Reviews and syntheses: Four Decades of Modeling Methane Cycling in Terrestrial Ecosystems

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Abstract

Over the past four 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_4) fluxes within terrestrial ecosystems. These CH_4 models are also used for integrating multi-scale CH_4 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_4 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_4 models has shifted from theoretical to site- and regional-level applications over the past four decades, (2) large discrepancies exist among models in terms of representing CH_4 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_4 models are: (1) CH_4 models should more explicitly represent the mechanisms underlying land-atmosphere CH_4

exchange, with an emphasis on improving and validating individual CH_4 processes over depth and horizontal space, (2) models should be developed that are capable of simulating CH_4 emissions across highly heterogeneous spatial and temporal scales, particularly hot moments and hot spots, 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 on CH_4 models would be beneficial for the Earth system models and further simulation of climate-carbon cycle feedbacks.

1. Introduction

Methane (CH_4) 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_4 exchange between land and the atmosphere is fundamental for understanding climate change (Bridgham 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_4 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_4 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_4 processes represented, CH_4 models fall into two broad categories: (1) empirical models that are used to estimate and extrapolate measured methanogenesis, methanotrophy, or CH_4 emission at plot, country, or continental scales (Christensen et al., 1996; Eliseev et al., 2008; Mokhov et al., 2007; Wania et al., 2010, 2009); and (2) process-based models that are used for prognostic understanding of individual CH_4 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_4 production, oxidation, and transport. Although this separation is rather arbitrary, it helps 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, 2000a), *ecosys* (Grant, 1998), HH (Cresto-Aleina et al., 2015), MEM (Cao et al., 1995), TEM (Zhuang et al., 2004), etc. 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_4 cycling in the terrestrial ecosystems and their representation in the models. The critical CH_4 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_4 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 from pure aquatic ecosystems and considering the important role of wetlands on CH_4 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 ecosystems, and marine systems (Elliott et al., 2011) were excluded. An early pioneering effort of multiplying wetland area by average CH_4 flux to estimate global CH_4 budget was excluded from this review as well (Matthews and Fungi, 1987). This review further excludes the CH_4 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”, “Gong model”. In this paper we first provide an overview of the range of processes that have been considered in CH_4 models over the past four 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_4 model for either understanding CH_4 cycling or quantifying CH_4 budget at various scales.

2. Primary CH_4 Processes

Biological CH_4 production in sediments was first noted in the late 18th century (Volta 1777), and the microbial oxidation of CH_4 was proposed at the beginning of the 20th century (Söhngen 1906). Since then, CH_4 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_4 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; Conrad, 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_4 processes in terrestrial ecosystems, and their environmental controls from a modeling perspective. In this context there exist three major methanogenesis mechanisms, two CH_4 methanotrophy mechanisms, and three aggregated CH_4 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_4 production (Conrad, 1999; Krüger et al., 2001): acetoclastic methanogenesis -- CH_4 production from acetate, and hydrogenotrophic methanogenesis – CH_4 production from hydrogen (H_2) and carbon dioxide (CO_2). Acetoclastic and hydrogenotrophic methanogenesis account for ~50% - 90% and ~10% - 43% of global annual CH_4 produced, respectively (Conrad and Klose, 1999; Kotsyurbenko et al., 2004; Mer and

Roger, 2001; Summons et al., 1998). Methylotrophic methanogenesis (producing CH_4 from methanol, methylamines, or dimethylsulfide) is usually considered a minor contributor of CH_4, but may be significant in marine systems (Summons et al., 1998). The proportion of CH_4 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, Heilman and Carlton 2001, Ström et al. 2005) and using CH_4 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_4 in soil contributes 1% - 90% (King, 1996; Ström et al., 2005), anaerobic oxidation of CH_4 within the soil profile contributes 0.3% - 5% (Blazewicz et al., 2012; Murase and Kimura, 1996), oxidation of CH_4 during transport in plant aerenchyma contributes <1% (Frenzel and Karofeld, 2000; Frenzel and Rudolph, 1998), and oxidation of atmospheric CH_4 contributes ~10 – 100% (ranging from ~10% for wetland to ~100% for upland) (Gulledge and Schimel, 1998a; Gulledge and Schimel, 1998b; Topp and Pattey, 1997) to total methanotrophy in the ecosystem. CH_4 is transported from the soil profile to the atmosphere in typical open-water wetlands by seven pathways which 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_4 produced in the soil that is emitted to the atmosphere. The plant-mediated transport includes diffusive and advective (associated with gas or liquid flow) transports, soil diffusion includes soil gaseous diffusion and advection and aqueous diffusion and advection.

Environmental factors affecting CH_4 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, etc. (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 on CH_4 processes have been mathematically described and incorporated in many CH_4 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, 2000a; Ren et al., 2011; Xu et al., 2010).

3. Model Representation of CH_4 Processes

[Insert Figure 1 here]

[Insert Figure 2 here]

We reviewed 40 CH_4 models (Fig. 1 & Table 1), which were developed for a variety of purposes. The first CH_4 model was published in 1986 by Lovley & Klug (1986) to simulate *methanogenesis* in freshwater sediments, and since then a number of CH_4 models have been developed and applied at numerous scales (Table 1). For example, Cao et al. developed the Methane Emission Model (MEM) and applied it to quantify the global CH_4 source in rice paddies and the sensitivity of the global CH_4 budget's response to climate change (Cao et al., 1995; Cao et al., 1998). Grant et al (1998) developed the *ecosys* model, which is currently the ecosystem-scale model that most mechanistically represents the many kinetic processes and microbial mechanisms for methanogenesis, methanotrophy, and CH_4 emission (Grant and Roulet, 2002). Riley et al (2011) developed CLM4Me, a CH_4 module for the Community Land Model, which is incorporated in 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_4 processes, but with different modules for CH_4 cycling; for example, LPJ-Bern and LPJ-WHyMe incorporate Walter CH_4 module (Walter and Heimann, 2000; Walter et al., 1996; Wania et al., 2009) while LPJ-WSL incorporates the CH_4 module from Christensen et al (Christensen et al., 1996).

The number of CH_4 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_4 processes to regional CH_4 budget (Fig. 1). For instance, the Lovley's model was built to understand the CH_4 production and sulfate reduction in freshwater sediment (Lovley and Klug, 1986); while all models published in the 2010s are applicable for CH_4 budget quantification, particularly at regional scale. This rapid increase in CH_4 model development indicates a growing effort to analyze CH_4 cycling and quantify CH_4 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_4 biogeochemistry has increased from 54% before 2000 to ~79% in the recent decade (2010-2015). The proportion of models with regional simulation capability (producing spatial map of CH_4 fluxes with inputs of spatial map of driving forces) has doubled from ~50% before the 2010s to almost 100% afterwards (Fig. 2).

[Insert Tables 1, 2, and 3 here]

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, 2000a; Walter et al., 1996) (Table 1). Not all of the models explicitly represented the belowground mechanistic processes for CH_4 production and consumption and the primary carbon biogeochemical processes (Christensen et al., 1996; Ding and Wang, 1996). The land-atmosphere CH_4 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 tradeoff in modeling CH_4 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_4 Model Classification

[Insert Figure 3 here]

[Insert Figure 4 here]

Based on a cluster analysis that considers model characteristics including acetoclastic methanogenesis, hydrogentrophic methanogenesis, methanotrophy, different CH_4 transport pathways, multiple soil layer, oxygen availability, current CH_4 models can be classified into three groups (Fig. 3 & 4). The first group of CH_4 models uses a very simple framework for land-surface CH_4 flux, and most were developed before the 2000s (e.g., Christensen's model, CASA, etc.) (Fig 4A). These models treated land-surface CH_4 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_4 transport. The second group of CH_4 models considers processes in a relatively simple manner (e.g., one or two primary CH_4 transport pathways, methanogenesis as a function of DOC, oxidation of atmospheric CH_4, etc.); however, the methanogenesis and methanotrophy mechanisms are still not mechanistically represented (Fig. 4B). For example, DLEM simulate CH_4 production with a Michaelis-Menten equation with DOC concentration as substrate (Tian et al., 2010); Walter's model simulates CH_4 production with a simple multiplier between substrate availability and environmental scalars and CH_4 oxidation with a Michaelis-Menten equation (Walter et al., 1996). The third group of CH_4 models explicitly simulates the processes for methanogenesis, methanotrophy, and CH_4 transport as well as their environmental controls, which allows comprehensive investigation of physical, chemical, or biological processes' contribution to land-surface CH_4 flux (Fig. 4C). Of the models in the third group, none fully represent 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_4 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 concentration of substrate (DOC); and (4) a suite of mechanistic processes simulated for methanogenesis.

Representation of the substrate for methanogenesis may be a key aspect of simulating CH_4 cycling in terrestrial ecosystems (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), which simulates the net flux of CH_4 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., 2010, 2009) 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_4 production [Eq. (3)]; examples are the MEM model (Cao et al., 1995; Cao et al., 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; van Bodegom et al., 2001), and the *ecosys* model (Grant, 1998).

Methanogenesis is a fundamental process for CH_4 cycling, and a majority of models simulate methanogenesis in either implicit or explicit ways (Tables 2 & 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 three out of 40 CH_4 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_4 flux temporally and spatially and needs to be addressed in future model improvements.

Michaelis-Menten-like equations, widely used for simulating CH_4 production and oxidation, consider substrates limiting factors (Segers and Kengen, 1998). A few CH_4 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, & 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 substrate.

3.3. Methanotrophy

Methanotrophy is another important process for simulating the land-atmosphere exchange of CH_4 (Table 2). Aerobic and anaerobic methanotrophy occurs in different locations in the soil profile, and affect both methanogenesis in the profile and CH_4 diffusing in from the atmosphere. For example, the oxidation of atmospheric CH_4, rhizosphere and bulk soil oxidation, and oxidation during CH_4 transport from soil to the atmosphere have been measured and modeled (Tables 1 & 2). Anaerobic CH_4

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_4 produced in the soil profile and aerobic oxidation of atmospheric CH_4 play a major role in CH_4 consumption in the system, and that anaerobic oxidation of CH_4 is a minor contributor. Currently, no models explicitly simulate the anaerobic oxidation of CH_4 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_4 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, 2015; Zhu et al., 2016). Although the ECA approach has not been applied for simulations of CH_4 emissions, CH_4 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_4 within the Soil/Water Profile

CH_4 produced in the soil profile or below the water table is not transported immediately into the atmosphere. The time required for CH_4 to migrate from 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_4 models assume that CH_4 transport to the atmosphere occurs immediately after CH_4 is produced, and a portion is oxidized (Tian et al., 2010; Fan et al., 2013); for models simulating CH_4 flux over minutes to days, the lack of modeled transport may produce unrealistic simulations.

Some models do simulate CH_4 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_4 flux (Table 2). For example, the recently observed CH_4 burst in the spring season in some field experiments confirms that the storage of CH_4 produced in winter can produce a strong emission outburst (Song et al., 2012). Without understanding the mechanism of CH_4 storage beneath the soil surface, this phenomenon will be difficult to simulate. In most of the models considering CH_4 storage, the CH_4 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_4 Transport from Soil to the Atmosphere

The transport of CH_4 produced and stored in soil column is the bottleneck for CH_4 leaving the system; therefore, this process is an important control on the instantaneous land-surface CH_4 flux. Several important pathways of CH_4 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_4 flux, with CH_4 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_4 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_4 (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:

(1) Most models treat transport implicitly; for example, the diffusion processes is treated simply as an excessive release of CH_4 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 to the atmosphere, which has been confirmed to be the key mechanism for hot-moment and hot-spot of CH_4 flux (Song et al., 2012) and for oxidation during transport.

(2) 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_4 emission in some natural wetlands (Aulakh et al., 2000; Colmer, 2003).

(3) Simultaneously representing aqueous and gaseous phases of CH_4 is one potentially important issue for simulating CH_4 transport from soil to the atmosphere (Tang and Riley, 2014). However, these processes are only explicitly represented in a few extant CH_4 models (Riley et al., 2011; Grant et al., 1998).

3.6. Environmental Controls on CH_4 Processes

Although a suite of environmental factors affects various CH_4 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 in the models, could indirectly affect CH_4 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_4 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_4 models for their representation of CH_4 production area. In this review, we specifically focus on temperature, moisture, and pH because these factors directly affect CH_4 processes in all environments, and they have been explicitly simulated in the many of the models.

Three types of mathematical functions have been used to simulate the temperature dependence of CH_4 processes: (1) linear functions of air or soil temperature (Eq. 9 in Table 3), (2) Q_{10} function (Eq. 10 in Table 4), and (3) 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.

[Insert Table 4 here]

Soil moisture is an important factor controlling CH_4 processes, because water limits O_2 diffusion from the air through the soil column and because microbes can become stressed at low matric potential. CH_4 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 (Keppler 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_4 processes. Four types of model representation are used to simulate moisture effects on CH_4 processes (Eqs. 13-16 in Table 3).

(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_4 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_4 processes are simulated as a bell-shaped curve although the mathematical functions used to describe pH impacts are different (Eq. 17a, 17b, and 17c). 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 pH_{min} (minimum pH value for CH_4 processes being active), pH_{opt} (optimal pH value for CH_4 processes being most active), and pH_{max} (minimum pH value for CH_4 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_4 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 (i.e. nitrate, sulfate, etc.) on CH_4 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_4 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_4 implementation in ESMs

The importance of CH_4 flux in simulating climate dynamics has been well recognized (IPCC 2013; Ringeval et al., 2011); yet few ESMs have implemented a CH_4 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_4 dynamic impacts on global climate system are rare (Eliseev et al., 2008; Hopcroft et al., 2011). For example, the SDGVM has been coupled within Fast Met Office UK Universities Simulator

(FAMOUS), a coupled general circulation model, to study the association between terrestrial CH_4 fluxes with rapid climate fluctuation during the last glacial period (Hopcroft et al., 2011). The IAP-RAP model was used to simulate terrestrial CH_4 flux and its contributions to atmospheric CH_4 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_4 dynamics on climate system (Ringeval et al., 2011). The CLM application within CESM framework has both CLM4Me and CLM-Microbe module for CH_4 dynamics, but none of them have been applied for a fully coupled simulation to evaluate CH_4-climate feedback. It should be a key research effort for CLM community in next five years to complete this coupling. All previous coupled ESM simulations have concluded that changes in terrestrial CH_4 flux have small impacts on climate change, while they also pointed out that large uncertainties exist. Given the importance of CH_4 as a greenhouse gas and uncertainties in current ESMs in simulating permafrost carbon and CH_4 flux, more efforts should be invested to implement CH_4 module in ESMs and further evaluate the CH_4-climate feedback under different climate scenarios.

3.8. Summary

Through the four decades of modeling CH_4 cycling in terrestrial ecosystems, consensus has been reached on several fronts. First, CH_4 cycling includes a suite of complicated processes, and both the simple and complex models are able to estimate land-surface CH_4 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_4 models have been developed, several gaps remain that need new model representations (e.g., dynamic linkage between inundation dynamics and the CH_4 module (Melton et al., 2013), and anaerobic oxidation of CH_4 (Gauthier et al., 2015)).

Two recent CH_4 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_4 emissions, but was poorly represented in CH_4 models; (2) the modeled response of land-surface CH_4 emission to elevated CO_2 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_4 models.

Although the primary individual CH_4 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_4 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 among individual processes; another reason is that the majority of CH_4 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_4 flux along environmental gradients or across biomes (Conrad, 2009; Krumholz et al., 1995; McCalley et al., 2014). Projecting CH_4 fluxes into future changing climate conditions requires not only accurate simulations of CH_4 processes, but also shifts among the various processes. In addition, CO_2 flux has been evaluated within the Earth System Modeling framework, but only a few studies have evaluated the CH_4 flux and its contribution to climate dynamics. Given the much higher warming potential and relatively faster rate of increase of atmospheric CH_4, fully coupled simulations are needed to represent the feedbacks between terrestrial CH_4 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_4 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_4 models.

4. Needs for Mechanistic CH_4 Models

During the last few years, the scientific community has continued to improve and optimize models to better simulate methanogenesis, methanotrophy, CH_4 transport, and their environmental and biological controls (Xu et al., 2015; Zhu. Q. 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_4 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_4 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_4 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. Q. et al., 2014).

Third, microbial processes need to be considered for incorporation into ecosystem models for simulating carbon cycling and CH_4 processes (DeLong et al., 2011; Xu et al., 2014). Although a few models explicitly simulate the microbial mechanisms of CH_4 cycling (Arah and Stephen, 1998; Grant, 1998; Li, 2000a; Segers and Kengen, 1998), none of them have been used for regional- or global-scale estimation of microbial contributions to the CH_4 budget. A reasonable experimental design and a well-validated microbial functional group-based CH_4 model should be combined to enhance our capability to apply models to estimate a regional CH_4 budget and to investigate the combination of microbial and environmental contributions to the land surface CH_4 flux (DeLong et al., 2011). Fourth, incorporating well-validated CH_4 modules into Earth System Modeling frameworks will allow a fully coupled simulation that provides a holistic understanding of the CH_4 processes, with its connections to many other processes and mechanisms in the atmosphere. Several recently developed models fall in 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_4 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 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.

[Insert Figure 5 here]

Based on the above-mentioned needs and model features as well as the mechanisms for the CH_4 models, the next generation of CH_4 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_4 production, consumption, and transport, and (4) support data assimilation and a model benchmarking system as auxiliary components.

5. Challenges for Developing Mechanistic CH_4 Models

5.1. Knowledge Gaps

Modeling CH_4 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_4 processes within terrestrial ecosystems can be achieved. The first gap is either confirmation or rejection of a few recently observed CH_4 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_4 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_4 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_4 budget, probably through a data model integration approach. Third, the aerobic production of CH_4 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. Forth, the large CH_4 emission 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_4 flux; particularly, the "hot spots" and "hot moments" of observed CH_4 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_4 emissions could underestimate the CH_4 flux because sparse sampling is unlikely to detect these foci or pulses of unusually high emissions. Better methods are also needed to measure CH_4 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_4 model development efforts. No model has yet been tested for simulating hot spots or hot moments over large spatial or long temporal scales. However, the high range (usually of factor 1-10) of the observed CH_4 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_4 cycling in terrestrial ecosystems requires improvement in the model structure to represent mechanistic CH_4 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_4 and extension to cover the majority of CH_4 models are needed. This vertical distribution of biogeochemistry is necessary for simulating the vertical distribution of CH_4 processes and CH_4 transport through the soil profile before reaching the atmosphere. A second challenge is incorporating tracer capability. Isotopic tracers (^{13}C, ^{14}C) have been widely used for quantifying the carbon flow and partitioning among individual CH_4 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_4 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_4 within heterogeneous landscapes (Weller et al., 1995). A fifth challenge is modeling CH_4 flux across spatial scales. Although a few studies have been used to demonstrate the approach for simulating CH_4 budget at plot scale and eddy covariance domain scale (Zhang et al., 2012), a mechanistic framework to link CH_4 processes at distinct scales is still lacking while highly valuable. Finally, a sixth challenge is accurate simulation of CH_4 within human-managed ecosystems. Human management practices are always hard to simulate and predict, and their impacts on CH_4 processes are challenging (Li et al., 2005).

5.3. Data Needs

First, a comprehensive dataset of field measurements of CH_4 fluxes across various landscape types is needed to effectively validate the CH_4 models. Although a number of datasets 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 as an important contributor to global CH_4 budget in the changing climate (IPCC, 2013; Koven et al., 2011), however, long-term dataset of CH_4 flux is lacking. It is well-known that inter-annual variation of climate may turn an ecosystem from a CH_4 sink to a CH_4 source (Nauta et al., 2015; Shoemaker et al., 2014); therefore, a long-term observational dataset that covers these temporal shifts in CH_4 flux and its associated ecosystem information would improve our understanding of the processes and our representation of them in CH_4 models. Second, microbial community shifts and their role in CH_4 processes are important, although information is incomplete for model representation of this mechanism (McCalley et al., 2014; Schimel and Gulledge, 1998). Although a number of studies have reported the microbial community structure and its potential association with changes in CH_4 processes (Monday et al., 2014; 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 dataset of all primary CH_4 processes within an individual ecosystem would be valuable for model optimization and validation. Although some datasets exist, no study has investigated all primary individual CH_4 processes within the same plot over the long term. Given the substantial spatial heterogeneity of CH_4 processes, this lack of process representation may cause bias in CH_4 simulations at regional scale. It should be noted that land surface net CH_4 flux is a measurable ecosystem-level process, whereas many individual CH_4 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_4 has been identified as a critical process for some ecosystem types, but no comprehensive dataset 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_4 models are critical for model development as well (Melton et al., 2013; Wania et al., 2013). Spatial distribution and dynamics of wetland area probably are the most important data need for CH_4 models (Wania et al., 2013). Spatial distribution of soil temperature, moisture, and texture are fundamental information because they serve as direct or indirectly environmental control on CH_4 processes. Recently launched Soil Moisture Active Passive (SMAP) satellite could be used as an important data source for soil moisture for driving CH_4 model (Entekhabi et al., 2010). It has been identified that soil texture and pH are important for simulating CH_4 processes (Xu et al., 2015). In addition, the atmospheric CH_4 concentration data from satellite could be used as important benchmark for model validation purposes, for example Scanning Imaging Absorption spectrometer for Atmospheric ChartographY (SCIAMACHY) (Frankenberg et al., 2005) and 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_4 processes and some progress has been made, integrating experiments and models presents multiple challenges, particularly, 1) the methods for integrating data with the models are not well developed for CH_4 cycling; 2) the metrics for evaluating data-model integration are not consistent in the scientific community; and 3) the regular communication between data scientists and modelers on various aspects of CH_4 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_4 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 the U.S. Department of Energy-sponsored project Next Generation Ecosystem Experiments - Arctic (ngee-arctic.ornl.gov), which was planned with inputs from field scientists, data scientists, and modelers. Another successful example is the U.S. DOE-sponsored project, Spruce and Peatland Responses Under Climatic and Environmental Change (SPRUCE) (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 model optimization algorithm into an ESM framework will enable more effective parameterization of newly developed CH_4 modules within CLM at site, regional, and global scales (Ricciuto et al, pers.).

6. Concluding Remarks

CH_4 dynamics in terrestrial ecosystems have been intensively studied, and model representation of CH_4 cycling has evolved as new knowledge becomes available. This is inherently a slow process. Currently, the primary mechanisms for CH_4 processes in terrestrial ecosystems are implicitly represented in many, but not all, terrestrial ecosystem models. Development of CH_4 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_4 budget quantification and integration with multiple sources of observational data. Although some current CH_4 models consider most of the relevant mechanisms, none of them consider all the processes for methanogenesis, methanotrophy, CH_4 transport, and their primary environmental controls. Further, 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_4 models for accurate projection of land-climate feedback in the next few decades should: (1) use mechanistic formulations for primary CH_4 processes, (2) be embedded in Earth System Models for the global evaluation of terrestrial-climate feedback associated with CH_4 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_4 processes and flux in the context of global change. These improvements for CH_4 modeling would be beneficial for ESMs and further simulation of climate-carbon cycle feedbacks.

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Table 1. Terrestrial ecosystem models for CH_4 cycling and the model representation of three pathways of CH_4 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; Huang et al., 2004; Li et al., 2012)
Christensen model	No	No	No	(Christensen et al., 1996)
CLASS	No	Yes	No	(Curry, 2009; Curry, 2007)
CLM4Me	Yes	Yes	Yes	(Riley et al., 2011)
CLM-Microbe	Yes	Yes	Yes	(Xu et al., 2015; Xu et al., 2014)
DAYCENT	No	Yes	No	(Del Grosso et al., 2002; Del Grosso et al., 2009; Del Grosso et al., 2000)
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, 2000b)
DOS-TEM	Yes	Yes	Yes	(Fan et al., 2013)
ecosys	No	Yes	Yes	(Grant, 2001, 1998)
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., 2010, 2009)
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; Cao et al., 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; Ringeval et al., 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 Q. 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; Van Bodegom et al., 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)

Table 2. Key mechanisms/features of CH_4 processes and their representations in CH_4 models

Key mechanisms	**Models**
Methanogenesis	Cartoon model, CASA, CH4MOD, Christensen model, CLM4Me, CLM-Microbe, Ding model, DLEM, DNDC, DOS-TEM, *ecosys*, 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's model, Xu's model
Methanotrophy	Cartoon model, CASA, CLASS, CLM4Me, CLM- Microbe, DAYCENT, DLEM, DNDC, DOS-TEM, *ecosys*, 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_4	CLM-Microbe, Martens model
Substrate (Acetate/DOC)	CH4MOD, CLM-Microbe, DLEM, DNDC, *ecosys*, Gong model, Kettunen model, Lovley model, Martens model, MEM, MERES, SDGVM, Segers model, TCF, van Bodegom model, Xu model
Microbial functional groups	CLM-Microbe, , *ecosys,* Segers model
CH_4 storage in soil profile	Beckett model, Cartoon model, CLM4Me, CLM-Microbe, *ecosys*, Kettunen model, Martens model, MERES, Nouchi model, ORCHIDEE, Segers model, UW-VIC, van Bodegom model, VISIT, De Visscher model, Walter model
O_2 availability for CH_4 oxidation	Beckett model, Cartoon model, CLM4Me, CLM-Microbe, *ecosys*, 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_4	None
Embedded in Earth System Model	CLASS, CLM4Me, CLM-Microbe, IAP-RAS, ORCHIDEE, SDGVM
Vertical resolved	Beckett model, Cartoon model, CLASS, CLM4Me, CLM-Microbe, DNDC,

biogeochemistry	DOS-TEM, *ecosys*, Gong model, HH model, IAP-RAS, Kettunen model, Lovley model, LPJ-Bern, LPJ-WHyMe, LPJ-WSL, Martens model, MERES, ORCHIDEE, Ridgwell model, SDGVM, Seger 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, *ecosys*, 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

Table 3. The mathematical equations used to described the CH$_4$ processes used in representative models (P_{CH4} is the CH$_4$ production rate; $Oxid_{CH4}$ is the CH$_4$ oxidation rate; T_{CH4} is the CH$_4$ transport rate; D_{CH4} is the CH$_4$ diffusion rate; some parameter may have been changed from original publication to keep relatively consistent in this table)

CH$_4$ processes	**Equations**		**Ecological description**	**Model examples**
CH$_4$ substrate and CH$_4$ production	1	$P_{CH_4} = f(T, W)$	A function of temperature (T) and moisture (W)	Christensen model, IAP-RAS, DAYCENT
	2a	$P_{CH_4} = r \times HR \times f(T, W)$	A portion of heterotrophic respiration, affected by temperature (T) and moisture (W)	LPJ family, CLM4Me, Ding model, MERES, TRIPLEX-GHG
	2b	$P_{CH_4} = r \times SOM \times f(T, W)$	A portion of soil organic matter (SOM), affected by temperature (T) and moisture (W); Walter's model use indirect association with NPP	CH4MOD, DOS-Tem, Gong model, HH model, Walter model
	3	$P_{CH_4} = V \times \frac{[DOC]}{K_{DOC} + [DOC]} \times f(T, W)$	A portion of dissolved organic carbon (DOC), affected by temperature (T) and moisture (W)	MEM, DLEM
	4	$P_{CH_4} = f(DOC, Acetate, CO_2) \times f(T, W)$	Mechanistic processes for CH$_4$ production are considered, affected by temperature (T) and moisture (W)	Kettunen model, Segers model, van Bodegoms model, and *ecosys*
CH$_4$ oxidation	5	$Oxid_{CH_4} = V \times \left(\frac{[CH_4]}{K_{CH_4} + [CH_4]}\right) \times f(T, W)$	Oxidation as a function of CH$_4$ concentration and temperature and moisture	DLEM, TRIPLEX-GHG, VISIT

	6	$Oxid_{CH_4}$ $= V$ $\times\left(\frac{[CH_4]}{K_{CH_4}+[CH_4]}\right)\left(\frac{[O_2]}{K_{O_2}+[O_2]}\right)$ $\times f(T,W)$	Oxidation as a function of CH_4 and O_2 concentration, temperature and moisture	Cartoon model, CLM4Me, CLM-Microbe, Kettunen model
CH_4 transport	7	$T_{CH_4} = V * ([CH_4] - \overline{[CH_4]})$	*V* is the parameter for distance, diffusion coefficient, etc.; $[CH_4]$ is the concentration of CH_4 in the soil/water profile (dissolvability for DLEM, 0 for DNDC); and $\overline{[CH_4]}$ is the threshold of CH_4 concentration above which CH_4 will be transported to the atmosphere via either of the three transport pathways	DLEM, DNDC, Walter model
	8a	$A = \frac{C(z) - C_a}{r_L z / D + r_a} pT\rho_r$	*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_4 was simulated following Fick's law; CLM4Me separate aqueous and gaseous diffusion	CLM4Me, CLM-Microbe, *ecosys*, 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	$V_T = V^0 \times \exp\,(\frac{\Delta E}{R}\left[\frac{1}{T^0} - \frac{1}{T}\right])$	Arrhenius equation	Cartoon model, Ding model
	11 b	$f_T = \frac{T_s \times \exp\,(A - \frac{H_a}{R\times T_s})}{\Big[1 + \exp\left(\frac{H_{dl} - S\times T_s}{R\times T_s}\right) + \exp\,(\frac{S\times}{}}$	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 mol^{-1}); R is universal gas constant (J mol^{-1} K^{-1}); H_{dl} and H_{dh} are energy of low and high temperature deactivation (J mol^{-1})	*ecosys*
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	$F_\vartheta = e^{-P/P_c}$	Water stress for oxidation, where P is soil moisture and Pe= -2.4×10^5 mm	CLM4Me
	14	$f(SM) = \begin{cases} 1, \\ \left[1 - \frac{log_{10}\varphi - log_{10}(0.2)}{log_{10}(100) - log_{10}(0.2)}\right]^\beta \\ 0, \end{cases}$	β is an arbitrary constant, ϕ is the soil water potential	CLASS
	15	$f_{prod}(SM) = \left(\frac{SM - SM_{fc}}{SM_{sat} - SM_{fc}}\right)^2 \times 0.368 \times e^{(\frac{SM - SM_{fc}}{SM_{sat} - SM_{fc}})}$ $f_{oxid}(SM) = 1 - f_{prod}(SM)$	Different impacts on CH_4 production and consumption; SM: soil moisture; SM_{fc}: field capacity; SM_{sat}: saturation soil moisture	DLEM

	16	$f(SM) = \frac{(M_V - M_{min})\times(M - M_{m}}{(M_V - M_{min})\times(M_V - M_{max}) - (}$	Bell-shape curve	TEM
pH effects	17a	$f(pH) = \frac{(pH - pH_{min})\times(pH - p}{(pH - pH_{min})\times(pH - pH_{max}) -}$	Bell-shape curve	CLM-Microbe, MEM, TEM,
	17 b	$f(pH) = 10^{-0.2335\times pH^2+2.7727\times pH-8.6}$	Bell-shape curve	CLM4Me
	17c	$f(pH) = \begin{cases} 0 & pH \le 4 \\ \frac{1.02}{1+1000000\times e^{(-2.5\times pH)}} & \\ \frac{1.02}{1+1000000\times e^{(-2.5\times(14-pH))}} & 7 \end{cases}$	Bell-shape curve	DLEM

Table 4. Temperature dependence of CH_4 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 $y = 0.209 * T + 0.845$	(Del Grosso et al., 2000)
LPJ family LPJ-Bern LPJ-WHyMe LPJ-WSL			Linear function was used for temperature impacts on diffusion	(Hodson et al., 2011; Spahni et al., 2011; Wania, 2007)
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	2	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)
Kettunenn'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., 2014a)
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 model		10	Arrhenius equation	(Arah and Stephen, 1998)
ecosys		30	Modified Arrhenius equation	(Grant et al., 1993)

Figure legend

Figure 1. Published CH_4 models and modeling trends in terms of applicability and mechanistic representation of CH_4 cycling processes over recent decades the envisioned CH_4 model capability

Figure 2. Percentage of CH_4 models with consideration of some key CH_4 mechanisms. The percentage was calculated as the number of models considering each mechanisms divided by the total number of published models in each time period

Figure 3. Cluster analysis showing three groups of CH_4 models based on model characteristics (lines with same color indicate CH_4 models in same group; green lines represent relatively simple model structure, red lines represent relatively mechanistic models, blue lines represent mechanistic models)

Figure 4. Three types of models with key mechanisms for CH_4 production and oxidation (*SOM*: Soil organic matter; *NPP*: net primary production; *DOC*: dissolved organic carbon; O_{atm}: oxidation of atmospheric CH_4; *P*: plant-mediated transport; *D*: diffusion transport; *E*: ebullition transport; O_{xid}: oxidation; O_{trans}: oxidation of CH_4 during transport)

Figure 5. Key features of future mechanistic CH_4 models with a full representation of primary CH_4 processes in the terrestrial ecosystems. The data assimilation system and model benchmarking system are also shown as auxiliary components to the future CH_4 models

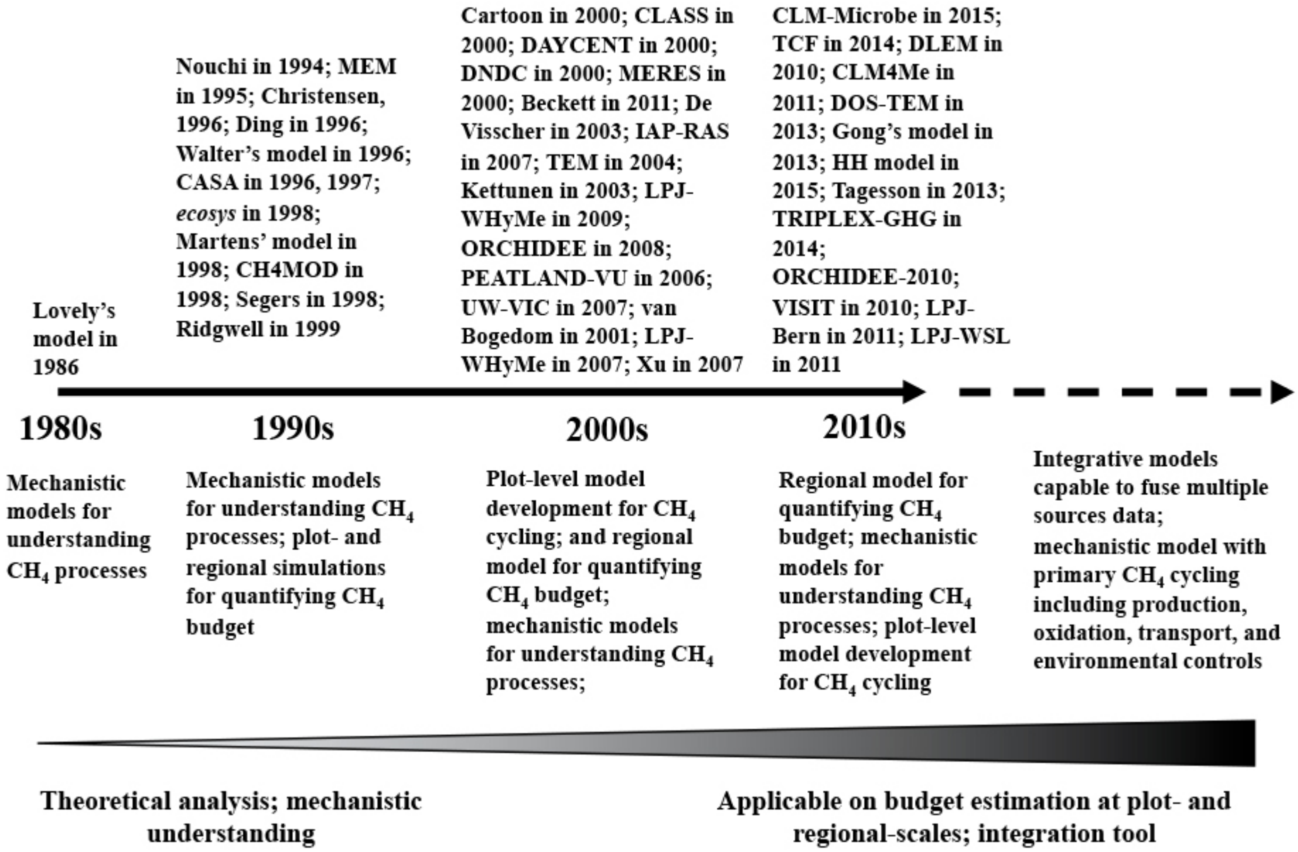
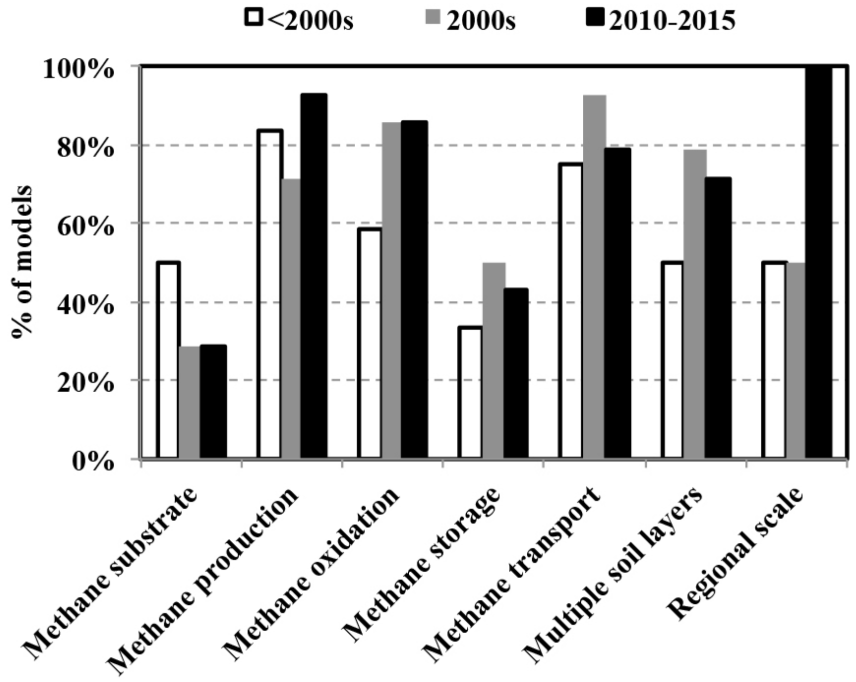

Lovely's model in 1986
Nouchi in 1994; MEM in 1995; Christensen, 1996; Ding in 1996; Walter's model in 1996; CASA in 1996, 1997; *ecosys* in 1998; Martens' model in 1998; CH4MOD in 1998; Segers in 1998; Ridgwell in 1999
Cartoon in 2000; CLASS in 2000; DAYCENT in 2000; DNDC in 2000; MERES in 2000; Beckett in 2011; De Visscher in 2003; IAP-RAS in 2007; TEM in 2004; Kettunen in 2003; LPJ-WHyMe in 2009; ORCHIDEE in 2008; PEATLAND-VU in 2006; UW-VIC in 2007; van Bogedom in 2001; LPJ-WHyMe in 2007; Xu in 2007
CLM-Microbe in 2015; TCF in 2014; DLEM in 2010; CLM4Me in 2011; DOS-TEM in 2013; Gong's model in 2013; HH model in 2015; Tagesson in 2013; TRIPLEX-GHG in 2014; ORCHIDEE-2010; VISIT in 2010; LPJ-Bern in 2011; LPJ-WSL in 2011
1980s
1990s
2000s
2010s
Mechanistic models for understanding CH_4 processes
Mechanistic models for understanding CH_4 processes; plot- and regional simulations for quantifying CH_4 budget
Plot-level model development for CH_4 cycling; and regional model for quantifying CH_4 budget; mechanistic models for understanding CH_4 processes;
Regional model for quantifying CH_4 budget; mechanistic models for understanding CH_4 processes; plot-level model development for CH_4 cycling
Integrative models capable to fuse multiple sources data; mechanistic model with primary CH_4 cycling including production, oxidation, transport, and environmental controls
Theoretical analysis; mechanistic understanding
Applicable on budget estimation at plot- and regional-scales; integration tool

Fig. 1.



<2000s
2000s
2010-2015
100%
80%
60%
40%
20%
0%
% of models
Methane substrate
Methane production
Methane oxidation
Methane storage
Methane transport
Multiple soil layers
Regional scale

Fig. 2.

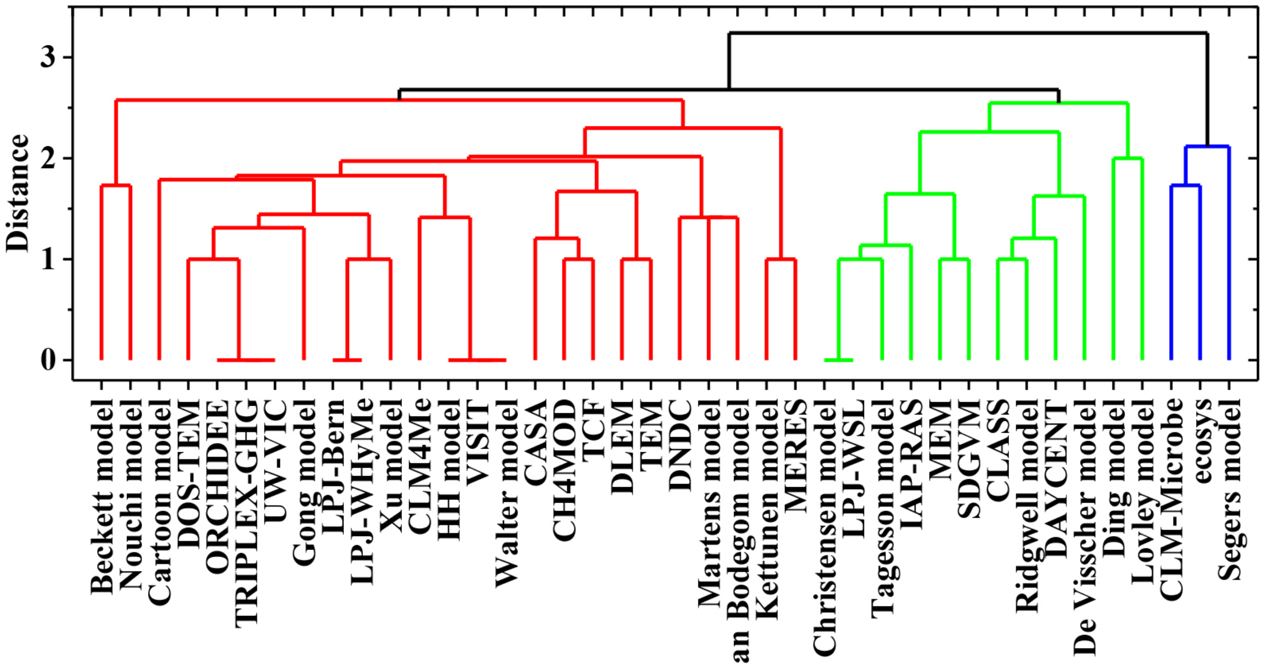

Distance
0
1
2
3
Beckett model
Nouchi model
Cartoon model
DOS-TEM
ORCHIDEE
TRIPLEX-GHG
UW-VIC
Gong model
LPJ-Bern
LPJ-WHyMe
Xu model
CLM4Me
HH model
VISIT
Walter model
CASA
CH4MOD
TCF
DLEM
TEM
DNDC
Martens model
van Bodegom model
Kettunen model
MERES
Christensen model
LPJ-WSL
Tagesson model
IAP-RAS
MEM
SDGVM
CLASS
Ridgwell model
DAYCENT
De Visscher model
Ding model
Lovley model
CLM-Microbe
ecosys
Segers model

Fig. 3

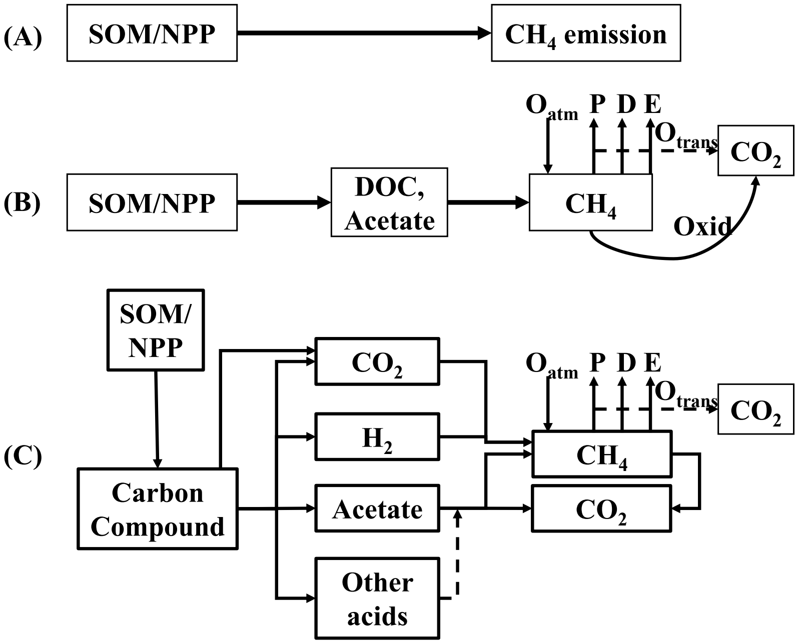

(A)
SOM/NPP
CH4 emission
(B)
SOM/NPP
DOC, Acetate
CH4
Oatm
P
D
E
Otrans
CO2
Oxid
(C)
SOM/NPP
Carbon Compound
CO2
H2
Acetate
Other acids
CH4
CO2
Oatm
P
D
E
Otrans
CO2

Fig. 4.

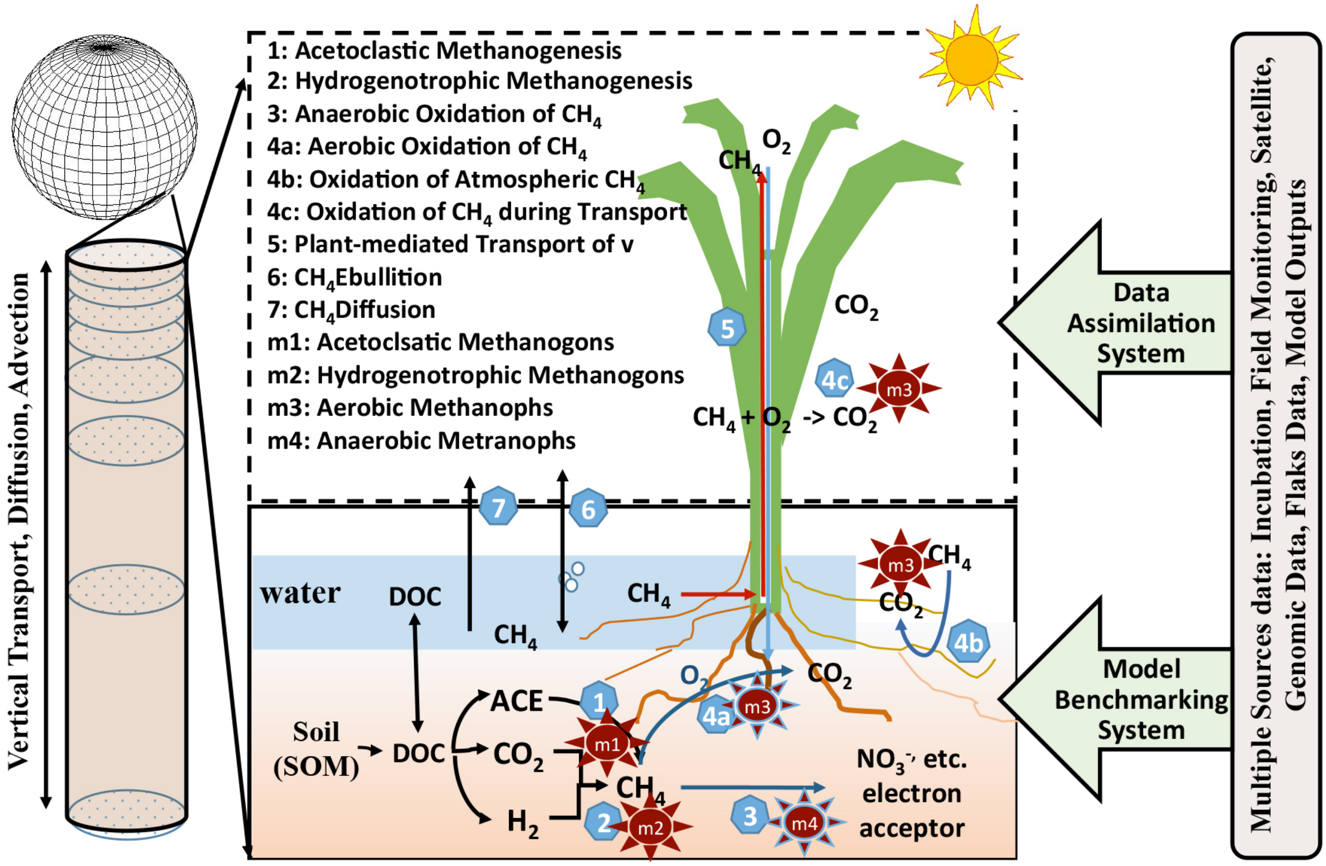

Vertical Transport, Diffusion, Advection
1: Acetoclastic Methanogenesis
2: Hydrogenotrophic Methanogenesis
3: Anaerobic Oxidation of CH_4
4a: Aerobic Oxidation of CH_4
4b: Oxidation of Atmospheric CH_4
4c: Oxidation of CH_4 during Transport
5: Plant-mediated Transport of v
6: CH_4Ebullition
7: CH_4Diffusion
m1: Acetoclsatic Methanogons
m2: Hydrogenotrophic Methanogons
m3: Aerobic Methanophs
m4: Anaerobic Metranophs
O_2
CH_4
CO_2
5
4c
m3
$CH_4 + O_2 \rightarrow CO_2$
7
6
water
DOC
CH_4
CH_4
m3
CH_4
CO_2
4b
O_2
CO_2
4a
m3
Soil (SOM)
DOC
ACE
1
m1
CO_2
H_2
CH_4
2
m2
3
m4
NO_3^- etc. electron acceptor
Data Assimilation System
Model Benchmarking System
Multiple Sources data: Incubation, Field Monitoring, Satellite, Genomic Data, Flaks Data, Model Outputs

Fig. 5