



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

Xiaofeng Xu^{1,2,3}, Fengming Yuan⁴, Paul J. Hanson⁴, Stan D. Wullschleger⁴, Peter E. Thornton⁴, William J. Riley⁵, Xia Song^{1,3}, David E. Graham⁶, Changchun Song², and Hanqin Tian⁷

¹Biology Department, San Diego State University, San Diego, CA, USA

²Northeast Institute of Geography and Agro-ecology, Chinese Academy of Sciences, Changchun, Jilin, China

³Department of Biological Sciences, University of Texas at El Paso, El Paso, TX, USA

⁴Climate Change Science Institute and Environmental Sciences Division, Oak Ridge National Laboratory, Oak Ridge, TN, USA

⁵Earth Sciences Division, Lawrence Berkeley National Laboratory, Berkeley, CA, USA

⁶Biosciences Division, Oak Ridge National Laboratory, Oak Ridge, TN, USA

⁷International Center for Climate and Global Change Research, School of Forestry and Wildlife Sciences, Auburn University, Auburn, AL, USA

Correspondence to: Xiaofeng Xu (xxu@mail.sdsu.edu)

Received: 3 February 2016 – Published in Biogeosciences Discuss.: 12 February 2016

Revised: 1 June 2016 – Accepted: 2 June 2016 – Published: 28 June 2016

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 (CH₄) fluxes within terrestrial ecosystems. These CH₄ models are also used for integrating multi-scale CH₄ 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 CH₄ 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 CH₄ 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 CH₄ 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 CH₄ models are that (1) CH₄ models should more explicitly represent the mechanisms underlying land–atmosphere CH₄ exchange, with an emphasis on improving and validating individual CH₄ processes over

depth and horizontal space, (2) models should be developed that are capable of simulating CH₄ 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 CH₄ models would be beneficial for the Earth system models and further simulation of climate–carbon cycle feedbacks.

1 Introduction

Methane (CH₄) 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 CH₄ 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 CH₄ 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 CH₄ 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 CH₄ processes represented, CH₄ models fall into two broad categories: (1) empirical models that are used to estimate and extrapolate measured methanogenesis, methanotrophy, or CH₄ 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 CH₄ 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 CH₄ 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 CH₄ cycling in the terrestrial ecosystems and their representation in the models. The critical CH₄ 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 CH₄ 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 CH₄ 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 CH₄ flux to estimate global CH₄ budget was excluded from this review as well (Matthews and Funghi, 1987). This review further excludes the CH₄ 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 CH₄ 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 CH₄ models for either understanding CH₄ cycling or quantifying CH₄ budgets at various scales.

2 Primary CH₄ processes

Biological CH₄ production in sediments was first noted in the late 18th century (Volta, 1777), and the microbial oxidation of CH₄ was proposed at the beginning of the 20th century (Söhnngen, 1906). Since then, CH₄ 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 CH₄ 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 CH₄ processes in terrestrial ecosystems and their environmental controls from a modeling perspective. In this context there exist three major methanogenesis mechanisms, two CH₄ methanotrophy mechanisms, and three aggregated CH₄ 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 CH₄ production (Conrad, 1999; Krüger et al., 2001): acetoclastic methanogenesis – CH₄ production from acetate – and hydrogenotrophic methanogenesis – CH₄

Table 1. Terrestrial ecosystem models for CH₄ cycling and the model representation of three pathways of CH₄ 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 (H₂) and carbon dioxide (CO₂). Acetoclastic and hydrogenotrophic methanogenesis account for ~50–90 and ~10–43 % of global annual CH₄ produced, respectively (Conrad and Klose, 1999; Kotsyurbenko et al., 2004; Mer and Roger, 2001; Summons et al., 1998). Methylo-trophic methanogenesis (producing CH₄ from methanol, methylamines, or dimethylsulfide) is usually considered a minor contributor of CH₄, but may be significant in marine systems (Summons et al., 1998). The proportion of CH₄ 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 CH₄ 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 CH₄ in soil contributes 1–90 % (King, 1996; Ström et al., 2005), anaerobic oxidation of CH₄ within the soil profile contributes 0.3–5 % (Blazewicz et al., 2012; Murase and Kimura, 1996), oxidation of CH₄ during transport in plant aerenchyma contributes < 1 % (Frenzel and Karofeld, 2000; Frenzel and Rudolph, 1998), and oxidation of atmospheric CH₄ 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. CH₄ 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 CH₄ 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 CH₄ 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 CH₄ processes have been mathematically described and incorporated into many CH₄ 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 CH₄ processes

We reviewed 40 CH₄ models (Fig. 1 and Table 1), which were developed for a variety of purposes. The first CH₄ model was published in 1986 by Lovley and Klug (1986) to simulate methanogenesis in freshwater sediments, and since then a number of CH₄ 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 CH₄ source in rice paddies and the sensitivity of the global CH₄ 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

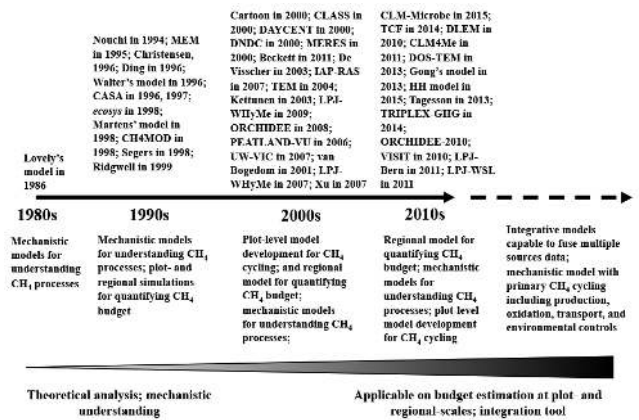


Figure 1. Published CH₄ models and modeling trends in terms of applicability and mechanistic representation of CH₄ cycling processes over recent decades; the envisioned CH₄ model capability.

the many kinetic processes and microbial mechanisms for methanogenesis, methanotrophy, and CH₄ emission (Grant and Roulet, 2002). Riley et al. (2011) developed CLM4Me, a CH₄ 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 CH₄ processes, but with different modules for CH₄ cycling; for example, LPJ-Bern and LPJ-WHyMe incorporate the Walter CH₄ module (Walter and Heimann, 2000; Walter et al., 1996; Wania et al., 2009), while LPJ-WSL incorporates the CH₄ module from Christensen et al. (1996). The number of CH₄ 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 CH₄ processes to the regional CH₄ budget (Fig. 1). For instance, Lovley's model was built to understand the CH₄ production and sulfate reduction in freshwater sediment (Lovley and Klug, 1986); while all models published in the 2010s are applicable for CH₄ budget quantification, particularly at regional scale. This rapid increase in CH₄ model development indicates a growing effort to analyze CH₄ cycling and quantify CH₄ 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 CH₄ 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 CH₄ fluxes with inputs of spatial forcing) has doubled from ~ 50 % before the 2010s to almost 100 % afterwards (Fig. 2).

Table 2. Key mechanisms/features of CH₄ processes and their representations in CH₄ 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 ₄ 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 ₄ 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 ₂ availability for CH ₄ 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 ₄	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 CH₄ production and consumption and the primary carbon biogeochemical processes (Christensen et al., 1996; Ding and Wang, 1996). The land-atmosphere CH₄ 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 CH₄ 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 CH₄ model classification

Based on a cluster analysis that considers model characteristics including acetoclastic methanogenesis, hydrogenotrophic methanogenesis, methanotrophy, different CH₄ transport pathways, multiple soil layers, and oxygen availability, current CH₄ models can be classified into three groups (Figs. 3 and 4). The first group of CH₄ models uses a very simple framework for land-surface CH₄ flux, and most were developed before the 2000s (Christensen's model, CASA, etc.) (Fig. 4a). These models treated land-surface CH₄ 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 CH₄ transport. The second group of CH₄ models considers processes in a relatively simple manner (one or two primary CH₄ transport pathways, methanogenesis as a function of DOC (dissolved organic carbon), oxidation of atmospheric CH₄, etc.); however, the methanogenesis and methanotrophy mechanisms are still

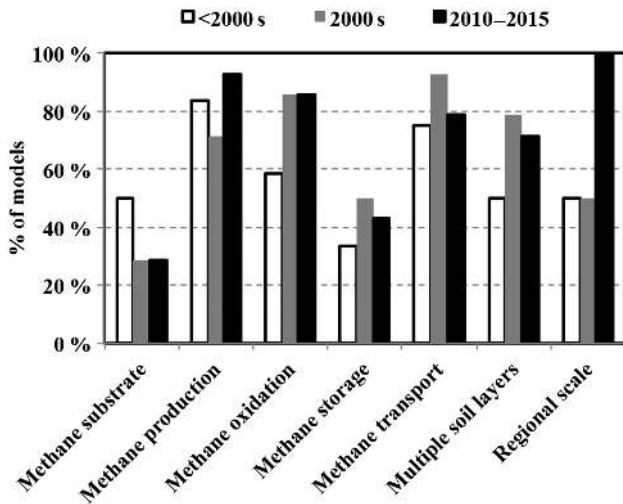


Figure 2. Percentage of CH₄ models with consideration of some key CH₄ mechanisms. The percentage was calculated as the number of models considering each mechanism divided by the total number of published models in each time period.

not mechanistically represented (Fig. 4b). For example, DLEM simulates CH₄ production with a Michaelis–Menten equation with DOC concentration as substrate (Tian et al., 2010); Walter’s model simulates CH₄ production with a simple multiplier between substrate availability and environmental scalars and CH₄ oxidation with a Michaelis–Menten equation (Walter et al., 1996). The third group of CH₄ models explicitly simulates the processes for methanogenesis, methanotrophy, and CH₄ transport as well as their environmental controls, which allows comprehensive investigation of physical, chemical, or biological processes’ contribution to land-surface CH₄ 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 CH₄ 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 CH₄ cycling in terrestrial ecosys-

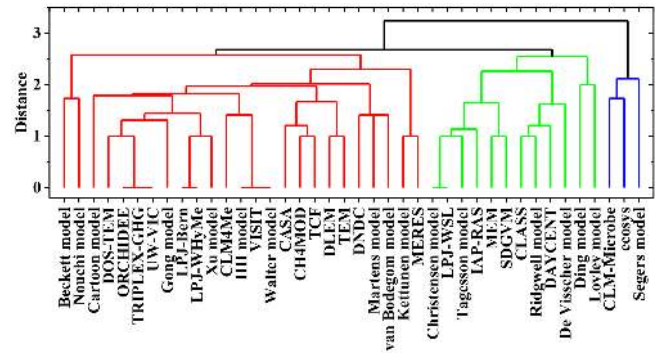


Figure 3. Cluster analysis showing three groups of CH₄ models based on model characteristics (lines with the same color indicate CH₄ models in the same group; green lines represent a relatively simple model structure, red lines represent relatively mechanistic models, and blue lines represent mechanistic models).

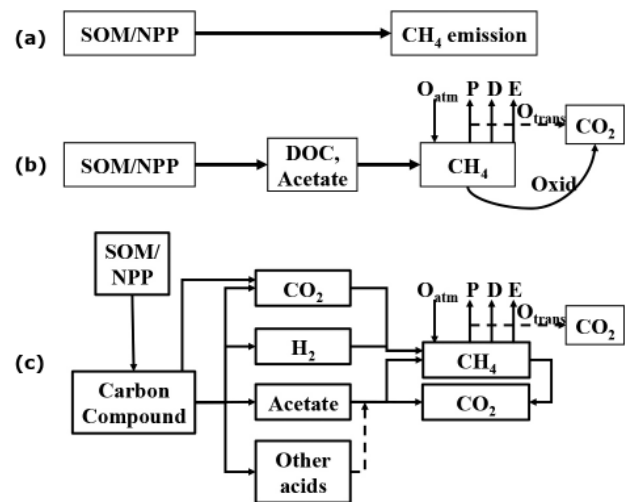


Figure 4. Three types of models with key mechanisms for CH₄ production and oxidation (SOM: soil organic matter; NPP: net primary production; DOC: dissolved organic carbon; O_{atm} : oxidation of atmospheric CH₄; P : plant-mediated transport; D : diffusion transport; E : ebullition transport; O_{xid} : oxidation; O_{trans} : oxidation of CH₄ 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 CH₄ processes used in representative models (P_{CH_4} is the CH₄ production rate; $Oxid_{CH_4}$ is the CH₄ oxidation rate; T_{CH_4} is the CH₄ transport rate; D_{CH_4} is the CH₄ diffusion rate; some parameters may have been changed from the original publication to keep relative consistency in this table).

CH ₄ processes	Equations	Ecological description	Model examples
CH ₄ substrate and CH ₄ 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 ₄ production are considered, affected by temperature (T) and moisture (W)	Kettunen model, Segers model, van Bodegom's model, and <i>ecosys</i>	
CH ₄ 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 ₄ concentration and temperature and moisture	DLEM, TRIPLEX-GHG, VISIT
	6 $Oxid_{CH_4} = V \times \left(\frac{[CH_4]}{K_{CH_4} + [CH_4]} \right) \left(\frac{[O_2]}{K_{O_2} + [O_2]} \right) \times f(TW)$	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 $T_{CH_4} = V \times ([CH_4] - \overline{[CH_4]})$	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 $A = \frac{C(z) - C_a}{r_{Lz}/D + r_a} pT \rho_r$	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 ₄ 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 $f(SM) = \begin{cases} 1, \varphi > 0.2 \text{ Mpa} \\ \left[1 - \frac{\log_{10} \varphi - \log_{10}(0.2)}{\log_{10}(100) - \log_{10}(0.2)} \right]^\beta, 0.2 > \varphi > 100 \text{ Mpa} \\ 0, \varphi > 100 \text{ Mpa} \end{cases}$	β is an arbitrary constant, ϕ is the soil water potential	CLASS	
15 $f_{prod}(SM) = \left(\frac{SM - SM_{fc}}{SM_{sat} - SM_{fc}} \right)^2 \times 0.368 \times e^{\left(\frac{SM - SM_{fc}}{SM_{sat} - SM_{fc}} \right)}$ $f_{oxid}(SM) = 1 - f_{prod}(SM)$	Different impacts on CH ₄ production and consumption; SM: soil moisture; SM _{fc} : field capacity; SM _{sat} : saturation soil moisture	DLEM	
16 $f(SM) = \frac{(M_V - M_{min}) \times (M - M_{max})}{(M_V - M_{min}) \times (M_V - M_{max}) - (M_V - M_{opt})^2}$	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 CH₄ 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 CH₄ 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 CH₄ 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 CH₄ 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 CH₄ flux temporally and spatially and needs to be addressed in future model improvements.

Michaelis–Menten-like equations, widely used for simulating CH₄ production and oxidation, consider substrates limiting factors (Segers and Kengen, 1998). A few CH₄ 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 CH₄ (Table 2). Aerobic and anaerobic methanotrophy occurs in different locations in the soil profile, and affects both methanogenesis in the profile and CH₄ diffusing in from the atmosphere. For example, the oxidation of atmospheric CH₄, rhizosphere and bulk soil oxidation, and oxidation during CH₄ transport from soil to the atmosphere have been measured and modeled (Tables 1 and 2). Anaerobic CH₄ 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 CH₄ produced in the soil profile and aerobic oxidation of atmospheric CH₄ play a major role in CH₄ consumption in the system, and that anaerobic oxidation of CH₄ is a minor contributor. Currently, no models explicitly simulate the anaerobic oxidation of CH₄ 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 CH₄ 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 CH₄ emissions, CH₄ 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 CH₄ within the soil/water profile

CH₄ produced in the soil profile or below the water table is not transported immediately into the atmosphere. The time required for CH₄ 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 CH₄ models assume that CH₄ transport to the atmosphere occurs immediately after CH₄ is produced, and a portion is oxidized (Tian et al., 2010; Fan et al., 2013); for models sim-

ulating CH₄ flux over minutes to days, the lack of modeled transport may produce unrealistic simulations.

Some models do simulate CH₄ 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 CH₄ flux (Table 2). For example, the recently observed CH₄ burst in the spring season in some field experiments confirms that the storage of CH₄ produced in winter can produce a strong emission outburst (Song et al., 2012). Without understanding the mechanism of CH₄ storage beneath the soil surface, this phenomenon will be difficult to simulate. In most of the models considering CH₄ storage, the CH₄ is treated as a simple gas pool, under the water table, which will be transported to the atmosphere through several transport pathways.

3.5 CH₄ transport from soil to the atmosphere

The transport of CH₄ produced and stored in the soil column is the bottleneck for CH₄ leaving the system; therefore, this process is an important control on the instantaneous land-surface CH₄ flux. Several important pathways of CH₄ 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 CH₄ flux, with CH₄ 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 CH₄ 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 CH₄ (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 CH₄ 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 CH₄ 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 CH₄ emission in some natural wetlands (Aulakh et al., 2000; Colmer, 2003).

Simultaneously representing aqueous and gaseous phases of CH₄ is one potentially important issue for simulating CH₄ transport from soil to the atmosphere (Tang and Riley, 2014). However, these processes are only explicitly represented in a few extant CH₄ models (Riley et al., 2011; Grant et al., 1998).

3.6 Environmental controls on CH₄ processes

Although a suite of environmental factors affects various CH₄ 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 CH₄ 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 CH₄ 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 CH₄ models for their representation of CH₄ production area. In this review, we specifically focus on temperature, moisture, and pH because these factors directly affect CH₄ 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 CH₄ 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 CH₄ processes, because water limits O₂ diffusion from the air through the soil column and because microbes can become stressed at low matric potential. CH₄ 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 CH₄ processes. Four types of model representation are used to simulate moisture effects on CH₄ processes (Eqs. 13–16 in Table 3).

Table 4. Temperature dependence of CH₄ 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 CH₄ 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 CH₄ 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 pH_{min} (minimum pH value for CH₄ processes being active), pH_{opt} (optimal pH value for

CH₄ processes being most active), and pH_{max} (minimum pH value for CH₄ 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 CH₄ 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 CH₄ 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 CH₄ 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 CH₄ implementation in ESMs

The importance of CH₄ flux in simulating climate dynamics has been well recognized (IPCC, 2013; Ringeval et al., 2011), yet few ESMs have implemented a CH₄ 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 CH₄ 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 CH₄ fluxes with rapid climate fluctuation during the last glacial period (Hopcroft et al., 2011). The IAP-RAP model was used to simulate terrestrial CH₄ flux and its contributions to atmospheric CH₄ 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 CH₄ dynamics on climate systems (Ringeval et al., 2011). The CLM application within the CESM framework has both CLM4Me and CLM-Microbe modules for CH₄ dynamics, but none of them have been applied for a fully coupled simulation to evaluate CH₄-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 CH₄ flux have small impacts on climate change, while they also pointed out that large uncertainties exist. Given the importance of CH₄ as a greenhouse gas and uncertainties in current ESMs in simulating permafrost carbon and CH₄ flux, more efforts should be invested to implement the CH₄ module in ESMs and further evaluate the CH₄-climate feedback under different climate scenarios.

3.8 Summary

Through the 4 decades of modeling CH₄ cycling in terrestrial ecosystems, consensus has been reached on several fronts. First, CH₄ cycling includes a suite of complicated processes, and both the simple and complex models are able to estimate land-surface CH₄ 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 CH₄ models have been developed, several gaps remain that need new model representations (e.g., dynamic linkage be-

tween inundation dynamics and the CH₄ module (Melton et al., 2013), and anaerobic oxidation of CH₄; Gauthier et al., 2015).

Two recent CH₄ 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 CH₄ emissions, but was poorly represented in CH₄ models; (2) the modeled response of land-surface CH₄ emission to elevated CO₂ 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 CH₄ models.

Although the primary individual CH₄ 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 CH₄ 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 CH₄ models do not explicitly represent all processes (Table 2). However, a number of studies report significant shifts in the processes contributing to the surface CH₄ flux along environmental gradients or across biomes (Conrad, 2009; Krumholz et al., 1995; McCalley et al., 2014). Projecting CH₄ fluxes into future changing climate conditions requires not only accurate simulations of CH₄ processes, but also shifts among the various processes. In addition, CO₂ flux has been evaluated within the Earth system modeling framework, but only a few studies have evaluated the CH₄ flux and its contribution to climate dynamics. Given the much higher warming potential and relatively faster rate of increase in atmospheric CH₄, fully coupled simulations are needed to represent the feedbacks between terrestrial CH₄ 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 CH₄ 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 CH₄ models.

4 Needs for mechanistic CH₄ models

During the last few years, the scientific community has continued to improve and optimize models to better simulate methanogenesis, methanotrophy, CH₄ 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 CH₄ 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 CH₄ 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 CH₄ 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 CH₄ processes (DeLong et al., 2011; Xu et al., 2014). Although a few models explicitly simulate the microbial mechanisms of CH₄ 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 CH₄ budget. A reasonable experimental design and a well-validated microbial functional group-based CH₄ model should be combined to enhance our capability to apply models to estimate a regional CH₄ budget and to investigate the combination of microbial and environmental contributions to the land-surface CH₄ flux (DeLong et al., 2011). Fourth, incorporating well-validated CH₄ modules into Earth system modeling frameworks will allow a fully coupled simulation that provides a holistic understanding of the CH₄ 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 CH₄ 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 CH₄ models, the next gen-

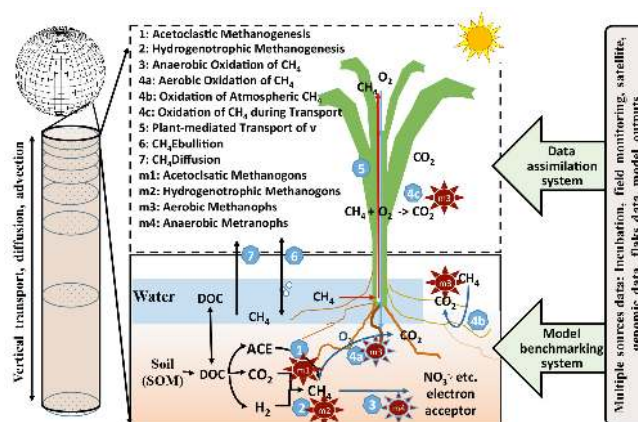


Figure 5. Key features of future mechanistic CH₄ models with a full representation of primary CH₄ processes in the terrestrial ecosystems. The data assimilation system and model benchmarking system are also shown as auxiliary components of the future CH₄ models.

eration of CH₄ 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 CH₄ production, consumption, and transport, and (4) support data assimilation and a model benchmarking system as auxiliary components.

5 Challenges in developing mechanistic CH₄ models

5.1 Knowledge gaps

Modeling CH₄ 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 CH₄ processes within terrestrial ecosystems can be achieved. The first gap is either confirmation or rejection of a few recently observed CH₄ 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 CH₄ 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 CH₄ 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 CH₄ budget, probably through a data–model integration approach. Third, the aerobic production of CH₄ 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 CH₄ 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 CH₄ flux; particularly, the “hot spots” and “hot moments” of observed CH₄ 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 CH₄ emissions could underestimate the CH₄ flux because sparse sampling is unlikely to detect these foci or pulses of unusually high emissions. Better methods are also needed to measure CH₄ 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 CH₄ 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 CH₄ 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 CH₄ cycling in terrestrial ecosystems requires improvement in the model structure to represent mechanistic CH₄ 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 CH₄ and extension to cover the majority of CH₄ models are needed. This vertical distribution of biogeochemistry is necessary for simulating the vertical distribution of CH₄ processes and CH₄ transport through the soil profile before reaching the atmosphere. A second challenge is incorporating tracer capability. Isotopic tracers (¹³C, ¹⁴C) have been widely used for quantifying the carbon flow and partitioning among individual CH₄ 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 CH₄ 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 CH₄ within heterogeneous landscapes (Weller et al., 1995). A fifth challenge is modeling CH₄ flux across spatial scales. Although a few studies have been used to demonstrate the approach for simulating CH₄ budget at plot scale and eddy covariance domain scale (Zhang et al., 2012), a mechanistic framework to link CH₄ processes at distinct scales is still lacking, while highly valuable. Finally, a sixth challenge is accurate simulation of CH₄ within human-managed ecosystems. Human management practices are always hard to simulate and predict, and their impacts on CH₄ processes are challenging (Li et al., 2005).

5.3 Data needs

First, a comprehensive data set of field measurements of CH₄ fluxes across various landscape types is needed to effectively validate the CH₄ 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 CH₄ budget in the changing climate (IPCC, 2013; Koven et al., 2011); however, a long-term data set of CH₄ flux is lacking. It is well known that inter-annual variation of climate may turn an ecosystem from a CH₄ sink to a CH₄ source (Nauta et al., 2015; Shoemaker et al., 2014); therefore, a long-term observational data set that covers these temporal shifts in CH₄ flux and its associated ecosystem information would improve our understanding of the processes and our representation of them in CH₄ models. Second, microbial community shifts and their role in CH₄ processes are important, although information is incomplete for model representation of this mechanism (McCalley et al., 2014; Schimel and Guldge, 1998). Although a number of studies have reported the microbial community structure and its potential association with changes in CH₄ 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 CH₄ 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 CH₄ processes within the same plot over the long term. Given

the substantial spatial heterogeneity of CH₄ processes, this lack of process representation may cause bias in CH₄ simulations at a regional scale. It should be noted that land-surface net CH₄ flux is a measurable ecosystem-level process, whereas many individual CH₄ 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 CH₄ 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 CH₄ 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 CH₄ 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 CH₄ processes. The recently launched Soil Moisture Active Passive (SMAP) satellite could be used as an important data source of soil moisture for driving CH₄ models (Entekhabi et al., 2010). It has been identified that soil texture and pH are important for simulating CH₄ processes (Xu et al., 2015). In addition, the atmospheric CH₄ 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 CH₄ 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 CH₄ 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 CH₄ 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 CH₄

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), 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 CH₄ modules within CLM at site, regional, and global scales (Ricciuto et al., personal communication, 16 December 2015).

6 Concluding remarks

CH₄ dynamics in terrestrial ecosystems have been intensively studied, and model representation of CH₄ cycling has evolved as new knowledge becomes available. This is inherently a slow process. Currently, the primary mechanisms for CH₄ processes in terrestrial ecosystems are implicitly represented in many, but not all, terrestrial ecosystem models. Development of CH₄ 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 CH₄ budget quantification and integration with multiple sources of observational data. Although some current CH₄ models consider most of the relevant mechanisms, none of them consider all the processes for methanogenesis, methanotrophy, CH₄ 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 CH₄ models for accurate projection of land-climate feedback in the next few decades should (1) use mechanistic formulations for primary CH₄ processes, (2) be embedded in Earth system models for the global evaluation of terrestrial-climate feedback associated with CH₄ 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 CH₄ processes and flux in the context of global change. These improvements for CH₄ modeling would be beneficial for ESMS and further simulation of climate-carbon cycle feedbacks.

Acknowledgements. The authors are grateful for financial and facility support from San Diego State University and the University of Texas at El Paso. The authors are grateful to Yiqi Luo at the University of Oklahoma for his comments on early versions of the manuscript. We are grateful to Jens-Arne Subke and five anonymous reviewers for their constructive comments that significantly improved this paper. This review is part of the CH₄ modeling tasks within the NGEE-Arctic and SPRUCE projects sponsored by the US Department of Energy Office of Science. Contributions by Fengming Yuan, Paul J. Hanson, Peter E. Thornton, Stan D. Wullschleger, and David E. Graham are supported by the US Department of Energy, Office of Science, Office of Biological and Environmental Research. Oak Ridge National Laboratory is managed by UT-Battelle, LLC, for the US Department of Energy under contract DE-AC05-00OR22725. Contributions by William J. Riley are supported by the US Department of Energy under contract no. DE-AC02-05CH11231. Changchun Song is supported by the National Natural Science Foundation of China (41125001), and Hanqin Tian is supported by the NASA Carbon Monitoring System Program (NNX14AO73G) and the NASA Interdisciplinary Science Program (NNX14AF93G).

Edited by: J.-A. Subke

References

- Anisimov, O. A.: Potential feedback of thawing permafrost to the global climate system through methane emission, *Environ. Res. Lett.*, 2, 045016, doi:10.1088/1748-9326/2/4/045016, 2007.
- Arah, J. R. M. and Kirk, G. J. D.: Modeling rice plant-mediated methane emission, *Nutr. Cycl. Agroecosys.*, 58, 221–230, 2000.
- Arah, J. R. M. and Stephen, K. D.: A model of the processes leading to methane emission from peatland, *Atmos. Environ.*, 32, 3257–3264, 1998.
- Aronson, E. and Helliker, B.: Methane flux in non-wetland soils in response to nitrogen addition: a meta-analysis, *Ecology*, 91, 3242–3251, 2010.
- Askaer, L., Elberling, B., Friborg, T., Jørgensen, C. J., and Hansen, B. U.: Plant-mediated CH₄ transport and C gas dynamics quantified in-situ in a *Phalaris arundinacea*-dominant wetland, *Plant Soil*, 343, 287–301, 2011.
- Aulakh, M. S., Wassmann, R., Rennenberg, H., and Fink, S.: Pattern and amount of aerenchyma relate to variable methane transport capacity of different rice cultivars, *Plant Biol.*, 2, 182–194, 2000.
- Banger, K., Tian, H., and Lu, C.: Do nitrogen fertilizers stimulate or inhibit methane emissions from rice fields?, *Glob. Change Biol.*, 18, 3259–3267, 2012.
- Barber, T. R., Burke, R. A., and Sackett, W. M.: Diffusive flux of methane from warm wetlands, *Global Biogeochem. Cy.*, 2, 411–425, 1988.
- Barlett, K. B. and Harriss, R. C.: Review and assessment of methane emissions from wetlands, *Chemosphere*, 26, 261–320, 1993.
- Becker, T., Kutzbach, L., Forbrich, I., Schneider, J., Jager, D., Thees, B., and Wilmking, M.: Do we miss the hot spots? – The use of very high resolution aerial photographs to quantify carbon fluxes in peatlands, *Biogeosciences*, 5, 1387–1393, doi:10.5194/bg-5-1387-2008, 2008.
- Beckett, P. M., Armstrong, W., and Armstrong, J.: Mathematical modelling of methane transport by *Phragmites*: the potential for diffusion within the roots and rhizosphere, *Aquat. Bot.*, 69, 293–312, 2001.
- Beerling, D. J., Gardiner, T., Leggett, G., Mcleod, A., and Quick, W. P.: Missing methane emissions from leaves of terrestrial plants, *Glob. Change Biol.*, 14, 1821–1826, 2008.
- Bellisario, L., Bubier, J., Moore, T., and Chanton, J.: Controls on CH₄ emissions from a northern peatland, *Global Biogeochem. Cy.*, 13, 81–91, 1999.
- Bhadra, A., Mukhopadhyay, S. N., and Ghose, T. K.: A kinetic model for methanogenesis of acetic acid in a multireactor system, *Biotechnol. Bioeng.*, 26, 257–264, 1984.
- Blazewicz, S. J., Petersen, D. G., Waldrop, M. P., and Firestone, M. K.: Anaerobic oxidation of methane in tropical and boreal soils: Ecological significance in terrestrial methane cycling, *J. Geophys. Res.-Biogeo.*, 117, G02033, doi:10.1029/2011JG001864, 2012.
- Blodau, C.: Carbon cycling in peatlands—A review of processes and controls, *Environ. Rev.*, 10, 111–134, 2002.
- Bohn, T. J. and Lettenmaier, D. P.: Systematic biases in large-scale estimates of wetland methane emissions arising from water table formulations, *Geophys. Res. Lett.*, 37, L22401, doi:10.1029/2010GL045450, 2010.
- Bohn, T. J., Lettenmaier, D. P., Sathulur, K., Bowling, L. C., Podest, E., McDonald, K. C., and Friborg, T.: Methane emissions from western Siberian wetlands: heterogeneity and sensitivity to climate change, *Environ. Res. Lett.*, 2, 045015, doi:10.1088/1748-9326/2/4/045015, 2007.
- Bohn, T. J., Melton, J. R., Ito, A., Kleinen, T., Spahni, R., Stocker, B. D., Zhang, B., Zhu, X., Schroeder, R., Glagolev, M. V., Maksyutov, S., Brovkin, V., Chen, G., Denisov, S. N., Eliseev, A. V., Gallego-Sala, A., McDonald, K. C., Rawlins, M. A., Riley, W. J., Subin, Z. M., Tian, H., Zhuang, Q., and Kaplan, J. O.: WETCHIMP-WSL: intercomparison of wetland methane emissions models over West Siberia, *Biogeosciences*, 12, 3321–3349, doi:10.5194/bg-12-3321-2015, 2015.
- Bridgman, S. D., Cadillo-Quiroz, H., Keller, J. K., and Zhuang, Q.: Methane emissions from wetlands: biogeochemical, microbial, and modeling perspective from local to global scales, *Glob. Change Biol.*, 19, 1325–1346, 2013.
- Butterbach-Bahl, K., Papen, H., and Rennenberg, H.: Impact of gas transport through rice cultivars on methane emission from rice paddy fields, *Plant Cell Environ.*, 20, 1175–1183, 1997.
- Cai, Z.: Greenhouse gas budget for terrestrial ecosystems in China, *Science China – Earth Sciences*, 55, 173–182, 2012.
- Caldwell, S. L., Laidler, J. R., Brewer, E. A., Eberly, J. O., Sandborgh, S. C., and Colwell, F. S.: Anaerobic oxidation of methane: mechanisms, bioenergetics, and ecology of associated microorganisms, *Environ. Sci. Technol.*, 42, 6791–6799, 2008.
- Cao, M. K., Dent, J. B., and Heal, O. W.: Modeling methane emissions from rice paddies, *Global Biogeochem. Cy.*, 9, 183–195, 1995.

- Cao, M. K., Gregson, K., and Marshall, S.: Global methane emission from wetlands and its sensitivity to climate change, *Atmos. Environ.*, 32, 3293–3299, 1998.
- Casella, G. and Robert, C. (Eds.): Monte Carlo statistical methods, Springer, New York, 2005.
- Chanton, J. P.: The effect of gas transport on the isotope signature of methane in wetlands, *Org. Geochem.*, 36, 753–768, 2005.
- Chanton, J. P., Martens, C. S., and Kelley, C. A.: Gas transport from methane-saturated, tidal freshwater and wetland sediments, *Limnol. Oceanogr.*, 34, 807–819, 1989.
- Chen, H., Zhu, Q., Peng, C., Wu, N., Wang, Y., Fang, X., Jiang, H., Xiang, W., Chang, J., Deng, X., and Yu, G.: Methane emissions from rice paddies natural wetlands, and lakes in China: synthesis and new estimate, *Glob. Change Biol.*, 19, 19–32, 2012.
- Christensen, T. and Cox, P.: Response of methane emission from Arctic tundra to climatic change: results from a model simulation, *Tellus B*, 47, 301–309, 1995.
- Christensen, T. R., Prentice, I. C., Kaplan, J. O., Haxeltine, A., and Sitch, S.: Methane flux from northern wetlands and tundra an ecosystem source modeling approach, *Tellus*, 48B, 652–661, 1996.
- Colmer, T.: Long distance transport of gases in plants: a perspective on internal aeration and radial oxygen loss from roots, *Plant Cell Environ.*, 26, 17–36, 2003.
- Conrad, R.: Contribution of hydrogen to methane production and control of hydrogen concentration in methanogenic soils and sediments, *FEMS Microbiol. Ecol.*, 28, 193–202, 1999.
- Conrad, R.: Control of methane production in terrestrial ecosystems, in: Exchange of trace gases between terrestrial ecosystems and the atmosphere, edited by: Andreae, M. O. and Schimel, D. S., Springer, New York, 39–58, 1989.
- Conrad, R.: Soil microbial processes involved in production and consumption of atmospheric trace gases, in: Advances in microbial ecology, Springer, 207–250, 1995.
- Conrad, R.: Soil microorganisms as controllers of atmospheric trace gases (H₂, CO, CH₄, OCS, N₂O, and NO), *Microbiol. Rev.*, 60, 609–640, 1996.
- Conrad, R.: Quantification of methanogenic pathways using stable carbon isotopic signatures: a review and a proposal, *Org. Geochem.*, 36, 739–752, 2005.
- Conrad, R.: The global methane cycle: recent advances in understanding the microbial processes involved, *Environ. Microbiol. Reports*, 1, 285–292, 2009.
- Conrad, R. and Claus, P.: Contribution of methanol to the production of methane and its ¹³C-isotopic signature in anoxic rice field soil, *Biogeochemistry*, 73, 381–393, 2005.
- Conrad, R. and Klose, M.: How specific is the inhibition by methyl fluoride of acetoclastic methanogenesis in anoxic rice field soil?, *FEMS Microbiol. Ecol.*, 30, 47–56, 1999.
- Cresto Aleina, F., Runkle, B. R. K., Kleinen, T., Kutzbach, L., Schneider, J., and Brovkin, V.: Modeling micro-topographic controls on boreal peatland hydrology and methane fluxes, *Biogeosciences*, 12, 5689–5704, doi:10.5194/bg-12-5689-2015, 2015.
- Curry, C. L.: Modeling the soil consumption of atmospheric methane at the global scale, *Global Biogeochem. Cy.*, 21, GB4012, doi:10.1029/2006GB002818, 2007.
- Curry, C. L.: The consumption of atmospheric methane by soil in a simulated future climate, *Biogeosciences*, 6, 2355–2367, doi:10.5194/bg-6-2355-2009, 2009.
- De Haas, Y., Windig, J., Calus, M., Dijkstra, J., De Haan, M., Bannink, A., and Veerkamp, R.: Genetic parameters for predicted methane production and potential for reducing enteric emissions through genomic selection, *J. Dairy Sci.*, 94, 6122–6134, 2011.
- De Kauwe, M. G., Medlyn, B. E., Zaehle, S., Walker, A. P., Dietze, M. C., Wang, Y. P., Luo, Y., Jain, A. K., El Masri, B., and Hickler, T.: Where does the carbon go? A model–data intercomparison of vegetation carbon allocation and turnover processes at two temperate forest free air CO₂ enrichment sites, *New Phytol.*, 203, 883–899, 2014.
- Del Grosso, S. J., Ojima, D., Parton, W. J., Mosier, A., Peterson, G., and Schimel, D.: Simulated effects of dryland cropping intensification on soil organic matter and greenhouse gas exchanges using the DAYCENT ecosystem model, *Environ. Pollut.*, 116, S75–S83, 2002.
- Del Grosso, S. J., Ojima, D. S., Parton, W. J., Stehfest, E., Heistermann, M., DeAngelo, B. J., and Rose, S.: Global scale DAYCENT model analysis of greenhouse gas emissions and mitigation strategies for cropped soils, *Global Planet. Change*, 67, 44–50, 2009.
- Del Grosso, S. J., Parton, W. J., Mosier, A. R., Ojima, D. S., Potter, C. S., Borken, W., Brumme, R., Butterbach-Bahl, K., Crill, P. M., Dobbie, K. E., and Smith, K. A.: General CH₄ oxidation model and comparisons of CH₄ oxidation in natural and managed systems, *Global Biogeochem. Cy.*, 14, 999–1019, 2000.
- DeLong, E. F., Harwood, C. S., Chisholm, P. W., Karl, D. M., Moran, M. A., Schmidt, T. M., Tiedje, J. M., Treseder, K. K., and Worden, A. Z.: Incorporating microbial processes into climate models, The American Academy of Microbiology, Washington DC, 2011.
- De Visscher, A. and Van Cleemput, O.: Simulation model for gas diffusion and methane oxidation in landfill cover soils, *Waste Manage.*, 23, 581–591, 2003.
- Ding, A. and Wang, M.: Model for methane emission from rice paddies and its application in southern China, *Adv. Atmos. Sci.*, 13, 159–168, 1996.
- Dueck, T. A., De Visser, R., Poorter, H., Persijn, S., Gorissen, A., De Visser, W., Schapendonk, A., Verhagen, J., Snel, J., and Harren, F. J.: No evidence for substantial aerobic methane emission by terrestrial plants: a ¹³C labelling approach, *New Phytol.*, 175, 29–35, 2007.
- Eliseev, A. V., Mokhov, I. I., Arzhanov, M. M., Demchenko, P. F., and Denisov, S. N.: Interaction of the methane cycle and processes in wetland ecosystems in a climate model of intermediate complexity, *Atmos. Ocean. Phys.*, 44, 139–152, 2008.
- Elliott, S., Maltrud, M., Reagan, M., Moridis, G., and Cameron Smith, P.: Marine methane cycle simulations for the period of early global warming, *J. Geophys. Res.-Biogeo.*, 116, G01010, doi:10.1029/2010JG001300, 2011.
- Entekhabi, D., Njoku, E. G., O'Neill, P. E., Kellogg, K. H., Crow, W. T., Edelstein, W. N., Entin, J. K., Goodman, S. D., Jackson, T. J., and Johnson, J.: The soil moisture active passive (SMAP) mission, *Proceedings of the IEEE*, 98, 704–716, 2010.
- Evans, M. R., Grimm, V., Johst, K., Knuuttila, T., de Langhe, R., Lessells, C. M., Merz, M., O'Malley, M. A., Orzack, S. H., and Weisberg, M.: Do simple models lead to generality in ecology?, *Trends Ecol. Evol.*, 28, 578–583, 2013.
- Falz, K. Z., Holliger, C., Grosskopf, R., Liesack, W., Nozhevnikova, A., Müller, B., Wehrli, B., and Hahn, D.: Vertical distribution

- of methanogens in the anoxic sediment of Rotsee (Switzerland), *Appl. Environ. Microb.*, 65, 2402–2408, 1999.
- Fan, Z., David McGuire, A., Turetsky, M. R., Harden, J. W., Michael Waddington, J., and Kane, E. S.: The response of soil organic carbon of a rich fen peatland in interior Alaska to projected climate change, *Glob. Change Biol.*, 19, 604–620, 2013.
- Forster, P., Ramaswamy, V., Artaxo, P., Bernsten, T., Betts, R., Fahey, D. W., Haywood, J., Lean, J., Lowe, D. C., Myhre, G., Nanga, J., Prinn, N. R., Raga, G., Schulz, M., and Dorland, R. V.: Changes in atmospheric constituents and in radiative forcing, in: *Climate change 2007: The physical science basis. Contribution of working group I to the fourth assessment report of the intergovernmental panel on climate change*, edited by: Solomon, S., Qin, D., Manning, M., and Chen, Z., Cambridge University Press, Cambridge, United Kingdom and New York, USA, 133–216, 2007.
- Frankenberg, C., Meirink, J. F., Van Weele, M., Platt, U., and Wagner, T.: Assessing methane emissions from global space-borne observations, *Science*, 308, 1010–1014, 2005.
- Frenzel, P. and Karofeld, E.: CH₄ emission from a hollow-ridge complex in a raised bog: the role of CH₄ production and oxidation, *Biogeochemistry*, 51, 91–112, 2000.
- Frenzel, P. and Rudolph, J.: Methane emission from a wetland plant: the role of CH₄ oxidation in *Eriophorum*, *Plant Soil*, 202, 27–32, 1998.
- Gao, C., Wang, H., Weng, E., Lakshmirarahan, S., Zhang, Y., and Luo, Y.: Assimilation of multiple data sets with the ensemble Kalman filter to improve forecasts of forest carbon dynamics, *Ecol. Appl.*, 21, 1461–1473, 2011.
- Gao, X., Schlosser, C. A., Sokolov, A., Anthony, K. W., Zhuang, Q., and Kicklighter, D.: Permafrost degradation and methane: low risk of biogeochemical climate-warming feedback, *Environ. Res. Lett.*, 8, 035014, doi:10.1088/1748-9326/8/3/035014, 2013.
- Gauthier, M., Bradley, R. L., and Šimek, M.: More evidence that anaerobic oxidation of methane is prevalent in soils: Is it time to upgrade our biogeochemical models?, *Soil Biol. Biochem.*, 80, 167–174, 2015.
- Gedney, N., Cox, P., and Huntingford, C.: Climate feedback from wetland methane emissions, *Geophys. Res. Lett.*, 31, L20503, doi:10.1029/2004GL020919, 2004.
- Gerard, G. and Chanton, J.: Quantification of methane oxidation in the rhizosphere of emergent aquatic macrophytes: defining upper limits, *Biogeochemistry*, 23, 79–97, 1993.
- Gong, J., Kellomaki, S., Wang, K., Zhang, C., Shurpali, N., and Martikainen, P. J.: Modeling CO₂ and CH₄ flux changes in pristine peatlands of Finland under changing climate conditions, *Ecol. Model.*, 263, 64–80, 2013.
- Grant, R. and Roulet, N.: Methane efflux from boreal wetlands: Theory and testing of the ecosystem model *Ecosys* with chamber and tower flux measurements, *Global Biogeochem. Cy.*, 16, 2-1–2-16, 2002.
- Grant, R., Juma, N., and McGill, W.: Simulation of carbon and nitrogen transformations in soil: mineralization, *Soil Biol. Biochem.*, 25, 1317–1329, 1993.
- Grant, R. F.: Simulation of methanogenesis in the mathematical model *Ecosys*, *Soil Biol. Biochem.*, 30, 883–896, 1998.
- Grant, R. F.: A review of the Canadian ecosystem model *ecosys*, in: *Modeling Carbon and Nitrogen Dynamics for Soil Management*, edited by: Shaffer, M. J., Ma, L., and Hansen, S., CRC Press, New York, 173–264, 2001.
- Gulledge, J. and Schimel, J. P.: Low-concentration kinetics of atmospheric CH₄ oxidation in soil and mechanism of NH₄⁺ inhibition, *Appl. Environ. Microb.*, 64, 4291–4298, 1998a.
- Gulledge, J. and Schimel, J. P.: Moisture control over atmospheric CH₄ consumption and CO₂ production in diverse Alaskan soils, *Soil Biol. Biochem.*, 30, 1127–1132, 1998b.
- Hakemian, A. S. and Rosenzweig, A. C.: The biochemistry of methane oxidation, *Annu. Rev. Biochem.*, 76, 223–241, 2007.
- Hanson, R. S. and Hanson, T. E.: Methanotrophic bacteria, *Microbiol. Mol. Biol. R.*, 60, 60, 439–471, 1996.
- Heilman, M. A. and Carlton, R. G.: Methane oxidation associated with submersed vascular macrophytes and its impact on plant diffusive methane flux, *Biogeochemistry*, 52, 207–224, 2001.
- Higgins, I. J., Best, D. J., Hammond, R. C., and Scott, D.: Methane-oxidizing microorganisms, *Microbiol. Rev.*, 45, 556–590, 1981.
- Hodson, E. L., Poulter, B., Zimmermann, N. E., Prigent, C., and Kaplan, J. O.: The El Niño-Southern Oscillation and wetland methane interannual variability, *Geophys. Res. Lett.*, 38, L08810, doi:10.1029/2011GL046861, 2011.
- Holgerson, M. A. and Raymond, P. A.: Large contribution to inland water CO₂ and CH₄ emissions from very small ponds, *Nat. Geosci.*, 9, 222–226, 2016.
- Hopcroft, P. O., Valdes, P. J., and Beerling, D. J.: Simulating idealized Dansgaard-Oeschger events and their potential impacts on the global methane cycle, *Quaternary Sci. Rev.*, 30, 3258–3268, 2011.
- Hosono, T. and Nouchi, I.: The dependence of methane transport in rice plants on the root zone temperature, *Plant Soil*, 191, 233–240, 1997.
- Huang, Y., Sass, R. L., and Fisher, F. M.: Model estimates of methane emission from irrigated rice cultivation of China, *Glob. Change Biol.*, 4, 809–821, doi:10.1046/j.1365-2486.1998.00175.x, 1998a.
- Huang, Y., Sass, R. L., and Fisher, F. M.: A semi-empirical model of methane emission from flooded rice paddy soils, *Glob. Change Biol.*, 4, 247–268, 1998b.
- Huang, Y., Zhang, W., Zheng, X., Li, J., and Yu, Y.: Modeling methane emission from rice paddies with various agricultural practices, *J. Geophys. Res.*, 109, D08113, doi:10.1029/2003JD004401, 2004.
- Inatomi, M., Ito, A., Ishijima, K., and Murayama, S.: Greenhouse gas budget of a cool-temperate deciduous broad-leaved forest in Japan estimated using a process-based model, *Ecosystems*, 13, 472–483, 2010.
- IPCC: Summary for policymakers, Cambridge, United Kingdom and New York, NY, USA, 2013.
- Ito, A. and Inatomi, M.: Use of a process-based model for assessing the methane budgets of global terrestrial ecosystems and evaluation of uncertainty, *Biogeosciences*, 9, 759–773, doi:10.5194/bg-9-759-2012, 2012.
- Karl, D. M., Beversdorf, L., Björkman, K. M., Church, M. J., Martinez, A., and Delong, E. F.: Aerobic production of methane in the sea, *Nat. Geosci.*, 1, 473–478, 2008.
- Keppler, F., Hamilton, J. T. G., Brass, M., and Rockmann, T.: Methane emissions from terrestrial plants under aerobic conditions, *Nature*, 439, 187–191, 2006.

- Kettunen, A.: Connecting methane fluxes to vegetation cover and water table fluctuations at microsite level: a modeling study, *Global Biogeochem. Cy.*, 17, 1051, doi:10.1029/2002GB001958, 2003.
- King, G. M.: In Situ Analyses of Methane Oxidation Associated with the Roots and Rhizomes of a Bur Reed, *Sparganium eurycarpum*, in a Maine Wetland, *Appl. Environ. Microb.*, 62, 4548–4555, 1996.
- Kotsyurbenko, O. R., Chin, K. J., Glagolev, M. V., Stubner, S., Simankova, M. V., Nozhevnikova, A. N., and Conrad, R.: Acetoclastic and hydrogenotrophic methane production and methanogenic populations in an acidic West Siberian peat bog, *Environ. Microbiol.*, 6, 1159–1173, 2004.
- Koven, C. D., Ringeval, B., Friedlingstein, P., Ciais, P., Cadule, P., Khvorostyanov, D., Krinner, G., and Tarnocai, C.: Permafrost carbon-climate feedbacks accelerate global warming, *P. Natl. Acad. Sci. USA*, 108, 14769–14774, 2011.
- Koven, C. D., Riley, W. J., Subin, Z. M., Tang, J. Y., Torn, M. S., Collins, W. D., Bonan, G. B., Lawrence, D. M., and Swenson, S. C.: The effect of vertically resolved soil biogeochemistry and alternate soil C and N models on C dynamics of CLM4, *Biogeosciences*, 10, 7109–7131, doi:10.5194/bg-10-7109-2013, 2013.
- Krüger, M., Frenzel, P., and Conrad, R.: Microbial processes influencing methane emission from rice fields, *Glob. Change Biol.*, 7, 49–63, 2001.
- Krumholz, L. R., Hollenback, J. L., Roskes, S. J., and Ringelberg, D. B.: Methanogenesis and methanotrophy within a Sphagnum peatland, *FEMS Microbiol. Ecol.*, 18, 215–224, 1995.
- Lai, D. Y. F.: Methane dynamics in Northern Peatlands: A Review, *Pedosphere*, 19, 409–421, 2009.
- Larsen, P. E., Gibbons, S. M., and Gilbert, J. A.: Modeling microbial community structure and functional diversity across time and space, *FEMS Microbiol. Lett.*, 332, 91–98, 2012.
- Lenhart, K., Bunge, M., Ratering, S., New, T. R., Schuttman, I., Greule, M., Kammann, C., Schnell, S., Müller, C., Zorn, H., and Keppler, F.: Evidence for methane production by saprotrophic fungi, *Nat. Commun.*, 3, 1046, doi:10.1038/ncomms2049, 2012.
- Li, C.: Modeling trace gas emissions from agricultural ecosystems, *Nutr. Cycl. Agroecosys.*, 58, 259–276, 2000.
- Li, C., Frohling, S., Xiao, X., Moore III, B., Boles, S., Qiu, J., Huang, Y., Salas, W., and Sass, R.: Modeling impacts of farming management alternatives on CO₂, CH₄, and N₂O emissions: a case study for water management of rice agriculture of China, *Global Biogeochem. Cy.*, 19, GB3010, doi:10.1029/2004GB002341, 2005.
- Li, T., Huang, Y., Zhang, W., and Yu, Y.-Q.: Methane emissions associated with the conversion of marshland to cropland and climate change on the Sanjiang Plain of northeast China from 1950 to 2100, *Biogeosciences*, 9, 5199–5215, doi:10.5194/bg-9-5199-2012, 2012.
- Liu, L. and Greaver, T.: A review of nitrogen enrichment effects on three biogenic GHGs: the CO₂ sink may be largely offset by stimulated N₂O and CH₄ emission, *Ecol. Lett.*, 12, 1103–1117, 2009.
- Lovley, D. P. and Klug, M. J.: Model for distribution of sulfate reduction and methanogenesis in freshwater sediments, *Geochim. Cosmochim. Ac.*, 50, 11–18, 1986.
- Luo, Y. Q., Randerson, J. T., Abramowitz, G., Bacour, C., Blyth, E., Carvalhais, N., Ciais, P., Dalmonech, D., Fisher, J. B., Fisher, R., Friedlingstein, P., Hibbard, K., Hoffman, F., Huntzinger, D., Jones, C. D., Koven, C., Lawrence, D., Li, D. J., Mahecha, M., Niu, S. L., Norby, R., Piao, S. L., Qi, X., Peylin, P., Prentice, I. C., Riley, W., Reichstein, M., Schwalm, C., Wang, Y. P., Xia, J. Y., Zaehle, S., and Zhou, X. H.: A framework for benchmarking land models, *Biogeosciences*, 9, 3857–3874, doi:10.5194/bg-9-3857-2012, 2012.
- Martens, C. S., Albert, D. B., and Alperin, M. J.: Biogeochemical processes controlling methane in gassy coastal sediments – Part 1, A model coupling organic matter flux to gas production, oxidation and transport, *Cont. Shelf Res.*, 18, 1741–1770, 1998.
- Martinson, G. O., Werner, F. A., Scherber, C., Conrad, R., Corre, M. D., Flessa, H., Wolf, K., Klose, M., Gradstein, S. R., and Veldkamp, E.: Methane emissions from tank bromeliads in neotropical forests, *Nat. Geosci.*, 3, 766–769, 2010.
- Massman, W., Sommerfeld, R., Mosier, A., Zeller, K., Hehn, T., and Rochelle, S.: A model investigation of turbulence driven pressure pumping effects on the rate of diffusion of CO₂, N₂O, and CH₄ through layered snowpacks, *J. Geophys. Res.-Atmos.*, 102, 18851–18863, 1997.
- Mastepanov, M., Sigsgaard, C., Dlugokencky, E. J., Houweling, S., Strom, L., Tamstorf, M. P., and Christensen, T. R.: Large tundra methane burst during onset of freezing, *Nature*, 456, 628–630, 2008.
- Matthews, E. and Fung, I.: Methane emissions from natural wetlands: global distribution, area and environmental characteristics of sources, *Global Biogeochem. Cy.*, 1, 61–86, 1987.
- Matthews, R. B., Wassmann, R., and Arah, J. R. M.: Using a crop/soil simulation model and GIS techniques to assess methane emissions from rice fields in Asia, I. model development, *Nutr. Cycl. Agroecosys.*, 58, 141–159, 2000.
- Mau, S., Bles, J., Helmke, E., Niemann, H., and Damm, E.: Vertical distribution of methane oxidation and methanotrophic response to elevated methane concentrations in stratified waters of the Arctic fjord Storfjorden (Svalbard, Norway), *Biogeosciences*, 10, 6267–6278, doi:10.5194/bg-10-6267-2013, 2013.
- McCalley, C. K., Woodcroft, B. J., Hodgkins, S. B., Wehr, R. A., Kim, E.-H., Mondav, R., Crill, P. M., Chanton, J. P., Rich, V. I., Tyson, G. W., and Saleska, S. R.: Methane dynamics regulated by microbial community response to permafrost thaw, *Nature*, 514, 478–481, 2014.
- Melloh, R. A. and Crill, P. M.: Winter methane dynamics in a temperate peatland, *Global Biogeochem. Cy.*, 10, 247–254, 1996.
- Melton, J. R., Wania, R., Hodson, E. L., Poulter, B., Ringeval, B., Spahni, R., Bohn, T., Avis, C. A., Beerling, D. J., Chen, G., Eliseev, A. V., Denisov, S. N., Hopcroft, P. O., Lettenmaier, D. P., Riley, W. J., Singarayer, J. S., Subin, Z. M., Tian, H., Zürcher, S., Brovkin, V., van Bodegom, P. M., Kleinen, T., Yu, Z. C., and Kaplan, J. O.: Present state of global wetland extent and wetland methane modelling: conclusions from a model inter-comparison project (WETCHIMP), *Biogeosciences*, 10, 753–788, doi:10.5194/bg-10-753-2013, 2013.
- Meng, L., Hess, P. G. M., Mahowald, N. M., Yavitt, J. B., Riley, W. J., Subin, Z. M., Lawrence, D. M., Swenson, S. C., Jauhainen, J., and Fuka, D. R.: Sensitivity of wetland methane emissions to model assumptions: application and model testing against site observations, *Biogeosciences*, 9, 2793–2819, doi:10.5194/bg-9-2793-2012, 2012.

- Mer, J. L. and Roger, P.: Production, oxidation, emission and consumption of methane by soils: a review, *Eur. J. Soil Biol.*, 37, 25–50, 2001.
- Miller, K. E., Lai, C.-T., Friedman, E. S., Angenent, L. T., and Lipson, D. A.: Methane suppression by iron and humic acids in soils of the Arctic Coastal Plain, *Soil Biol. Biochem.*, 83, 176–183, 2015.
- Mokhov, I. I., Eliseev, A. V., and Denisov, S. N.: Model diagnostics of variations in methane emissions by wetlands in the second half of the 20th century based on reanalysis data, *Dokl. Earth Sci.*, 417, 1293–1297, 2007.
- Monechi, S., Coccioni, R., and Rampino, M. R.: Large ecosystem perturbations: causes and consequences, Geological Society of America, Boulder, Colo., 2007.
- Morrissey, L. and Livingston, G.: Methane emissions from Alaska arctic tundra: An assessment of local spatial variability, *J. Geophys. Res.-Atmos.*, 97, 16661–16670, 1992.
- Mosier, A., Delgado, J., Cochran, V., Valentine, D., and Parton, W.: Impact of agriculture on soil consumption of atmospheric CH₄ and a comparison of CH₄ and N₂O flux in subarctic, temperate and tropical grasslands, *Nutr. Cycl. Agroecosys.*, 49, 71–83, 1997.
- Murase, J. and Kimura, M.: Methane production and its fate in paddy fields: IX. Methane flux distribution and decomposition of methane in the subsoil during the growth period of rice plants, *Soil Sci. Plant Nutr.*, 42, 187–190, 1996.
- Nauta, A. L., Heijmans, M. M., Blok, D., Limpens, J., Elberling, B., Gallagher, A., Li, B., Petrov, R. E., Maximov, T. C., and van Huissteden, J.: Permafrost collapse after shrub removal shifts tundra ecosystem to a methane source, *Nature Climate Change*, 5, 67–70, 2015.
- Nazaries, L., Murrell, J. C., Millard, P., Baggs, L., and Singh, B. K.: Methane, microbes and models: fundamental understanding of the soil methane cycle for future predictions, *Environ. Microbiol.*, 15, 2395–417, doi:10.1111/1462-2920.12149, 2013.
- Nouchi, I., Mariko, S., and Aoki, K.: Mechanism of methane transport from the rhizosphere to the atmosphere through rice plants, *Plant Physiol.* 94, 59–66, 1990.
- Nouchi, I., Hosono, T., Aoki, K., and Minami, K.: Seasonal variation in methane flux from rice paddies associated with methane concentration in soil water, rice biomass and temperature, and its modelling, *Plant Soil*, 161, 195–208, 1994.
- Ogle, K. and Barber, J. J.: Bayesian data–model integration in plant physiological and ecosystem ecology, in: *Progress in botany*, Springer Verlag, Berlin, Heidelberg, 281–311, 2008.
- Pareek, S., Matsui, S., Kim, S. K., and Shimizu, Y.: Mathematical modeling and simulation of methane gas production in simulated landfill column reactors under sulfidogenic and methanogenic environments, *Water Sci. Technol.*, 39, 235–242, 1999.
- Peng, C., Guiot, J., Wu, H., Jiang, H., and Luo, Y.: Integrating models with data in ecology and palaeoecology: advances towards a model–data fusion approach, *Ecol. Lett.*, 14, 522–536, 2011.
- Philippot, L., Andersson, S. G., Battin, T. J., Prosser, J. I., Schimel, J. P., Whitman, W. B., and Hallin, S.: The ecological coherence of high bacterial taxonomic ranks, *Nat. Rev. Microbiol.*, 8, 523–529, 2010.
- Potter, C. S.: An ecosystem simulation model for methane production and emission from wetlands, *Global Biogeochem. Cy.*, 11, 495–506, 1997.
- Potter, C. S., Davidson, E. A., and Verchot, L. V.: Estimation of global biogeochemical controls and seasonality in soil methane consumption, *Chemosphere*, 32, 2219–2246, 1996.
- Ren, W., Tian, H., Xu, X., Liu, M., Lu, C., Chen, G., Melillo, J., Reilly, J., and Liu, J.: Spatial and temporal patterns of CO₂ and CH₄ fluxes in China's croplands in response to multifactor environmental changes, *Tellus B*, 63, 222–240, 2011.
- Riccio, D. M., Davis, K. J., and Keller, K.: A bayesian calibration of a simple carbon cycle model: the role of observations in estimating and reducing uncertainty, *Global Biogeochem. Cy.*, 22, GB2030, doi:10.1029/2006GB002908, 2008.
- Ridgwell, A. J., Marshall, S. J., and Gregson, K.: Consumption of atmospheric methane by soils: a process-based model, *Global Biogeochem. Cy.*, 13, 59–70, 1999.
- Riley, W. J., Subin, Z. M., Lawrence, D. M., Swenson, S. C., Torn, M. S., Meng, L., Mahowald, N. M., and Hess, P.: Barriers to predicting changes in global terrestrial methane fluxes: analyses using CLM4Me, a methane biogeochemistry model integrated in CESM, *Biogeosciences*, 8, 1925–1953, doi:10.5194/bg-8-1925-2011, 2011.
- Ringeval, B., de Noblet-Ducoudre, N., Ciais, P., Bousquet, P., Prigent, C., Para, F., and Rossow, W. B.: An attempt to quantify the impact of changes in wetland extent on methane emissions on the seasonal and interannual time scales, *Global Biogeochem. Cy.*, 24, GB2003, doi:10.1029/2008GB003354, 2010.
- Ringeval, B., Friedlingstein, P., Koven, C., Ciais, P., de Noblet-Ducoudré, N., Decharme, B., and Cadule, P.: Climate-CH₄ feedback from wetlands and its interaction with the climate-CO₂ feedback, *Biogeosciences*, 8, 2137–2157, doi:10.5194/bg-8-2137-2011, 2011.
- Rodhe, H.: A comparison of the contribution of various gases to the greenhouse effect, *Science*, 248, 1217–1219, 1990.
- Schimel, J.: Ecosystem consequences of microbial diversity and community structure, in: *Arctic and alpine biodiversity: patterns, causes and ecosystem consequences*, Springer, Springer-Verlag, Berlin, Heidelberg, 239–254, 1995.
- Schimel, J. P. and Gullledge, J.: Microbial community structure and global trace gases, *Glob. Change Biol.*, 4, 745–758, 1998.
- Schleip, C., Rais, A., and Menzel, A.: Bayesian analysis of temperature sensitivity of plant phenology in Germany, *Agr. Forest Meteorol.*, 149, 1699–1708, 2009.
- Schütz, H., Seiler, W., and Conrad, R.: Processes involved in formation and emission of methane in rice paddies, *Biogeochemistry*, 7, 33–53, 1989.
- Segers, R.: Methane production and methane consumption: a review of processes underlying wetland methane fluxes, *Biogeochemistry*, 41, 23–51, 1998.
- Segers, R. and Kengen, S. W. M.: Methane production as a function of anaerobic carbon mineralization: a process model, *Soil Biol. Biochem.*, 30, 1107–1117, 1998.
- Segers, R. and Leffelaar, P. A.: Modeling methane fluxes in wetlands with gas-transporting plants 1, single-root scale, *J. Geophys. Res.*, 106, 3511–3528, 2001a.
- Segers, R. and Leffelaar, P. A.: Modeling methane fluxes in wetlands with gas-transporting plants 3, plot scale, *J. Geophys. Res.*, 106, 3541–3558, 2001b.
- Segers, R., Rappoldt, C., and Leffelaar, P. A.: Modeling methane fluxes in wetlands with gas-transporting plants 2, soil layer scale, *J. Geophys. Res.*, 106, 3529–3540, 2001.

- Shoemaker, J. K., Keenan, T. F., Hollinger, D. Y., and Richardson, A. D.: Forest ecosystem changes from annual methane source to sink depending on late summer water balance, *Geophys. Res. Lett.*, 41, 673–679, 2014.
- Smemo, K. A. and Yavitt, J. B.: Anaerobic oxidation of methane: an underappreciated aspect of methane cycling in peatland ecosystems?, *Biogeosciences*, 8, 779–793, doi:10.5194/bg-8-779-2011, 2011.
- Söhngen, N.: Über Bakterien, welche Methan als Kohlenstoffnahrung und Energiequelle gebrauchen, *Zentrabl Bakteriell Parasitenk Infektionskr.*, 15, 513–517, 1906.
- Song, C., Xu, X., Sun, X., Tian, H., Sun, L., Miao, Y., Wang, X., and Guo, Y.: Large methane emission upon spring thaw from natural wetlands in the northern permafrost region, *Environ. Res. Lett.*, 7, 034009, doi:10.1088/1748-9326/7/3/034009, 2012.
- Spahni, R., Wania, R., Neef, L., van Weele, M., Pison, I., Bousquet, P., Frankenberg, C., Foster, P. N., Joos, F., Prentice, I. C., and van Velthoven, P.: Constraining global methane emissions and uptake by ecosystems, *Biogeosciences*, 8, 1643–1665, doi:10.5194/bg-8-1643-2011, 2011.
- Ström, L., Mastepanov, M., and Christensen, T. R.: Species-specific effects of vascular plants on carbon turnover and methane emissions from wetlands, *Biogeochemistry*, 75, 65–82, 2005.
- Summons, R. E., Franzmann, P. D., and Nichols, P. D.: Carbon isotopic fractionation associated with methylophilic methanogenesis, *Org. Geochem.*, 28, 465–475, 1998.
- Tagesson, T., Mastepanov, M., Mölder, M., Tamstorf, M. P., Eklundh, L., Smith, B., Sigsgaard, C., Lund, M., Ekberg, A., and Falk, J. M.: Modelling of growing season methane fluxes in a high-Arctic wet tundra ecosystem 1997–2010 using in situ and high-resolution satellite data, *Tellus B*, 65, 19722, doi:10.3402/tellus.v65i0.19722, 2013.
- Tang, J. and Zhuang, Q.: Equifinality in parameterization of process based biogeochemistry models: A significant uncertainty source to the estimation of regional carbon dynamics, *J. Geophys. Res.-Biogeo.*, 113, G04010, doi:10.1029/2008JG000757, 2008.
- Tang, J., Zhuang, Q., Shannon, R. D., and White, J. R.: Quantifying wetland methane emissions with process-based models of different complexities, *Biogeosciences*, 7, 3817–3837, doi:10.5194/bg-7-3817-2010, 2010.
- Tang, J. Y. and Riley, W. J.: A total quasi-steady-state formulation of substrate uptake kinetics in complex networks and an example application to microbial litter decomposition, *Biogeosciences*, 10, 8329–8351, doi:10.5194/bg-10-8329-2013, 2013.
- Tang, J. Y. and Riley, W. J.: Technical Note: Simple formulations and solutions of the dual-phase diffusive transport for biogeochemical modeling, *Biogeosciences*, 11, 3721–3728, doi:10.5194/bg-11-3721-2014, 2014.
- Tian, H., Xu, X., Liu, M., Ren, W., Zhang, C., Chen, G., and Lu, C.: Spatial and temporal patterns of CH₄ and N₂O fluxes in terrestrial ecosystems of North America during 1979–2008: application of a global biogeochemistry model, *Biogeosciences*, 7, 2673–2694, doi:10.5194/bg-7-2673-2010, 2010.
- Tokida, T., Mizoguchi, M., Miyazaki, T., Kagemoto, A., Nagata, O., and Hatano, R.: Episodic release of methane bubbles from peatland during spring thaw, *Chemosphere*, 70, 165–171, 2007.
- Topp, E. and Pattey, E.: Soils as sources and sinks for atmospheric methane, *Can. J. Soil Sci.*, 77, 167–177, 1997.
- Tveit, A. T., Urlich, T., Frenzel, P., and Svenning, M. M.: Metabolic and trophic interactions modulate methane production by Arctic peat microbiota in response to warming, *P. Natl. Acad. Sci. USA*, 112, E2507–E2516, 2015.
- Valentine, D. L. and Reeburgh, W. S.: New perspectives on anaerobic methane oxidation, *Environ. Microbiol.*, 2, 477–484, 2000.
- van Bodegom, P. M., Leffelaar, P. A., Stams, A. J. M., and Wassmann, R.: Modeling methane emissions from rice fields: variability, uncertainty, and sensitivity analysis of processes involved, *Nutr. Cycl. Agroecosys.*, 58, 231–248, 2000.
- van Bodegom, P. M., Wassmann, R., and Metra-Corton, T. M.: A process-based model for methane emission predictions from flooded rice paddies, *Global Biogeochem. Cy.*, 15, 247–263, 2001.
- Van Oijen, M., Rougier, J., and Smith, R.: Bayesian calibration of process-based forest models: bridging the gap between models and data, *Tree Physiol.*, 25, 915–927, 2005.
- Volta, A.: Lettere dell'illustrissimo Signor Volta Alessandro sull'aria infiammabile native delle paludi, in: Giuseppe Marelli, Milano, 1777.
- Wagner, D., Lipski, A., Embacher, A., and Gatterer, A.: Methane fluxes in permafrost habitats of the Lena Delta: effects of microbial community structure and organic matter quality, *Environ. Microbiol.*, 7, 1582–1592, 2005.
- Wahlen, M.: The global methane cycle, *Annu. Rev. Earth Pl. Sc.*, 21, 407–426, 1993.
- Walter, B. P. and Heimann, M.: A process-based, climate-sensitive model to derive methane emissions from natural wetlands: Application to five wetland sites, sensitivity to model parameters, and climate, *Global Biogeochem. Cy.*, 14, 745–765, 2000.
- Walter, B. P., Heimann, M., Shannon, R. D., and White, J. R.: A process-based model to derive methane emissions from natural wetlands, *Geophys. Res. Lett.*, 23, 3731–3734, 1996.
- Wang, Z., Han, X., Wang, G. G., Song, Y., and Gullledge, J.: Aerobic methane emission from plants in the Inner Mongolia Steppe, *Environ. Sci. Technol.*, 42, 62–68, 2007.
- Wania, R.: Modelling northern peatland land surface processes, vegetation dynamics and methane emissions, *Doktorarbeit, University of Bristol, Bristol*, 1–140, 2007.
- Wania, R., Ross, I., and Prentice, I. C.: Integrating peatlands and permafrost into a dynamic global vegetation model: 1. Evaluation and sensitivity of physical land surface processes, *Global Biogeochem. Cy.*, 23, GB3014, doi:10.1029/2008GB003412, 2009.
- Wania, R., Ross, I., and Prentice, I. C.: Implementation and evaluation of a new methane model within a dynamic global vegetation model: LPJ-WHyMe v1.3.1, *Geosci. Model Dev.*, 3, 565–584, doi:10.5194/gmd-3-565-2010, 2010.
- Wania, R., Melton, J. R., Hodson, E. L., Poulter, B., Ringeval, B., Spahni, R., Bohn, T., Avis, C. A., Chen, G., Eliseev, A. V., Hopcroft, P. O., Riley, W. J., Subin, Z. M., Tian, H., van Bodegom, P. M., Kleinen, T., Yu, Z. C., Singarayer, J. S., Zürcher, S., Lettenmaier, D. P., Beerling, D. J., Denisov, S. N., Prigent, C., Papa, F., and Kaplan, J. O.: Present state of global wetland extent and wetland methane modelling: methodology of a model inter-comparison project (WETCHIMP), *Geosci. Model Dev.*, 6, 617–641, doi:10.5194/gmd-6-617-2013, 2013.
- Wassmann, R., Neue, H., Lantin, R., Makarim, K., Chareonsilp, N., Buendia, L., and Rennenberg, H.: Characterization of methane

- emissions from rice fields in Asia. II. Differences among irrigated, rainfed, and deepwater rice, *Nutr. Cycl. Agroecosys.*, 58, 13–22, 2000.
- Watanabe, K. and Ito, M.: In situ observation of the distribution and activity of microorganisms in frozen soil, *Cold Reg. Sci. Technol.*, 54, 1–6, 2008.
- Watts, J. D., Kimball, J. S., Parmentier, F. J. W., Sachs, T., Rinne, J., Zona, D., Oechel, W., Tagesson, T., Jackowicz-Korczynski, M., and Aurela, M.: A satellite data driven biophysical modeling approach for estimating northern peatland and tundra CO₂ and CH₄ fluxes, *Biogeosciences*, 11, 1961–1980, doi:10.5194/bg-11-1961-2014, 2014.
- Weller, G., Chapin, F. S., Everett, K. R., Hobbie, J. E., Kane, D., Oechel, W. C., Ping, C. L., Reeburgh, W. S., Walker, D., and Walsh, J.: The arctic flux study: A regional view of trace gas release, *J. Biogeogr.*, 22, 365–374, 1995.
- Whiting, G. J. and Chanton, J. P.: Control of the diurnal pattern of methane emission from emergent aquatic macrophytes by gas transport mechanisms, *Aquat. Bot.*, 54, 237–253, 1996.
- Xu, S., Jaffe, P. R., and Mauzerall, D. L.: A process-based model for methane emission from flooded rice paddy systems, *Ecol. Model.*, 205, 475–491, 2007.
- Xu, X.: Modeling methane and nitrous oxide exchanges between the atmosphere and terrestrial ecosystems over North America in the context of multifactor global change, PhD Dissertation, School of Forestry and Wildlife Sciences, Auburn University, Auburn, 199 pp., 2010.
- Xu, X., Schimel, J. P., Thornton, P. E., Song, X., Yuan, F., and Goswami, S.: Substrate and environmental controls on microbial assimilation of soil organic carbon: a framework for Earth system models, *Ecol. Lett.*, 17, 547–555, 2014.
- Xu, X., Elias, D. A., Graham, D. E., Phelps, T. J., Carrol, S. L., Wullschleger, S. D., and Thornton, P. E.: A microbial functional group based module for simulating methane production and consumption: application to an incubation permafrost soil, *J. Geophys. Res.-Biogeo.*, 120, 1315–1333, 2015.
- Xu, X. and Tian, H.: Methane exchange between marshland and the atmosphere over China during 1949–2008, *Global Biogeochem. Cy.*, 26, GB2006, doi:10.1029/2010GB003946, 2012.
- Xu, X. F., Tian, H. Q., Zhang, C., Liu, M. L., Ren, W., Chen, G. S., Lu, C. Q., and Bruhwiler, L.: Attribution of spatial and temporal variations in terrestrial methane flux over North America, *Biogeosciences*, 7, 3637–3655, doi:10.5194/bg-7-3637-2010, 2010.
- Xu, X. F., Hahn, M., Kumar, J., Yuan, F. M., Tang, G. P., Thornton, P., Torn, M., and Wullschleger, S.: Upscaling plot-scale methane flux to an eddy covariance tower domain in Barrow, AK: integrating in-situ data with a microbial functional group-based model, AGU Annual Fall meeting, San Francisco, 2014.
- Yokota, T., Yoshida, Y., Eguchi, N., Ota, Y., Tanaka, T., Watanabe, H., and Maksyutov, S.: Global concentrations of CO₂ and CH₄ retrieved from GOSAT: First preliminary results, *Sola*, 5, 160–163, 2009.
- Yvon-Durocher, G., Allen, A. P., Bastviken, D., Conrad, R., Gudasz, C., St-Pierre, A., Thanh-Duc, N., and Del Giorgio, P. A.: Methane fluxes show consistent temperature dependence across microbial to ecosystem scales, *Nature*, 507, 488–491, 2014.
- Zhang, Y., Sachs, T., Li, C., and Boike, J.: Upscaling methane fluxes from closed chambers to eddy covariance based on a permafrost biogeochemistry integrated model, *Glob. Change Biol.*, 18, 1428–1440, 2012.
- Zhu, X., Zhuang, Q., Chen, M., Sirin, A., Melillo, J., Kicklighter, D., Sokolov, A., and Song, L.: Rising methane emissions in response to climate change in Northern Eurasia during the 21st century, *Environ. Res. Lett.*, 6, 045211, doi:10.1088/1748-9326/6/4/045211, 2011.
- Zhu, Q., Riley, W. J., Tang, J., and Koven, C. D.: Multiple soil nutrient competition between plants, microbes, and mineral surfaces: model development, parameterization, and example applications in several tropical forests, *Biogeosciences*, 13, 341–363, doi:10.5194/bg-13-341-2016, 2016.
- Zhuang, Q., Melillo, J. M., Kicklighter, D. W., Prinn, R. G., McGuire, A. D., Steudler, P. A., Felzer, B. S., and Hu, S.: Methane fluxes between terrestrial ecosystems and the atmosphere at northern high latitudes during the past century: A retrospective analysis with a process-based biogeochemistry model, *Global Biogeochem. Cy.*, 18, GB3010, doi:10.1029/2004GB002239, 2004.
- Zona, D., Gioli, B., Commane, R., Lindaas, J., Wofsy, S. C., Miller, C. E., Dinardo, S. J., Dengei, S., Sweeney, C., Karion, A., Chang, R. Y.-W., Henderson, J. M., Murphy, P. C., Goodrich, J. P., Moreaux, V., Liljedahi, A., Watts, J. D., Kimball, J. S., Lipson, D. A., and Oechel, W. C.: Cold season emissions dominate the Arctic tundra methane budget, *P. Natl. Acad. Sci. USA*, 113, 40–45, 2016.