Soil Methanotrophy Model (MeMo v1.0): a process-based model to quantify global uptake of atmospheric methane by soil

5 Fabiola Murguia-Flores[1], Sandra Arndt[1,2], Anita L. Ganesan[1], Guillermo N. Murray-Tortarolo[3,4], Edward R.C. Hornibrook[5,6]

[1]School of Geographical Sciences, University of Bristol, Bristol, BS8 1SS, United Kingdom
[2]*Current address:* Department of Geosciences, Environment and Society, Université Libre de Bruxelles, Brussels, Belgium
[3]University of Exeter, Devon, EX4, United Kingdom
10 [4] *Current address:* Instituto de Investigaciones en Ecosistemas y Sustentabilidad (IIES), UNAM.
[5]School of Earth Sciences, University of Bristol, Bristol, BS8 1RJ. United Kingdom
[6]*Current address:* Earth, Environmental and Geographic Sciences, The University of British Columbia, Okanagan Campus, Kelowna, BC, Canada V4V 1C7

Correspondence to: Fabiola Murguia-Flores (fmurguia84@gmail.com)

15 **Abstract.**

Soil bacteria known as methanotrophs are the sole biological sink for atmospheric methane (CH_4), a powerful greenhouse gas that is responsible for ~20% of the human-driven increase in radiative forcing since pre-industrial times. Soil methanotrophy is controlled by a plethora of different factors, including temperature, soil texture and moisture or nitrogen content, resulting in spatially and temporally heterogeneous rates of soil methanotrophy. As a
20 **consequence, the exact magnitude of the global soil sink, as well as its temporal and spatial variability remains poorly constrained. We developed a process-based model (Methanotrophy Model; MeMo v1.0) to simulate and quantify the uptake of atmospheric CH_4 by soils on the global scale. MeMo builds on previous models by Ridgwell et al. (1999) and Curry (2007) by introducing several advances, including: (1) a general analytical solution of the one-dimensional diffusion-reaction equation in porous media, (2) a refined representation of nitrogen inhibition on soil**
25 **methanotrophy, and (3) updated factors governing the influence of soil moisture and temperature on CH_4 oxidation rates. We show that the improved representation of these key drivers of soil methanotrophy resulted in a better fit to observational data. A global simulation of soil methanotrophy for the period 1990-2009 using MeMo yielded an average annual sink of 34.3 ± 4.3 Tg CH_4 yr^{-1}. Warm and semiarid regions (tropical deciduous forest, dense and open shrubland) had the highest CH_4 uptake rates of 630 and 580 mg CH_4 m^{-2} y^{-1}, respectively. In these regions, favorable**
30 **annual soil moisture content (~20% saturation) and low seasonal temperature variations (variations < ~6 ºC) provided optimal conditions for soil methanotrophy and soil-atmosphere gas exchange. In contrast to previous model**

analyses, but in agreement with recent observational data, MeMo predicted low fluxes in wet tropical regions because of refinements in describing the influence of excess soil moisture on methanotrophy. Tundra and boreal forest had the lowest simulated CH_4 uptake rates of 179 and 187 mg CH_4 m^{-2} y^{-1}, respectively, due to their marked seasonality driven by temperature. Soil uptake of atmospheric CH_4 was attenuated by up to 10% in regions receiving high rates

5   of nitrogen deposition. Globally, nitrogen deposition reduced soil uptake of atmospheric CH_4 by 0.34 Tg y^{-1}, which is an order of magnitude lower than reported previously. In addition to improved characterization of the contemporary soil sink for atmospheric CH_4, MeMo provides an opportunity to quantify more accurately the relative importance of soil methanotrophy in the global CH_4 cycle in the past and its capacity to contribute to reduction of atmospheric CH_4 levels under future global change scenarios.

10   **1 Introduction**

Methane (CH_4) is the most abundant organic trace gas in the atmosphere and responsible for approximately 20% of the human-driven increase in radiative forcing since preindustrial times (Myhre et al., 1998; Ciais et al., 2013). Anthropogenic activities during the last 200 years have increased the concentration of CH_4 in the atmosphere from pre-industrial levels of approximately 710 parts per billion (ppb) to the current mixing ratio of approximately 1800 ppb (Etheridge et al., 1998;

15   Kirschke et al., 2013). The atmospheric lifetime of CH_4 is 9.1 ± 0.9 years (Prather et al., 2012) and most CH_4 is consumed in the troposphere via oxidation by OH radicals, which represents ~90% of the global CH_4 sink (Prather et al., 2012; Ciais et al., 2013). Soil bacteria known as methanotrophs consume ~9 to 10% of atmospheric CH_4 and a further ~1% is oxidized by reaction with chlorine radicals from sea salt in the marine boundary layer (Allan et al., 2007; Ciais et al., 2013).

Soil methanotrophy is the only biological sink for CH_4 and its rate is highly dependent on environmental conditions.

20   The total global soil sink is similar in size to global emissions of CH_4 from rice paddies (Kirschke et al., 2013) and consequently year-to-year changes in factors that impact rates of soil CH_4 oxidation may contribute to variability in the interannual growth rate of atmospheric CH_4. Moreover, soil methanotrophy consumes up to 90% of CH_4 produced via methanogenesis in persistently or periodically wet soil and thus factors that impact soil uptake of atmospheric CH_4 may reduce the capacity of soil methanotrophs to attenuate emission of soil-produced CH_4 (Oremland and Culbertson, 1992;

25   Singh et al., 2010).

The rate of methanotrophy in soil is controlled by several environmental factors including temperature, soil texture, moisture and nitrogen (N) content (Czepiel et al., 1995; Le Mer and Roger, 2001; Wang et al., 2005). The influence of these factors on rates of CH_4 oxidation has been widely studied both at the ecosystem level and under laboratory conditions. Positive correlations have been consistently reported between temperature and rates of CH_4 oxidation in soil (Castro et al.,

30   1995; Butterbach-Bahl and Papen, 2002; Rosenkranz et al., 2006; Luo et al., 2013). Atypically low and high soil moisture levels both have a negative impact on rates of atmospheric CH_4 consumption. A soil moisture content of ~20% appears to

yield optimum rates of CH_4 uptake in different ecosystems, including tropical forests, short grass steppe and tundra (Adamsen and King, 1993; Mosier, 2002; Burke et al., 1999; Castro et al., 1995; Epstein et al., 1998; Klemedtsson and Klemedtsson, 1997; McLain and Ahmann, 2007; West et al., 1999). Soil texture impacts the ability of soil to retain water and influences diffusion of atmospheric CH_4 and O_2 into soil because of its control on pore size and connectivity. Thus

5   sandy soil generally exhibits higher rates of CH_4 uptake than silt-rich soil followed by clayey soil (Born et al., 1990; Dörr et al., 1993). The influence of N input from atmospheric deposition and fertilizer application is more complex; however, the majority of studies report inhibition of soil methanotrophy with increased addition of N (Aronson and Helliker, 2010; Bodelier and Laanbroek, 2004; Fang et al., 2014).

There is a large year-to-year uncertainty in the accounting of the global CH_4 budget, particularly for processes that

10   consume CH_4 (Kirschke et al., 2013). Our understanding of the main drivers of CH_4 uptake in soils and how those factors respond to climate change is incomplete. Estimates of the soil CH_4 sink based upon field data (Dutaur and Verchot, 2007) show high variability globally and within different ecosystems. Numerical models provide an efficient means to deal with the spatial and temporal heterogeneity and to evaluate mechanistic understanding of physical and biological processes that influence soil methanotrophy. Ultimately, models enable derivation of regional and global estimates of soil uptake of

15   atmospheric CH_4 and provide the ability to predict the response of soil methanotrophy to past and future global change. In addition, they provide a platform of interdisciplinary knowledge synthesis, help identify the most important parameters and environmental controls and can thus inform future field and laboratory research.

Several biogeochemical models have been developed to quantify global consumption of atmospheric CH_4 by soil. The model of Potter et al. (1996) (hereafter referred to as 'P96' model) estimated terrestrial uptake of CH_4 by calculating

20   diffusive flux of atmospheric CH_4 into soil using a modified version of Fick´s first law. Ridgwell et al. (1999) (hereafter referred to as 'R99' model) improved the P96 model by explicitly accounting for microbial CH_4 oxidation in soil. The R99 model quantifies CH_4 oxidation rates as a function of soil temperature, moisture and N content. The latter parameter was estimated using agricultural land area as a proxy for fertilizer application. Solution of the resulting one-dimensional diffusion-reaction equation was approximated semi-numerically assuming steady state conditions. Curry (2007) (hereafter

25   referred to as 'C07'model) employed a steady state analytical solution of the one-dimensional diffusion-reaction equation and introduced a scalar modifier to account for the regulation of CH_4 oxidation rates by soil moisture and the impact of temperature below 0°C. The C07 model continued to use the R99 agricultural land area approximation to evaluate the effect of N loading on CH_4 uptake. The C07 model has been employed as a reference model for the Global Carbon Project (Kirschke et al., 2013) and has been used to estimate global CH_4 uptake in dynamic global vegetation models, such as the

30   Lund-Potsdam-Jena model (LPJ-WHy-Me; Wania et al., 2010; Spahni et al., 2011).

Over the past decade, the increased availability of new observational and experimental data has led to an improved characterisation of CH_4 oxidation processes in soil and thus, an opportunity to revise and enhance model parameterization and validation. For example, new global datasets quantifying N deposition now enable better representation of this key inhibitory effect on soil uptake of atmospheric CH_4 (Lamarque et al., 2013).

Here we present an updated process-based model to quantity the global sink for atmospheric CH_4 by soil (hereafter referred to as 'MeMo': soil **Me**thanotrophy **Mo**del). MeMo builds on the R99 and C07 models; however, it is based on a more general analytical solution of the one-dimensional diffusion-reaction equation, which makes obsolete the *a priori* assumption of complete CH_4 consumption in the model domain applied in the C07 model. The refinement now also

5   provides the opportunity to account for CH_4 flux from below (*i.e.*, due to CH_4 production in soil, if present). In addition, MeMo revisits and improves R99 and C07 model formulations to incorporate advances in the mechanistic understanding of soil methanotrophy that have resulted from availability of new data. Finally, MeMo utilizes for the first time N deposition data to explore more accurately the effect of land-use and land-use changes on the global CH_4 sink. We present a comprehensive description of the new model, a comparison of MeMo with the R99 and C07 models, and a critical discussion

10   of model formulations and assumptions based on observational data. We then provide an assessment of global and regional soil uptake and variability across ecosystem types and seasons.

2.0 Model Description

The following sections provide a detailed description of MeMo in the context of existing global soil CH_4 uptake. Table 1 provides a summary of all terms, names and units used in the model description section, while Table 2 contains a short

15   summary of the four existing global CH_4 uptake models.

Table 1. Terms, names and units used in the model description section.

Terms	Name	Units
CH_4	CH_4 concentration	mg m^{-3}
J_{CH4}	CH_4 flux uptake	mg CH_4 m^{-2} mo^{-1}
C_{CH4}	Atmospheric CH_4 concentration	ppb
F_{CH4}	CH_4 flux through L	mg CH_4 m^{-2} mo^{-1}
A and B	Integration constants	dimensionless
z	Depth in the soil profile	cm
L	Depth of 99.9% penetration of atmospheric CH_4 into the soil	cm
D_{CH4}	Diffusion coefficient of CH_4 into soil	cm^2 s^{-1}
k_d	CH_4 oxidation activity	s^{-1}
$D_{0CH4} = 0.196$	CH_4 diffusion in free air at standard temperature and pressure STP= 0°C and 1 atm pressure	cm^2 s^{-1}
G_T	Soil temperature response	°C
G_{soil}	Soil structure response	dimensionless
Φ	Total pore volume	cm^3 cm^{-3}
ρ	Bulk density	cm^{-3} g^{-1}
$\mathfrak{d} = 2.65$	Soil particle density	g cm^{-3}
Φ_{air}	Air-filled porosity	cm^3 cm^{-3}
θ	Soil water content	%
w	Saturation soil water potential	MPa
b	Clay soil content factor	dimensionless
f_{clay}	Clay soil content	%
k_0	Base oxidation rate constant for uncultivated moist soil at 0°C	s^{-1}

Geoscientific
Model Development
Discussions

r_{SM}	Microbial CH_4 oxidation, soil moisture response	dimensionless
r_T	Microbial CH_4 oxidation, temperature response	dimensionless
r_N	Microbial CH_4 oxidation, nitrogen response	dimensionless
N_{soil}	Nitrogen deposition into soil	g N m^{-2} mo^{-1}
$\alpha = 0.33$	Average coefficient of N deposition inhibition	% mol N^{-1}

2.1 Conservation Equation

The general, one-dimensional mass conservation equation for CH_4 in soil is given by:

$$\frac{\partial CH_4}{\partial t} = -\frac{\partial J_{CH4}}{\partial z} + \sum R \tag{1}$$

Where J_{CH4} denotes the flux of CH_4 and ΣR is the sum of all production and consumption processes that affect CH_4 concentrations in soil. The flux J_{CH4} in the soil is generally controlled by diffusion. Consequently, the P96 model assumes that global uptake of atmospheric CH_4 by soil is diffusion limited and thus describes the soil CH_4 sink as a purely diffusive process (*i.e.*, $\sum R = 0$). However, CH_4 is consumed by microbial activity in the soil and the simplified diffusion model may thus underestimate total uptake of CH_4. Consequently, R99 extended the diffusion model by explicitly accounting for microbial oxidation of CH_4 through a first order rate expression. The resulting diffusion- reaction equation forms the basis of the R99 model, the C07 model and MeMo:

$$\frac{\partial CH4}{\partial t} = -D_{CH4} \frac{\partial^2 CH4}{\partial z^2} + k_d * CH_4 \tag{2}$$

Where D_{CH4} is the CH_4 diffusion coefficient and k_d the first-order rate constant for microbial CH_4 oxidation. Under steady-state conditions (*i.e.*, $\partial CH_4/\partial t=0$), soil CH_4 uptake is controlled by the balance between diffusion of CH_4 into soil and the rate of microbial CH_4 oxidation. Hence, accurate characterization of D_{CH4} and k_d is essential for a robust quantification of CH_4 uptake by soil.

2.2 Solution of Reaction-Transport Equation

The R99 model solved Eq. (2) semi-numerically by (i) assuming steady-state, (ii) numerically approximating the diffusion term similar to the approach applied in the P96 model (Table 2, Eq. 11), and (iii) assigning CH_4 oxidation exclusively to a distinct soil layer of thickness ϵ at depth $z_d = 6$ cm (Table 2, Eq. 12). However, CH_4 consumption can occur throughout a soil profile and thus Eq. (12) (Table 2) may either overestimate or underestimate the CH_4 sink.

Geoscientific
Model Development
Discussions

In the C07 model, Eq. (2) was solved analytically, providing a more accurate and mathematically robust estimate of CH$_4$ uptake Eq. (13) (Table 2). Assuming steady-state and constant D_{CH4} and k_d throughout the soil profile, integration of Eq. (2) provides a general solution for determining CH$_4$ concentration at depth z in soil:

5
$$CH_4(z) = A * exp\left(-\sqrt{\frac{k_d}{D_{CH4}}}z\right) + B\ exp\left(\sqrt{\frac{k_d}{D_{CH4}}}z\right) \tag{3}$$

Where A and B are integration constants that can be determined by setting upper and lower boundary conditions for the soil profile. The concentration of CH$_4$ at the soil-atmosphere interface is defined by the atmospheric concentration of CH$_4$ (C_{CH4}) and thus, a Dirichlet boundary (*i.e.*, fixed concentration) is applied at the upper boundary. Conditions at the lower boundary

10 are more challenging to ascribe because the soil depth at which atmospheric CH$_4$ is completely consumed is not known *a priori*.

Negligible CH$_4$ flux through the lower boundary (C07 Solution)

The C07 model circumvents the problem by applying a homogenous Neumann (no-flux) condition at the lower model

15 boundary: $\frac{dCH_4}{d_z}\big|_{z->\infty} = 0$

The application of this boundary condition allows derivation of the integration constants $A = C_{CH4}$ and $B = 0$, which simplifies Eq. (3) to:

$$CH_4(z) = C_{CH4} * exp\left(-\sqrt{\frac{k_d}{D_{CH4}}} * z\right) \tag{4}$$

20

The diffusive uptake of atmospheric CH$_4$ at the soil-atmosphere interface can then be calculated using the derivative of Eq. (4) at $z = 0$:

$$J_{CH4} = -D_{CH4} * \frac{dCH4}{d_z}\big|_{z=0} = D_{CH4} * C_{CH4} * \sqrt{\frac{k_d}{D_{CH4}}} = C_{CH4}\sqrt{D_{CH4}k_d} \tag{5}$$

25

This formulation of soil uptake is the simplest analytical solution to Eq. (2). It represents an improvement from the semi-numerical representation used in the R99 model and enables complete consumption of CH$_4$ to be accounted for within the soil layer; however, the homogeneous Neumann boundary condition applied here is only an approximation, which is not generally valid. The simulation will not be influenced if the Neumann boundary is infinitely far from the consumption depth

30 of CH$_4$ and thus, the corresponding Neumann boundary conditions can be neglected. However, if this is not the case, it will result in simulation error.

Geoscientific
Model Development
Discussions

Complete consumption of CH$_4$ at an a priori unknown depth L (MeMo solution)

Therefore, we adopted an approach similar to the C07 model but one that is generally valid. We assume that methanotrophy

consumes atmospheric CH$_4$ in the soil until CH$_4$ is fully depleted at an *a priori* unknown depth L (i.e. CH$_4$ (L) = 0). The

integration constants in Eq. (3) thus become:

$$A = \frac{c_{CH4} * exp\left(\sqrt{\frac{k_d}{D_{CH4}}}L\right)}{\left[-exp\left(-\sqrt{\frac{k_d}{D_{CH4}}}L\right) + exp\left(\sqrt{\frac{k_d}{D_{CH4}}}L\right)\right]} \tag{6}$$

$$B = \frac{c_{CH4} * exp\left(-\sqrt{\frac{k_d}{D_{CH4}}}L\right)}{\left[-exp\left(-\sqrt{\frac{k_d}{D_{CH4}}}L\right) + exp\left(\sqrt{\frac{k_d}{D_{CH4}}}L\right)\right]} \tag{7}$$

In addition to the concentration condition CH_4 (L)= 0, a flux condition also is imposed on the lower boundary in order to

determine depth L: $-D_{CH4} * \frac{dCH4}{d_z}|_{z=L} = F_{CH4}$

Where F_{CH4} denotes a potential CH$_4$ flux across the lower boundary that can be specified or set equal to zero. The

unknown depth L at which $CH_4 = 0$ is then calculated by substituting the derivative of Eq. (3) into the expression for the

lower boundary condition:

$$-D_{CH4} * \frac{dCH4}{dz}|L = -D_{CH4} * \left(A\left(-\sqrt{\frac{k_d}{D_{CH4}}}\right) * exp\left(-\sqrt{\frac{k_d}{D_{CH4}}}L\right) + B\sqrt{\frac{k_d}{D_{CH4}}} * exp\left(\sqrt{\frac{k_d}{D_{CH4}}}L\right)\right) = F_{CH4} \tag{8}$$

Rearranging Eq. (8) and finding its root allows determination of the initially unknown depth L:

$$0 = \frac{-2*c_{CH4} * exp\left(\sqrt{\frac{k_d}{D_{CH4}}}L\right) * \sqrt{\frac{k_d}{D_{CH4}}} * exp\left(-\sqrt{\frac{k_d}{D_{CH4}}}L\right)}{\left[-exp\left(-\sqrt{\frac{k_d}{D_{CH4}}}L\right) + exp\left(\sqrt{\frac{k_d}{D_{CH4}}}L\right)\right]} - F_{CH4} \tag{9}$$

Once L is known total CH$_4$ uptake can be calculated from:

$$J_{CH4} = -D_{CH4} * \frac{dCH4}{d_z}|_{z->z=0} = -D_{CH4}\left(-A\sqrt{\frac{k_d}{D_{CH4}}} + B\sqrt{\frac{k_d}{D_{CH4}}}\right) \tag{10}$$

Geoscientific
Model Development
Discussions

Where A and B are defined by Eqs. (6) and (7). When L tends to infinity Eq. (10) is equivalent to C07 solution; however, Eq. (10) also allows for (i) complete consumption of CH_4 within the soil interval, and (ii) influx of CH_4 from beneath the soil profile (*e.g.*, from thawing permafrost or production of CH_4 in oxygen-depleted soils).

Figure 1 illustrates CH_4 soil profiles and the penetration depth of CH_4 into soil, L, for different k_d values, $F_{CH4} = 0$

5 and $D_{CH4} = D_{0CH4}$ (diffusivity in free air) (Table1). It is expected that L will vary spatially depending on local k_d, D_{CH4} and soil properties.
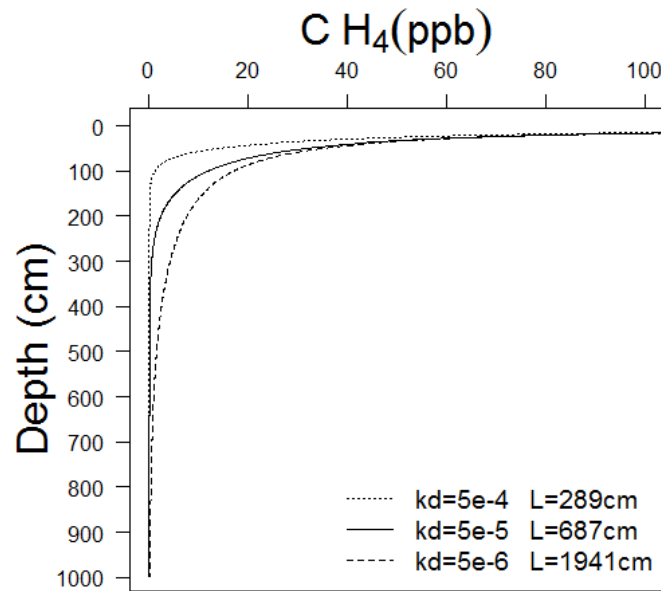
Figure 1: Computational solution of Eq. (9) for different values of k_d. Parameter L is defined as the depth where 99.9% of CH_4 in soil pore spaces is removed.

10

Table 2. Descriptions of four soil methanotrophy models.

Model / Study	Description	CH_4 uptake calculation (J_{CH4})	Eq.
P96 Potter et al. (1996)	Model based on Fick's first law. The calculation of the uptake flux is approximated numerically and based on the diffusion of CH_4 into soil.	$J_{CH4} = D_{CH4} \frac{\Delta C_{CH4}}{\Delta_z}$	(11)
R99 Ridgwell et al. (1999)	R99 extends the P96 model by including an explicit term for microbial oxidation of CH_4 in soil. The uptake flux is approximated numerically, using Fick's first law and adopting a first	$J_{CH4} = \frac{C_{CH4} D_{CH4}}{z_d}\left(1 - \frac{D_{CH4}}{D_{CH4} + k_d z_d}\right)$	(12)

	order rate law for microbial oxidation, assuming that oxidation occurs in a thin ϵ cm layer located at 6 cm depth.		
C07 Curry (2007)	C07 adopts the diffusion-reaction equation that underlies R99. However, C07 solves the equation analytically (as opposed to semi-numerically). The model also improves representation of soil moisture influence on the microbial oxidation rate. C07 refines methanotrophy response at subzero temperatures on the basis of observations.	$J_{CH4} = C_{CH4} r_N r_w \sqrt{D_{CH4} k_d}$	(13)
MeMo This study	Incorporates a general mathematical description of CH_4 uptake flux, allowing for complete consumption of CH_4 at an initially unknown depth L and CH_4 flux through the lower boundary. Refines representation of the influence of soil moisture, temperature and nitrogen deposition on CH_4 oxidation.	$J_{CH4} = -D_{CH4} \left(-A \sqrt{\frac{k_d}{D_{CH4}}} + B \sqrt{\frac{k_d}{D_{CH4}}} \right)$	(10)

MeMo is based on the more general solution (Eq. (10)) and uses local methanotrophy rates (k_d) and diffusion coefficients (D_{CH4}) based upon soil conditions to determine CH_4 penetration depths (L). We assume no *in situ* production of CH_4 or upward CH_4 flux from below (*i.e.*, $F_{CH4} = 0$) because of a scarcity of field data for model validation. However, a flux
5   from below can be employed in MeMo to enable a more comprehensive quantification of soil CH_4 uptake that also potentially accounts for consumption of upward migrating CH_4 and autochthonous CH_4 produced in oxygen-depleted microsites of finely textured soil.

2.3 Parameters

The rate of CH_4 uptake by soil is controlled by the balance between gaseous diffusion of atmospheric CH_4 into soil and the
10   rate of CH_4 oxidation by methanotrophic bacteria as described by Eq. (14) and Eq. (20), respectively. Thus, D_{CH4} and k_d are key parameters and accurate characterization of their values is essential for robust quantification of the soil CH_4 sink.

Geoscientific
Model Development
Discussions

Open Access

2.3.1 Soil CH$_4$ Diffusivity, D_{CH4}

Similar to the R99 and C07 model, D_{CH4} in MeMo is determined from the diffusivity of CH$_4$ in free air (D_{0CH4}; Table 1) adjusted for the influence of temperature (G_T) and soil structure (G_{soil}):

$$D_{CH4} = D_{0CH4} * G_T * G_{soil} \tag{14}$$

The gaseous diffusion coefficient of CH$_4$ in soil increases linearly with temperature T (°C) (Potter et al., 1996) according to the relationship:

$$G_T = 1.0 + 0.0055\, T\ (\text{°C}) \tag{15}$$

The soil structure factor (G_{soil}) accounts for the effects of pore size, connectivity and tortuosity on gaseous diffusion and is determined according to the parameterization of Moldrup et al. (1996):

$$G_{soil} = \Phi^{4/3} \left(\frac{\Phi_{air}}{\Phi} \right)^{1.5+3/b} \tag{16}$$

Where Φ is total pore volume (cm^3 cm^{-3}), Φ_{air} is air-filled porosity (cm^3 cm^{-3}) and b is a scalar that accounts for soil structure. Total pore volume is defined as a function of bulk density ρ (g cm^{-3}) and average particle density d (Table 1) (Brady et al., 1999):

$$\Phi = 1 - \left(\frac{\rho}{d} \right) \tag{17}$$

The scalar b in Eq. (16) is calculated as a function of soil clay content (f_{clay}; %) as proposed by Saxton et al. (1986):

$$b = 15.9\, f_{clay} + 2.91 \tag{18}$$

Air-filled porosity (Φ_{air}) is determined from the difference between total pore volume and soil water content θ (%):

$$\Phi air = \Phi - \theta \tag{19}$$

10

Geoscientific
Model Development
Discussions

2.3.2 Rate Constant for CH$_4$ Oxidation, k_d

The CH$_4$ oxidation rate (k_d) is defined as the base oxidation rate constant (k_0) for an uncultivated moist soil at 0° C scaled by three factors to account for the influence of soil moisture (r_{SM}), soil temperature (r_T), and nitrogen content (r_N):

5    $$k_d = k_0 * r_{SM} * r_T * r_N \qquad\qquad (20)$$

The R99 and C07 models used a similar equation to estimate k_d but without the r_N parameter, opting instead to employ intensity of agricultural activity as a proxy to account for the inhibitory effects of N deposition on soil methanotrophy. Moreover, model C07 excluded r_N from the k_d formulation and used a N deposition term to modify total CH$_4$ uptake flux
10   (Table 2, Eq. 13), which results in a larger N inhibition effect. The approach employed in MeMo is to use N deposition data directly to modify k_d.

2.3.3 Base Oxidation Rate Constant, k_0

The base oxidation rate constant (k_0) is a key parameter that exerts significant control on k_d and thus the estimated CH$_4$
15   uptake flux. For example, a 10-fold change in k_0 (and thus k_d) leads to a 3-fold decrease in the depth L at which CH$_4$ is fully depleted from soil pores (Fig. 1) and a ~3-fold increase in total uptake of CH$_4$ (Fig. 2).
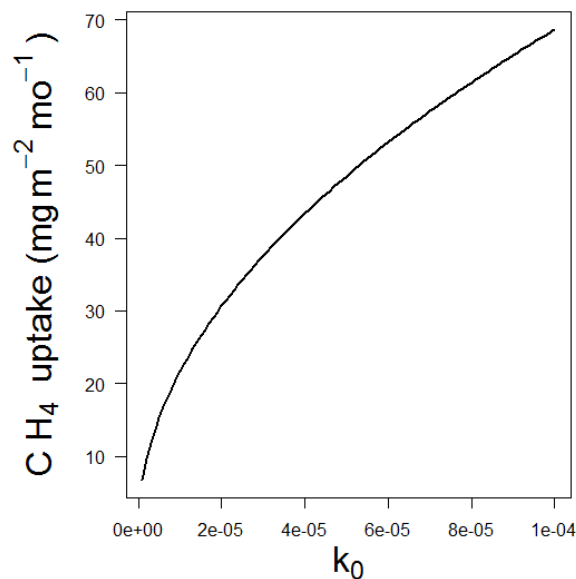

Figure 2: Total CH$_4$ uptake for different values of k_0 (s^{-1}), assuming a constant value of $D_{CH4} = D_{0CH4}$ and no modification by soil temperature, moisture or nitrogen deposition.

20

Geoscientific
Model Development
Discussions

Rate constants can be defined either on the basis of theoretical considerations or through site-specific field and laboratory observations. Rates of soil microbial processes, such as CH_4 oxidation, are controlled by microbial biomass dynamics and community structure, and, thus a complex array of environmental factors, including temperature, substrate (CH_4) concentration, land use, moisture, pH and soil type (Ho et al., 2013). The influence of these environmental factors on

5   microbial CH_4 oxidation rates is not well characterized and thus all factors are not explicitly represented in models. Consequently, apparent rate constants implicitly account for some environmental factors via fitting field observations or laboratory experiments, resulting in parameter values that may be more environment- and model-specific. A possible limitation of such an approach is reduced transferability and predictive capacity in other environments or from a regional to the global scale. For example, Ridgwell et al. (1996) derived a single global estimate of $k_0 = 8.7 \times 10^{-4}$ s^{-1} by fitting Eq. (12)

10   to 13 measured values of J_{CH4}, D_{CH4} and soil temperature from four different studies. In contrast, Curry (2007) estimated a global k_0 of 5.0×10^{-5} s^{-1} based upon fitting Eq. (13) to a five-year time series of J_{CH4} and soil temperature, moisture and CH_4 flux measurements from a single site in Colorado (Mosier et al., 1996). The order of magnitude difference in k_0 between the R99 and C07 models illustrates the potential model-specific nature of parameter values derived from experimental and observational data, as well as the limits and challenges for transferability. Soil methanotrophy is not unique in this regard

15   and parameterization of microbially mediated processes remains a common problem more generally in modelling approaches (*e.g.*, Arndt et al., 2013; Bradley et al., 2016).

Parameterization of k_0 in MeMo has been refined using recently time-series data published by Luo et al., (2013) and consisting of daily soil CH_4 uptake, temperature and soil moisture from three contrasting environments: temperate forest (Hoglwald Germany), tropical rainforest (Bellenden Ker Australia) and steppe (Inner Mongolia, China). The data sets were

20   used to explore potential variations in apparent k_0 values in different environments, including comparison with k_0 values from models R99 and C07. Data from each site were interpolated according to Eq. (10) to derive an apparent k_0 value for each biome. The k_0 values for temperate forest and steppe are similar to the k_0 value employed in the C07 model; however, the apparent k_0 for tropical forest is approximately three times smaller than the C07 k_0 value. The three newly derived k_0 values were employed in MeMo for their respective biomes and the k_0 value from the C07 model ($k_0 = 5.0 \times 10^{-5}$ s^{-1}) was

25   used for all other regions for which no biome specific k_0 values exist (Table 3). Similar k_0 values of 5.0×10^{-5} s^{-1} for temperate forest, steppe and short grass steppe indicate that this magnitude of k_0 is appropriate for many ecosystems. Yet, apart from the tropical wet forest, the data clearly indicate additional controls and the use of $k_0 = 1.6 \times 10^{-5}$ s^{-1} will thus prevent an overestimation of simulated fluxes. Nevertheless, further research is required to better characterize this key parameter.

30

Table 3. k_0 values from models R99 and C07 and new k_0 values employed in MeMo that were determined based upon temperate forest, tropical forest and steppe data from Luo et al. (2013).

Model	Biome	k_0 (s^{-1})

R99	Global	8.7×10^{-4}
C07	Global	5.0×10^{-5}
MeMo	Temperate forest	4.0×10^{-5}
	Tropical forest	1.6×10^{-5}
	Steppe	3.6×10^{-5}
	Other ecosystems	5.0×10^{-5}

2.3.4. Soil Moisture Factor, r_{SM}

Both low and high soil moisture levels can negatively impact soil uptake of atmospheric CH_4 (Schnell and King, 1996; von Fischer et al., 2009). Scarcity of soil water generally inhibits soil microbial activity while excessive moisture attenuates gas diffusion, limiting entry of atmospheric CH_4 and O_2 into soil (Burke et al., 1999; McLain et al., 2002; McLain and Ahmann, 2007; West et al., 1999).

The R99 and C07 models incorporated parameters to address the limiting effects of low soil moisture levels on CH_4 uptake fluxes. The R99 model applied a soil moisture factor adopted from Potter et al. (1986) where r_{SM} was calculated as a proportional ratio of precipitation (P) plus soil moisture (SM) divided by potential evapotranspiration (ET; Table 4, Eq. (21)). It was assumed that r_{SM} decreases linearly when $(P+SM)/ET$ is less than one. The C07 model modified the response of soil methanotrophy to moisture using an empirical water stress parameterization and soil water potential based on findings from Clapp and Hornberger (1978) (Table 4, Eq. (22)). A consequence of that approach is that r_{SM} decreases logarithmically to zero at an absolute soil water potential of $w < 0.2$ MPa (Fig. 3).

In MeMo, soil moisture (%) is used to calculate r_{SM} and a formulation similar to the C07 model is used for low soil moisture values. A threshold of <20% soil moisture is applied because that value corresponds to optimum conditions for CH_4 oxidation in soil (Castro et al., 1995; Whalen and Reeburgh, 1996) and because inclusion of a water stress parameter better captures CH_4 uptake flux in dry ecosystems (Fig. 3; Curry, 2007).

Establishing parameters to quantify the impact of excess moisture on soil methanotrophy has proven more challenging. The C07 model relied upon soil pore space characteristics in factor G_{soil} (Eq. (16)) to account for decreased gas diffusion and limitation of k_d at high soil moisture content. However, attenuation of gas diffusion is only one impact of high soil water content and it is necessary also to account for the inhibitory effects of excessive moisture on k_d (Boeckx and Van Cleemput, 1996; Dasselaar et al., 1998; Visvanathan et al., 1999). Soil moisture content >20% reduces CH_4 uptake due to a restricted diffusion of CH_4 and supply of O_2. The R99 and C07 models assume that microbial CH_4 oxidation remains active at a soil moisture content of 80%, an assumption that contradicts field investigations, which show that CH_4 uptake decreases rapidly at soil moisture levels >50% (Dasselaar et al., 1998). Thus, the soil moisture factor employed in MeMo also accounts for limitation of microbial CH_4 oxidation at a soil moisture content >20% after which rates of CH_4 uptake begin to decrease (Adamsen and King, 1993; Visvanathan et al., 1999). The r_{SM} factor used in MeMo was determined by fitting a

Gaussian function to laboratory experimental data (Table 4, Eq. (23); Fig. 3a), following the approach of Grosso et al. (2000). The mean r_{SM} and standard deviation determined using this approach were 0.2 ± 0.2.

Table 4. Model R99, C07 and MeMo formulations for r_{SM} response.

Model	Formulation	Eq.	Variable definitions
R99	$r_{SM} = 1$ for P+SM/ETp>1	(21)	P=precipitation
	$r_{SM} = P + SM/ETp$ for P+SM/ET p≤1		SM=soil moisture stored at 30 cm depth
			ETp=potential evapotranspiration
C07	$r_{SM} = 1$ for w<0.2MPa	(22)	w=saturation soil water potential
	$r_{SM} = \left[1 - \dfrac{log_{10}w - log_{10}(0.2)}{log_{10}(100) - log_{10}(0.2)}\right]^{0.8}$ for w≥0.2≤100MPa		
MeMo	$r_{SM} = \left[1 - \dfrac{log_{10}\frac{1}{SM} - log_{10}(0.2)}{log_{10}(100) - log_{10}(0.2)}\right]^{0.8}$ for SM<0.2	(23)	SM=soil moisture
	$r_{SM} = \dfrac{1}{\sqrt[\sigma]{2\pi}} e^{-\frac{1}{2}\left(\frac{SM-0.2}{0.2}\right)^2}$ for SM>0.2		

A soil moisture factor (r_{SM}) was calculated for each set of observational data from independent field sites (Supplementary 1, Table S1) based upon an optimum rate of CH_4 uptake occurring at a soil moisture content of 20% (r_{SM} = 1). The remaining r_{SM} values were computed as a linear ratio of the CH_4 uptake rate at 20% water content. Figure 3b illustrates the pattern of response in methanotrophy rates to changes in soil moisture content in the R99, C07 models and MeMo and the net effect on CH_4 uptake fluxes across a range of absolute soil moisture levels used to force parameter r_{SM}. The CH_4 uptake fluxes were calculated by varying soil moisture content while holding constant all other environmental parameters (temperature, C_{CH4} and N_{dep}). The R99 and C07 models both predict greater CH_4 uptake fluxes than MeMo at soil moisture contents >20% with the R99 model yielding the highest flux rates; however, the C07 model and MeMo yield similar CH_4 uptake rates for much of the soil moisture range. Reduction of CH_4 uptake flux at high soil moisture levels due to attenuation of gas diffusion cannot be managed solely through the term G_{soil} (*i.e.*, reduction in free pore space). MeMo also accounts for inhibition of microbial CH_4 oxidation rates at elevated soil moisture content, predicting lower CH_4 uptake flux as a result of more realistic r_{SM} values determined from the Gaussian response observed in field data from three different global biomes (Luo et al., 2013).

2.3.5. Temperature Factor, r_T

Temperature exerts an important influence on rates of microbial processes and consequently all models parameterize for the effects of temperature on soil methanotrophy. The R99 model employs a Q10 function derived from experimental data with a Q10 factor of 2 change over the temperature interval 0 to 15°C. The model assumes that bacterial methanotrophy ceases at

5   temperatures <0°C (Table 5, Eq. (24)). The C07 model adopts the same Q10 factor as R99 for temperatures >0°C but employs a different response below 0°C. Soil water generally does not freeze at a surface temperature of 0°C and observations from cold regions provide ample evidence for the presence of methanotrophic activity at temperatures <0°C (Vecherskaya et al. 2013). The C07 model allows for a parabolic decrease of methanotrophy rates from 0 to -10°C (Table 5, Eq. (25)) based upon observations of CH_4 uptake in soil at subzero temperatures (Grosso et al., 2000).

10   Parameterization of a temperature factor (r_T) is revisited in MeMo based upon availability of new experimental data for soil from different biomes (Supplementary 1, Table S2). A Q10 factor having a value of 1.95 was determined for the temperature interval 0 to 15 °C by curve fitting and minimizing linear errors ($r^2 = 0.75$, p=1.9 e^{-11}; Table 5, Eq. (26)). The factor r_T was determined by using the observed CH_4 uptake flux at 10°C at each site as the base of the Q10 function (Fig. 3c). An exponential decrease in CH_4 uptake flux was assigned to the temperature range 0 to -5°C as recommend by Castro

15   et al. (1995) and Grosso et al. (2000). Moreover, the amount of frozen soil increases exponentially with decreasing temperatures (Low et al., 1968) and consequently, CH_4 uptake also should decline exponentially.

Table 5. Model R99, C07 and MeMo formulations for r_T response.

Model	T<0°C	T≥0°C	Eq.
R99	$r_T = 0$	$r_T = \exp(0.0693T - 8.56 \times 10^{-7} T^4)$	(24)
C07	$r_T = (0.1T + 1.0)^2$ if T>-10°C	$r_T = \exp(0.0693T - 8.56 \times 10^{-7} T^4)$	(25)
MeMo	$r_T = 1/\exp(-T)$	$r_T = \exp(0.1515 + 0.05238T - 5.946 \times 10^{-7} T^4)$	(26)

20   The pattern of change in the r_T factor and CH_4 uptake flux for the temperature range -10 to 60°C is shown in Fig. 3d. The CH_4 uptake fluxes shown were calculated by varying temperature while holding other environmental factors constant (*i.e.*, soil moisture, N deposition or agricultural land use, and C_{CH4}). All models exhibit an optimum in CH_4 uptake at 25°C characterized by a maximum r_T and CH_4 oxidation rate. The key differences between models are the behavior of r_T at temperatures below 0°C and the amplitude of response curves. The R99 model assumes that methanotrophy activity

25   ceases at 0°C and consequently, CH_4 uptake rates decrease sharply at that temperature. In contrast, models C07 and MeMo both allow for methanotrophy at temperatures <0°C. In general, the exponential decrease of r_T employed in MeMo more closely resembles natural patterns of soil methanotrophy at subzero temperatures than the parabolic decline employed in the C07 model consistent with observations reported by Castro et al. (1999) and Grosso et al. (2000). Although our

parameterization yields a fit similar to C07 to the limited observations available at temperatures <0°C the r_T used in MeMo provides a simpler solution because it does not require multiple conditions to be met. In contrast, the C07 parameterization increases parabolically at temperatures <-10° C, which requires an additional condition to be incorporated into the model to prevent increased rates of CH_4 uptake at very low temperatures. Soil CH_4 uptake fluxes predicted by the C07 model are

5   greater than those calculated using MeMo because of the different parameterization at temperatures <0°C. Finally, the amplitude of the temperature response curve is greater and similar in models C07 and MeMo compared to model R99, in particular, at temperatures >25°C as a result of differences in the formulation and solution for CH_4 uptake flux (Fig. 3d).
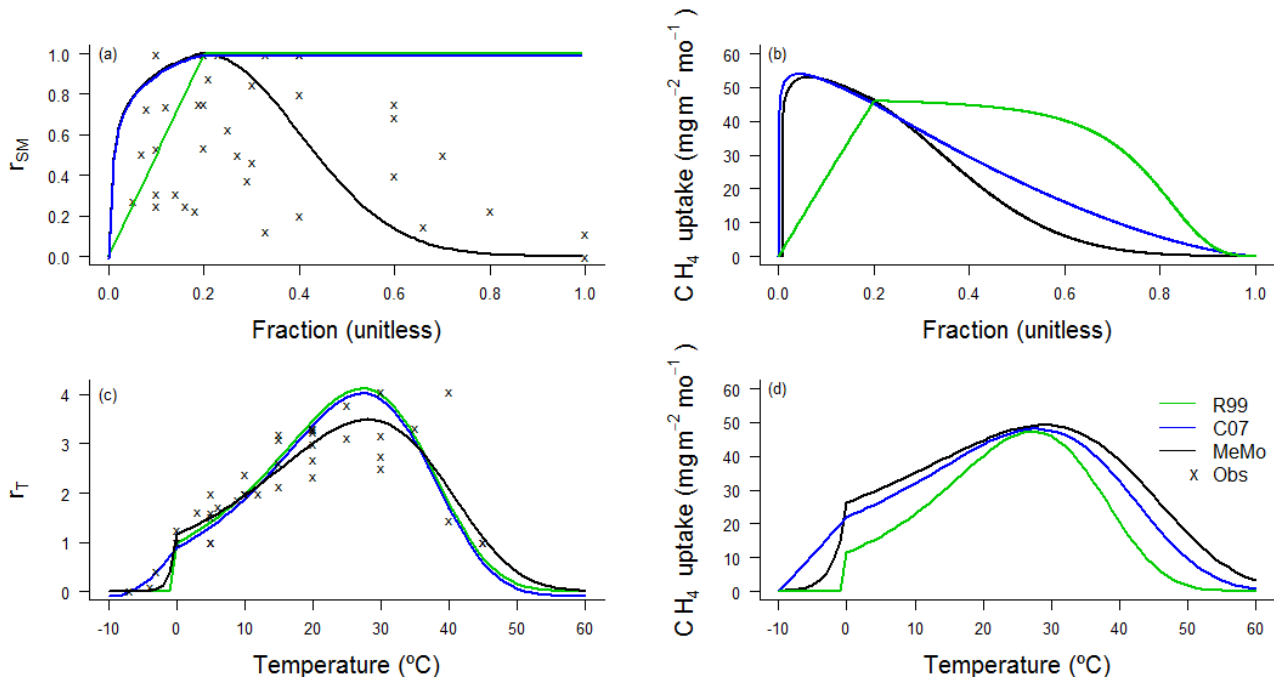
Figure 3: CH_4 uptake response factors (a, c) and uptake fluxes (b, d) as a function of soil moisture (r_{SM}) and temperature (r_T).
10 **Observations (shown as crosses) (r_{SM}, Supplementary 1, Table S1; r_T, Supplementary 1, Table S2), MeMo (black line), C07 (blue line) and R99 (green line).**

2.3.6 Nitrogen Deposition factor, r_N

The effect of nitrogen (N) deposition on CH_4 uptake is not as well constrained as the effects of temperature and soil
15 moisture. In general, field observations have shown that CH_4 consumption rates and thus, uptake fluxes decrease with N additions (Aronson and Helliker, 2010; Butterbach-Bahl and Papen, 2002; Steinkamp et al., 2001). Different processes have been suggested to explain this negative effect. Firstly, methanotrophs and ammonia oxidizers are capable of switching substrates (although the latter microorganisms typically consume N compounds preferentially if available) and therefore the presence of N compound reduces CH_4 consumption (Bradford et al., 2001; Gulledge and Schimel, 1998; Phillips et al., 2001;

Wang and Ineson, 2003; Whalen, 2000). In addition, intermediate and end products from methanotrophic ammonia oxidation (*i.e.*, hydroxilamida and nitrite) can be toxic to methanotrophic bacteria (Bronson and Mosier, 1994; MacDonald et al., 1996; Sitaula et al., 2000). Finally, large amounts of mineral fertilizers (*i.e.*, ammonium salts) can induce osmotic stress in methanotrophs inhibiting CH_4 consumption (Whalen, 2000). However, other studies suggest a positive effect of N

5   fertilization on CH_4 oxidation rates. One of the mechanism invoked to explain the positive effect is a stimulation of nitrifying bacteria to consume CH_4 by increased inputs of N due to an improvement in living conditions (Cai and Mosier, 2000; De Visscher and Cleemput, 2003; Rigler and Zechmeister-Boltenstern, 1999). The positive effect of N addition on CH_4 oxidation rates has been observed primarily under experimental conditions and also greatly depends on the local microbial community structure. Therefore, we assumed that N has an inhibitory effect on uptake of atmospheric CH_4 in all scenarios.

10   The C07 and R99 models both account for the negative effect of N inputs on CH_4 uptake fluxes via a N deposition factor r_N. In model R99, r_N directly affects k_d while in model C07 r_N directly modifies the uptake flux. Both models parameterize the negative effect of N inputs on CH_4 oxidation rates as a function of agricultural intensity (as a fraction of area) as a proxy for fertilizer application (Table 6, Eq. (27)). However, the mathematical description of r_N used by R99 and C07 does not account for the enhanced N deposition by anthropogenic activity because its global distribution was not well

15   known at the time of model development. Here, we suggest a mathematical description of r_N that accounts for all anthropogenic N deposition sources: fossil fuel combustion, biomass burning and fertilizer application (Lamarque, 2013).

The computation of r_N in MeMo is a function of: i) the inhibitory effect on CH_4 uptake, and ii) the distribution and amount of N deposition in soil (Zhuang et al., 2013). We estimated the percent reduction of CH_4 uptake per mol of N added based on field and laboratory observations (Supplementary 1, Table S3). We determined an average inhibition α of 0.33

20   %mol N^{-1} based on the mean uptake reduction per mol of N added. The N response function r_N was governed by Eq. (29):
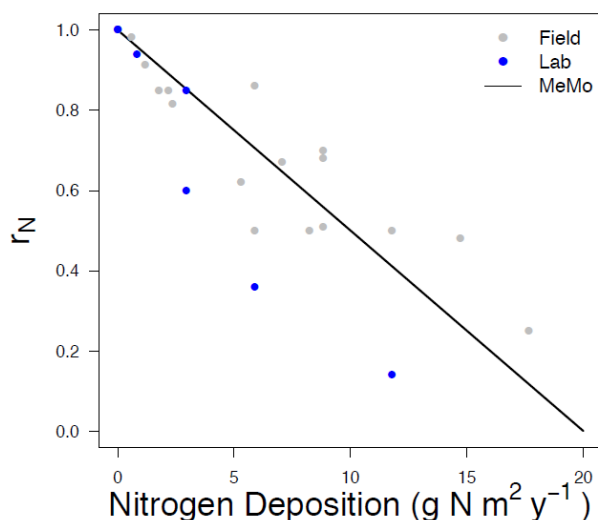
$$r_N = 1 - (N_{soil} * \alpha) \tag{29}$$

Figure 4: CH4 uptake response as a function of nitrogen deposition factor r_N. The linear fit (black line) is based on observations from field and laboratory measurements (gray and blue dots; Supplementary 1, Table S3).

In cases where entry of N deposition into soil is limited by bulk density ρ, ninety percent of N compounds tend to remain at depths $z <= 5$ cm before exponentially decreasing in concentration with depth (Schnell and King, 1994). Thus, N_{soil} was calculated as N deposition (kg N ha^{-1} y^{-1}) divided by ρ at $z = 5$cm:

$$N_{soil} = \frac{Ndep}{(\rho*z)} \qquad (30)$$

Figure 4 shows the change in r_N in relation to N deposition rate and the form of Equation (29).

Table 6. Model R99, C07 and MeMo formulations for r_N response.

Model	Formulation	Eq.	Driving data	
R99	$r_N = 1.0 - (0.75 \times I)$	(27)	I = fractional intensity of cultivation	
C07	$r_N = 1.0 - (0.75 \times I)$	(28)	I = fractional intensity of cultivation (r_N outside of k_d parameterization)	
MeMo	$r_N = 1-(N_{soil}) * \alpha$	(29)	$N_{soil} = \frac{Ndep}{(\rho*z)}$	(30)

3.0 Model implementation

MeMo was implemented in R (version 3.0.1) and simulations were carried out with a spatial resolution of 1°x1° and a monthly temporal resolution for the period between 1990 and 2009. The model code, a simple model case study for year 2000 and output for 1990-2009 are available as a supplement to this manuscript. To enable model-model comparisons and assess the combined effect of all refinements introduced in MeMo on the global CH4 uptake flux estimate, the R99 and C07 models were also implemented in R at identical spatial and temporal resolutions and forced using the same driving data.

3.1 Forcing data

MeMo, the C07 and the R99 model were forced using global, monthly observations of soil moisture, temperature, atmospheric CH4 concentrations, N deposition, soil bulk density, and clay content for the period 1990-2009. Information about data sources and maps of the forcing data are provided in Supplementary 2.

Satellite observations of soil moisture at a spatial resolution of 1x1° and a monthly temporal resolution are available for the period 1990-2009 from Dorigo et al. (2011); however, the data set contains gaps in some regions (*e.g.*, in areas of high-density vegetation). The use of MeMo as a predictive tool to estimate the past and future global CH_4 soil sink relies strongly on the use of soil moisture from standard climate models, such as output from land surface models or Dynamic Global Vegetation Models (DGVMs). Therefore, gaps in the Dorigo et al. (2011) data set were filled using soil moisture data from an ensemble of 9 DGVMs (TRENDY; Sitch et al., 2015). The R99 model parameterizes the effect of soil moisture on CH_4 uptake fluxes as a function of precipitation and evaporation and therefore, R99 was forced using monthly data sets of precipitation (CRU3.1; Harris et al., 2014) and evapotranspiration (TRENDY; Sitch et al., 2015). Temperature forcing is constrained by global data sets for surface temperature as a proxy for soil temperature (CRU3.1; Harris et al., 2014). Monthly mean global atmospheric CH_4 concentrations multiplied by the latitudinal atmospheric CH_4 gradient were calculated from Rigby et al. (2008). The N deposition data were obtained from an atmospheric chemical transport model embedded in an Earth System Model (Lamarque et al., 2013). Because the R99 and C07 models express the influence of N deposition on CH_4 uptake fluxes as a function of agricultural fraction rather than N deposition (see section 2.3.6), R99 and C07 were forced using annual global gridded land-use change data from Hurtt et al. (2011). Finally, global gridded observations for bulk density and clay content were taken from Shangguan et al. (2014).

Areas that have less than 0.5% average annual soil moisture content were masked (*e.g.*, Sahara Desert) because it was assumed CH_4 uptake is negligible under such conditions. If the areas were left unmasked, then MeMo would overestimate CH_4 uptake across the regions due to high temporal variability in the driving data (*e.g.*, a month with no moisture followed by a month with >20%). Irregular short-lived precipitation events in deserts lead to unreliable estimates of soil uptake of atmospheric CH_4 because such areas are unlikely to host well-established communities of methanotrophic bacteria capable of responding rapidly to short-term increases in soil moisture.

4.0 Results and Discussion

The following sections critically evaluate MeMo estimates of the global CH_4 sink (section 4.1), as well as the regional distribution of CH4 uptake and its main drivers (section 4.2) in the context of available field data and published model predictions.

4.1 Global CH4 Uptake by Soils

MeMo predicts an average annual global flux of 34.3 ± 0.6 Tg CH_4 y^{-1} for the period 1990 to 2009. The estimated global uptake compares well with estimates from terrestrial ecosystem models, DGVMs and global atmospheric inversions (Table 7). Zhuang et al. (2013) determined a similar average global uptake flux of 34 ± 2 Tg CH_4 y^{-1} during the 21st century using a modified version of the Terrestrial Ecosystem Model (TEM) while Spahni et al. (2011) estimated an uptake flux of 38.9 Tg CH_4 y^{-1} using the LPJ-WHyMe DGVM. Hein et al. (1997) predicted a similar flux through atmospheric inversions but with a greater level of uncertainty (30 ± 15 Tg CH_4 y^{-1}). Upscaling of field measurements of soil methanotrophy rates from 120

different studies spanning a wide range of ecosystems yielded a value of 36 ± 23 Tg CH_4 y^{-1} (Dutaur and Verchot, 2007). In contrast, flux estimates based upon extrapolation of long-term records of CH_4 uptake in a smaller number of soil types resulted in an estimated flux of 28.7 Tg CH_4 y^{-1} (Dörr et al. 1993). Similarly, global extrapolation of measurements made solely on northern European soils yielded a sink strength of 29 Tg CH_4 y^{-1} (Smith et al. 2000).

5

Table 7. Global CH₄ uptake estimations

Methodology	Reference	Global uptake by soils (Tg CH_4 y^{-1})
Observation	Dörr et al. (1993)	28.7
Observation	Smith et al. (2000)	29
Observation	Dutaur and Verchot (2007)	36 ± 23
Atmospheric inversions	Hein et al. (1997)	30 ± 15
Model (P96)	Potter et al. (1996)	20 ± 3
Model (R99)	Ridgwell et al. (1999)	38.1 ± 1.1
Model	Spahni et al. (2011)	38.9
Model (C07)	Curry (2007)	29.3 ± 0.6
Model	Zhuang et al. (2013)	34 ± 2
Model (MeMo)	**(This study)**	**34.3 ± 0.6**

The average annual soil sink for atmospheric CH_4 estimated by MeMo (34.3 ± 0.6 Tg CH_4 y^{-1}) is greater than global uptake predicted using the P96 and C07 model (20 ± 3 Tg CH_4 y^{-1} and 29.3 ± 0.6 Tg CH_4 y^{-1}, respectively). The R99 model

10   predicts a global sink of 38.1 ± 1.1 Tg CH_4 y^{-1}, which compares more favorably with the MeMo estimate. The observed differences in mean global soil uptake of atmospheric CH_4 estimated using models R99, C07 and MeMo forced with identical data are attributed primarily to three factors: (i) their respective mathematical solutions of reaction-transport equations (section 2.2), (ii) differences in parameterization of k_0 (section 2.3.3), and (iii) differences in formulation of r_N (section 2.3.6). The R99 model predicts soil uptake that is 10% and 24% greater, respectively, than fluxes estimated using

15   MeMo and the C07 model. These differences are due to the R99 model applying a k_0 that is one order of magnitude greater than k_0 values used in the C07 model and MeMo. The amplifying effect of the large k_0 is partially offset by the semi-numerical approximation (Eq. 12) employed in the R99 model, which results in the final global CH_4 uptake flux being of similar magnitude to the MeMo and the C07 model estimates. Finally, the low uptake predicted by the C07 model is a consequence of the parameterization of the nitrogen inhibition effect ($r_{N,}$) and its direct modification of the CH_4 flux rather

20   than the CH_4 oxidation activity (k_d) (section 2.3.3). Nitrogen inhibition was responsible for a global reduction in CH_4 uptake of 0.34 Tg y^{-1} in MeMo compared to 7.3 and 2.3 Tg y^{-1} in the C07 and R99 models, respectively.

Geoscientific
Model Development
Discussions

4.2 Regional CH₄ Uptake by Soils

The latitudinal distribution of soil uptake rates of atmospheric CH_4 predicted using the R99 model, the C07 model and MeMo are shown in Fig. 5 accompanied by direct measurements of CH_4 oxidation rates from Dutaur and Verchot (2007) and a 10° running average. Figure 6 provides globally gridded maps of average simulated CH_4 uptake fluxes from the three
5   models for the period 1990 to 2009 and a comparison between MeMo and the R99 and C07 models.
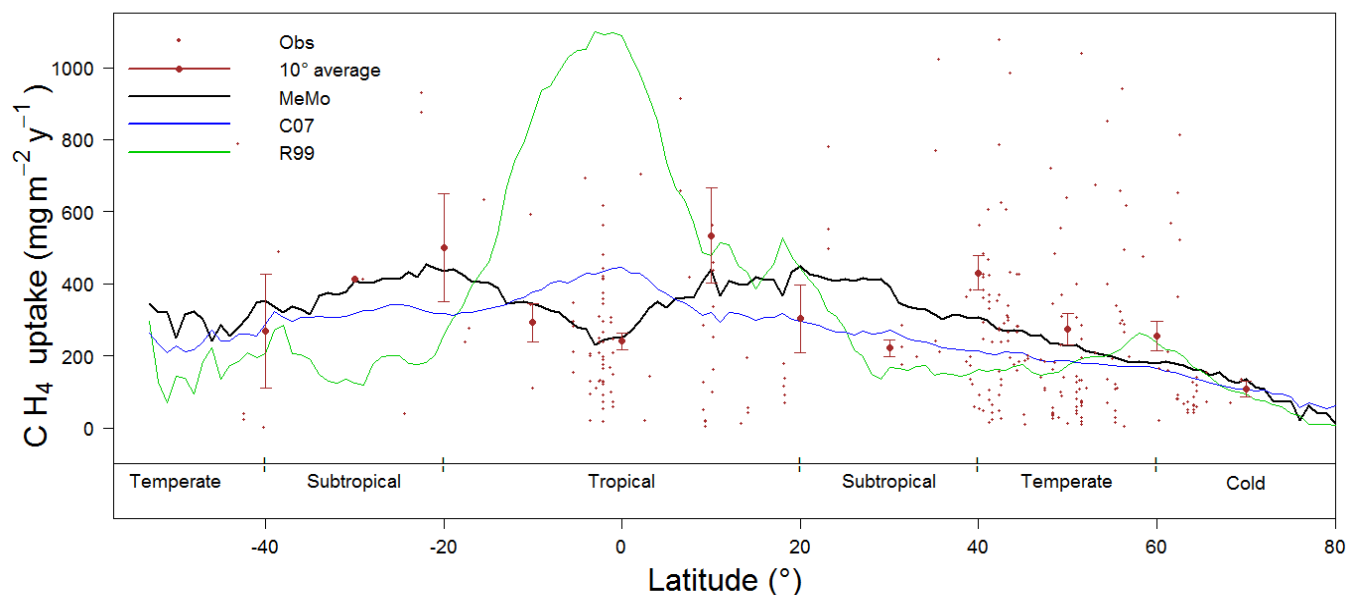
Figure 5. Latitudinal distribution of the soil uptake predicted by models R99 (green line), C07 (blue line) and MeMo (black line). Measurements of CH₄ uptake (small brown dots; Dutaur and Verchot, 2007) and a 10° running mean of direct observations (large brown dots for average with bars representing one standard deviation error).

10

The latitudinal distribution of observations reveals a scarcity of direct measurements of soil methanotrophy from sites in the southern hemisphere. Additionally, the frequency of measurements generally is low and rarely encompasses a full twelve-month period, which creates challenges for verifying model estimates of annual CH_4 uptake fluxes. Observations at specific latitudes typically exhibit a wide range of values, which are reflected in the large standard error bars calculated for
15   the 10° running means (Fig. 5). Nevertheless, the averages of direct observations calculated for each 10° latitude interval show a distinct bimodal pattern with the lowest soil CH_4 uptake fluxes in the tropics and at high latitudes. Maximum rates of CH_4 uptake occur between 10 to 20° in both hemispheres (Fig. 5). MeMo simulates a similar bimodal latitudinal distribution of CH_4 uptake fluxes with an RSME that is 16.6 mg CH_4 m^{-2} y^{-1} lower than other models when fitted to 10° latitudinal averages of observational data. In contrast, the C07 and R99 models both predict a latitudinal distribution of soil
20   methanotrophy that has CH_4 uptake maxima in equatorial regions and lower rates of CH_4 oxidation at mid-latitudes (~40°N and 20 to 40° S), resulting in higher RSMEs of 28 and 72 mg CH_4 m^{-2} y^{-1}, respectively, when fitted to the 10° latitude

averaged data. the R99 model significantly overestimates CH_4 uptake fluxes in the tropics (20°N to 20°S) and underestimates CH_4 oxidation in the subtropics (20 to 40° N and S), resulting in large differences for these regions relative to the MeMo simulations (Fig. 6e). The C07 model predicts a latitudinal pattern of simulated CH_4 fluxes that is similar to R99; however, with much lower uptake fluxes in the tropics and no pronounced minima in the subtropics. Consequently, the

5 RSME of the fit to observational data is much lower and regional differences relative to MeMo generally are smaller, ranging from 30% in the tropics to 20% in the subtropics (Fig. 6d).

The regional differences between MeMo and the R99 and C07 models result from differences in the parameterization of factors that govern CH_4 oxidation rates in the models: k_0, $r_{SM,}$, r_T and r_N. The lower k_0 assigned to tropical wet forest (see section 2.3.3) accounts for the reduction in CH_4 uptake by tropical soil in MeMo. The strong

10 agreement between MeMo simulation results and CH_4 uptake measurements presented in Fig. 5 suggests that the empirically derived lower k_0 value more accurately reflects soil CH_4 oxidation rates in the tropics. However, we note the possibility that additional factors, or unexpected combinations of current factors, may influence rates of atmospheric CH_4 uptake in the tropics in ways that are not explicitly represented in the models.
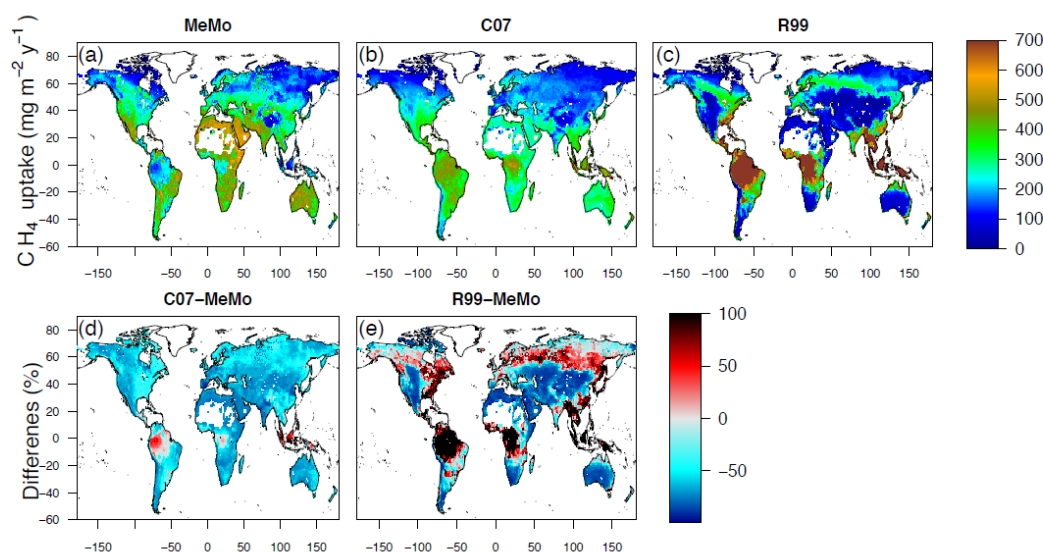

Figure 6: Annual mean CH_4 uptake by soil predicted using models (a) MeMo, (b) C07 and (c) R99 for the period 1990-2009. Differences between models expressed in percent are shown in panels (d) C07 minus MeMo and (e) R99 minus MeMo.

The influence of different environmental factors on soil CH_4 uptake was assessed by calculating the global CH_4 uptake flux while varying each factor (temperature, soil moisture and nitrogen deposition) independently and keeping other

20 factors constant (Figs. 7, 8 and 9). Comparison of r_{SM} values reveals large differences across models in tropical wet regions (Fig. 7), which explains the contrasting predictions of CH_4 uptake by MeMo (213 mg CH_4 m^{-2} y^{-1}) versus models R99 (689 mg CH_4 m^{-2} y^{-1}) and C07 (329 mg CH_4 m^{-2} y^{-1}). Formulation of r_{SM} in MeMo (section 2.3.4) accounts for limitation of methanotrophic oxidation rates when soil moisture levels are >20% water content, a feature that is absent in the R99 and C07

models. In addition, the R99 model implements a linear decrease of r_{SM} for soil moisture conditions <20%, which results in a 60 to 80% reduction in CH$_4$ oxidation rates in the subtopics. The absence of this condition in models MeMo and C07 explains the significant differences in CH$_4$ uptake fluxes in subtropical regions (Figs. 5 and 6).
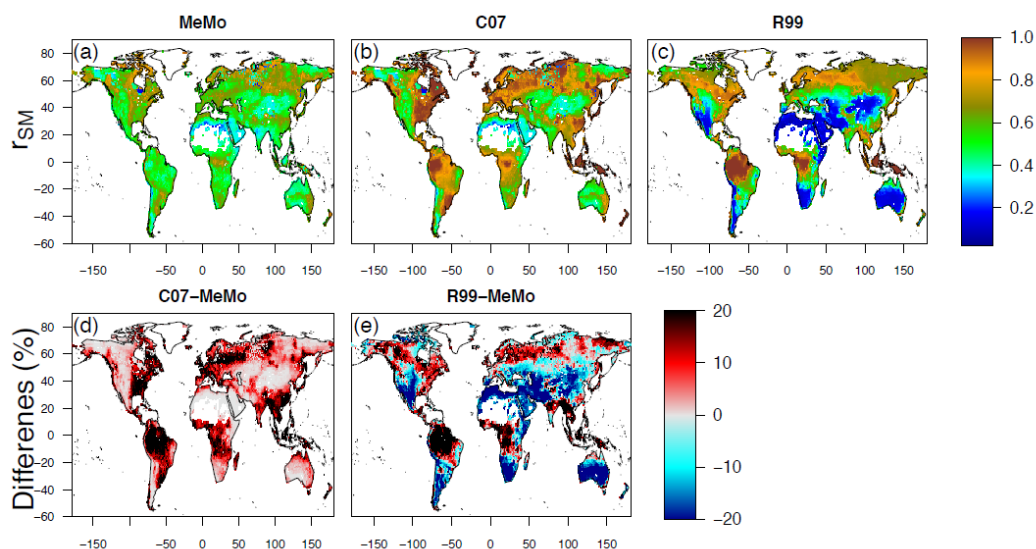
Figure 7. Soil moisture response (r_{SM}) of CH$_4$ oxidation simulated by models (a) MeMo, (b) C07 and (c) R99. Differences in model response expressed in percent are shown in panels (d) C07 minus MeMo, and (e) R99 minus MeMo.

Formulations of r_T are similar in the three models (section 2.3.5) and consequently, gridded maps of simulated r_T values exhibit broadly similar global patterns in which high r_T values are present at warm low latitudes and low r_T values are predicted at cold high latitudes. Notably, MeMo generally simulates r_T values that are approximately 20% lower than those predicted by the C07 and R99 models (Fig. 8) because of the revised formulation of the Q$_{10}$ value. MeMo and the C07 model simulate higher r_T values than R99 at high latitudes because of differences in parameterization of r_T at temperatures near 0°C.
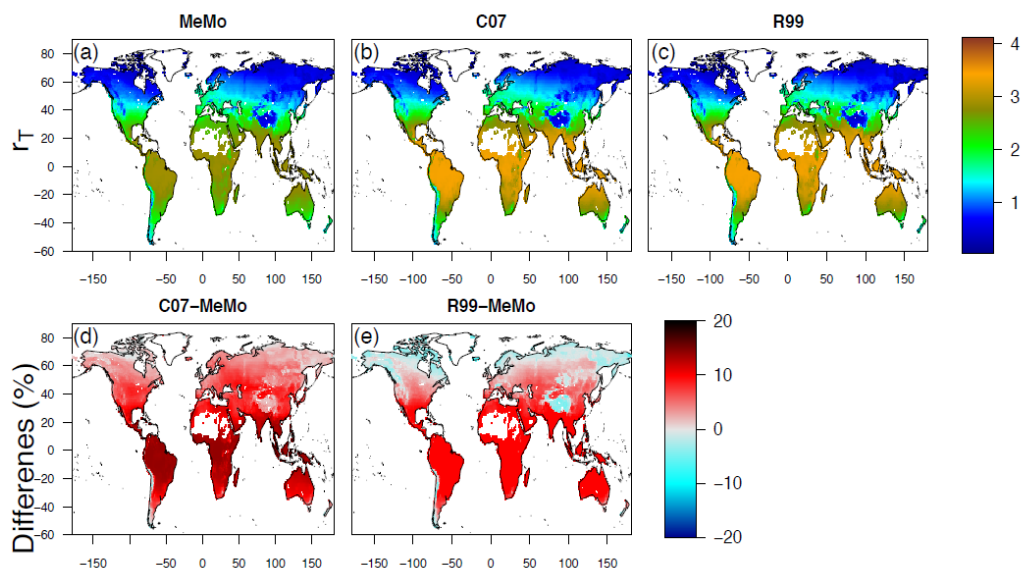
Geoscientific
Model Development
Discussions

Figure 8: Temperature response (r_T) of soil methanotrophy simulated by models (a) MeMo, (b) C07, and (c) R99. Differences in model response expressed in percent are shown in panels (d) C07 minus MeMo, and (e) R99 minus MeMo.

Inhibition of soil methanotrophy due to N deposition (r_N) differs significantly between the three models. Nitrogen

5 inhibition of CH_4 oxidation rates is lower in MeMo compared to the R99 and C07 models, in particular, at mid-latitudes (Fig. 9). The R99 and C07 models formulate r_N as a function of agricultural intensity in contrast to MeMo which uses modelled N deposition. The difference in approach results in an ~20% higher r_N factor in MeMo across most regions with the exception of high latitude areas (Fig. 9). In regions of intense agricultural activity and high N deposition (5 kg N ha^{-1}), such as Europe or the mid-western USA, the R99 and C07 models predict a reduction of up to 60% in CH_4 oxidation rates

10 compared to a decrease of only ~10% simulated in MeMo. Two recent studies reported that high rates of N deposition (10 kg N ha^{-1} y^{-1}) can reduce soil uptake of atmospheric CH_4 by ~8.6% (Fang et al., 2014; Zhang et al., 2008), which is consistent with the lower r_N values employed in MeMo. The key limitation of the N effect approach adopted in the R99 and C07 models is the generalization of N inhibitory effects across different agricultural areas, crops and types of management, which results in excessive attenuation of CH_4 oxidation rates. For example, the R99 and C07 models predict a 75%

15 reduction in CH_4 uptake rates for areas characterized by an agricultural intensity of 100%; however, Veldkamp et al. (2001) reported that inhibition of soil methanotrophy at such levels requires N addition >300 kg N ha^{-1} y^{-1}, a loading rate which greatly exceeds N input levels typically associated with agriculture. Although a more conservative r_N factor is employed in MeMo, the importance of accurate characterization of the attenuating effects of N addition on soil methanotrophy highlights the need for additional efforts to verify and refine parameterization of this key factor.
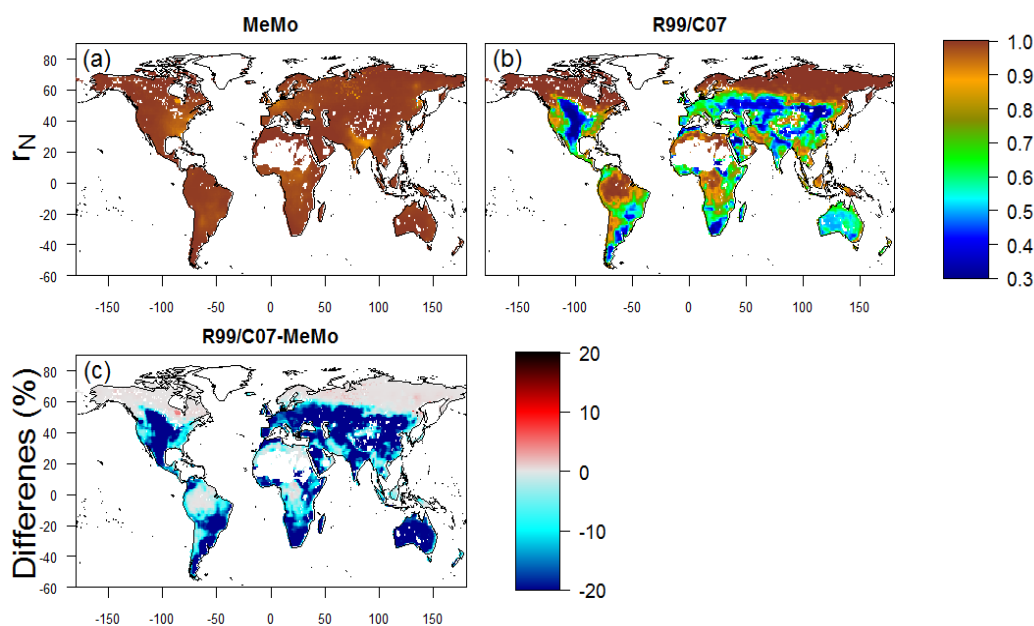
Geoscientific
Model Development
Discussions

Figure 9. Response of soil methanotrophy to nitrogen effect (r_N) simulated by models (a) MeMo, (b) R99, and C07. The responses for models R99 and C07 are both shown in panel (b) because they have the same formulation. The difference in model response between models R99/C07 minus MeMo expressed in percent is shown in panel (c).

4.3 Temporal and Spatial Variability of Soil CH₄ Uptake

Field observations of soil uptake of atmospheric CH₄ are generally sparse both spatially and temporally. Consequently, our quantitative understanding of CH₄ uptake fluxes across different ecosystems and seasons is limited. Models provide a means to quantitatively explore spatial and temporal patterns of soil methanotrophy on scales that cannot be readily captured by field-based observations. Therefore, once tested and validated (see section 4.2), MeMo was used to quantitatively assess the variability of soil CH₄ uptake in different climate zones and ecosystems on seasonal time scales.

4.3.1 Regional Variability

The relative contribution of soil in each climatic zone to global uptake of atmospheric CH₄ as predicted by MeMo is summarized in Table 8. Soil in the northern hemisphere is estimated to account for approximately two thirds (67%) of the total global sink for atmospheric CH₄ because of the uneven distribution of landmasses between the northern and southern hemispheres. Notably, terrestrial areas in the northern subtropical and temperate zones collectively account for ~46% of the global soil sink for atmospheric CH₄. The southern tropical zone contributes a further ~19% to soil uptake of CH₄. The southern subtropical and northern tropical zones are estimated to contribute almost equally (~14%) to total CH₄ uptake (Table 8). The smallest proportion of soil CH₄ oxidation occurs in the southern temperate (0.5%) and northern polar (6%) zones due to a combination of small land area and low rates of CH₄ uptake. Model predictions of CH₄ uptake by climatic

zone provides insights into the relative importance of each region in the global CH_4 cycle but additionally begins to facilitate analysis of potential responses of the soil CH_4 sink within each zone to global change both due to climate and land management.

Table 8. MeMo CH₄ uptake estimates by region.

Regions	Regional gridded mean (mg CH_4 m^{-2} y^{-1})	Total land area (10^{12} m^{-2})	Total CH_4 uptake (Tg CH_4 y^{-1})	% of total
Cold zone (60°-90° N)	102	18.7	2.2	6.4
Temperate zone (40°-60° N)	217	31.0	6.9	20.1
Subtropic zone (20°-40° N)	344	26.4	9.1	26.5
Tropical zone (0°- 20° N)	313	15.1	4.7	13.7
Northern Hemisphere Total:		**91.2**	**22.9**	**66.7**
Temperate zone (40°-60° S)	212	1.1	0.2	0.5
Subtropic zone (20°-40° S)	385	13.3	4.7	13.7
Tropical zone (0°- 20° S)	322	20.8	6.5	18.9
Southern Hemisphere Total:		**35.2**	**11.4**	**33.3**

5

Further analysis of soil CH_4 uptake by ecosystem types (Table 9) shows that the highest gridded mean rates of CH_4 oxidation are associated with tropical deciduous forests (630 mg CH_4 m^{-2} y^{-1}). The relatively low soil moisture content during the dry season (Supplementary 2, Figure S3) and the consistently high mean annual temperature (Supplementary 2, Figure S6) in such ecosystems promote high rates of soil methanotrophy. Furthermore, the soil typically possesses a low

10 clay content (Supplementary 2, Figure S2), which results in higher porosity that enhances gas diffusion and promotes higher rates of CH_4 oxidation. In comparison, rates of CH_4 uptake by soil in open and dense shrubland, temperate evergreen forest and savanna ecosystems (Table 9) are ~100 mg CH_4 m^{-2} y^{-1} lower but still highly significant globally.

Dense and open shrubland are characterized by constant climatic conditions (temperate and relatively low soil moisture; Supplementary 2 Figures S6 and S3, respectively) throughout the year, which in combination with a texture that

15 typically is sandy results in high annual CH_4 uptake rates (Tate et al., 2007). In contrast, high annual rates of CH_4 uptake in temperate evergreen forests result from elevated rates of soil methanotrophy during summer months (section 2.3.4), indicating that temperature is a key driver of CH_4 oxidation in such ecosystems (Borken et al., 2006; Ueyama et al., 2015; Wang and Ineson, 2003). Savannas share many climatic conditions with tropical deciduous forests but also commonly experience wildfire during the dry season. Both ecosystem types though are characterized by a marked seasonality driven by

20 the presence or absence of precipitation in combination with a consistent high mean annual temperature (Supplementary 2, Figure S6 and S3), which collectively support high rates of CH_4 uptake by soil.

Tundra, taiga, polar desert and other ecosystem types that are common at high latitudes (Supplementary 2, Figure S9) are characterized by the lowest mean annual rates of soil methanotrophy (<108 mg CH_4 m^{-2} y^{-1}) because of low temperatures throughout most of the year. MeMo also predicts low rates of CH_4 uptake in tropical humid forest (330 mg

CH_4 m^{-2} y^{-1}) due to low rates of bacterial CH_4 oxidation and the negative impact of high soil moisture levels on gas diffusion (see section 2.3.5). The CH_4 uptake rates estimated by MeMo are consistent with field observations by Dasselar et al. (1998) and Luo et al. (2013) which indicate that excess soil moisture strongly attenuates CH_4 uptake rates across a range of ecosystem types.

5   Finally, the global significance of each ecosystem type as a CH_4 sink depends strongly on spatial extent as well as CH_4 oxidation rates. Open shrubland (18.7%), grassland and steppe (12.7%), and savanna (11.3%) are the most important ecosystem types contributing to the global CH_4 soil sink (~46% collectively; Table 9) in MeMo because of high mean rates of CH_4 uptake (339 to 571 mg CH_4 m^{-2} y^{-1}) in combination with a large areal extent globally (14 x 10^{12} to 23 x 10^{12} m^2). This finding is similar to the estimation by Potter et al. (1996) that warm and relatively dry ecosystems, such as semi-arid

10   steppe, tropical savanna, tropical seasonal forest, and chaparral, account for 40% of soil uptake of atmospheric CH_4 globally. Moreover, Luo et al. (2013) reported the highest annual CH_4 uptakes rates in dry savanna as part of a long-term field investigation of soil methanotrophy in several ecosystem types. Singh et al. (1997) also observed CH_4 uptake rates that were higher in savannah than temperate forest. Although both model simulations and available field observations suggest these ecosystems are important global sinks for atmospheric CH_4 there is presently a dearth of field measurements for warm and

15   dry environments relative to temperate ecosystems.

Table 9. MeMo CH_4 uptake estimates by ecosystem type from Ramankutty and Foley (1999) land cover classification.

Ecosystem type	Global gridded mean (mg CH_4 m^{-2} y^{-1})	Total land area (x10^{12} m^{-2})	Total CH_4 uptake (Tg CH_4 y^{-1})	% of total
Tropical Deciduous Forest	630 ± 59	4.2	1.7	5.0
Dense Shrubland	580 ± 104	6.1	2.4	6.9
Open Shrubland	571 ± 132	23.3	7.3	21.2
Temperate Broadleaf Evergreen Forest	526 ± 70	2.0	0.7	2.0
Savanna	504 ± 128	14.1	4.5	13.1
Temperate Needleleaf Evergreen Forest	359 ± 90	3.9	1.2	3.4
Grassland/Steppe	339 ± 92	15.8	4.3	12.5
Temperate Deciduous Forest	331 ± 68	5.2	1.4	4.0
Tropical Evergreen Forest	330 ± 44	12.5	2.5	7.2
Boreal Deciduous Forest	288 ±119	5.7	1.5	4.3
Boreal Evergreen Forest	275 ± 96	9.1	2.4	7.0
Mixed Forest	187 ± 86	13.4	2.7	7.8
Tundra	179 ± 144	6.2	1.7	4.9
Polar Desert/Rock/Ice	108 ± 48	0.4	0.01	0.0
Total		**124.1**	**34.3**	**100**

4.3.2 Seasonal Variability

Global annual uptake of atmospheric CH_4 by soil exhibits a marked seasonality that reflects the dominance of the northern hemisphere in soil methanotrophy. The highest simulated CH_4 uptake fluxes occur during June, July, August (JJA) (10.4 Tg CH_4) followed by September, October and November (SON) (10.2 Tg CH_4), March, April and May (MAM) (7.2 Tg CH_4), and finally, December, January and February (DJF) (6.5 Tg CH_4) (Fig. 10).

Methane uptake in the cold and temperate regions of the northern hemisphere generally is characterized by the largest seasonality exhibiting an amplitude of 30 mg CH_4 m^{-2} mo^{-1}. In these regions, modeled uptake of CH_4 by soil is controlled strongly by temperature and consequently, ecosystems common at these latitudes (*e.g.,* boreal, needle leaf, temperate deciduous, mixed forest, polar deserts/rock/ice and tundra) show pronounced seasonal trends (Fig. 11), which also are evident in field measurements (*e.g*., Priemé and Christensen, 1997) and emphasized in local mechanistic models (*e.g*., Oh et al., 2016). These finding suggest that the soil CH_4 sink in such ecosystems may be more sensitive to future change as a result of global warming.

In contrast, soil methanotrophy in temperate regions in the southern hemisphere are characterised by a weaker seasonality having an amplitude of 17 mg CH_4 m^{-2} mo^{-1} due to the prevalence of grassland and steppe, which contrasts with a dominance of forest in the northern hemisphere. Seasonality of soil CH_4 uptake fluxes is even more muted in tropical and subtropical environments (<10 mg CH_4 m^{-2} mo^{-1}) because of favourable and stable environmental conditions. Tropical deciduous forest and tropical evergreen forest, which are common in these climate zones are characterized by relatively constant CH_4 uptake fluxes throughout the year (Fig. 11); however, MeMo predicts greater seasonality (20 mg CH_4 m^{-2} mo^{-1}) of CH_4 uptake by soil in drier subtropical ecosystems, such as open shrubland, savanna and grasslands (Fig. 11) because of seasonality in soil moisture.

Notably, northern temperate forest in summer (JJA) was the ecosystem and time period possessing the highest average monthly CH_4 uptake fluxes (137 mg CH_4 m^{-2} mo^{-1}) simulated by MeMo. During the rest of the year, the largest soil sink for atmospheric CH_4 occurred in the southern hemisphere in tropical deciduous forest of central Africa (DJF, 132 mg CH_4 m^{-2} mo^{-1}; MAM, 131 mgCH_4 m^{-2} mo^{-1}; SON, 129 mg CH_4 m^{-2} mo^{-1}). This finding is significant because field observations of soil methanotrophy in northern temperate forest during summer are the measurements most commonly extrapolated to an annual basis, which may lead to a possible overestimation of global CH_4 uptake fluxes.
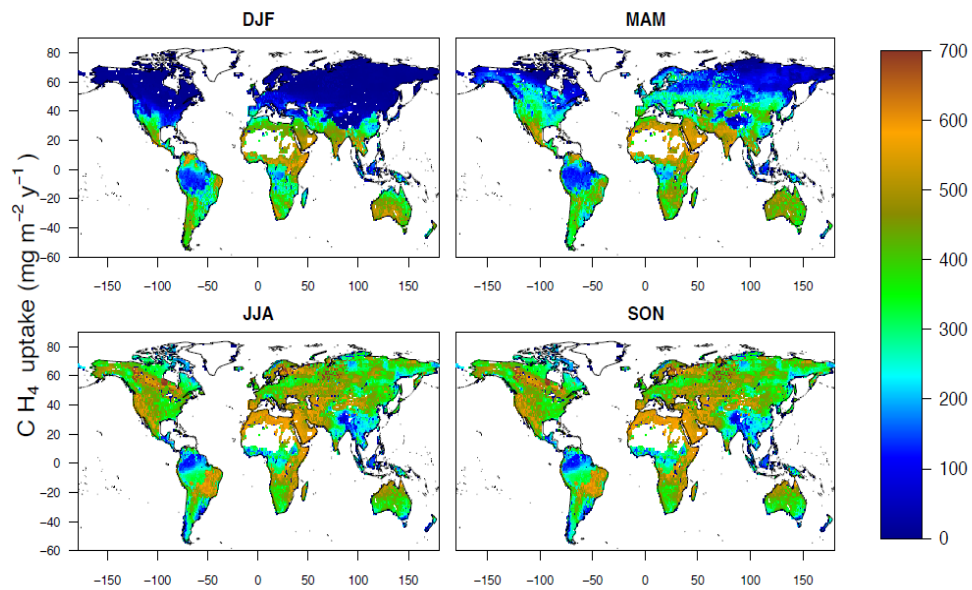
Figure 10: Seasonal uptake of atmospheric CH$_4$ by global soils predicted by MeMo for the period 1990 to 2009.
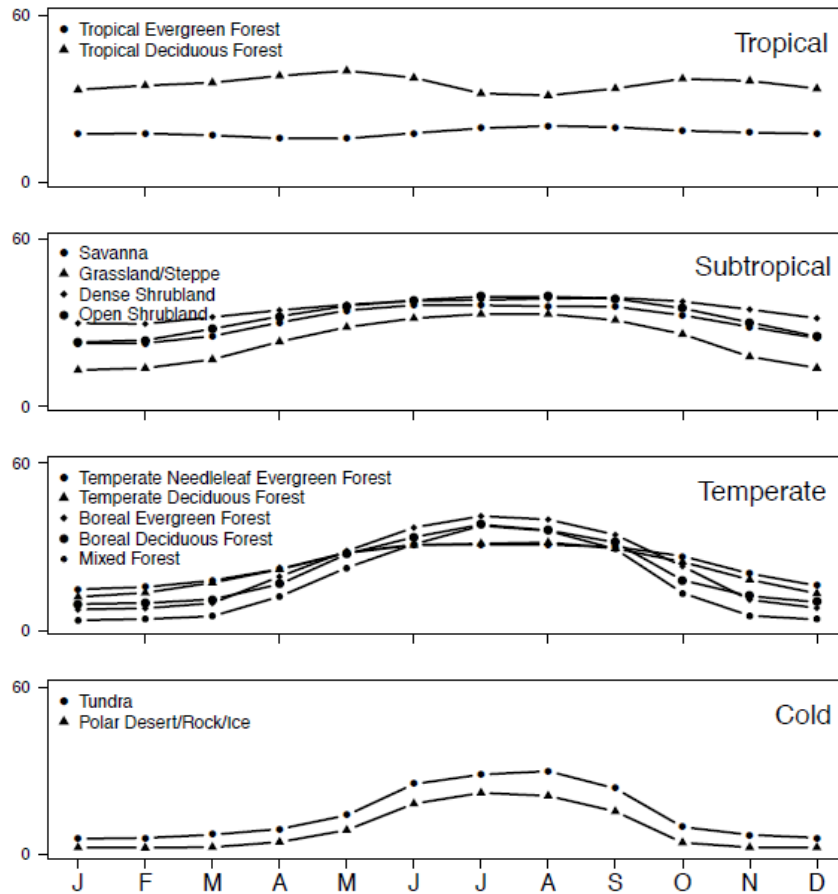
Figure 11: Seasonal patterns of soil uptake of atmospheric CH$_4$ by ecosystem for the four regions: cold, temperate, tropical and subtropical using MeMo model for the period 1990-2009.

4.4 Model Limitations and Scope of Applicability

Several aspects of MeMo can be developed further, pending availability of additional field data, to improve estimation of global soil uptake of atmospheric CH$_4$. Firstly, the base oxidation rate of bacterial methanotrophy at 0°C (k_0) is a critical parameter necessary for accurate estimation of CH$_4$ uptake rates. There is presently a general dearth of published k_0 values for soil methanotrophy and moreover, ecosystem coverage is incomplete. Additionally, our parametrization for k_d accounts for methanotrophic activity in a one-dimensional soil matrix; however, other studies have separated CH$_4$ uptake in soil from methanotrophy in the rhizosphere to improve estimates of total CH$_4$ uptake (*e.g.*, Savrekov et al., 2016). This refinement has been modeled for local conditions but insufficient data about rhizosphere CH$_4$ oxidation rates prevent inclusion in MeMo and extension to a global scale.

Secondly, the Q_{10} response of soil methanotrophy has been determined to date in only a small subset of ecosystems in which soils function as a sink for atmospheric CH_4. The majority of Q_{10} values have been determined for bacterial oxidation of CH_4 under laboratory conditions and there is considerable variability in values across different ecosystems.

Thirdly, additional field observations of CH_4 uptake by soil are needed, in particular, long-term measurements at individual sites that capture seasonality and inter-annual variability and from regions that presently have minimal or no representation (*i.e.*, the southern hemisphere, semi-arid ecosystems, etc.) in the current pool of observations.

Fourthly, additional observations and characterization of the effects of N deposition on soil methanotrophy are needed. The measurements ideally should be conducted *in situ* using N input rates that are appropriate for different environments and land use practices.

Finally, MeMo is parameterized to accommodate input of CH_4 from below (*i.e.*, subsurface methanogenesis or upward migration of deeply sourced CH_4); however, rigorous validation of that aspect of the model will require additional field observations, including better characterization of conditions under which CH_4 is produced in finely textured soils and deep sub-horizons. The presence, or periodic input, of high concentrations of CH_4 (*e.g.*, from permafrost melting) may impact competition for oxygen and niche space between low affinity CH_4-oxidizing bacteria and the high affinity methanotrophs responsible for uptake of atmospheric CH_4. Refinement and validation of the capacity for MeMo to account for upward migrating or autochthonous CH_4 will enable the model to be used to estimate CH_4 flux from intermittently wet environments, which may currently fall outside the scope of process-based wetland models.

The process-based nature of MeMo and the breadth of conditions for which it has been validated provide scope for using the model to quantify CH_4 uptake in soil in a broad range of scenarios. For example, MeMo could be used to determine global uptake of CH_4 by soil in the past during glacial or former interglacial periods. It may also be used to assess potential uptake rates of atmospheric CH_4 in future climate scenarios and further elevated tropospheric CH_4 mixing ratios.

5.0 Conclusions

We developed a processed-based model to simulate uptake of atmospheric CH_4 by soil, which was refined using newly reported experimental data and the introduction of recent insights into physical and biological mechanisms that drive soil methanotrophy. We modified the general analytical solution proposed by Ridgwell et al. (1999) and Curry (2007) to account for a maximum depth of CH_4 uptake and to quantify upward migration and consumption of CH_4 produced *in situ*. Representation of the effects of nitrogen deposition, soil moisture and temperature on methanotrophy were improved based upon newly available data and recent advances in characterization of these processes. Finally, we proposed utilization of a different base oxidation rate k_0 for methanotrophy in different regions because its value changes in relation to environmental conditions.

MeMo simulations produced a closer fit to observational data than two previous soil methanotrophy models (Ridgwell et al., 1999; Curry 2007). MeMo and observational data show a similar bi-modal latitudinal distribution of atmospheric CH_4 uptake by soil with the lowest fluxes at the equator and high-latitudes, and largest uptake fluxes at mid-

Geoscientific
Model Development
Discussions

latitudes. Previous models simulated a dissimilar pattern with large uptake fluxes in equatorial regions, a difference that results primarily from improved representation of the soil moisture effect in MeMo.

MeMo simulations supported by observational data indicate that warm and semiarid regions are the most efficient soil sink for atmospheric CH_4. In these regions, tropical deciduous forest and dense open shrubland are characterized by

5 relatively low soil moisture and constant temperature during the year, which are key factors that promote high rates of CH_4 uptake by soil. In contrast, cold regions possessed the lowest CH_4 uptake rates, in particular, tundra and boreal forest, which have a marked seasonality driven by temperature, making soil methanotrophy in such areas potentially sensitive to future global climate change. The warm and wet tropical evergreen forest biome has CH_4 uptake rates that are ~50% less than warm and semiarid regions because excess soil moisture impacts soil-atmosphere gas exchange, resulting in a smaller k_0 (1.6

10 x10^{-5} s^{-1}). The extensive area of shrubland, grassland, steppe and savanna globally yields a high total uptake of CH_4; however, there is presently a dearth of experimental data for these biomes and additional field observations are required to strengthen validation of MeMo simulations for these globally extensive areas.

MeMo simulations indicate that soil uptake of atmospheric CH_4 is reduced by as much as 10% in regions that receive high rates of nitrogen deposition. Globally, nitrogen deposition attenuates the soil sink for atmospheric CH_4 by 0.34

15 Tg yr^{-1}, which is an order of magnitude lower than previously reported because of the refined representation of the nitrogen inhibition effect in MeMo.

The accuracy of quantifying the modern soil sink for atmospheric CH_4 is improved using MeMo. In addition, the model can be used to explore changes in the relative importance of soil methanotrophy in the global CH_4 cycle in the past and the capacity of the soil sink to consume atmospheric CH_4 under future global change scenarios.

20

Code and Data Availability

MeMo was implemented in R (version 3.0.1). The model code and model output for 1990-2009 are available as a supplement to this manuscript. In addition, we also provide a post-processed driving dataset to run a simple, example model

25 case study for year 2000. All the forcing data used in this study are available from the following sources:

- temperature from CRU3.1, Harris et al. (2014): https://crudata.uea.ac.uk/cru/data/hrg/;
- vegetation mask from Ramankutty and Foley (1999): https://nelson.wisc.edu/sage/data-and-models/global-potential-vegetation/index.php;
- soil moisture from Dorigo et al. (2011) (Satellite): http://www.esa-soilmoisture-cci.org;
30 - soil moisture from TRENDY: (Sitch et al., 2015): http://www-lscedods.cea.fr/invsat/RECCAP/;
- nitrogen deposition from Lamarque et al. (2013): 1) https://www.isimip.org/gettingstarted/downloading-input-data/, 2) https://www.isimip.org/gettingstarted/details/24/; and
- clay content and bulk density from Shangguan et al. (2014): http://globalchange.bnu.edu.cn

References

Adamsen, A.P.S., King, G.M.: Methane Consumption in Temperate and Subarctic Forest Soils: Rates, Vertical Zonation, and Responses to Water and Nitrogen, Appl. Environ, Microbiol., 59, 485–490, 1993.

Allan, W., Struthers, H., Lowe, D.C.: Methane carbon isotope effects caused by atomic chlorine in the marine boundary layer: Global model results compared with Southern Hemisphere measurements. J. Geophys. Res. Atmospheres, 112, D04306, doi:10.1029/2006JD007369, 2007

Arndt, S., Jørgensen, B.B., LaRowe, D.E., Middelburg, J.J., Pancost, R.D., Regnier, P.: Quantifying the degradation of organic matter in marine sediments: A review and synthesis, Earth-Sci. Rev., 123, 53–86. doi:10.1016/j.earscirev.2013.02.008, 2013.

Aronson, E.L., Helliker, B.R.: Methane flux in non-wetland soils in response to nitrogen addition: a meta-analysis, Ecology, 91, 3242–3251, doi:10.1890/09-2185.1, 2010.

Bodelier, P.L.E., Laanbroek, H.J.: Nitrogen as a regulatory factor of methane oxidation in soils and sediments, FEMS Microbiol. Ecol., 47, 265–277, doi:10.1016/S0168-6496(03)00304-0, 2004.

Boeckx, P., Van Cleemput, O.: Methane Oxidation in a Neutral Landfill Cover Soil: Influence of Moisture Content, Temperature, and Nitrogen-Turnover, J. Environ. Qual., 25, 178, doi:10.2134/jeq1996.00472425002500010023x, 1996.

Borken, W., Davidson, E.A., Savage, K., Sundquist, E.T., Steudler, P.: Effect of summer throughfall exclusion, summer drought, and winter snow cover on methane fluxes in a temperate forest soil, Soil Biol. Biochem., 38, 1388–1395, doi:10.1016/j.soilbio.2005.10.011, 2006.

Born, M., Dörr, H., Levin, I.: Methane consumption in aerated soils of the temperate zone, Tellus, B, 42, 2–8, doi:10.1034/j.1600-0889.1990.00002.x, 1990.

Geoscientific
Model Development
Discussions

Bradford, M.A., Ineson, P., Wookey, P.A., Lappin-Scott, H.M.: The effects of acid nitrogen and acid sulphur deposition on CH4 oxidation in a forest soil: a laboratory study, Soil Biol. Biochem., 33, 1695–1702, doi:10.1016/S0038-0717(01)00091-8, 2001.

Bradley, J.A., Anesio, A.M., Arndt, S.: Bridging the divide: a model-data approach to Polar and Alpine microbiology, FEMS Microbiol. Ecol., 92, fiw015, doi:10.1093/femsec/fiw015, 2016.

Brady, N.C., Weil, R.R., Weil, R.: The Nature and Properties of Soils, Prentice-Hall, Upper Sadler River, 881 pp, 1999.

Bronson, K.F., Mosier, A.R.: Suppression of methane oxidation in aerobic soil by nitrogen fertilizers, nitrification inhibitors, and urease inhibitors, Biol. Fertil. Soils, 17, 263–268, doi:10.1007/BF00383979, 1994.

Burke, R.A., Meyer, J.L., Cruse, J.M., Birkhead, K.M., Paul, M.J.: Soil-atmosphere exchange of methane in adjacent cultivated and floodplain forest soils, J. Geophys. Res. Atmospheres, 104, 8161–8171, doi:10.1029/1999JD900015, 1999.

Butterbach-Bahl, K., Papen, H.: Four years continuous record of CH4-exchange between the atmosphere and untreated and limed soil of a N-saturated spruce and beech forest ecosystem in Germany, Plant Soil, 240, 77–90, doi:10.1023/A:1015856617553, 2002.

Cai, Z.C., Mosier, A.R.: Effect of NH4Cl addition on methane oxidation by paddy soils, Soil Biol. Biochem., 32, 1537–1545, doi:10.1016/S0038-0717(00)00065-1, 2000.

Castro, M.S., Steudler, P.A., Melillo, J.M., Aber, J.D., Bowden, R.D.: Factors controlling atmospheric methane consumption by temperate forest soils, Glob. Biogeochem. Cycles, 9, 1–10, doi:10.1029/94GB02651, 1995.

Ciais, P., Sabine C., Bala G., Bopp L., Brovkin, V. Canadell, J. Chhabra, A. DeFries, R. Galloway, J. Heimann, M. Jones, C. Le Quéré, C. Myneni, R.B. Piao S. and Thornton P.: Carbon and Other Biogeochemical Cycles. In: Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Stocker, T.F., Qin, D., Plattner, G.-K., Tignor, M., Allen, S.K., Boschung, J., Nauels, A., Xia, Y., Bex, V., and Midgley, P.M. (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA. 2013

Clapp, R.B., Hornberger, G.M.: Empirical equations for some soil hydraulic properties, Water Resour. Res., 14, 601–604, doi:10.1029/WR014i004p00601, 1978.

Czepiel, P.M., Crill, P.M., Harriss, R.C.: Environmental factors influencing the variability of methane oxidation in temperate zone soils, J. Geophys. Res. Atmospheres, 100, 9359–9364, doi:10.1029/95JD00542, 1995.

Curry, C.L.: Modeling the soil consumption of atmospheric methane at the global scale, Glob. Biogeochem. Cycles, 21, GB4012, doi:10.1029/2006GB002818, 2007.

Dasselaar, A. van den P., Beusichem, M.L. van, Oenema, O.: Effects of soil moisture content and temperature on methane uptake by grasslands on sandy soils, Plant Soil, 204, 213–222, doi:10.1023/A:1004371309361, 1998.

De Visscher, A., Cleemput, O.V.: Induction of enhanced CH4 oxidation in soils: NH4+ inhibition patterns, Soil Biol. Biochem., 35, 907–913, doi:10.1016/S0038-0717(03)00122-6, 2003.

Dorigo, W.A., Wagner, W., Hohensinn, R., Hahn, S., Paulik, C., Xaver, A., Gruber, A., Drusch, M., Mecklenburg, S., van Oevelen, P., Robock, A., Jackson, T.: The International Soil Moisture Network: a data hosting facility for global in situ soil moisture measurements, Hydrol. Earth Syst. Sci., 15, 1675–1698. doi:10.5194/hess-15-1675-2011, 2011.

Dörr, H., Katruff, L., Levin, I.: Proceedings of the NATO advanced research workshop Soil texture parameterization of the methane uptake in aerated soils, Chemosphere, 26, 697–713, doi:10.1016/0045-6535(93)90454-D, 1993.

Dunfield, P., knowles, R., Dumont, R., Moore, T.R.: Methane production and consumption in temperate and subarctic peat soils: Response to temperature and pH, Soil Biol. Biochem., 25, 321–326, doi:10.1016/0038-0717(93)90130-4, 1993.

Dutaur, L., Verchot, L.V.: A global inventory of the soil CH4 sink. Glob, Biogeochem. Cycles, 21, GB4013, doi:10.1029/2006GB002734, 2007.

Epstein, H.E., Burke, I.C., Mosier, A.R., Hutchinson, G.L.: Plant functional type effects on trace gas fluxes in the shortgrass steppe, in: Breemen, N.V. (Ed.), Plant-Induced Soil Changes: Processes and Feedbacks, Developments in Biogeochemistry, Springer Netherlands, pp. 145–168, 1998.

Etheridge, D.M., Steele, L.P., Francey, R.J., Langenfelds, R.L.: Atmospheric methane between 1000 A.D. and present: Evidence of anthropogenic emissions and climatic variability. J. Geophys. Res. Atmospheres 103, 15979–15993. doi:10.1029/98JD00923, 1998.

Geoscientific
Model Development
Discussions

Fang, H., Cheng, S., Yu, G., Cooch, J., Wang, Y., Xu, M., Li, L., Dang, X., Li, Y.: Low-level nitrogen deposition significantly inhibits methane uptake from an alpine meadow soil on the Qinghai–Tibetan Plateau, Geoderma, 213, 444–452, doi:10.1016/j.geoderma.2013.08.006, 2014.

Gulledge, J., Schimel, J.P.: Low-Concentration Kinetics of Atmospheric CH4 Oxidation in Soil and Mechanism of NH4 + Inhibition, Appl. Environ. Microbiol., 64, 4291–4298, 1998.

Grosso, S.J.D., Parton, W.J., Mosier, A.R., Ojima, D.S., Potter, C.S., Borken, W., Brumme, R., Butterbach-Bahl, K., Crill, P.M., Dobbie, K., Smith, K.A.: General CH4 oxidation model and comparisons of CH4 Oxidation in natural and managed systems, Glob. Biogeochem. Cycles, 14, 999–1019, doi:10.1029/1999GB001226, 2000.

Harris, I., Jones, P.D., Osborn, T.J., Lister, D.H.: Updated high-resolution grids of monthly climatic observations - the CRU TS3.10 Dataset, Int., J. Climatol., 34, 623–642, doi:10.1002/joc.3711, 2014.

Hein, R., Crutzen, P.J., Heimann, M.: An inverse modelling approach to investigate the global atmospheric methane cycle, Glob. Biogeochem. Cycles, 11, 43–76, doi:10.1029/96GB03043, 1997.

Ho, A., Kerckhof, F.-M., Luke, C., Reim, A., Krause, S., Boon, N., Bodelier, P.L.E.: Conceptualizing functional traits and ecological characteristics of methane-oxidizing bacteria as life strategies, Environ. Microbiol. Rep., 5, 335–345, doi:10.1111/j.1758-2229.2012.00370.x, 2013.

Hurtt, G.C., Chini, L.P., Frolking, S., Betts, R.A., Feddema, J., Fischer, G., Fisk, J.P., Hibbard, K., Houghton, R.A., Janetos, A., Jones, C.D., Kindermann, G., Kinoshita, T., Goldewijk, K.K., Riahi, K., Shevliakova, E., Smith, S., Stehfest, E., Thomson, A., Thornton, P., Vuuren, D.P. van, Wang, Y.P.: Harmonization of land-use scenarios for the period 1500–2100: 600 years of global gridded annual land-use transitions, wood harvest, and resulting secondary lands, Clim. Change, 109, 117–161, doi:10.1007/s10584-011-0153-2, 2011.

Kirschke, S., Bousquet, P., Ciais, P., Saunois, M., Canadell, J.G., Dlugokencky, E.J., Bergamaschi, P., Bergmann, D., Blake, D.R., Bruhwiler, L., Cameron-Smith, P., Castaldi, S., Chevallier, F., Feng, L., Fraser, A., Heimann, M., Hodson, E.L., Houweling, S., Josse, B., Fraser, P.J., Krummel, P.B., Lamarque, J.-F., Langenfelds, R.L., Le Quéré, C., Naik, V., O'Doherty, S., Palmer, P.I., Pison, I., Plummer, D., Poulter, B., Prinn, R.G., Rigby, M., Ringeval, B., Santini, M., Schmidt, M., Shindell, D.T., Simpson, I.J., Spahni, R., Steele, L.P., Strode, S.A., Sudo, K., Szopa, S., van der Werf, G.R., Voulgarakis, A., van Weele, M., Weiss, R.F., Williams, J.E., Zeng, G.: Three decades of global methane sources and sinks, Nat. Geosci., 6, 813–823, doi:10.1038/ngeo1955, 2013.

Klemedtsson, Å. K., Klemedtsson, L.: Methane uptake in Swedish forest soil in relation to liming and extra N-deposition, Biol. Fertil. Soils., 25, 296–301, doi:10.1007/s003740050318, 1997.

Lamarque, J.-F., Dentener, F., McConnell, J., Ro, C.-U., Shaw, M., Vet, R., Bergmann, D., Cameron-Smith, P., Dalsoren, S., Doherty, R., Faluvegi, G., Ghan, S.J., Josse, B., Lee, Y.H., MacKenzie, I.A., Plummer, D., Shindell, D.T., Skeie, R.B., Stevenson, D.S., Strode, S., Zeng, G., Curran, M., Dahl-Jensen, D., Das, S., Fritzsche, D., Nolan, M.: Multi-model mean nitrogen and sulfur deposition from the Atmospheric Chemistry and Climate Model Intercomparison Project (ACCMIP): evaluation of historical and projected future changes, Atmos Chem Phys., 13, 7997–8018, doi:10.5194/acp-13-7997-2013, 2013.

Le Mer, J., Roger, P.: Production, oxidation, emission and consumption of methane by soils: A review. Eur. J. Soil Biol., 37, 25–50, doi:10.1016/S1164-5563(01)01067-6, 2001.

Low, P.F., Hoekstra, P., Anderson, D.M.: Some Thermodynamic Relationships for Soils at or Below the Freezing Point: 2. Effects of Temperature and Pressure on Unfrozen Soil Water, Water Resour. Res., 4, 541–544. doi:10.1029/WR004i003p00541, 1968.

Luo, G.J., Kiese, R., Wolf, B., Butterbach-Bahl, K.: Effects of soil temperature and moisture on methane uptake and nitrous oxide emissions across three different ecosystem types, Biogeosciences, 10, 3205–3219, doi:10.5194/bg-10-3205-2013, 2013.

MacDonald, J.A., Skiba, U., Sheppard, L.J., Hargreaves, K.J., Smith, K.A., Fowler, D.: Soil environmental variables affecting the flux of methane from a range of forest, moorland and agricultural soils, Biogeochemistry, 34, 113–132, doi:10.1007/BF00000898, 1996.

Mclain, J.E.T., Kepler, T.B., Ahmann, D.M.:Belowground factors mediating changes in methane consumption in a forest soil under elevated CO2, Glob. Biogeochem. Cycles, 16, doi:10.1029/2001GB001439, 2002.

McLain, J.E.T., Ahmann, D.M.: Increased moisture and methanogenesis contribute to reduced methane oxidation in elevated CO2 soils, Biol. Fertil. Soils, 44, 623–631, doi:10.1007/s00374-007-0246-2, 2007.

Moldrup, P., et al.: Modelling diffusion and reaction in soils: III. Predicting gas diffusivity from the Campbell soil-water retention model, Soil science,161.6: 366-375, 1996.

Mosier, A.R., Parton, W.J., Valentine, D.W., Ojima, D.S., Schimel, D.S., Delgado, J.A.: CH4 and N2O fluxes in the Colorado shortgrass steppe: 1. Impact of landscape and nitrogen addition, Glob. Biogeochem. Cycles, 10, 387–399, doi:10.1029/96GB01454, 1996.

Mosier, A.R., Morgan, J.A., King, J.Y., LeCain, D., Milchunas, D.G.: Soil-atmosphere exchange of CH4, CO2, NOx, and N2O in the Colorado shortgrass steppe under elevated CO2, Plant Soil, 240, 201–211, doi:10.1023/A:1015783801324, 2002.

Myhre, G., Highwood, E.J., Shine, K.P., Stordal, F.: New estimates of radiative forcing due to well mixed greenhouse gases, Geophys. Res. Lett, 25, 2715–2718, doi:10.1029/98GL01908, 1998.

Oh, Y., Stackhouse, B., Lau, M.C.Y., Xu, X., Trugman, A.T., Moch, J., Onstott, T.C., Jørgensen, C.J., D'Imperio, L., Elberling, B., Emmerton, C.A., St. Louis, V.L., Medvigy, D.: A scalable model for methane consumption in arctic mineral soils, Geophys. Res. Lett., 43, 2016GL069049, doi:10.1002/2016GL069049, 2016

Oremland, R.S., Culbertson, C.W.: Importance of methane-oxidizing bacteria in the methane budget as revealed by the use of a specific inhibitor, Nature, 356, 421–423, doi:10.1038/356421a0, 1992.

Phillips, R.L., Whalen, S.C., Schlesinger, W.H.: Response of soil methanotrophic activity to carbon dioxide enrichment in a North Carolina coniferous forest, Soil Biol. Biochem., 33, 793–800, doi:10.1016/S0038-0717(00)00227-3, 2001.

Potter, C.S., Davidson, E.A., Verchot, L.V.: Estimation of global biogeochemical controls and seasonality in soil methane consumption, Chemosphere, 32, 2219–2246, doi:10.1016/0045-6535(96)00119-1, 1996.

Prather, M.J., Holmes, C.D., Hsu, J.: Reactive greenhouse gas scenarios: Systematic exploration of uncertainties and the role of atmospheric chemistry. Geophys. Res. Lett. 39, L09803. doi:10.1029/2012GL051440, 2012

Priemé, A., Christensen, S.: Seasonal and spatial variation of methane oxidation in a Danish spruce forest, Soil Biol. Biochem., 29, 1165–1172, doi:10.1016/S0038-0717(97)00038-2, 1997.

Ramankutty, N., Foley, J.A.: Estimating historical changes in global land cover: Croplands from 1700 to 1992, Glob. Biogeochem. Cycles, 13, 997–1027, doi:10.1029/1999GB900046, 1999.

Ridgwell, A.J., Marshall, S.J., Gregson, K.: Consumption of atmospheric methane by soils: A process-based model, Glob. Biogeochem. Cycles, 13, 59–70, doi:10.1029/1998GB900004, 1999.

Rigby, M., Prinn, R.G., Fraser, P.J., Simmonds, P.G., Langenfelds, R.L., Huang, J., Cunnold, D.M., Steele, L.P., Krummel, P.B., Weiss, R.F., O'Doherty, S., Salameh, P.K., Wang, H.J., Harth, C.M., Mühle, J., Porter, L.W.: Renewed growth of atmospheric methane, Geophys. Res. Lett., 35, L22805, doi:10.1029/2008GL036037, 2008.

Rigler, E., Zechmeister-Boltenstern, S.: Oxidation of ethylene and methane in forest soils—effect of CO2 and mineral nitrogen, Geoderma, 90, 147–159, doi:10.1016/S0016-7061(98)00099-8, 1999.

Rosenkranz, P., Brüggemann, N., Papen, H., Xu, Z., Horváth, L., Butterbach-Bahl, K.: Soil N and C trace gas fluxes and microbial soil N turnover in a sessile oak (Quercus petraea (Matt.) Liebl.) forest in Hungary, Plant Soil, 286, 301–322, doi:10.1007/s11104-006-9045-z, 2006.

Sabrekov, A.F., Glagolev, M.V., Alekseychik, P.K., Smolentsev, B.A., Terentieva, I.E., Krivenok, L.A., Maksyutov, S.S.: A process-based model of methane consumption by upland soils, Environ. Res. Lett., 11, 075001. doi:10.1088/1748-9326/11/7/075001, 2016.

Saxton, K.E., Rawls, W.J., Romberger, J.S., Papendick, R.I.: Estimating Generalized Soil-water Characteristics from Texture, Soil Sci. Soc. Am. J., 50, 1031, doi:10.2136/sssaj1986.03615995005000040039x, 1986.

Schnell, S., King, G.M.: Responses of Methanotrophic Activity in Soils and Cultures to Water Stress, Appl. Environ. Microbiol., 62, 3203–3209, 1996.

Schnell, S., King, G.M.: Mechanistic Analysis of Ammonium Inhibition of Atmospheric Methane Consumption in Forest Soils, Appl. Environ. Microbiol., 60, 3514–3521, 1994.

Shangguan, W., Dai, Y., Duan, Q., Liu, B., Yuan, H.: A global soil data set for earth system modelling, J. Adv. Model. Earth Syst., 6, 249–263, doi:10.1002/2013MS000293, 2014.

Singh, B.K., Bardgett, R.D., Smith, P., Reay, D.S.: Microorganisms and climate change: terrestrial feedbacks and mitigation options. Nat. Rev. Microbiol. 8, 779–790. doi:10.1038/nrmicro2439, 2010.

Geoscientific
Model Development
Discussions

Singh, J.S., Singh, S., Raghubanshi, A.S., Singh, S., Kashyap, A.K., Reddy, V.S.: Effect of soil nitrogen, carbon and moisture on methane uptake by dry tropical forest soils, Plant Soil, 196, 115–121, doi:10.1023/A:1004233208325, 1997.

Sitaula, B.K., Hansen, S., Sitaula, J.I.B., Bakken, L.R.: Methane oxidation potentials and fluxes in agricultural soil: Effects of fertilisation and soil compaction, Biogeochemistry, 48, 323–339, doi:10.1023/A:1006262404600, 2000.

Sitch, S., Friedlingstein, P., Gruber, N., Jones, S.D., Murray-Tortarolo, G., Ahlström, A., Doney, S.C., Graven, H., Heinze, C., Huntingford, C., Levis, S., Levy, P.E., Lomas, M., Poulter, B., Viovy, N., Zaehle, S., Zeng, N., Arneth, A., Bonan, G., Bopp, L., Canadell, J.G., Chevallier, F., Ciais, P., Ellis, R., Gloor, M., Peylin, P., Piao, S.L., Le Quéré, C., Smith, B., Zhu, Z., Myneni, R.: Recent trends and drivers of regional sources and sinks of carbon dioxide, Biogeosciences, 12, 653–679, doi:10.5194/bg-12-653-2015, 2015.

Smith, K.A., Dobbie, K.E., Ball, B.C., Bakken, L.R., Sitaula, B.K., Hansen, S., Brumme, R., Borken, W., Christensen, S., Priemé, A., Fowler, D., Macdonald, J.A., Skiba, U., Klemedtsson, L., Kasimir-Klemedtsson, A., Degórska, A., Orlanski, P.: Oxidation of atmospheric methane in Northern European soils, comparison with other ecosystems, and uncertainties in the global terrestrial sink, Glob. Change Biol., 6, 791–803, doi:10.1046/j.1365-2486.2000.00356.x, 2000.

Spahni, R., Wania, R., Neef, L., van Weele, M., Pison, I., Bousquet, P., Frankenberg, C., Foster, P.N., Joos, F., Prentice, I.C., van Velthoven, P.: Constraining global methane emissions and uptake by ecosystems, Biogeosciences, 8, 1643–1665, doi:10.5194/bg-8-1643-2011, 2011.

Steinkamp, R., Butterbach-Bahl, K., Papen, H.: Methane oxidation by soils of an N limited and N fertilized spruce forest in the Black Forest, Germany, Soil Biol. Biochem., 33, 145–153, doi:10.1016/S0038-0717(00)00124-3, 2001.

Tate, K.R., Ross, D.J., Saggar, S., Hedley, C.B., Dando, J., Singh, B.K., Lambie, S.M.: Methane uptake in soils from Pinus radiata plantations, a reverting shrubland and adjacent pastures: Effects of land-use change, and soil texture, water and mineral nitrogen, Soil Biol. Biochem., 39, 1437–1449, doi:10.1016/j.soilbio.2007.01.005, 2007.

Ueyama, M., Takeuchi, R., Takahashi, Y., Ide, R., Ataka, M., Kosugi, Y., Takahashi, K., Saigusa, N.: Methane uptake in a temperate forest soil using continuous closed-chamber measurements, Agric. For. Meteorol., 213, 1–9, doi:10.1016/j.agrformet.2015.05.004, 2015.

Vecherskaya, M.S., Galchenko, D.V.F., Sokolova, E.N., Samarkin, V.A.: Activity and species composition of aerobic methanotrophic communities in tundra soils, Curr. Microbiol., 27, 181–184, doi:10.1007/BF01576018, 2013.

Veldkamp, E., Weitz, A.M., Keller, M.: Management effects on methane fluxes in humid tropical pasture soils, Soil Biol. Biochem., 33, 1493–1499, doi:10.1016/S0038-0717(01)00060-8, 2001.

Visvanathan, C., Pokhrel, D., Cheimchaisri, W., Hettiaratchi, J.P.A., Wu, J.S.: Methanotrophic activities in tropical landfill cover soils: effects of temperature, moisture content and methane concentration. Waste Manag. Res., 17, 313–323, doi:10.1034/j.1399-3070.1999.00052.x, 1999.

von Fischer, J.C., Butters, G., Duchateau, P.C., Thelwell, R.J., Siller, R.: In situ measures of methanotroph activity in upland soils: A reaction-diffusion model and field observation of water stress, J. Geophys. Res. Biogeosciences, 114, G01015, doi:10.1029/2008JG000731, 2009.

Wang, Y., Xue, M., Zheng, X., Ji, B., Du, R., Wang, Y.: Effects of environmental factors on N2O emission from and CH4 uptake by the typical grasslands in the Inner Mongolia. Chemosphere 58, 205–215. doi:10.1016/j.chemosphere.2004.04.043, 2005.

Wang, Z.-P., Ineson, P.: Methane oxidation in a temperate coniferous forest soil: effects of inorganic N, Soil Biol. Biochem., 35, 427–433, doi:10.1016/S0038-0717(02)00294-8, 2003.

Wania, R., Ross, I., 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.

West, A.E., Brooks, P.D., Fisk, M.C., Smith, L.K., Holland, E.A., Iii, C.H.J., Babcock, S., Lai, R.S., Schmidt, S.K.: Landscape patterns of CH4 fluxes in an alpine tundra ecosystem, Biogeochemistry, 45, 243–264, doi:10.1023/A:1006130911046, 1999.

Whalen, S.C.: Influence of N and non-N salts on atmospheric methane oxidation by upland boreal forest and tundra soils, Biol. Fertil. Soils, 31, 279–287, doi:10.1007/s003740050657, 2000.

Whalen, S.C., Reeburgh, W.S.: Moisture and temperature sensitivity of CH4 oxidation in boreal soils, Soil Biol. Biochem., 28, 1271–1281, doi:10.1016/S0038-0717(96)00139-3, 1996.

Zhang, W., Mo, J., Zhou, G., Gundersen, P., Fang, Y., Lu, X., Zhang, T., Dong, S.: Methane uptake responses to nitrogen deposition in three tropical forests in southern China, J. Geophys. Res. Atmospheres, 113, D11116, doi:10.1029/2007JD009195, 2008.

Zhuang, Q., Chen, M., Xu, K., Tang, J., Saikawa, E., Lu, Y., Melillo, J.M., Prinn, R.G., McGuire, A.D.: Response of global soil consumption of atmospheric methane to changes in atmospheric climate and nitrogen deposition, Glob. Biogeochem. Cycles, 27, 650–663, doi:10.1002/gbc.20057, 2013.

5