past decades, many empirical and process-based models have been developed, for example, CASA (Potter, 1997), CH4MOD (Huang et al., 1998b), CLM4Me (Riley et al., 2011), DAYCENT (Del Grosso et al., 2000), DLEM (Tian et al., 2010; Xu and Tian, 2012), DNDC (Li, 2000), *ecosys* (Grant, 1998), HH (Cresto Aleina et al., 2015), MEM (Cao et al., 1995), and TEM (Zhuang et al., 2004). However, recent analyses and model inter-comparisons have shown that most of these models poorly reproduce regional- to global-scale observations (Bohn and Lettenmaier, 2010; Bohn et al., 2015; Melton et al., 2013; Wania et al., 2013). A comprehensive synthesis and evaluation of the mechanisms incorporated into these models is lacking. This review focuses on primary processes of CH<sub>4</sub> cycling in the terrestrial ecosystems and their representation in the models. The critical CH<sub>4</sub> processes include substrate cycling, methanogenesis, methanotrophy, and transport in the soil profile, and their environmental controls. Emphasis is given to how these mechanisms were simulated in various models and how they were categorized in terms of complexity and ecosystem function. The review focuses on CH<sub>4</sub> models developed for terrestrial ecosystems, which is defined as ecosystems on land and wetlands with less than 2 m standing water. This classification is used to distinguish them from pure aquatic ecosystems and considering the important role of wetlands in CH<sub>4</sub> cycling. Therefore, models for understanding reactions in bioreactors (Bhadra et al., 1984; Pareek et al., 1999), mining plots (De Visscher and Van Cleemput, 2003), aquatic ecosys-

tems, and marine systems (Elliott et al., 2011) were excluded. An early pioneering effort of multiplying wetland area by average CH<sub>4</sub> flux to estimate global CH<sub>4</sub> budget was excluded from this review as well (Matthews and Fung, 1987). This review further excludes the CH<sub>4</sub> emission from biomass burning, termites, and ruminants, because this paper primarily focuses on soil biogeochemical processes represented in ecosystem models. The model names are determined by two criteria: (1) if the model has been named in the original publication, it will be used to represent the model; (2) if the model has not been named, the last name of the first author will be used to name the model: for example, “Segers model” or “Gong model”. In this paper we first provide an overview of the range of processes that have been considered in CH<sub>4</sub> models over the past 4 decades, and then further classify existing models as determined by the range of processes considered. We finished with several suggested research topics, which would be beneficial for better developing and applying CH<sub>4</sub> models for either understanding CH<sub>4</sub> cycling or quantifying CH<sub>4</sub> budgets at various scales.

## 2 Primary CH<sub>4</sub> processes

Biological CH<sub>4</sub> production in sediments was first noted in the late 18th century (Volta, 1777), and the microbial oxidation of CH<sub>4</sub> was proposed at the beginning of the 20th century (Söhngen, 1906). Since then, CH<sub>4</sub> cycling processes have been intensively studied and documented (Christensen et al., 1996; Hakemian and Rosenzweig, 2007; Lai, 2009; Melloh and Crill, 1996; Mer and Roger, 2001), and most have been described mathematically and incorporated into ecosystem models (Table 1). Herein, we do not attempt to review all CH<sub>4</sub> processes, as a number of reviews have been published on this topic (Barlett and Harriss, 1993; Blodau, 2002; Bridgham et al., 2013; Cai, 2012; Chen et al., 2012; Conrad, 1995, 1996; Hakemian and Rosenzweig, 2007; Higgins et al., 1981; Lai, 2009; Monechi et al., 2007; Segers, 1998; Wahlen, 1993). Rather, we focus on primary CH<sub>4</sub> processes in terrestrial ecosystems and their environmental controls from a modeling perspective. In this context there exist three major methanogenesis mechanisms, two CH<sub>4</sub> methanotrophy mechanisms, and three aggregated CH<sub>4</sub> transport pathways in plants and soils. We note that most models do not explicitly represent all of these transport pathways, and that the relative importance of these pathways varies substantially in time, space, and with ecosystem types. We also pay attention to several other modeling features, including capability for plot- or regional-level simulations, vertical representation of biogeochemical processes, and whether the model is embedded in an Earth system model (ESM).

The published literature concludes that two processes dominate biological CH<sub>4</sub> production (Conrad, 1999; Krüger et al., 2001): acetoclastic methanogenesis – CH<sub>4</sub> production from acetate – and hydrogenotrophic methanogenesis – CH<sub>4</sub>

**Table 1.** Terrestrial ecosystem models for CH<sub>4</sub> cycling and the model representation of three pathways of CH<sub>4</sub> transport (models are in alphabetical order; author's last name is used if the model name is not available).

Model	Aerenchynma	Diffusion	Ebullition	References
Beckett model	Yes	Yes	No	Beckett et al. (2001)
Cartoon model	Yes	Yes	Yes	Arah and Stephen (1998); Arah and Kirk (2000)
CASA	Yes	Yes	Yes	Potter (1997); Potter et al. (1996)
CH4MOD	Yes	Yes	Yes	Huang et al. (1998b, 2004); Li et al. (2012)
Christensen model	No	No	No	Christensen et al. (1996)
CLASS	No	Yes	No	Curry (2007, 2009)
CLM4Me	Yes	Yes	Yes	Riley et al. (2011)
CLM-Microbe	Yes	Yes	Yes	Xu et al. (2014, 2015)
DAYCENT	No	Yes	No	Del Grosso et al. (2000, 2002, 2009)
Ding model	Yes	No	No	Ding and Wang (1996)
DLEM	Yes	Yes	Yes	Tian et al. (2010); Xu and Tian (2012)
DNDC	Yes	Yes	Yes	Li (2000)
DOS-TEM	Yes	Yes	Yes	Fan et al. (2013)
<i>ecosys</i>	No	Yes	Yes	Grant (1998, 2001)
Gong model	Yes	Yes	Yes	Gong et al. (2013)
HH model	Yes	Yes	Yes	Cresto Aleina et al. (2015)
IAP-RAS	No	No	No	Eliseev et al. (2008); Mokhov et al. (2007)
Kettunen model	Yes	Yes	Yes	Kettunen (2003)
Lovley model	No	No	No	Lovley and Klug (1986)
LPJ-Bern	Yes	Yes	Yes	Spahni et al. (2011)
LPJ-WHyMe	Yes	Yes	Yes	Wania et al. (2009, 2010)
LPJ-WSL	No	No	No	Hodson et al. (2011)
Martens model	Yes	Yes	Yes	Martens et al. (1998)
MEM	No	No	No	Cao et al. (1995, 1998)
MERES	Yes	Yes	No	Matthews et al. (2000)
Nouchi model	Yes	Yes	No	Hosono and Nouchi (1997); Nouchi et al. (1994)
ORCHIDEE	Yes	Yes	Yes	Ringeval et al. (2010, 2011)
Ridgwell model	No	Yes	No	Ridgwell et al. (1999)
SDGVM	No	No	No	Hopcroft et al. (2011)
Segers model	Yes	Yes	Yes	Segers and Kengen (1998); Segers and Leffelaar (2001a, b); Segers et al. (2001)
Tagesson model	No	No	No	Tagesson et al. (2013)
TCF	Yes	Yes	Yes	Watts et al. (2014)
TEM	Yes	Yes	Yes	Zhuang et al. (2004)
TRIPLEX-GHG	Yes	Yes	Yes	Zhu et al. (2014)
UW-VIC	Yes	Yes	Yes	Bohn and Lettenmaier (2010); Bohn et al. (2007)
van Bodegom model	Yes	Yes	Yes	van Bodegom et al. (2000, 2001)
VISIT	Yes	Yes	Yes	Inatomi et al. (2010); Ito and Inatomi (2012)
De Visscher model	No	Yes	No	De Visscher and Van Cleemput (2003)
Walter model	Yes	Yes	Yes	Walter and Heimann (2000); Walter et al. (1996)
Xu model	Yes	Yes	Yes	Xu et al. (2007)

production from hydrogen (H<sub>2</sub>) and carbon dioxide (CO<sub>2</sub>). Acetoclastic and hydrogenotrophic methanogenesis account for ~50–90 and ~10–43 % of global annual CH<sub>4</sub> produced, respectively (Conrad and Klose, 1999; Kotsyurbenko et al., 2004; Mer and Roger, 2001; Summons et al., 1998). Methylo-trophic methanogenesis (producing CH<sub>4</sub> from methanol, methylamines, or dimethylsulfide) is usually considered a minor contributor of CH<sub>4</sub>, but may be significant in marine systems (Summons et al., 1998). The proportion of CH<sub>4</sub> produced via any of these pathways varies widely in time, space, and across ecosystem types.

Methanotrophy occurs under aerobic (Gerard and Chanton, 1993) and anaerobic (Smemo and Yavitt, 2011) conditions. These oxidative processes can occur in several locations in soil and plants (Frenzel and Rudolph, 1998; Heil-

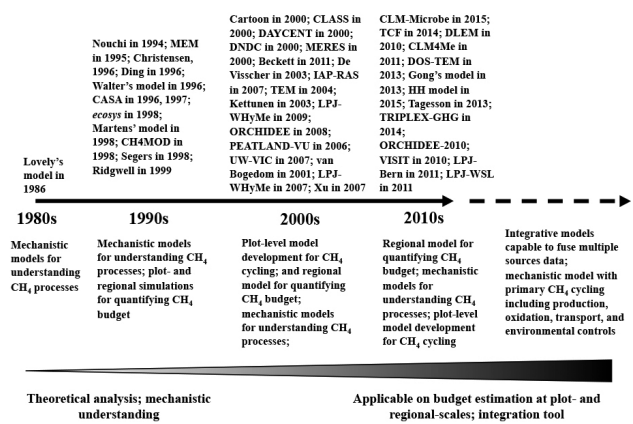
man and Carlton, 2001, Ström et al., 2005) and using CH<sub>4</sub> either produced in the soil column or transported from the atmosphere (Mau et al., 2013). Large variation in the relative magnitudes of these pathways as a percentage of total methanotrophy has been observed: aerobic oxidation of CH<sub>4</sub> in soil contributes 1–90 % (King, 1996; Ström et al., 2005), anaerobic oxidation of CH<sub>4</sub> within the soil profile contributes 0.3–5 % (Blazewicz et al., 2012; Murase and Kimura, 1996), oxidation of CH<sub>4</sub> during transport in plant aerenchyma contributes < 1 % (Frenzel and Karofeld, 2000; Frenzel and Rudolph, 1998), and oxidation of atmospheric CH<sub>4</sub> contributes ~10–100 % (ranging from ~10 % for wetland to ~100 % for upland) (Gulledge and Schimel, 1998a, b; Topp and Pattey, 1997) to total methanotrophy in the ecosystem. CH<sub>4</sub> is transported from the soil profile to the at-

mosphere in typical open-water wetlands by seven pathways that could be aggregated into three: plant-mediated transport accounts for 12–98 % (Butterbach-Bahl et al., 1997; Mer and Roger, 2001; Morrissey and Livingston, 1992), diffusion accounts for ~ 5 % for wetlands and > 90 % for upland systems (Barber et al., 1988; Mer and Roger, 2001), and ebullition accounts for 10–60 % (Chanton et al., 1989; Tokida et al., 2007) of the CH<sub>4</sub> produced in the soil that is emitted into the atmosphere. The plant-mediated transport includes diffusive and advective (associated with gas or liquid flow) transports; soil matrix transport includes soil gaseous diffusion and advection and aqueous diffusion and advection. Because diffusion normally dominates soil matrix transport, we only consider here the model's representation of diffusion, consistent with other studies (Mer and Roger, 2001; Bridgham et al., 2013).

Environmental factors affecting CH<sub>4</sub> processes have many direct and indirect controls. The dominant direct factors controlling methanogenesis and methanotrophy in most ecosystems include oxygen availability, dissolved organic carbon concentration, soil pH, soil temperature, soil moisture, nitrate and other reducers, ferric iron, microbial community structure, active microbial biomass, wind speed (Askaer et al., 2011), plant root structure (Nouchi et al., 1990), etc. Indirect factors include soil texture and mineralogy, vegetation, air temperature, soil fauna, nitrogen input, irrigation, agricultural practices, sulfate reduction, and carbon quality (Banger et al., 2012; Bridgham et al., 2013; Hanson and Hanson, 1996; Higgins et al., 1981; Mer and Roger, 2001). The complicated effects induced by a few key factors in CH<sub>4</sub> processes have been mathematically described and incorporated into many CH<sub>4</sub> models, for example, direct factors such as soil temperature, moisture, oxygen availability, soil pH, and soil redox potential (Grant, 1998; Riley et al., 2011; Tian et al., 2010; Zhuang et al., 2004). The indirect factors such as nitrogen input (Banger et al., 2012), irrigation (Wassmann et al., 2000), and agricultural practices were not reviewed in this study as their impacts are indirect and were modeled through impacts on vegetation and hydrology (Li, 2000; Ren et al., 2011; Xu et al., 2010).

### 3 Model representation of CH<sub>4</sub> processes

We reviewed 40 CH<sub>4</sub> models (Fig. 1 and Table 1), which were developed for a variety of purposes. The first CH<sub>4</sub> model was published in 1986 by Lovley and Klug (1986) to simulate methanogenesis in freshwater sediments, and since then a number of CH<sub>4</sub> models have been developed and applied at numerous scales (Table 1). For example, Cao et al. (1995) developed the Methane Emission Model (MEM) and applied it to quantify the global CH<sub>4</sub> source in rice paddies and the sensitivity of the global CH<sub>4</sub> budget's response to climate change (Cao et al., 1995, 1998). Grant et al. (1998) developed the *ecosys* model, which is currently the ecosystem-scale model that most mechanistically represents



**Figure 1.** Published CH<sub>4</sub> models and modeling trends in terms of applicability and mechanistic representation of CH<sub>4</sub> cycling processes over recent decades; the envisioned CH<sub>4</sub> model capability.

the many kinetic processes and microbial mechanisms for methanogenesis, methanotrophy, and CH<sub>4</sub> emission (Grant and Roulet, 2002). Riley et al. (2011) developed CLM4Me, a CH<sub>4</sub> module for the Community Land Model, which is incorporated into the Community Earth System Model. The family of LPJ models (LPJ-Bern, LPJ-WHyMe, LPJ-WSL) was developed under the LPJ framework to simulate CH<sub>4</sub> processes, but with different modules for CH<sub>4</sub> cycling; for example, LPJ-Bern and LPJ-WHyMe incorporate the Walter CH<sub>4</sub> module (Walter and Heimann, 2000; Walter et al., 1996; Wania et al., 2009), while LPJ-WSL incorporates the CH<sub>4</sub> module from Christensen et al. (1996). The number of CH<sub>4</sub> models has steadily increased since the 1980s (Fig. 1): 1 in the 1980s, 11 in the 1990s, 14 in the 2000s, and 14 for 2010–2015. This increase in model developments is driven by many factors, including a desire to understand the contribution of CH<sub>4</sub> processes to the regional CH<sub>4</sub> budget (Fig. 1). For instance, Lovley's model was built to understand the CH<sub>4</sub> production and sulfate reduction in freshwater sediment (Lovley and Klug, 1986); while all models published in the 2010s are applicable for CH<sub>4</sub> budget quantification, particularly at regional scale. This rapid increase in CH<sub>4</sub> model development indicates a growing effort to analyze CH<sub>4</sub> cycling and quantify CH<sub>4</sub> budgets across spatial scales. Meanwhile, the key mechanisms represented in the models have increased at a slower pace (Fig. 2). The most important changes are representation of vertically resolved processes within the soil and regional model simulation. For example, the percentage of the newly developed models with vertically resolved CH<sub>4</sub> biogeochemistry has increased from 54 % before 2000 to ~ 79 % in the most recent decade (2010–2015). The proportion of models with regional simulation capability (producing a spatial map of CH<sub>4</sub> fluxes with inputs of spatial map of driving forces) has doubled from ~ 50 % before the 2010s to almost 100 % afterwards (Fig. 2).

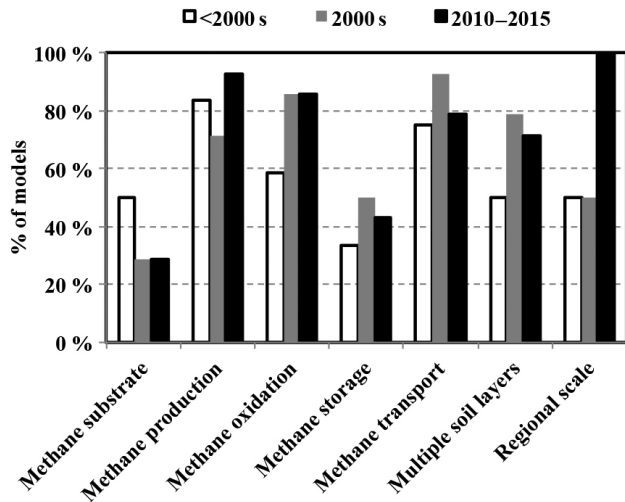
**Table 2.** Key mechanisms/features of CH<sub>4</sub> processes and their representations in CH<sub>4</sub> models.

Key mechanisms	Models
Methanogenesis	Cartoon model, CASA, CH4MOD, Christensen model, CLM4Me, CLM-Microbe, Ding model, DLEM, DNDC, DOS-TEM, <i>ecosys</i> , Gong model, IAP-RAS, Kettunen model, Lovley model, LPJ-Brn, LPJ-WHyMe, LPJ-WSL, Martens model, MEM, MERES, ORCHIDEE, SDGVM, Segers model, TCF, TEM, TRIPLEX-GHG, UW-VIC, van Bodegom's model, VISIT, Walter model, Xu's model
Methanotrophy	Cartoon model, CASA, CLASS, CLM4Me, CLM-Microbe, DAYCENT, DLEM, DNDC, DOS-TEM, <i>ecosys</i> , Gong model, Kettunen model, LPJ-Bern, LPJ-WHyMe, Martens model, MEM, MERES, ORCHIDEE, Ridgwells model, SDGVM, Segers model, TCF, TEM, TRIPLEX-GHG, UW-VIC, van Bodegom's model, VISIT, De Visscher model, Walter model, Xu model
Anaerobic oxidation of CH <sub>4</sub> Substrate (acetate/DOC)	CLM-Microbe, Martens model CH4MOD, CLM-Microbe, DLEM, DNDC, <i>ecosys</i> , Gong model, Kettunen model, Lovley model, Martens model, MEM, MERES, SDGVM, Segers model, TCF, van Bodegom model, Xu model
Microbial functional groups CH <sub>4</sub> storage in soil profile	CLM-Microbe, <i>ecosys</i> , Segers model Beckett model, Cartoon model, CLM4Me, CLM-Microbe, <i>ecosys</i> , Kettunen model, Martens model, MERES, Nouchi model, ORCHIDEE, Segers model, UW-VIC, van Bodegom model, VISIT, De Visscher model, Walter model
O <sub>2</sub> availability for CH <sub>4</sub> oxidation	Beckett model, Cartoon model, CLM4Me, CLM-Microbe, <i>ecosys</i> , Kettunen model, MERES, Segers model, van Bodegom model, De Visscher model, Xu model
Iron biogeochemistry	van Bodegom model
Sulfate biogeochemistry	Lovley model, Martens model, van Bodegom model
Frozen trapped CH <sub>4</sub>	None
Embedded in the Earth system model	CLASS, CLM4Me, CLM-Microbe, IAP-RAS, ORCHIDEE, SDGVM
Vertical resolved biogeochemistry	Beckett model, Cartoon model, CLASS, CLM4Me, CLM-Microbe, DNDC, DOS-TEM, <i>ecosys</i> , Gong model, HH model, IAP-RAS, Kettunen model, Lovley model, LPJ-Bern, LPJ-WHyMe, LPJ-WSL, Martens model, MERES, ORCHIDEE, Ridgwell model, SDGVM, Segers model, TRIPLEX-GHG, UW-VIC, VISIT, De Visscher model, Walter model, Xu model
Regional-scale, capacity for up-scaling	CASA, CH4MOD, Christensen model, CLASS, CLM4Me, CLM-Microbe, DAYCENT, DLEM, <i>ecosys</i> , Gong model, HH model, IAP-RAS, LPJ-Bern, LPJ-WHyMe, LPJ-WSL, Martens model, MEM, MERES, ORCHIDEE, Ridgwell model, SDGVM, Tagesson model, TCF, TEM, TRIPLEX-GHG, UW-VIC, VISIT, Walter model

The majority of these models were designed to simulate land-surface exchange in saturated ecosystems (primarily natural wetlands and rice paddies) (Huang et al., 1998b; Li, 2000; Walter et al., 1996) (Table 1). Not all of the models explicitly represented the belowground mechanistic processes for CH<sub>4</sub> production and consumption and the primary carbon biogeochemical processes (Christensen et al., 1996; Ding and Wang, 1996). The land–atmosphere CH<sub>4</sub> exchange is a net balance of many processes, including production, oxidation, and transport, which are represented in models with different complexities (Table 2). Some models are quite complicated, while some are relatively simple. The obvious trade-off in modeling CH<sub>4</sub> cycling is to represent mechanisms as accurately as possible while managing complexity (Evans et al., 2013), and ensuring that additional complexity enhances predictability (Tang and Zhuang, 2008).

### 3.1 CH<sub>4</sub> model classification

Based on a cluster analysis that considers model characteristics including acetoclastic methanogenesis, hydrogenotrophic methanogenesis, methanotrophy, different CH<sub>4</sub> transport pathways, multiple soil layers, and oxygen availability, current CH<sub>4</sub> models can be classified into three groups (Figs. 3 and 4). The first group of CH<sub>4</sub> models uses a very simple framework for land-surface CH<sub>4</sub> flux, and most were developed before the 2000s (Christensen's model, CASA, etc.) (Fig. 4a). These models treated land-surface CH<sub>4</sub> flux as an empirical function and link it to environmental controls or soil organic carbon. This group of models ignored the mechanistic processes of methanogenesis, methanotrophy, and CH<sub>4</sub> transport. The second group of CH<sub>4</sub> models considers processes in a relatively simple manner (one or two primary CH<sub>4</sub> transport pathways, methanogenesis as a function of DOC (dissolved organic carbon), oxidation of atmospheric CH<sub>4</sub>, etc.); however, the methanogenesis and methanotrophy mechanisms are still



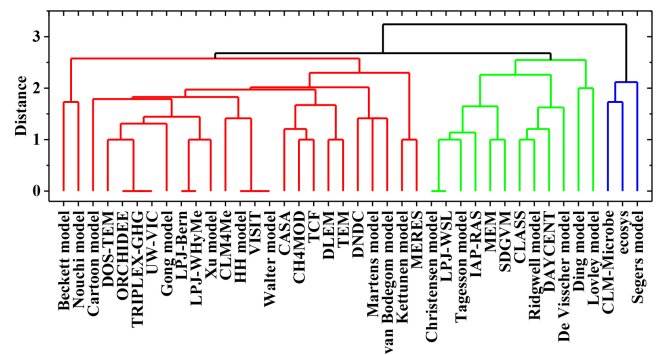
**Figure 2.** Percentage of CH<sub>4</sub> models with consideration of some key CH<sub>4</sub> mechanisms. The percentage was calculated as the number of models considering each mechanism divided by the total number of published models in each time period.

not mechanistically represented (Fig. 4b). For example, DLEM simulates CH<sub>4</sub> production with a Michaelis–Menten equation with DOC concentration as substrate (Tian et al., 2010); Walter’s model simulates CH<sub>4</sub> production with a simple multiplier between substrate availability and environmental scalars and CH<sub>4</sub> oxidation with a Michaelis–Menten equation (Walter et al., 1996). The third group of CH<sub>4</sub> models explicitly simulates the processes for methanogenesis, methanotrophy, and CH<sub>4</sub> transport as well as their environmental controls, which allows comprehensive investigation of physical, chemical, or biological processes’ contribution to land-surface CH<sub>4</sub> flux (Fig. 4c). Of the models in the third group, none fully represents all these processes (although some have most of the features described); for example, the *ecosys* model is one of the few models to represent most of the CH<sub>4</sub> cycling processes shown in Fig. 4c, although it has not been embedded in an Earth system model.

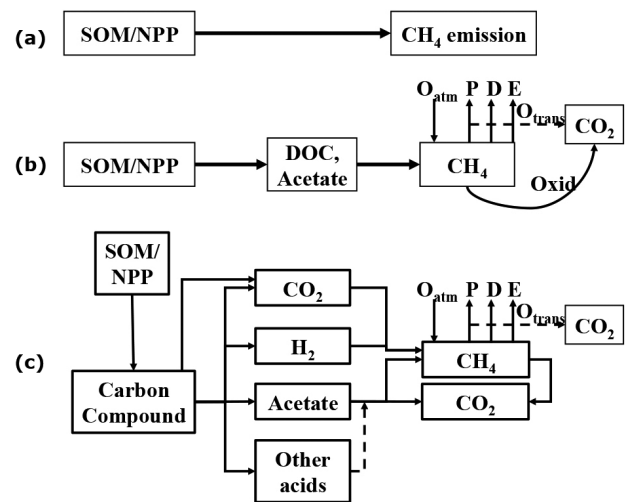
### 3.2 Methanogenesis

Models make use of four types of modeling frameworks (Table 3) to relate methanogenesis to substrate requirements. Similar to Eqs. (1)–(4) in Table 3, there are four model algorithms to represent methanogenesis: (1) empirical association between methanogenesis and environmental condition, including temperature and water table; (2) empirical correlation of methanogenesis with biological variables (particularly heterotrophic respiration and soil organic matter); (3) methanogenesis as a function of DOC concentration; and (4) a suite of mechanistic processes simulated for methanogenesis.

Representation of the substrate for methanogenesis may be a key aspect of simulating CH<sub>4</sub> cycling in terrestrial ecosys-



**Figure 3.** Cluster analysis showing three groups of CH<sub>4</sub> models based on model characteristics (lines with the same color indicate CH<sub>4</sub> models in the same group; green lines represent a relatively simple model structure, red lines represent relatively mechanistic models, and blue lines represent mechanistic models).



**Figure 4.** Three types of models with key mechanisms for CH<sub>4</sub> production and oxidation (SOM: soil organic matter; NPP: net primary production; DOC: dissolved organic carbon;  $O_{atm}$ : oxidation of atmospheric CH<sub>4</sub>;  $P$ : plant-mediated transport;  $D$ : diffusion transport;  $E$ : ebullition transport;  $O_{xid}$ : oxidation;  $O_{trans}$ : oxidation of CH<sub>4</sub> during transport).

tems (Bellisario et al., 1999); however, more than half of the models examined do not explicitly simulate substrates for methanogenesis. We note, however, that explicit representation of substrates and their effects on methanogenesis requires additional model parameters, and therefore degrees of freedom in the model, which can lead to increased equifinality (Tang and Zhuang, 2008). The optimum complexity level for methanogenesis and consumption models remains to be determined.

The first model algorithm correlates methanogenesis with environmental factors and ignores substrate production and its influence on methanogenesis (Eq. 1) (Table 3). This group includes Christensen’s model (Christensen et al., 1996),

**Table 3.** The mathematical equations used to describe the CH<sub>4</sub> processes used in representative models ( $P_{CH_4}$  is the CH<sub>4</sub> production rate;  $Oxid_{CH_4}$  is the CH<sub>4</sub> oxidation rate;  $T_{CH_4}$  is the CH<sub>4</sub> transport rate;  $D_{CH_4}$  is the CH<sub>4</sub> diffusion rate; some parameters may have been changed from the original publication to keep relative consistency in this table).

CH <sub>4</sub> processes	Equations	Ecological description	Model examples
CH <sub>4</sub> substrate and CH <sub>4</sub> production	1 $P_{CH_4} = f(TW)$	A function of temperature ( $T$ ) and moisture ( $W$ )	Christensen model, IAP-RAS, DAYCENT
	2a $P_{CH_4} = r \times HR \times f(TW)$	A portion of heterotrophic respiration, affected by temperature ( $T$ ) and moisture ( $W$ )	LPJ family, CLM4Me, Ding model, MERES, TRIPLEX-GHG
	2b $P_{CH_4} = r \times SOM \times f(TW)$	A portion of soil organic matter (SOM), affected by temperature ( $T$ ) and moisture ( $W$ ); Walter's model uses indirect association with NPP	CH4MOD, DOS-Tem, Gong model, HH model, Walter model
	3 $P_{CH_4} = V \times \frac{[DOC]}{K_{DOC} + [DOC]} \times f(TW)$	A portion of dissolved organic carbon (DOC), affected by temperature ( $T$ ) and moisture ( $W$ )	MEM, DLEM
4 $P_{CH_4} = f(DOCAcetate, CO_2) \times f(TW)$	Mechanistic processes for CH <sub>4</sub> production are considered, affected by temperature ( $T$ ) and moisture ( $W$ )	Kettunen model, Segers model, van Bodegom's model, and <i>ecosys</i>	
CH <sub>4</sub> oxidation	5 $Oxid_{CH_4} = V \times \left( \frac{[CH_4]}{K_{CH_4} + [CH_4]} \right) \times f(TW)$	Oxidation as a function of CH <sub>4</sub> concentration and temperature and moisture	DLEM, TRIPLEX-GHG, VISIT
	6 $Oxid_{CH_4} = V \times \left( \frac{[CH_4]}{K_{CH_4} + [CH_4]} \right) \left( \frac{[O_2]}{K_{O_2} + [O_2]} \right) \times f(TW)$	Oxidation as a function of CH <sub>4</sub> and O <sub>2</sub> concentration, temperature and moisture	Cartoon model, CLM4Me, CLM-Microbe, Kettunen model
CH <sub>4</sub> transport	7 $T_{CH_4} = V \times ([CH_4] - \overline{[CH_4]})$	$V$ is the parameter for distance, diffusion coefficient, etc.; $[CH_4]$ is the concentration of CH <sub>4</sub> in the soil/water profile (dissolvability for DLEM, 0 for DNDC); and $\overline{[CH_4]}$ is the threshold of CH <sub>4</sub> concentration above which CH <sub>4</sub> will be transported to the atmosphere via either of the three transport pathways	DLEM, DNDC, Walter model
	8a $A = \frac{C(z) - C_a}{r_{Lz}/D + r_a} pT \rho_r$	Aerenchyma transport	CLM4Me
	8b Moves to first unsaturated layer and then released to gaseous phase	Ebullition	CLM4Me
	8c $D_{CH_4} = D \times \frac{\Delta[CH_4]}{\Delta z}$	Diffusion of CH <sub>4</sub> was simulated following Fick's law; CLM4Me separates aqueous and gaseous diffusion	CLM4Me, CLM-Microbe, <i>ecosys</i> , Ridgwell model, TRIPLEX-GHG; Sergers model
Temperature effects	9 $f(T) = a \times T + b$ $f(T) = a \times T^2 + b \times T + c$ $f(T) = b \times e^{0.2424 \times T}$	Linear regression on temperature or degree days; DNDC simulate temperature impact on production not on oxidation	DAYCENT, DNDC, IAP-RAS, LPJ family
	10 $f(T) = Q_{10}^{\frac{(T - T_{ref})}{10}}$	$Q_{10}$ equations; $T_{ref}$ is the reference temperature	CH4MOD, CLM-Microbe, CLM4Me, DLEM, VISIT, Kettunen model
	11a $V_T = V^0 \times \exp\left(\frac{\Delta E}{R} \left[ \frac{1}{T^0} - \frac{1}{T} \right]\right)$	Arrhenius equation	Cartoon model, Ding model
	11b $f_T = \frac{T_s \times \exp(A - \frac{H_a}{R \times T_s})}{1 + \exp\left(\frac{H_{dl} - S \times T_s}{R \times T_s}\right) + \exp\left(\frac{S \times T_s - H_{dh}}{R \times T_s}\right)}$	Modified Arrhenius equation; $T_s$ is soil temperature at $K$ ; $A$ is the parameter for $f_T = 1.0$ at $T_s = 303.16$ K; $H_a$ is the energy of activation ( $J \text{ mol}^{-1}$ ); $R$ is universal gas constant ( $J \text{ mol}^{-1} \text{ K}^{-1}$ ); $H_{dl}$ and $H_{dh}$ are energy of low and high temperature deactivation ( $J \text{ mol}^{-1}$ )	<i>ecosys</i>
Moisture effects on methanogenesis and methanotrophy	12 No moisture effect is simulated, rather inundation area is simulated	No equation, while a temporal and spatial variation of inundation and saturation impacts	CASA
	13 $F_\phi = e^{-P/P_c}$	Water stress for oxidation, where $P$ is soil moisture and $P_c = -2.4 \times 10^5$ mm	CLM4Me
14 $f(SM) = \begin{cases} 1, \phi > 0.2 \text{ Mpa} \\ \left[ 1 - \frac{\log_{10} \phi - \log_{10}(0.2)}{\log_{10}(100) - \log_{10}(0.2)} \right]^\beta, 0.2 > \phi > 100 \text{ Mpa} \\ 0, \phi > 100 \text{ Mpa} \end{cases}$	$\beta$ is an arbitrary constant, $\phi$ is the soil water potential	CLASS	
15 $f_{prod}(SM) = \left( \frac{SM - SM_{fc}}{SM_{sat} - SM_{fc}} \right)^2 \times 0.368 \times e^{\left( \frac{SM - SM_{fc}}{SM_{sat} - SM_{fc}} \right)}$ $f_{oxid}(SM) = 1 - f_{prod}(SM)$	Different impacts on CH <sub>4</sub> production and consumption; SM: soil moisture; $SM_{fc}$ : field capacity; $SM_{sat}$ : saturation soil moisture	DLEM	
16 $f(SM) = \frac{(M_V - M_{min}) \times (M - M_{max})}{(M_V - M_{min}) \times (M_V - M_{max}) - (M_V - M_{opt})^2}$	Bell-shape curve	TEM	
pH effects	17a $f(pH) = \frac{(pH - pH_{min}) \times (pH - pH_{max})}{(pH - pH_{min}) \times (pH - pH_{max}) - (pH - pH_{opt})^2}$	Bell-shape curve	CLM-Microbe, MEM, TEM,
	17b $f(pH) = 10^{-0.2335 \times pH^2 + 2.7727 \times pH - 8.6}$	Bell-shape curve	CLM4Me
	17c $f(pH) = \begin{cases} 0, pH \leq 4 \text{ or } pH \geq 10 \\ \frac{1.02}{1 + 1\,000\,000 \times e^{(-2.5 \times pH)}} & 4 > pH > 7 \\ \frac{1.02}{1 + 1\,000\,000 \times e^{(-2.5 \times (14 - pH))}} & 7 > pH > 10 \end{cases}$	Bell-shape curve	DLEM



which simulates the net flux of CH<sub>4</sub> based on fraction of saturated soil column and soil temperature, and the IAP-RAS model (Mokhov et al., 2007), which calculates methanogenesis as an empirical equation of soil temperature. This group has a role in site-specific interpolation of observations for scaling over time at a given site, but does not explicitly represent carbon or acetate substrate. The second model algorithm directly links methanogenesis with heterotrophic respiration or soil organic matter content, but does not explicitly represent carbon or acetate substrate availability (Eq. 2); examples are the LPJ model family (Hodson et al., 2011; Spahni et al., 2011; Wania et al., 2009, 2010) and CLM4Me (Riley et al., 2011). The third model algorithm simulates dissolved organic carbon (DOC) or different pools of soil organic carbon, which are treated as a substrate pool influencing CH<sub>4</sub> production (Eq. 3); examples are the MEM (Cao et al., 1995, 1998) and DLEM (Tian et al., 2010). The fourth model algorithm considers the primary substrates for methanogenesis, that is, acetate and single-carbon compounds (Eq. 4); examples are Kettunen's model (Kettunen, 2003), Segers' model (Segers and Kengen, 1998; Segers and Leffelaar, 2001a, b; Segers et al., 2001), van Bodegom's model (van Bodegom et al., 2000, 2001), and the *ecosys* model (Grant, 1998).

Methanogenesis is a fundamental process for CH<sub>4</sub> cycling, and the majority of models simulate methanogenesis in either implicit or explicit ways (Tables 2 and 3). For example, 32 models (i.e., Cartoon model, CASA, CH4MOD, Christensen model, CLM4Me, Ding model, DLEM, DNDC, DOS-TEM, *ecosys*, Gong model, HH model, IAP-RAS, Kettunen model, Lovley model, LPJ-Brn, LPJ-WHyMe, LPJ-WSL, Martens model, MEM, MERES, ORCHIDEE, SDGVM, Segers model, TCF, TEM, TRIPLEX-GHG, UW-VIC, van Bodegom model, VISIT, Walter model, and Xu model) simulate methanogenesis as one individual process. As a comparison, only 3 out of 40 CH<sub>4</sub> models reviewed explicitly simulate two methanogenesis pathways (acetoclastic methanogenesis and hydrogenotrophic methanogenesis) (Table 3). As mentioned earlier, it is well recognized that there are two dominant methanogenesis pathways, and their relative combination changes significantly across environmental gradients, for example, along the soil profile (Falz et al., 1999) and across landscape types (McCalley et al., 2014). This lack of representation of two methanogenesis mechanisms might have caused dramatic bias in simulating CH<sub>4</sub> flux temporally and spatially and needs to be addressed in future model improvements.

Michaelis–Menten-like equations, widely used for simulating CH<sub>4</sub> production and oxidation, consider substrates limiting factors (Segers and Kengen, 1998). A few CH<sub>4</sub> models in the third category of methanogenesis models (linking methanogenesis with a substrate) use the Michaelis–Menten-like equation to compute methanogenesis and methanotrophy rates (Eqs. 3, 5, and 6). For example, DLEM simulates methanogenesis as a function of DOC concentration and other environmental controls, and Michaelis–Menten-

like functions were used to compute methanogenesis on the basis of DOC as a substrate.

### 3.3 Methanotrophy

Methanotrophy is another important process for simulating the land–atmosphere exchange of CH<sub>4</sub> (Table 2). Aerobic and anaerobic methanotrophy occurs in different locations in the soil profile, and affects both methanogenesis in the profile and CH<sub>4</sub> diffusing in from the atmosphere. For example, the oxidation of atmospheric CH<sub>4</sub>, rhizosphere and bulk soil oxidation, and oxidation during CH<sub>4</sub> transport from soil to the atmosphere have been measured and modeled (Tables 1 and 2). Anaerobic CH<sub>4</sub> oxidation has been measured (Blazewicz et al., 2012) and has been proposed to be incorporated into ecosystem models (Gauthier et al., 2015).

It has been confirmed that the aerobic oxidation of CH<sub>4</sub> produced in the soil profile and aerobic oxidation of atmospheric CH<sub>4</sub> play a major role in CH<sub>4</sub> consumption in the system, and that anaerobic oxidation of CH<sub>4</sub> is a minor contributor. Currently, no models explicitly simulate the anaerobic oxidation of CH<sub>4</sub> in soil, although a few recent studies highlighted the importance of this process (Blazewicz et al., 2012; Caldwell et al., 2008; Conrad, 2009; Smemo and Yavitt, 2011; Valentine and Reeburgh, 2000). The key reasons for this omission are that the process has not been mathematically described, the key parameters are uncertain (Gauthier et al., 2015), and the biochemical mechanism is not fully understood.

Methanotrophy has been simulated with dual Monod Michaelis–Menten-like equations with CH<sub>4</sub> and oxygen as limiting factors (Table 3). Recent work has shown that the Michaelis–Menten approach may be inaccurate when representing multi-substrate, multi-consumer networks, and that a new approach (called equilibrium chemistry approximation, ECA) can ameliorate this problem (Tang and Riley, 2013, 2014; Zhu et al., 2016). Although the ECA approach has not been applied for simulations of CH<sub>4</sub> emissions, CH<sub>4</sub> dynamics are inherently multi-consumer, including transformations associated with methanogens, heterotrophs, ebullition, advection, diffusion, and aerenchyma transport, even if only one substrate is considered.

### 3.4 CH<sub>4</sub> within the soil/water profile

CH<sub>4</sub> produced in the soil profile or below the water table is not transported immediately into the atmosphere. The time required for CH<sub>4</sub> to migrate from a deep soil profile to the atmosphere ranges from minutes to days (depending on temperature, water, soil texture, and emissivity of plant roots), or even a season if the surface is frozen. The majority of current CH<sub>4</sub> models assume that CH<sub>4</sub> transport to the atmosphere occurs immediately after CH<sub>4</sub> is produced, and a portion is oxidized (Tian et al., 2010; Fan et al., 2013); for models sim-

ulating CH<sub>4</sub> flux over minutes to days, the lack of modeled transport may produce unrealistic simulations.

Some models do simulate CH<sub>4</sub> dynamics within the soil and water profile (e.g., *ecosys*, CLM4Me), which produces a lag between methanogenesis and emission, allowing for oxidation to be explicitly represented during transport, and is valuable for simulating the seasonality of CH<sub>4</sub> flux (Table 2). For example, the recently observed CH<sub>4</sub> burst in the spring season in some field experiments confirms that the storage of CH<sub>4</sub> produced in winter can produce a strong emission outburst (Song et al., 2012). Without understanding the mechanism of CH<sub>4</sub> storage beneath the soil surface, this phenomenon will be difficult to simulate. In most of the models considering CH<sub>4</sub> storage, the CH<sub>4</sub> is treated as a simple gas pool, under the water table, which will be transported to the atmosphere through several transport pathways.

### 3.5 CH<sub>4</sub> transport from soil to the atmosphere

The transport of CH<sub>4</sub> produced and stored in the soil column is the bottleneck for CH<sub>4</sub> leaving the system; therefore, this process is an important control on the instantaneous land-surface CH<sub>4</sub> flux. Several important pathways of CH<sub>4</sub> transport to the atmosphere are identified: plant-mediated diffusive and advective transport, aqueous and gaseous diffusion, and ebullition (Beckett et al., 2001; Chanton, 2005; Mer and Roger, 2001; Whiting and Chanton, 1996). Model simulation of these transport pathways uses direct control of simulated land-surface CH<sub>4</sub> flux, with CH<sub>4</sub> transport simulation considered in a manner similar to Eq. (7) (Table 3).

The majority (83 %) of the current models simulate at least one transport pathway. Specifically, 70 % of the models simulate CH<sub>4</sub> transport via aerenchyma, 80 % simulate gaseous diffusive transport, and 60 % simulate ebullition transport (Table 1). More than 50 % of models simulated these three transport pathways. Some models simulate explicitly the aqueous and gaseous diffusion of CH<sub>4</sub> (Riley et al., 2011), while most models do not simulate advective transport. Many models simulate diffusion and plant-mediated transport in very simple ways. For model improvement in this area, three issues remain as challenges.

Most models treat transport implicitly; for example, the diffusion processes are treated simply as an excessive release of CH<sub>4</sub> when its concentration exceeds a threshold (Tian et al., 2010). This treatment prevents the model from simulating the lag between methanogenesis and its final release into the atmosphere, which has been confirmed to be the key mechanism for hot moments and hotspots of CH<sub>4</sub> flux (Song et al., 2012) and for oxidation during transport.

The parameters for plant species capable of transporting gas (i.e., aerenchyma) are poorly constrained (Riley et al., 2011), although plant-mediated transport has been identified as the dominant pathway for CH<sub>4</sub> emission in some natural wetlands (Aulakh et al., 2000; Colmer, 2003).

Simultaneously representing aqueous and gaseous phases of CH<sub>4</sub> is one potentially important issue for simulating CH<sub>4</sub> transport from soil to the atmosphere (Tang and Riley, 2014). However, these processes are only explicitly represented in a few extant CH<sub>4</sub> models (Riley et al., 2011; Grant et al., 1998).

### 3.6 Environmental controls on CH<sub>4</sub> processes

Although a suite of environmental factors affects various CH<sub>4</sub> processes, many of these factors are not explicitly simulated in many models. These factors include soil temperature, soil moisture, substrate, soil pH, soil redox potential, and oxygen availability. Many other factors not incorporated into the models could indirectly affect CH<sub>4</sub> cycling. For example, nitrogen fertilizer affects methanogenesis through its stimulating impacts on ecosystem productivity, which in turn affects DOC, soil moisture and soil temperature (Xu et al., 2010). The CLM4Me model simulates permafrost and its effects on CH<sub>4</sub> dynamics, and has a simple relationship for soil pH impacts on methanogenesis (Riley et al., 2011). Wania et al. (2013) reviewed a number of active CH<sub>4</sub> models for their representation of CH<sub>4</sub> production area. In this review, we specifically focus on temperature, moisture, and pH because these factors directly affect CH<sub>4</sub> processes in all environments, and they have been explicitly simulated in many of the models.

Three types of mathematical functions have been used to simulate the temperature dependence of CH<sub>4</sub> processes: (1) linear functions of air or soil temperature (Eq. 9 in Table 3), (2) the  $Q_{10}$  function (Eq. 10 in Table 4), and (3) the Arrhenius type function (Eq. 11 in Table 3). Of these three model representations of temperature dependence, the  $Q_{10}$  equation is the most common mathematical description. However, the parameters for these empirical functions vary widely across the models (Table 4). Actual temperature responses may diverge significantly from the models at low temperatures, close to the freezing point of water, and high temperatures, close to the denaturation point of enzymes.

Soil moisture is an important factor controlling CH<sub>4</sub> processes, because water limits O<sub>2</sub> diffusion from the air through the soil column and because microbes can become stressed at low matric potential. CH<sub>4</sub> is produced typically under conditions with a low reduction potential, which is normally associated with long-term inundation. Although methanogenesis occurs solely under reducing conditions (methanogenesis within plant biomass under aerobic condition has never been simulated, although it has been reported in experiments; Kepler et al., 2006), methanotrophy occurs under drier, aerobic conditions. A low water content can also limit microbial activity in frozen soils or soils with high osmolarity (Watanabe and Ito, 2008). Therefore, soil moisture has different impacts on different CH<sub>4</sub> processes. Four types of model representation are used to simulate moisture effects on CH<sub>4</sub> processes (Eqs. 13–16 in Table 3).

**Table 4.** Temperature dependence of CH<sub>4</sub> processes in various models (blank indicates the  $Q_{10}$  function is not used; all temperatures are expressed as °C; 273.15 was used for unit conversion).

Model	$Q_{10}$	Reference temperature (°C)	Note	Sources
CASA			Based on a linear equation with temperature	Potter (1997)
DAYCENT			Linear equation $y = 0.209 \times T + 0.845$	Del Grosso et al. (2000)
LPJ family			Linear function was used for temperature impacts on diffusion.	Hodson et al. (2011); Spahni et al. (2011); Wania (2007)
LPJ-Bern				
LPJ-WHyMe				
LPJ-WSL				
Christensen's model	2	2	For temperature >0, the temperature impact is set to zero when <0.	Christensen and Cox (1995)
CH4MOD	3	30	$T = 30$ for $30 < T \leq 40$	Huang et al. (1998b)
CLM4Me	2 for production, 1.9 for oxidation	22	Parameters for baseline simulation	Riley et al. (2011)
CLM-Microbe	1.5	13.5		Xu et al. (2015)
DLEM	2.5	30	For a temperature range of [-5, 30]; temperature impact is set to zero when <-5 or >30.	Tian et al. (2010)
Kettunen's model	4.0 for production, 2.0 for oxidation	10	Standard $Q_{10}$ function	Kettunen (2003)
ORCHIDEE	Abisko site, 2.6; Michigan site, 3.2; Panama site, 1.2	Mean annual temperature	$Q_{10}$ function with different parameters across biomes	Ringeval et al. (2010)
TEM	Alpine tundra: wetland, 3.5; upland, 0.8. Wet tundra: wetland, 2.2; upland, 1.1. Boreal forest: wetland, 1.9; upland, 1.5	Alpine tundra: wetland, -3.0; upland, 8.0. Wet tundra: wetland, -5.5; upland, 8.0. Boreal forest: wetland, 1.0; upland, 7.0	$Q_{10}$ function with different parameters across biomes	Zhuang et al. (2004)
TRIPLEX-GHG	1.7–16 for production, 1.4–2.4 for oxidation	25 for optimal, 45 for highest temperature	Modified $Q_{10}$ equation	Zhu et al. (2014)
VISIT		Mean annual temperature		Ito and Inatomi (2012)
Walter's model	2	Ombrotrophic bog, 12; poor fen, 6.5; oligotrophic pine fen, 3.5; Arctic tundra, 0; swamp, 27	$Q_{10}$ function with different parameters across biomes	Walter and Heimann (2000)
Cartoon model		10	Arrhenius equation	Arah and Stephen (1998)
<i>ecosys</i>		30	Modified Arrhenius equation	Grant et al. (1993)

1. Methanogenesis occurs only in the saturated zone and an exponential function for soil moisture is used to control methanotrophy (e.g., CLM4Me).
2. Linear function for moisture impacts (e.g., CLASS use linear function for moisture impact on methanotrophy) (Curry, 2007).
3. Reciprocal responsive curves for moisture impacts on methanogenesis and methanotrophy (e.g., DLEM) (Tian et al., 2010).
4. A bell-shaped curve for methanogenesis (e.g., TEM uses a function similar to Eq. (16) for moisture impacts) (Zhuang et al., 2004).

Soil pH has been included in a number of CH<sub>4</sub> models (Cao et al., 1995; Zhuang et al., 2004). Methanogens and methanotrophs depend on proton and sodium ion translocation for energy conservation; thus, they are directly affected by pH. The pH impacts on CH<sub>4</sub> processes are simulated as a bell-shaped curve although the mathematical functions used to describe pH impacts are different (Eqs. 17a, b, and c). Moreover, even when the same functions were used in different models, they were associated with different parameter values, indicating slightly different response functions; for example, the MEM model sets  $\text{pH}_{\min}$  (minimum pH value for CH<sub>4</sub> processes being active),  $\text{pH}_{\text{opt}}$  (optimal pH value for

CH<sub>4</sub> processes being most active), and  $\text{pH}_{\max}$  (minimum pH value for CH<sub>4</sub> processes being active) values of 5.5, 7.5, and 9 (Cao et al., 1995). This set of parameter values was adopted in the TEM model (Zhuang et al., 2004), whereas the DLEM model uses values of 4, 7, and 10 (Tian et al., 2010). The CLM4Me model uses a different function while keeping the impact curve at the same shape, but its peak has an optimal pH of 6.2 (Meng et al., 2012). It should be noted that while pH has been confirmed to significantly affect CH<sub>4</sub> production (Xu et al., 2015), the simulation of pH dynamics caused by organic acid in soils remains a key challenge for the incorporation of this phenomenon.

For the other environmental factors, model representation is still in its infancy; however, several models consider oxygen availability as an electron acceptor for methanotrophy (e.g., Beckett model, Cartoon model, CLM4Me, *ecosys*, Kettunen model, MERES, Segers model, van Bodegom model, De Visscher model, and Xu model). In addition, only a few models simulate the impacts of the electron acceptor (nitrate, sulfate, etc.) on CH<sub>4</sub> processes (Table 2). For example, the van Bodegom model simulates iron biogeochemistry, and the Lovley model, Marten model, and van Bodegom model all simulate sulfate as the electron acceptor and its impacts on methanogenesis and methanotrophy (Lovley and Klug, 1986; Martens et al., 1998; van Bodegom et al., 2001). Explicitly representing these processes enables future coupling

of CH<sub>4</sub> cycling to processes that are regionally significant, such as iron reduction on the Alaskan North Slope (Miller et al., 2015). These models have the potential advantage of more accurately simulating biogeochemical processes of carbon and ions, although large uncertainties still exist because of the lack of data for constraining model parameters.

### 3.7 CH<sub>4</sub> implementation in ESMs

The importance of CH<sub>4</sub> flux in simulating climate dynamics has been well recognized (IPCC, 2013; Ringeval et al., 2011), yet few ESMs have implemented a CH<sub>4</sub> module (Ringeval et al., 2011; Riley et al., 2011; Xu et al., 2014; Hopcroft et al., 2011; Eliseev et al., 2008). While these models have been claimed to be coupled within ESMs, truly fully coupled simulations within ESMs to evaluate CH<sub>4</sub> dynamic impacts on global climate systems are rare (Eliseev et al., 2008; Hopcroft et al., 2011). For example, the SDGVM has been coupled within the Fast Met Office UK Universities Simulator (FAMOUS), a coupled general circulation model, to study the association between terrestrial CH<sub>4</sub> fluxes with rapid climate fluctuation during the last glacial period (Hopcroft et al., 2011). The IAP-RAP model was used to simulate terrestrial CH<sub>4</sub> flux and its contributions to atmospheric CH<sub>4</sub> concentrations and, further on, climate change. The quasi-coupling between ORCHIDEE\_WET with an ocean–atmosphere general circulation model was used to theoretically evaluate terrestrial CH<sub>4</sub> dynamics on climate systems (Ringeval et al., 2011). The CLM application within the CESM framework has both CLM4Me and CLM-Microbe modules for CH<sub>4</sub> dynamics, but none of them have been applied for a fully coupled simulation to evaluate CH<sub>4</sub>-climate feedback. It should be a key research effort for the CLM community in the next 5 years to complete this coupling. All previous coupled ESM simulations have concluded that changes in terrestrial CH<sub>4</sub> flux have small impacts on climate change, while they also pointed out that large uncertainties exist. Given the importance of CH<sub>4</sub> as a greenhouse gas and uncertainties in current ESMs in simulating permafrost carbon and CH<sub>4</sub> flux, more efforts should be invested to implement the CH<sub>4</sub> module in ESMs and further evaluate the CH<sub>4</sub>-climate feedback under different climate scenarios.

### 3.8 Summary

Through the 4 decades of modeling CH<sub>4</sub> cycling in terrestrial ecosystems, consensus has been reached on several fronts. First, CH<sub>4</sub> cycling includes a suite of complicated processes, and both the simple and complex models are able to estimate land-surface CH<sub>4</sub> flux to a certain level of confidence, although models of different complexity do provide different results (Tang et al., 2010). Second, although a number of CH<sub>4</sub> models have been developed, several gaps remain that need new model representations (e.g., dynamic linkage be-

tween inundation dynamics and the CH<sub>4</sub> module (Melton et al., 2013), and anaerobic oxidation of CH<sub>4</sub>; Gauthier et al., 2015).

Two recent CH<sub>4</sub> model–model inter-comparison projects raised several important points (Bohn et al., 2015; Melton et al., 2013): (1) the distribution of the inundation area is important for accurately simulating global CH<sub>4</sub> emissions, but was poorly represented in CH<sub>4</sub> models; (2) the modeled response of land-surface CH<sub>4</sub> emission to elevated CO<sub>2</sub> is likely biased as a number of global change factors were missing, which indicates the need for modeling with multiple global environmental factors; and (3) the need for comparison with high-frequency observational data is identified as an important task for future model–model inter-comparison. These lessons will be helpful for, and likely addressed during, model improvements and applications of more mechanistic CH<sub>4</sub> models.

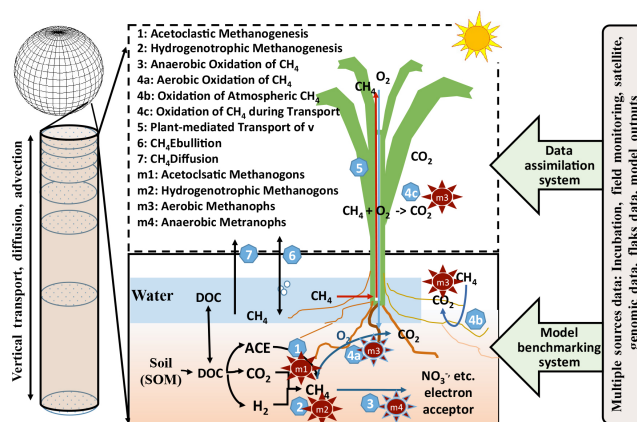
Although the primary individual CH<sub>4</sub> processes have been studied and quantified at a certain level of confidence, only a few modeling studies have reported these individual processes as previously discussed. For example, three pathways of CH<sub>4</sub> transports were represented in Kettunen (2003) and Walter et al. (1996), but none of those modeled results have been evaluated against observational results for those individual processes. One reason is that measurements rarely distinguish between individual processes; another reason is that the majority of CH<sub>4</sub> models do not explicitly represent all processes (Table 2). However, a number of studies report significant shifts in the processes contributing to the surface CH<sub>4</sub> flux along environmental gradients or across biomes (Conrad, 2009; Krumholz et al., 1995; McCalley et al., 2014). Projecting CH<sub>4</sub> fluxes into future changing climate conditions requires not only accurate simulations of CH<sub>4</sub> processes, but also shifts among the various processes. In addition, CO<sub>2</sub> flux has been evaluated within the Earth system modeling framework, but only a few studies have evaluated the CH<sub>4</sub> flux and its contribution to climate dynamics. Given the much higher warming potential and relatively faster rate of increase in atmospheric CH<sub>4</sub>, fully coupled simulations are needed to represent the feedbacks between terrestrial CH<sub>4</sub> exchanges and climate. We note that a few recent studies reported a relatively small climate warming–methane feedback from global wetlands and permafrost (Gao et al., 2013; Gedney et al., 2004; Riley et al., 2011). A fully mechanistic CH<sub>4</sub> model that accounts for all the important features is critically needed. In addition, a modeling framework to integrate multiple sources of data, such as microbial community structure and functional activities, ecosystem-level measurements, and global-scale satellite measurements of gas concentration and flux is needed with these mechanistic CH<sub>4</sub> models.

#### 4 Needs for mechanistic CH<sub>4</sub> models

During the last few years, the scientific community has continued to improve and optimize models to better simulate methanogenesis, methanotrophy, CH<sub>4</sub> transport, and their environmental and biological controls (Xu et al., 2015; Zhu et al., 2014). A number of emerging tasks have been identified, and progress in these directions is expected. First, linking genomic data with large-scale CH<sub>4</sub> flux measurements will be an important, while challenging, task for the entire community; for example, some work has been carried out in this direction (De Haas et al., 2011; Larsen et al., 2012). An effort has been initialized to develop a new microbial functional group-based CH<sub>4</sub> model, which has the advantages of linking genomic information for each individual process with the four microbial functional groups (Xu et al., 2015). Second, data–data and model–model comparisons are another important effort for model comparison and improvement. One ongoing encouraging feature that all recently developed CH<sub>4</sub> models possess is the capability for regional simulations as well as the possibility to be run at the site level (Riley et al., 2011; Zhu et al., 2014).

Third, microbial processes need to be considered for incorporation into ecosystem models for simulating carbon cycling and CH<sub>4</sub> processes (DeLong et al., 2011; Xu et al., 2014). Although a few models explicitly simulate the microbial mechanisms of CH<sub>4</sub> cycling (Arah and Stephen, 1998; Grant, 1998; Li, 2000; Segers and Kengen, 1998), none of them have been used for regional- or global-scale estimation of microbial contributions to the CH<sub>4</sub> budget. A reasonable experimental design and a well-validated microbial functional group-based CH<sub>4</sub> model should be combined to enhance our capability to apply models to estimate a regional CH<sub>4</sub> budget and to investigate the combination of microbial and environmental contributions to the land-surface CH<sub>4</sub> flux (DeLong et al., 2011). Fourth, incorporating well-validated CH<sub>4</sub> modules into Earth system modeling frameworks will allow a fully coupled simulation that provides a holistic understanding of the CH<sub>4</sub> processes, with its connections to many other processes and mechanisms in the atmosphere. Several recently developed models fall into the framework of Earth system models (Riley et al., 2011; Ringeval et al., 2010), which provide a foundation for this application in a relatively easy way. This effort will likely contribute not only to the CH<sub>4</sub> modeling community, but also to the entire global change science community (Koven et al., 2011). Iron and sulfate biogeochemistry has so far been modeled implicitly by only a few models (Table 2), as mechanisms are as yet poorly understood, and there is a paucity of data. Accordingly, these processes have not been incorporated into recently developed models, and a more explicit inclusion, based on improved biogeochemistry understanding, will hopefully be achieved in the long term.

Based on the above-mentioned needs and model features as well as the mechanisms for the CH<sub>4</sub> models, the next gen-



**Figure 5.** Key features of future mechanistic CH<sub>4</sub> models with a full representation of primary CH<sub>4</sub> processes in the terrestrial ecosystems. The data assimilation system and model benchmarking system are also shown as auxiliary components of the future CH<sub>4</sub> models.

eration of CH<sub>4</sub> models will likely include several important features (Fig. 5). The models should (1) be embedded in an Earth system model, (2) consider the vertical distribution of thermal, hydrological, and biogeochemical transport and processes, (3) represent mechanistic processes for microbial CH<sub>4</sub> production, consumption, and transport, and (4) support data assimilation and a model benchmarking system as auxiliary components.

## 5 Challenges in developing mechanistic CH<sub>4</sub> models

### 5.1 Knowledge gaps

Modeling CH<sub>4</sub> cycling is a dynamic process. As new mechanisms are identified, the modeling community should ensure that the mechanisms are well studied and mathematically described, as has occurred over the past decades (Conrad, 1989; McCalley et al., 2014; Schütz et al., 1989; Xu et al., 2015). However, a number of knowledge gaps need to be filled before a full modeling framework of CH<sub>4</sub> processes within terrestrial ecosystems can be achieved. The first gap is either confirmation or rejection of a few recently observed CH<sub>4</sub> mechanisms; these mechanisms need to be fully vetted before being considered for incorporation into a model. One well-known mechanism still under debate is aerobic CH<sub>4</sub> production within plant tissue (Beerling et al., 2008; Keppler et al., 2006). Since its first report in 2006 (Keppler et al., 2006), a few studies have confirmed the mechanism in multiple plant species (Wang et al., 2007). While its existence in nature is still under debate (Dueck et al., 2007), this mechanism will likely not be incorporated into an ecosystem model before solid evidence is presented and consensus is reached. The second new mechanism is CH<sub>4</sub> production

by fungi (Lenhart et al., 2012). More field- or lab-based experiments are needed to investigate this mechanism and its contribution to the global CH<sub>4</sub> budget, probably through a data–model integration approach. Third, the aerobic production of CH<sub>4</sub> from the cleavage of methylphosphonate has been demonstrated in marine systems (Karl et al., 2008), but the significance of this process in terrestrial systems is unknown. Fourth, the large CH<sub>4</sub> emissions from rivers and small ponds are still not fully understood (Holgerson and Raymond, 2016; Martinson et al., 2010), which will likely be a direction for future model improvement.

Another knowledge gap is the missing comprehensive understanding of spatial and temporal variations in CH<sub>4</sub> flux; particularly, the “hot spots” and “hot moments” of observed CH<sub>4</sub> flux are still not completely understood (Becker et al., 2008; Mastepanov et al., 2008; Song et al., 2012). The traditional static chamber method of measuring CH<sub>4</sub> emissions could underestimate the CH<sub>4</sub> flux because sparse sampling is unlikely to detect these foci or pulses of unusually high emissions. Better methods are also needed to measure CH<sub>4</sub> cycling during the shoulder seasons in the Arctic and subarctic when fluxes may be most variable (Zona et al., 2016). These knowledge gaps are key hurdles for CH<sub>4</sub> model development efforts. No model has yet been tested for simulating hotspots or hot moments over large spatial or long temporal scales. However, the high range (usually of factor 1–10) of the observed CH<sub>4</sub> flux might cause regional budgets to vary substantially (Song et al., 2012); therefore, mechanistic model representations of these mechanisms are highly needed.

## 5.2 Modeling challenges

Better simulation of CH<sub>4</sub> cycling in terrestrial ecosystems requires improvement in the model structure to represent mechanistic CH<sub>4</sub> processes. First is the challenge to simulate the vertical profile of soil biogeochemical processes and validate such models with observational results. Although some models have a capability for vertical distribution of carbon and nitrogen (Koven et al., 2013; Tang et al. 2013; Mau et al., 2013), a better framework for CH<sub>4</sub> and extension to cover the majority of CH<sub>4</sub> models are needed. This vertical distribution of biogeochemistry is necessary for simulating the vertical distribution of CH<sub>4</sub> processes and CH<sub>4</sub> transport through the soil profile before reaching the atmosphere. A second challenge is incorporating tracer capability. Isotopic tracers (<sup>13</sup>C, <sup>14</sup>C) have been widely used for quantifying the carbon flow and partitioning among individual CH<sub>4</sub> processes (Conrad, 2005; Conrad and Claus, 2005), but for ecosystem models this capability has not been represented even though it is very important to understanding CH<sub>4</sub> processes and integrating field observational data. A third challenge is to simulate microbial functional groups. Microbial processes are carried out by different functional groups of microbes (Lenhart et al., 2012; McCalley et al., 2014). Therefore, model comparison with individual processes requires representing the microbial

population sizes (or active biomass) for specific functional groups (Tveit et al., 2015). This goal has proved more difficult than representing plant functional types or traits in models, because not all microbial taxonomic groups have ecologically coherent functions (Philippot et al., 2010). A fourth challenge is to simulate the lateral transport of dissolved and particulate biogeochemical variables that are necessary to better simulate the storage and transport of CH<sub>4</sub> within heterogeneous landscapes (Weller et al., 1995). A fifth challenge is modeling CH<sub>4</sub> flux across spatial scales. Although a few studies have been used to demonstrate the approach for simulating CH<sub>4</sub> budget at plot scale and eddy covariance domain scale (Zhang et al., 2012), a mechanistic framework to link CH<sub>4</sub> processes at distinct scales is still lacking, while highly valuable. Finally, a sixth challenge is accurate simulation of CH<sub>4</sub> within human-managed ecosystems. Human management practices are always hard to simulate and predict, and their impacts on CH<sub>4</sub> processes are challenging (Li et al., 2005).

## 5.3 Data needs

First, a comprehensive data set of field measurements of CH<sub>4</sub> fluxes across various landscape types is needed to effectively validate the CH<sub>4</sub> models. Although a number of data sets have been compiled (Aronson and Helliker, 2010; Chen et al., 2012; Liu and Greaver, 2009; Mosier et al., 1997; Yvon-Durocher et al., 2014), some landscape types are still not fully covered. Meanwhile, high-frequency field observational data are also needed, particularly long-term observational data in some less-studied ecosystems; for example, Arctic tundra ecosystems have been considered an important contributor to the global CH<sub>4</sub> budget in the changing climate (IPCC, 2013; Koven et al., 2011); however, a long-term data set of CH<sub>4</sub> flux is lacking. It is well known that inter-annual variation of climate may turn an ecosystem from a CH<sub>4</sub> sink to a CH<sub>4</sub> source (Nauta et al., 2015; Shoemaker et al., 2014); therefore, a long-term observational data set that covers these temporal shifts in CH<sub>4</sub> flux and its associated ecosystem information would improve our understanding of the processes and our representation of them in CH<sub>4</sub> models. Second, microbial community shifts and their role in CH<sub>4</sub> processes are important, although information is incomplete for model representation of this mechanism (McCalley et al., 2014; Schimel and Gullledge, 1998). Although a number of studies have reported the microbial community structure and its potential association with changes in CH<sub>4</sub> processes (Schimel, 1995; Wagner et al., 2005), none of this progress has been documented in a mathematical manner suitable for a modeling representation.

Third, a comprehensive data set of all primary CH<sub>4</sub> processes within an individual ecosystem would be valuable for model optimization and validation. Although some data sets exist, no study has investigated all primary individual CH<sub>4</sub> processes within the same plot over the long term. Given

the substantial spatial heterogeneity of CH<sub>4</sub> processes, this lack of process representation may cause bias in CH<sub>4</sub> simulations at a regional scale. It should be noted that land-surface net CH<sub>4</sub> flux is a measurable ecosystem-level process, whereas many individual CH<sub>4</sub> processes are difficult to accurately measure. Therefore, designing field- or lab-based experiments suitable for measuring these processes is a fundamental need. For example, the anaerobic oxidation of CH<sub>4</sub> has been identified as a critical process for some ecosystem types, but no comprehensive data set on it is available for model development or improvement.

Last but not least, high-quality spatial data as driving forces and validation data for CH<sub>4</sub> models are critical for model development as well (Melton et al., 2013; Wania et al., 2013). Spatial distribution and dynamics of wetland areas probably are the most important data need for CH<sub>4</sub> models (Wania et al., 2013). Spatial distributions of soil temperature, moisture, and texture are fundamental information because they serve as direct or indirect environmental control on CH<sub>4</sub> processes. The recently launched Soil Moisture Active Passive (SMAP) satellite could be used as an important data source of soil moisture for driving CH<sub>4</sub> models (Entekhabi et al., 2010). It has been identified that soil texture and pH are important for simulating CH<sub>4</sub> processes (Xu et al., 2015). In addition, the atmospheric CH<sub>4</sub> concentration data from satellites could be used as an important benchmark for model validation purposes, for example, the Scanning Imaging Absorption spectrometer for Atmospheric Chartography (SCIAMACHY) (Frankenberg et al., 2005) and the Greenhouse gas Observing SATellite (GOSAT) (Yokota et al., 2009).

#### 5.4 Data–model integration

Model development and data collection are two important but historically independent scientific approaches; the integration between model development and data collection is much stronger for advancing science (De Kauwe et al., 2014; Luo et al., 2012; Peng et al., 2011). Although data–model integration is recognized as very important for understanding and predicting CH<sub>4</sub> processes and some progress has been made, integrating experiments and models presents multiple challenges, particularly because (1) the methods for integrating data with the models are not well developed for CH<sub>4</sub> cycling; (2) the metrics for evaluating data–model integration are not consistent in the scientific community; and (3) regular communication between data scientists and modelers on various aspects of CH<sub>4</sub> processes and their model representation is lacking.

Methods for data–model integration have been recently created, for example, Kalman filter (Gao et al., 2011), Bayesian (Ogle and Barber, 2008; Ricciuto et al., 2008; Schleip et al., 2009; Van Oijen et al., 2005), and Markov chain Monte Carlo (Casella and Robert, 2005). However, no studies have evaluated these methods for integrating CH<sub>4</sub>

data with models. In addition, the metric for evaluating the data–model integration is still not well developed. A very helpful strategy for data–model integration is to solicit timely input from modelers when designing a field experiment. A good example of this is US Department of Energy-sponsored project Next Generation Ecosystem Experiments – Arctic (<http://ngee-arctic.ornl.gov>), which was planned with inputs from field scientists, data scientists, and modelers. Another successful example is the US DOE-sponsored project, Spruce and Peatland Responses Under Climatic and Environmental Change (SPRUCE) ([mnspruce.ornl.gov](http://mnspruce.ornl.gov)), in which the experiment design for data–model integration created an opportunity for modeling needs to be adopted by the field scientists. A modeling framework that focuses on model parameterization and validation ability is under development at Oak Ridge National Laboratory; building a model optimization algorithm into an ESM framework will enable more effective parameterization of newly developed CH<sub>4</sub> modules within CLM at site, regional, and global scales (Ricciuto et al., personal communication, 16 December 2015).

#### 6 Concluding remarks

CH<sub>4</sub> dynamics in terrestrial ecosystems have been intensively studied, and model representation of CH<sub>4</sub> cycling has evolved as new knowledge becomes available. This is inherently a slow process. Currently, the primary mechanisms for CH<sub>4</sub> processes in terrestrial ecosystems are implicitly represented in many, but not all, terrestrial ecosystem models. Development of CH<sub>4</sub> models began in the late 1980s, and the pace of growth has been fast since the 1990s. Model development shifted from theoretical analysis in the 1980s and 1990s to being more applied in the 2000s and 2010s, expressed as being more focused on regional CH<sub>4</sub> budget quantification and integration with multiple sources of observational data. Although some current CH<sub>4</sub> models consider most of the relevant mechanisms, none of them consider all the processes for methanogenesis, methanotrophy, CH<sub>4</sub> transport, and their primary environmental controls. Furthermore, evidence demonstrating that incorporating all of these processes would lead to more accurate prediction is needed. Incorporating sophisticated parameter assimilation, uncertainty quantification, equifinality quantification, and metrics of the benefits associated with increased model complexity would also facilitate scientific discovery.

The CH<sub>4</sub> models for accurate projection of land-climate feedback in the next few decades should (1) use mechanistic formulations for primary CH<sub>4</sub> processes, (2) be embedded in Earth system models for the global evaluation of terrestrial-climate feedback associated with CH<sub>4</sub> fluxes, (3) have the capacity to integrate multiple sources of data, which makes the model not only a prediction tool but also an integrative tool, and (4) be developed in association with model benchmarking frameworks. These four characteristics pave the way for

examining CH<sub>4</sub> processes and flux in the context of global change. These improvements for CH<sub>4</sub> modeling would be beneficial for ESMs and further simulation of climate-carbon cycle feedbacks.

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