Reviewer #1

[We are deeply appreciated for the comments, which significantly improve the manuscript in terms of clarity and organization. Specifically, we 1) reorganized the introduction section; 2) defined the terrestrial ecosystems; 3) defined the primary CH_4 processes; 4) revised the section for model purposes; and 5) addressed many other minor comments. All detailed point-by-point responses are listed below.]

General comments: This manuscript provides an overview and a synthesis of the evolution of models focusing on methane emissions from terrestrial ecosystems. The manuscript is based on a comparison among 39 methane models described in peer- reviewed articles, followed by a general synthesis that includes outlines of future challenges and directions in the field. I read the review with interest; it is a review which as far as I know has not been done before. Understanding the current state and potential future challenges of methane modelling will be of interest both to field researchers and for new modelling projects. The manuscript also has shortcomings that I think should be addressed before publication is considered. First, I find that the overall presentation can be improved for increased clarity, particularly with regards to sentence and paragraph structure. I have several examples in the specific comments below, but an overall assessment is recommended.

[We have made a substantial revision to address the shortcomings as stated. See below for the specific responses to reviewers.]

I also think the introduction could do a better job in outlining the scope of the manuscript, particularly I would favor some more specific information, e.g "first we will give an overview of the range of processes that have been considered in methane models, based on this we will classify existing models as determined by the range of processes considered. The following sections will review and synthesize how models deal specifically with methane production, consumption and transport within soils. . . . etc." I also recommend the authors to better define several key concepts in the manuscript. This would include your definition of a terrestrial ecosystem (see further comment below), and a definition of what constitutes a "primary process” with regards to methane dynamics (is this just your ranking of which processes that are more likely to have a stronger influence on the resulting emissions magnitude?).

[We have revised the manuscript accordingly. Specifically, we re-organized the last paragraph of the Introduction. The logic of the manuscript has been outlined at the end of the section. It highlights what we did for this review, which also addressed other minor comments in later section. The primary methane processes have been clearly described and listed.]

The term “terrestrial ecosystems” is particularly important for this manuscript, since it defines the scope of the models that have been reviewed. How do you define terrestrial ecosystems? I.e. what is the distinction from aquatic ecosystems and why are not models of aquatic ecosystem methane emissions considered in this review? The review emphasizes the need to be able to estimate methane emissions at large regional to global scales, but aquatic ecosystems might (depending on your definition) have greater emissions than terrestrial ecosystems at the regional/global scale, so the omission of aquatic ecosystems is important. How do you define wetlands in terms of being terrestrial or aquatic ecosystems? The US and Canadian definitions of wetlands include open water wetlands with up to 2 m of standing water – are all these considered terrestrial in this review? Would it be considered a future challenge to extent the current models to include aquatic ecosystems, particularly streams, rivers, ponds and lakes?

[We have added text to clearly define the terrestrial ecosystems covered in this review, indicating the differences from aquatic ecosystems. The definition of wetlands is used. We agreed that future expansion of review to cover aquatic ecosystems might be an interesting research effort, while it is not the focus for our current review.]

Another topic that I do not think get sufficient attention in the manuscript relate to the diversity of goals for different models, and how that influences the choices made in the model development. In the introduction you bring up the fact that models can be developed for extrapolation to regional or global scales, or for process-level models that are developed to understand methane dynamics at the site level. The latter type of model requires information on many site-specific parameters (soil microbial community, iron and sulfur data etc etc), data which is not available for large regions. One recommendation in this manuscript it that more processes should be considered for methane model – however, for models aimed at regional to global scales this is likely to lead to highly unconstrained models since the data to run the models does not exist and is highly unlikely to be mapped. In short, I think there is a need to discuss how modelling goals will influence model development, particularly how this relates to available model data inputs.

[We totally agree with the reviewer on the comment for the modeling purpose. Therefore, we added short paragraph to discuss model development and its association with the shift of models from mechanistic understanding to applicable model development. For the data requirements for parameterizing, and driving mechanistic models, we agree with the reviewer's comments, yet we believe more and more data will be generated and more insightful understandings are needed, which requires mechanistic models to fully understand the internal interaction and feedback between different processes.]

The issue of spatial data availability, used as model input, is also not discussed in the manuscript. It is my belief is that improved spatial data on wetland extents and wet- land characteristics are likely to improve our accuracy of regional to global estimates of methane emissions (both magnitude and spatial patterns) much more than the in- corporation of additional processes in the models. The use of different spatial products (wetland maps, inundation maps etc) for estimating global methane emissions is known to produce wildly different spatial patterns of regional methane emissions. I believe a discussion on how available data, and the use of available data, affect model development and modelling results deserve some attention in this review.

[We agree that accurate data might result in more reliable model output, which would be important than model development. But model development

remains a critical improvement we need to work on in order to reduce uncertainties in quantifying CH_4 budget. In addition, model development will likely provide guidance for experimental design, which is the core of data-model integration.]

Specific comments:

P2 L37. I strongly discourage use the concept of global warming potential when dis- cussing methane emissions from wetlands. GWP are only applicable when considering "new" sources, i.e. changes in emissions, but cannot be used when evaluating sustained emissions. Wetlands have been emitting methane for millennia, thus their methane emissions have a much lesser additional impact on climate forcing at this point than would be concluded based on GWP (unless they have increased as a result of climate change or by other means). See Frolking and Roulet et al 2007 Glob Change Biol.P3 L70-72. This is a weak sentence to finish an introduction. P3 L74-76. Is it possible to reference the original sources?

[We have removed the term GWP and its usage for describing CH_4 flux in the revision.]

P4 L83. What is meant by "primary CH4 processes"? How do you distinguish primary processes from other processes? Do these primary processes include the 3 methanogenesis processes, 2 methanotrophy processes, and the 7 transport mechanisms? Several of these processes, which I assume are what you consider primary processes since they are listed in the sentence after your statement on primary processes, are not discussed in regards to how they are represented in models. E.g. methylotrophic methanogenesis is only mentioned once, and is not discussed with regards to how it is considered by models. Also, of the seven transport mechanisms you only discuss ebullition, diffusion and plant-mediated transport – what are the other four processes? Overall, I think you need a better framework for how you classify the different processes, including a motivation on why some of these processes are to be considered in the review and why other are not.

[We have rewritten this section; 1) we defined the primary CH_4 processes; 2) we reorganized the detailed CH_4 processes section. We organized them into two methanogenesis, two methanotropy and three transport processes. Each transport process is composed of one or more mechanisms. The CH_4 transport is discussed at higher level of three transport mechanisms. See primary CH_4 processes section.]

P4 L85. Clumsy sentence structure, omit "(depending on how one counts)".

[We have removed the phrase as suggested.]

P4 L87. Importance in time and space – and you should probably highlight that it varies by wetland characteristics.

[Revised as suggested.]

P4 L92. Perhaps a brief description is needed that explains the differences between acetoclastic and hydrogenotrophic processes, in terms of under what conditions they are more likely to dominate and why.

[We added explanations of acetoclastic and hydrogenotrophic processes.]

P4 L107. This is a awkward way of saying that upland soils are net sinks of atmospheric methane.

[We revised this sentence to emphasize that it is a range not exactly 100% for all upland. Yet we still kept ~100% to make it consistent with other sentences. The percentage is used to help understand how much each single mechanism contribute to the total production, oxidation, or transport processes.]

P4-5 L09-15. This sentence is very long and introduced several new concepts not previously described.

[The sentence has been reorganized into two sentences. Meanwhile, we define the newly added terms diffusive and advective transports.]

P5 L16. This is the third time I have seen the same point being raised already - “process vary significantly depending on temporal and spatial scales”.

[This sentence has been removed to reduce redundancies.]

P5 L17. How do you define direct and indirect effects with regards to wetland methane emissions? It is not clear to me given the examples brought up. Is the classification of direct and indirect processes different from that of primary and other processes introduced earlier?

[In our manuscript, we have information that the direct and indirect impacts are based on their associations with CH_4 production, oxidation, or transport processes.]

P5 L35. “Water sediments”, do you mean “Aquatic sediments”?

[We changed it to freshwater sediment, to keep consistent with original publication.]

P5-P6 L36-57. I’m not sure this listing of the different methane models is effective. I would recommend merging this section with the section below (L181-199) on the different groups of model, i.e. to bring these models up as examples of each group.

[We have significantly shortened the paragraph by removing more than half of the listed models. And this section has been merged with the following section as suggested.]

P7 L66. What is your definition of regional simulation capability? This has not been presented.

[We added text to define the regional simulation capability. The models are defined with regional simulation capability if models directly read in and produce spatial maps.]

P8 L09. Do you have any field data that can support your statement that substrate characterization is key for modelling methane production?

[We added one citation to support our statement of strong control of substrate on methanogenesis.]

P10 L62. Unclear if you mean the third group of the three groups described in the "Model Classification' section or the third group described in the "Methanogenesis" section. I would recommend separating the models into groups once, rather than a new division of models in each section.

[We have revised the manuscript to clearly describe how we separated models based on model representation of CH_4 processes. The section describing groups for methanogenesis has been reorganized as model algorithms.]

P10 L264. Seems appropriate to discuss substrate limitation and Michelis-Menten dynamics of methanogenesis in the section on methanogenesis rather than methan- otrophy.

[We have separated that section and moved the discussion of Michelis-Menten function into methanogenesis section, while keeping the discussion on methanotrophy in original section as appropriate.]

P17, L43. This sentence has poor structure, also, what is meant by "was not included in any of the three groups because that effort will likely be achieve over the long term"?

[We have revised this sentence for the purpose of improved clarity.]

P19, L09. Can you give examples of less-studies ecosystems?

[We added one sentence to show that the Arctic tundra ecosystem is an important contributor to global CH_4 budget but long-term datasets of CH_4 flux are lacking.]

P20, L31. Sentence structure: "integration between model development and data collection is much stronger for advancing science", do you mean that integration is important for advancing our scientific understanding of methane dynamics?

[We agree with reviewer. Yet we would like to keep sentence as it was because that sentence is used for general scientific studies. Meanwhile, we added a detailed description of data-model integration for CH_4 cycling in the following sentences.]

Reviewer #2

[We really appreciate the reviewer for the comments, which significantly improve the manuscript in terms of clarity and organization. Specifically, we 1) removed redundancies; 2) emphasized the importance of spatial maps of wetland data; and 3) addressed many other minor comments. All detailed point-by-point responses are listed below.]

General comments

In this manuscript, the authors reviewed 39 terrestrial methane models and discussed their limitations and future opportunities. This kind of model review has been partly conducted in introduction of model intercomparison project (e.g., WETCHIMP; Melton et al., 2013, Wania et al., 2013), but I agree that this manuscript gives a more thorough overview. The 39 models were classified into several categories (or generations) from the points of processes and complexity. Also, the authors gave good overview of underlying mechanisms of methane production, consumption, and transportation. In the light of its importance as the second important anthropogenic greenhouse gas, this manuscript is timely and within the scope of the journal.

[We appreciate the positive comments.]

The manuscript is fairly prepared, but I have several recommendations. First, I felt redundancies in the manuscript. For example, influential factors of methane processes are similarly listed in Page 5 Line 118 and Page 12 Line 322. I recommend refining the manuscript by reducing redundancies. Second, I recommend giving a broader picture of terrestrial models that include methane processes. The authors mentioned that methane schemes would be implemented into Earth system models (ESMs). Similarly, integrated terrestrial models (other than ESMs) should include methane processes to evaluate e.g. the effect of mitigation practices. Overall, I recommend that the manuscript be worth publication after moderate to major revision.

[We have carefully revised the manuscript and removed redundancies. We have also added a paragraph to discuss the implementations of CH_4 module

in ESMs.]

Specific comments

Page 3 Line 65

This manuscript does not cover several quantitatively important processes such as methane emissions from biomass burning, termites, and ruminants. Please justify here for ignorance of these processes.

[We totally agree that CH_4 emissions from biomass burning, termites, and ruminants are important. While important, these processes have not been included in this manuscript because they are not the focus of this paper.]

Page 5 Line 133

In the 1980s, E. Mattews and I. Fung (1987) achieved a pioneering work in which not only terrestrial but also atmospheric methane dynamics were simulated at the global scale. I think that their work should be mentioned in text.

[We acknowledge this pioneering work, although we did not include it because the approach in their paper is simply multiplying wetland area with measured CH_4 fluxes. It is not a modeling approach as we described. In this revision, we did cite this important work but did not treat as an independent ecosystem CH_4 model.]

Page 6 Line 159

In Figure 6 of Wania et al. (2013), estimations of methane production area in the contemporary models are well summarized.

[In the revised manuscript, we added text to emphasize the importance of spatial maps of wetland distribution, and acknowledge the review of CH_4

production area has been done for a group of models in Wania et al. (2013).]

Page 7 Line 190 Can you give several examples for the second group model?

[We have added few model examples as suggested.]

Page 8 Line 193 Can you give several examples for the third group model?

[We have added model examples as suggested.]

Page 9 Line 233Can you show the 31 models by adding a column in Table 1?
Page 9 Line 244"address" should be "addressed".

[We appreciate the comment, yet we did not add it as a new column because the information has been shown in the Table 2 in a different format.]

Page 10 Line 246 and Table 1. In addition to Ridgwell et al. (1999), several methane oxidation models have been presented and could be mentioned here: e.g., Del Grosso et al. (2000) and Curry (2007).

[We do have DAYCNET, CLASS models reviewed and summarized in the Table 1.]

Page 10 Line 251 Can you indicate a typical value of the contribution of anaerobic methane oxidation in total oxidation?

[We did have this rough estimates in the primary CH_4 processes section.]

Page 11 Line 275 In terms of the modeling of vertical profile, parameterization of methane diffusion coefficient within soil is critically important. Do you agree?

[We totally agree that diffusion parameter is very important in terms of simulating vertical profile of the biogeochemical processes and CH_4 flux. Yet it is not focus of current review as current paper emphasizes model structure and mechanisms. We did discuss this important parameter in our revision.]

Page 13 Line 35 Yvon-Durocher et al. (2014) implied that the temperature response of methane emission would be evaluated using a single consistent model. If correct, the divergence in present models would be largely reduced. Do you agree?

[We would agree that Yvon-Durocher et al's approach is applicable for single CH_4 process. Since the observed CH_4 flux is a combination of many different processes. Using a single consistent model might not be the best way to represent CH_4 flux. Yvon-Durocher's approach provides a theoretical understanding of some consistencies between observed CH_4 fluxes across space.]

Page 14 Line 356 As long as I know, only a few global dataset of soil pH is available. Also, in situ measurement and model prediction of soil pH are rather difficult. I think these difficulties in using soil pH should be noted.

[We agree that global dataset of soil pH is lacking, yet a number of field experiments and modeling studies do confirm the importance of soil pH to CH_4 flux. We did note the difficulties for modeling soil pH in the revision.]

Page 15 Line 380 It looks wired to give a summary at this place, because it is usually given at the end of the manuscript. Actually, the statements around Page 16 Line 411 are as if your conclusion.

[This summary section is a short paragraph for CH_4 modeling section only, while the last conclusion section is for high-level summary and key findings

for the whole manuscript. We would still keep this section but make it as a sub-section of modeling section.]

Page 18 Line 460 A few more processes not mentioned here have been presented: e.g., emission from tank bromeliads (Martinson et al., 2010) and emission from small ponds (Holgerson and Raymond, 2016).

[We have included these new findings in the manuscript and identified them as a knowledge gap and future direction for modeling community.]

Page 19 Line 504 I recommend adding one more (6th?) challenge. Modeling of human-natural processes such as emission from managed ponds and estuaries is important in terms of mitigation. Namely, we should consider both natural biogeochemical processes and human management effects.

[We have added it in the revised manuscript as suggested. We appreciated the reviewer for pointing this out.]

Page 21 Line 540Do you mean “Markov Chain Monte Carlo (MCMC)”?

[Mistake corrected.]

Page 25 Line 623Please correct information for Bohn et al. (2015):

[Mistake corrected, thanks.]

Bohn, T. J., Melton, J. R., Ito, A., Kleinen, T., Spahni, R., Stocker, B. D., Zhang, B., Zhu, X., Schroeder, R., Glagorev, M. V., Maksyutov, S., Brovkin, V., Chen, G., Denisov, S. N., Eliseev, A. V., Gallego-Sala, A., McDonald, K. C., Rawlins, M. A., Riley, W. J., Subin, Z. M., Tian, H., Zhuang, Q., and Kaplan, J. O.: WETCHIMP-WSL: Intercomparison of wetland methane emissions over West Siberia, Biogeosciences, 12, 3321–3349, doi: 10.5194/bg-12-3321-2015, 2015.

Figure 4

Can you include the microbial community factor into the figure?

[We have revised the figure to show several different functional groups of microbes that control the CH_4 processes.]

References

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

Del Grosso, S. J., Parton, W. J., Mosier, A. R., Ojima, D. S., Potter, C. S., Borken, W., Brumme, R., Butterbach-Bahl, K., Crill, P. M., Dobbie, K., and Smith, K. A.: Gen- eral CH4 oxidation model and comparisons of CH4 oxidation in natural and managed systems, Global Biogeochem. Cycles, 14, 999-1019, 2000.

Holgerson, M. A., and Raymond, P. A.: Large contribution to inland water CO2 and CH4 emissions from very small ponds, Nature Geoscience, 9, 222–226, doi:10.1038/NGEO2654, 2016.

Martinson, G. O., Werner, F. A., Scherber, C., Conrad, R., Corre, M. D., Flessa, H., Wolf, K., Klose, M., Gradstein, S. R., and Veldkamp, E.: Methane emis- sion from tank bromeliads in neotropical forests, Nature Geoscience, 3, 766–769, doi:10.1038/ngeo980, 2010.

Matthews, E., and Fung, I.: Methane emission from natural wetlands: global distribu- tion, area, and environmental characteristics of sources, Global Biogeochem. Cycles, 1, 61-86, 1987.

Melton, J. R., Wania, R., Hadson, E. L., Poulter, B., Ringeval, B., Spahni, R., Bohn, T., Avis, C. A., Beerling, D. J., Chen, G., Eliseev, A. V., Denisov, S. N., Hopcroft, P. O., Lettenmaier, D. P., Riley, W. J., Singarayer, J. S., Subin,

Z. M., Tian, H., Zürcher, S., Brovkin, V., van Bodegom, P. M., Kleinen, T., Yu, Z. C., and Kaplan, J. O.: Present state of global wetland extent and wetland methane modelling: conclusions from a model inter-comparison project (WETCHIMP), Biogeosciences, 10, 753–788, doi:10.5194/bg- 10-753-2013, 2013.

Wania, R., Melton, J. R., Hodson, E. L., Poulter, B., Ringeval, B., Spahni, R., Avis, C. A., Chen, G., Eliseev, A. V., Hopcroft, P. O., Riley, W. J., Subin, Z. M., Tian, H., van Bodegom, P. M., Kleinen, T., Yu, Z. C., Singarayer, J. S., Zürcher, S., Lettenmaier, D. P., Beerling, D. J., Denisov, S. N., Prigent, C., Papa, F., and Kaplan, J. O.: Present state of global wetland extent and wetland methane modelling: methodology of a model inter-comparison project (WETCHIMP), Geoscientific Model Development, 6, 617–641, 10.5194/gmd-6-617-2013, 2013.

Reviewer #3

[We really appreciate the comments, which significantly improve the manuscript in terms of clarity and organization. All detailed point-by-point responses are listed below.]

Overall Evaluation

This manuscript presents a review of approaches used to model methane dynamics in terrestrial ecosystems in the last four decades. The review largely focuses on describing the variability in structure and mathematical descriptions of processes among 39 terrestrial methane models. Parameterization issues are touched upon in the section on environmental controls, mostly with respect to variability in Q10 (which affects temperature sensitivity of processes). The discussion makes suggestions for adding more complexity to methane models, primarily along the lines of more explicitly considering microbial processes and dynamics. The discussion finishes with identifying knowledge gaps, modeling challenges, data needs, and the need for data-model integration.

[We appreciated the positive comments.]

This manuscript tries to cover a lot of ground. The primary strength of the manuscript, in my opinion, is largely in the description of variability in mathematical descriptions of processes. The other aspects of the review didn't provide a lot insight in my opinion, as the issues discussed were in many cases just touched upon and were not well developed. My main concern about this manuscript is that in trying to cover a lot of ground, it covers some of that ground poorly. I think there are several issues to address to improve the review. First, I think there are some general organization issues that could be addressed to improve the manuscript. Second, there are a number of cases in the presentation of putting the "cart" before the "horse". Third, I didn't find that the description in the variability in structure (as depicted in Figure 3) was based on an objective evaluation of the 39 terrestrial models. Fourth, there a number of assertions in the manuscript that should be presented as more open issues. Fifth, the challenge of scaling is only touched upon in the manuscript and needs to be better developed, and there is a need for some discussion of reconciliation with atmospheric data analyses. Sixth, beside the scaling/reconciliation issue, I also found several issues that need to be better developed/discussed including the modeling of ebullition, vertical representation of processes, model benchmarking, and data-model integration. Below I go into more depth on each of these issues, and finish my review with a listing of specific comments.

[We have made a substantial revision to address the comments. Specifically, (1) we reorganized several sections to make them clearer, particularly the modeling section; (2) we clearly revised some statements to make them more consistent with the results; (3) scaling is not the key focus of this review, therefore, we did not expand writing on scaling and its reconciliation with atmospheric data analysis; yet we did emphasize that satellite data of atmospheric CH_4 concentration could be used for model validation; (4) we added a section for discussing presenting CH_4 module in ESMs.]

Issue 1: Organizational issues in the manuscript. The manuscript starts out well, but then gradually gets more and more disorganized. There is a lot of overlap of material between some of the later sections of the manuscript that could be eliminated with a more effective organization. Perhaps consider the organization of Luo et al. (2016, Global Biogeochemical Cycles), which review soil carbon models. The organization of that paper is (1) model structure, (2) model parameterization, and (3) external forcing. I think additional in this manuscript concerns scaling and reconciliation with atmospheric data. The strength of this manuscript is that it generally does a good job of reviewing model structure, but a rather inadequate job of reviewing model parameterization, external forcing, scaling, and reconciliation issues.

[We did remove some redundancies in different sections. This manuscript is not designed to cover model parameterization and external forcing specifically. Those two sections were discussed briefly model development perspective.]

Issue 2: “Cart” before the “Horse” issues. There are a number of places in the manuscript where the “cart” comes before the “horse”, from the perspective of this being a review paper. For example, the citation to Figure 2 on line 162 talks about the timeline for inclusion of “key mechanisms”, but these mechanisms haven’t been described in a general sense yet. Table 2, which contains the list of “key mechanisms” isn’t cited until line 175. Even when Table 2 is cited, the general reader gets no background on these mechanisms/features of models, as it is not used beyond a simple citation at the end of a sentence. Other rough spots in the manuscript involve adequately describing terms used in the manuscript. For example, acetoclastic and hydrogenotrophic methanogenesis suddently appears on lines 238-240 without any prior description. “Advective transport” (line 203) is also not described.

[For the citation to Figure 2, although those processes and their representation in models have not been reviewed, yet the processes themselves have been reviewed in “primary CH_4 processes” section. For the acetoclastic and hydrogenotrophic methanogenesis, we have included detailed definitions at their early occurrences. The advective transport has been defined as well.]

Issue 3: Analysis of the variability in structure. What is the basis for defining three different types of models? It seems to me that this could be done in a much more objective fashion by doing some sort of cluster analysis among the 39 models reviewed in this study. Information from Tables 1, 2, and 3 could be put into an objective cluster analysis so that we better understood what factors seem to cause models to be distinct (or not distinct) from each other.

[We really appreciated the suggestion of doing a cluster analysis. We did a cluster analysis based on model characteristics of representation of methanogenesis processes, methanotrophy processes, transport pathways, oxygen availability, multiple soil layers etc. All 40 models could be classified into three groups, which is consistent with our previous classification. See the

updated Figure 3 and relevant text.]

Issue 4: There are a number of assertions in the manuscript that have not been justified by any sort of rational analysis/argument. For example, why make a recommendation in the last sentence of section 4 (lines 196-198) on the third types of models as the means of moving forward with respect to improving reduced form models for application in Earth System Model applications? First of all, this is too early in the manuscript. Second, doesn't making this recommendation conflict with the sentence on lines 211- 212 that the optimum complexity remains to be determined? At the end of section 6 there are four recommendations for models "based on the above-mentioned needs" and a citation to Figure 4. I didn't find the previous text in section 6 as being very helpful for establishing these as the top needs. This all comes before the section 7, which talks about knowledge gaps and data needs. The arrows for benchmarking and data assimilation in Figure 4 have not been developed, and the issues of vertical trans- port/diffusion have only been touched upon. Also, the top recommendation that "the models (features?) should be embedded in an Earth System Model" seems strange to make here. The point here is that arguments have not been well enough organized and crafted to effectively make these recommendations. This sort of all gets back to issues 1 and 2 above. Finally, I can't say that I'm very fond of Figure 4 as being the synthetic figure for this manuscript – we've seen a lot of these sort of figures over the years. I suggest thinking about something that is truly synthetic based on this manuscript.

[We have revised the manuscript to address all comments. The recommendation of the third group of model in the early section of the paper has been removed as suggested. Then it is not in conflict with later section as reviewer suggested. We added description and summary of CH_4 model representation in ESMs, the model classification have been done in a mathematical way -- a cluster analysis. Other writing issues have been addressed as well. The original Figure 4 is a framework showing future model development as we envisioned, it is combination of summarized and visionary framework. Although it is little lack of evidence, we do believe it will be the key direction for CH_4 model development and application.]

Issue 5: The issues of scaling and reconciliation with atmospheric data. Scaling is an important issue. It does pop up several places in the manuscript as a sort of "between the lines" issue, but it really needs its own section. I also think that the issue of reconciling model applications at particular scales with data from atmospheric analyses needs to be part of the discussion.

[Since scaling and reconciliation are not the key focus of this manuscript, we did not plan to expand that section in this revision.]

Issue 6: Other issues. I also found several issues that need to be better developed/discussed including the modeling of ebullition, vertical representation of processes, model benchmarking, and data-model integration. For example, transport mechanisms don't even show up as key features in Table 2, although they do appear somewhat in Table 1. These issues are touched upon in several places in the manuscript, but are not really effectively dealt with in a meaningful way.

[We have added more text and wordings to make those statements strong and solid.]

Specific comments

Line 104-105: "contributes" is not really the right verb to use here. Just says "varies from 1 to 90%", for example.

[We still keep "contributes" because it emphasizes the contribution of individual process to the total oxidation or production.]

Line 106-107: I really don't know what you mean by "oxidation of atmospheric CH_4 contributes". Aren't all of the previous mechanisms in this paragraph ultimately oxidation of atmospheric CH_4, albeit in the open pore space of the soil.

[It emphasizes the oxidation of atmospheric CH_4, taking up CH_4 from atmosphere. This process is defined to distinguish from oxidation of CH_4 produced from soils.]

Line 109: Perhaps start a new paragraph after "methanotrophy.".

[We separated it as a new paragraph.]

Lines 109-116: There is no information for the uninitiated reader to understand how these pathways differ from each other.

[We added one small paragraph to define different transport pathways.]

Line 120: I think this might be the only occurrence of "wind speed" in the manuscript. What do you mean by "wind speed" as an environmental factor.

[We revised the manuscript to have a bit more description of wind speed impacts on CH_4 flux.]

Line 121: Define what you mean by "indirect" vs. "direct" environmental factors.

[We revised the manuscript to define the direct and indirect environmental factors.]

Line 147: I don't think Fan et al. (2013, Peatland DOS-TEM) has anything to do with the Zhuang et al. (2014) model in that it has a number of different features and to my understanding the two models do not share any code base.

[We have confirmed with Dr. Zhaosheng Fan, and treated the DOS-TEM as another independent CH_4 model in the revision.]

Line 162: As mentioned earlier, the reader needs to know more about the key mechanisms before you present/interpret Figure 2.

[We have added definition for some key mechanisms in the manuscript.]

Line 175: Need to make better use of Table 2 in the manuscript. As I indicated earlier, transport mechanisms need to be included in Table 2.

[We expanded the Table 2 to include the model information on CH_4 transport pathway.]

Line 213: Does use of "first group of models" refer to model types in Figure 3, or to the first set of empirical models referred to in the first paragraph of section 4.1?

[We have revised the manuscript to be clearer on this issue. The CH_4 models were classified as groups, while methangoenesis was categorized as model algorithms.]

Line 238-240: Where does the information on acetoclastic and hydrogenotropic methanogenesis appear in Table 3? Note that these production processes have not been defined for the reader.

[We have added definitions for acetoclastic and hydrogenotropic methanogenesis in the revised manuscript.]

Line 280: Why is Zhuang (2004) cited here in the context of immediately transporting CH_4? This model is primarily a monthly model with a pseudo-daily time step. This transport issue is an important temporal scaling issue, and one which should appear in a separate section on temporal scaling.

[Thanks for pointing out this inappropriate expression. We have removed citation of Zhuang (2004), and added another model as an example.]

Line 286: I think you should change “will likely” to “can”.Line 287: I think you should change “impossible” to “not straight forward”.

[Revised as suggested.]

Line 291: I note that ebullition is not adequately treated in this section (section 4.4).

[We do have ebullition in the section. In the revision, we have revised the section to have more specific information for ebullition.]

Line 292: Why is this the “final” bottleneck, or why is even referred to as a “bottleneck”. Line 303: Define advective transport.

[We revised it to bottleneck, and added definition of advective transport.]

Line 313: I think you should change “most” to “some”. Note that ebullition seems to be ignored in these three “transport” challenges. It is a dominant pathway in some systems.

[Revised as suggested.]

Line 319: I note that the simulation of variability in some environmental controls is not adequately treated in section 4.5 on environmental controls.

[We have revised the section to better describe variability in environmental controls.]

Lines 331-332: I think that this sentence needs to refer to Eq 9, 10, and 11 instead of 10, 11, and 12. Note that the third function in Eq 9 is essentially equivalent to Eq 10 in that the Q_{10} can be derived from the exponent.

[Mistake corrected.]

Line 347: I think you mean Eqs. 13-16 instead of 12-15.

[Mistake corrected.]

Lines 356-367: Do any models represent pH variability in time? It would be useful to know how models represent pH variability in space.

[We agree that pH variability is important and only few models consider dynamics of pH in soil over time and across space. Due to recent studies suggesting the importance of pH on CH_4 flux, it would be noteworthy to point out its importance for future model development.]

Lines 393-394: Why is the comparison of high frequency observational data needed for future model-model inter-comparison? I think it would be most important to high quality seasonal and interannual estimates derived from observations to effectively test and compare models.

[We have revised to reflect this point.]

Line 405: With respect to shifts, are you referring to shifts in time or in space?

[We have revised to clarify it is temporal shifts.]

Line 479: What do you mean by "order 1-10". Do you mean by a "factor of 1-10"? The language could be confused for "orders of magnitude".

[We have revised it to a factor of 1-10.]

Luo, Y., A. Ahlstrom, S.D. Allison, N.H. Batjes, V. Brovkin, N. Carvalhais, A. Chappell, P. Ciais, E.A. Davidson, A. Finzi, K. Georgiou, B. Guenet, O. Hararuk, J.W. Harden, Y. He, F. Hopkins, L. Jiang, C. Koven, R.B. Jackson, C.D. Jones, M.J. Lara, J. Liang, A.D. McGuire, W. Parton, C. Peng, J.T. Randerson, A. Salazar, C.A. Sierra, M.J. Smith, H. Tian, K.E.O. Todd-Brown, M. Torn, K.J. van Groenigen, Y.P. Wang, T.O. West, Y. Wei, W.R. Wieder, J. Xia, X. Xu, X. Xu, and T. Zhou. 2016. Toward more realistic projections of soil carbon dynamics by Earth system models. Global Biogeochemical Cycles 30:40-56, doi:10.1002/2015GB005239.

Reviewer #4

[We really appreciate the reviewer for the comments, which significantly improve the manuscript in terms of clarity and organization. All detailed point-by-point responses are listed below.]

This is an excellent and timely review of the current state of process-based methane modeling. While other recent literature on particular methane models typically pro- vide some brief review in the introduction and/or discussion sections, this review paper provides a very useful level of detail for understanding where, how, and why, process- based models of methane differ. As the authors note, these current methane models often poorly reproduce observed patterns, so this is an important reflective manuscript to assess the field before moving forward. That said, I do believe that the manuscript could be improved and clarified before publication. There are several relatively minor terms and phrases that require clarification that are detailed below. On a larger point, I think that it would be helpful to provide more information about representations of CH_4 processes that are included within ESMs, since this is a major suggestion by the authors. They could include basic information on which models are in ESMs in Table 1, but it would also be helpful to detail plans for future representations.

[We agree with the description of this work, and the needs for more discussion of CH_4 model representation in ESMs. We have added one paragraph to summarize how ESMs include CH_4 module; what is the likely future direction for ESMs development in terms of CH_4 representation.]

Within the conclusions of their review, the authors argue that researchers should focus on the development of a fully mechanistic CH_4 model that accounts for all features, and can integrate data on microbial community structure and function. There is always some tradeoff with model complexity and functionality, and I would be more convinced by the authors' conclusions that a more complex mechanistic model should be developed with all components if there was some evidence that this improves simulations over simpler representations. And furthermore, how can the increasing number of plot- to ecosystem-scale measurements of net CH_4 flux be used to constrain such a complex model, except for validation? This type of very complex model would even more so require the aggregation of experimental data on microbial ecophysiology that can be used to parameterize and develop robust uncertainties for these processes, and the authors appropriately note that much of this experimental work is yet to be done. It would be helpful if the authors provided some context for understanding how much data exist to constrain these individual CH_4 processes (a handful of experiments, or potentially hundreds?) and within which ecosystems. Within the section on model-data integration, I also think that it would be useful for the authors to provide more specific detail regarding ways to integrate these different data types (from net CH_4 flux data to process-based experimental data).

[We have added discussion about the tradeoff of developing a more mechanistic model and a simple empirical model. Meanwhile, the classification of empirical model and process-based model has been expanded. Meanwhile, we totally agreed that constraining mechanistically model is really challenging, yet it is becoming more and more applicable as the scientific community is expanding measurements of CH_4 flux and processes, as well as developing new model optimization algorithms. For example, SPRUCE, NGEE-Arctic and NGEE-Tropic projects within DOE are taking this intensive measurements and integration with models. A new model optimization algorithm has been developed associated with CLM framework and ALM framework, we believe the mechanistic models will be more powerful in near future along with these lines of advancements.]

Line by line comments follow:

L102-109: I'm confused about the reference number for the percentages: is it the percent of total carbon respiration? Or percent of total methane produced?

[Those percentage numbers emphasize specific processes to the single function of CH_4 cycling. For example, acetoclastic methanogenesis contributes to ~60-100% to the total CH_4 production.]

L235: You should also consider citing Matthews & Fung (1987) in this history: Matthews, E., and I. Fung (1987), Methane emission from natural wetlands: Global distribution, area, and environmental characteristics of sources, Global Biogeochem. Cycles, 1(1), 61–86, doi:10.1029/GB001i001p00061.

[We totally agree that the pioneering work by Matthews and Fung is important and should be cited in the manuscript. We have cited it in the revised manuscript.]

Table 1: Since the table is already large, I think that it would be useful to add which models are within ESMs (and if so, which ESM) and which models were developed for particular regions/species (rice, Arctic, etc.).

[We appreciated the reviewer for pointing out this issue. The information of which CH_4 models are embedded in ESMs has been summarized in the Table.]

L280-295: I think it would be helpful to add a bit more context for how and why these CH4 models are added into ESMs. The authors recommend that the third group be the focus to understand potential for reduction into ESM models, but what does it take to reduce a CH4 model into an ESM?

[We have added texts to emphasize the importance of representing CH_4 module in ESMs.]

L315-330: This section is a bit hard to follow with respect to what exactly the differences are here among the models. I think that it would be useful to restructure this with a bit more of an introduction (like the environmental controls section) about the differences among the four distinct classes of substrate representation, with explicit list of the four classes before listing which model is in each class.

[This section has been re-organized little bit for clarity purpose.]

L345: I'm not sure what the authors mean by "dramatic bias" caused by a lack of representation, and this should be clarified.

[We have revised the sentence to clearly reflect the importance of representing these two mechanisms; the bias in surface CH_4 flux will likely be biased if we do not represent these two mechanisms. Studies have confirmed that the surface layer and bottom layer have different mechanisms dominated CH_4 production (McCalley et al., 2014), therefore, if we do not consider two mechanisms, we will not be able to simulate this shift and likely the surface fluxes caused by this function shift in response to environmental change.

McCalley, C. K., Woodcroft, B. J., Hodgkins, S. B., Wehr, R. A., Kim, E.-H., Mondav, R., Crill, P. M., Chanton, J. P., Rich, V. I., Tyson, G. W., and Saleska, S. R.: Methane dynamics regulated by microbial community response to permafrost thaw, Nature, 514, 478-481, 2014.]

L363: It's hard to follow the many different categories that the authors are creating, and I'm not completely sure which category three refers to as described here.

[We have revised the manuscript. The three groups of CH_4 models are remained, while we changed four groups of methanogenesis to four modeling algorithms for methanogenesis. The classification of three groups of CH_4 models have been demonstrated with a cluster analysis as suggested by another reviewer (new Figure 3).]

L370: It would be helpful to provide a bit more context for why Michaelis-Menten representation fails for multi-substrate, multi-consumer networks. Is it purely an equifinality problem?

[We rewrote this sentence to acknowledge the new approach developed by Riley's group. The ECA approach might be good for multi-substrate, multi-consumer biogeochemistry reaction network. We added a short description in this aspect.]

L398: Unclear what "reported these individual processes" is referring to.L479: I'm not sure what the "high range" refers to within this context.

[L398 emphasizes the individual processes discussed in previous section. While L479 primarily focuses on processes caused hot spot and hot moments in CH_4 flux. In the revised manuscript, we revised those two sentences for clarity purpose.]

L567: Unclear what is meant by "integrative tool" . . . for integrative assessment?

[We used "integrative tool" to emphasize that the model can be used to integrate multiple sources of data to reach a better understanding of the system and better budget quantification.]

Reviewer #5

[We really appreciate the reviewer for the comments, which significantly improve the manuscript in terms of clarity and organization. All detailed point-by-point responses are listed below.]

The manuscript by Xu et al. reviews the past four decades of modeling methane emissions from terrestrial ecosystems. The authors provide a timeline and structure for assessing both the level of detail in terms of the processes represented and also in terms of how the processes are represented. Overall, the authors do a very nice job of comprehensively summarizing the current state of art in methane modeling and tracing the history of model development over the past four decades.

[We appreciate the positive comments.]

My main comments are : 1. The authors categorize the representation of processes into empirical to mechanistic approaches. This is rather subjective and it would be very helpful for the reader to have a section (1-2 paragraphs) describing how the authors define these terms. For example, even some of the mechanistic representation of processes rely on empirical response functions, and are thus only semi-mechanistic. In an ideal setting, what would be the definition of a purely mechanistic modeling approach?

[We totally agree that separation of mechanistic and empirical is rather arbitrary, while it does help understand the model representation of CH_4 processes. In this revised manuscript, we provideddetailed description to show how to define the empirical and mechanistic models in terms of modeling CH_4 dynamics.]

2. Some of the descriptions of the processes are fairly vague. For example, even the description of methanogenesis is abbreviated to just mentioning "acetoclastic and hydrogenotrophic methanogenesis". Given that the authors

are trying to emphasize a more mechanistic modeling approach, increasing the level of detail for each process would be helpful.

[We agree that it is important to have more detailed description of two methanogenesis processes. Yet the processes themselves have been reviewed, while for all the present CH_4 model, only few models simulate acetoclastic and hydrogenotrophic methanogenesis; which are not sufficient for a detailed review section.]

3. The discussion on substrate is particularly useful because most methane models do not consider this explicitly. Given the rise of atmospheric CO2, addressing how substrate has changed due to CO2 interactions, and what this means for modeling approaches and methane emissions is necessary to be mentioned.

[We added a short paragraph to discuss the potential impacts of elevated CO_2 and substrate on CH_4 emission.]

4. Lastly, in the discussion for data needs, the list and ideas for integration within models is also very helpful. However, some discussion of the benchmark targets that the modeling community should aim for, and how to handle the uncertainties in bench- marks, would be very useful.

[We have added one small paragraph to summarize the benchmarking targets of the benchmarking system and uncertainties in benchmark.]

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

Xiaofeng Xu[1, 2, 3], Fengming Yuan[4], Paul J. Hanson[4], Stan D.Wullschleger[4], Peter E. Thornton[4], William J. Riley[5], Xia Song[1, 3], David E. Graham[6], Changchun Song[2], and Hanqin Tian[7]

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2. Northeast Institute of Geography and Agro-ecology, Chinese Academy of Sciences, Changchun, Jilin, China
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5. Earth Sciences Division, Lawrence Berkeley National Laboratory, Berkeley, CA, USA
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Abstract

Over the past four decades, a number of numerical models have been developed to quantify the magnitude, investigate the spatial and temporal variations, and understand the underlying mechanisms and environmental controls of methane (CH_4) fluxes within terrestrial ecosystems. These CH_4 models are also used for integrating multi-scale CH_4 data, such as laboratory-based incubation and molecular analysis, field observational experiments, remote sensing, and aircraft-based measurements across a variety of terrestrial ecosystems. Here we summarize 40 terrestrial CH_4 models to characterize their strengths and weaknesses and to suggest a roadmap for future model improvement and application. Our key findings are that: (1) the focus of CH_4 models has shifted from theoretical to site- and regional-level applications over the past four decades, (2) large discrepancies exist among models in terms of representing CH_4 processes and their environmental controls, and (3) significant data-model and model-model mismatches are partially attributed to different representations of landscape characterization and inundation dynamics. Three areas for future improvements and applications of terrestrial CH_4 models are: (1) CH_4 models should more explicitly represent the mechanisms underlying land-atmosphere CH_4

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exchange, with an emphasis on improving and validating individual CH_4 processes over depth and horizontal space, (2) models should be developed that are capable of simulating CH_4 emissions across highly heterogeneous spatial and temporal scales, particularly hot moments and hot spots, and (3) efforts should be invested to develop model benchmarking frameworks that can easily be used for model improvement, evaluation, and integration with data from molecular to global scales. These improvements on CH_4 models would be beneficial for the Earth system models and further simulation of climate-carbon cycle feedbacks.

1. Introduction

Methane (CH_4) is the second most important anthropogenic greenhouse gas, accounting for ~15% of anthropogenic forcing to climate change (Forster et al., 2007; IPCC, 2013; Rodhe, 1990). Therefore, an accurate estimate of CH_4 exchange between land and the atmosphere is fundamental for understanding climate change (Bridgham et al., 2013; Nazaries et al., 2013; Spahni et al., 2011). The ecosystem modeling approach has been one of the most broadly used integrative tools for examining mechanistic processes, quantifying the budget of CH_4 flux across spatial and temporal scales (Arah and Kirk, 2000; Arah and Stephen, 1998; Cao et al., 1995; Curry, 2007; Fung et al., 1991; Huang et al., 1998b; Nouchi et al., 1994; Potter, 1997; Riley et al., 2011; Walter et al., 1996; Xu et al., 2007; Zhuang et al., 2004), and predicting future flux (Anisimov, 2007). Specifically, many CH_4 models have been developed to integrate data, improve process understanding, quantify budgets, and project exchange with the atmosphere under a changing climate (Cao et al., 1995; Grant, 1998; Huang et al., 1998a; Potter, 1997; Riley et al., 2011; Tian et al., 2010; Zhuang et al., 2004). In addition, model sensitivity analyses help to design field and laboratory experiments by identifying the most uncertain processes and parameters in the models (Massman et al., 1997; Xu, 2010).

Based on the complexity of the CH_4 processes represented, CH_4 models fall into two broad categories: (1) empirical models that are used to estimate and extrapolate measured methanogenesis, methanotrophy, or CH_4 emission at plot, country, or continental scales (Christensen et al., 1996; Eliseev et al., 2008; Mokhov et al., 2007; Wania et al., 2010, 2009); and (2) process-based models that are used

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for prognostic understanding of individual CH_4 processes in response to multiple environmental drivers and budget quantification (reviewed below). This separation emphasizes the high-level model structure rather than the specific processes represented, therefore, models with many processes represented with empirical functions are still classified as process-based models if they represent many key processes of CH_4 production, oxidation, and transport. Although this separation is rather arbitrary, it helps understand the characteristics and purpose of models in a systems perspective.

Over the past decades, many empirical and process-based models have been developed, for example CASA (Potter, 1997), CH4MOD (Huang et al., 1998b), CLM4Me (Riley et al., 2011), DAYCENT (Del Grosso et al., 2000), DLEM (Tian et al., 2010; Xu and Tian, 2012), DNDC (Li, 2000a), *ecosys* (Grant, 1998), HH (Cresto-Aleina et al., 2015), MEM (Cao et al., 1995), TEM (Zhuang et al., 2004), etc. However, recent analyses and model inter-comparisons have shown that most of these models poorly reproduce regional- to global-scale observations (Bohn and Lettenmaier, 2010; Bohn et al., 2015; Melton et al., 2013; Wania et al., 2013). A comprehensive synthesis and evaluation of the mechanisms incorporated into these models is lacking. This review focuses on primary processes of CH_4 cycling in the terrestrial ecosystems and their representation in the models. The critical CH_4 processes include substrate cycling, methanogenesis, methanotrophy, and transport in the soil profile, and their environmental controls. Emphasis is given to how these mechanisms were simulated in various models and how they were categorized in terms of complexity and ecosystem function. The review focuses on CH_4 models developed for terrestrial ecosystems, which is defined as ecosystems on land and wetlands with less than 2 m standing water. This classification is used to distinguish from pure aquatic ecosystems and considering the important role of wetlands on CH_4 cycling. Therefore, models for understanding reactions in bioreactors (Bhadra et al., 1984; Pareek et al., 1999), mining plots (De Visscher and Van Cleemput, 2003), aquatic ecosystems, and marine systems (Elliott et al., 2011) were excluded. An early pioneering effort of multiplying wetland area by average CH_4 flux to estimate global CH_4 budget was excluded from this review as well (Matthews and Fungi, 1987). This review excludes the CH_4 emission from biomass burning, termites and ruminants, because this paper primarily focuses on soil biogeochemical processes represented in ecosystem models. The model names are determined

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by two criteria: (1) if the model has been named in the original publication, it will be used to represent the model; (2) if the model has not been named, the last name of the first author will be used to name the model; for example, "Segers model", "Gong model". In this paper we first provide an overview of the range of processes that have been considered in methane models over the past four decades, and then further classify existing models as determined by the range of processes considered. We finished with several suggested research topics, which would be beneficial for better developing and applying CH_4 model for either understanding CH_4 cycling or quantifying CH_4 budget at various scales.

2. Primary CH_4 Processes

Biological methane production in sediments was first noted in the late 18th century (Volta 1777), and the microbial oxidation of methane was proposed at the beginning of the 20th century (Söhngen 1906). Since then, methane cycling processes have been intensively studied and documented (Christensen et al., 1996; Hakemian and Rosenzweig, 2007; Lai, 2009; Melloh and Crill, 1996; Mer and Roger, 2001), and most have been described mathematically and incorporated into ecosystem models (Table 1). Herein, we do not attempt to review all CH_4 processes, as a number of reviews have been published on this topic (Barlett and Harriss, 1993; Blodau, 2002; Bridgham et al., 2013; Cai, 2012; Chen et al., 2012; Conrad, 1995; Conrad, 1996; Hakemian and Rosenzweig, 2007; Higgins et al., 1981; Lai, 2009; Monechi et al., 2007; Segers, 1998; Wahlen, 1993). Rather, we focus on primary CH_4 processes in terrestrial ecosystems, and their environmental controls from a modeling perspective. In this context there exist three major methanogenesis mechanisms, two CH_4 methanotrophy mechanisms, and three aggregated CH_4 transport pathways in plants and soils. We note that most models do not explicitly represent all of these transport pathways, and that the relative importance of these pathways varies substantially in time, space, and with ecosystem types. We also pay attention to several other modeling features including capability for plot- or regional-level simulations, vertical representation of biogeochemical processes, and whether the model is embedded in an Earth System Model (ESM).

The published literature concludes that two processes dominate biological CH_4 production (Conrad, 1999; Krüger et al., 2001): acetoclastic methanogenesis -- CH_4 production from acetate, and hydrogenotrophic methanogenesis – CH_4 production from hydrogen (H_2) and carbon dioxide (CO_2).

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Acetoclastic and hydrogenotrophic methanogenesis account for ~50% - 90% and ~10% - 43% of global annual CH_4 produced, respectively (Conrad and Klose, 1999; Kotsyurbenko et al., 2004; Mer and Roger, 2001; Summons et al., 1998). Methylotrophic methanogenesis (producing CH_4 from methanol, methylamines, or dimethylsulfide) is usually considered a minor contributor of CH_4, but may be significant in marine systems (Summons et al., 1998). The proportion of CH_4 produced via any of these pathways varies widely in time, space, and across ecosystem types.

Methanotrophy occurs under aerobic (Gerard and Chanton 1993) and anaerobic (Smemo and Yavitt 2011) conditions. These oxidative processes can occur in several locations in soil and plants (Frenzel and Rudolph 1998, Heilman and Carlton 2001, Ström et al. 2005) and using CH_4 either produced in the soil column or transported from the atmosphere (Mau et al. 2013). Large variation in the relative magnitudes of these pathways as a percentage of total methanotrophy has been observed: aerobic oxidation of CH_4 in soil contributes 1% - 90% (King, 1996; Ström et al., 2005), anaerobic oxidation of CH_4 within the soil profile contributes 0.3% - 5% (Blazewicz et al., 2012; Murase and Kimura, 1996), oxidation of CH_4 during transport in plant aerenchyma contributes <1% (Frenzel and Karofeld, 2000; Frenzel and Rudolph, 1998), and oxidation of atmospheric CH_4 contributes ~10 – 100% (ranging from ~10% for wetland to ~100% for upland) (Gulledge and Schimel, 1998a; Gulledge and Schimel, 1998b; Topp and Pattey, 1997) to total methanotrophy in the ecosystem. CH_4 is transported from the soil profile to the atmosphere in typical open-water wetlands by seven pathways which could be aggregated into three: plant-mediated transport accounts for 12~98% (Butterbach-Bahl et al., 1997; Mer and Roger, 2001; Morrissey and Livingston, 1992), diffusion accounts for ~5% for wetlands and > 90% for upland systems (Barber et al., 1988; Mer and Roger, 2001), and ebullition accounts for 10~60% (Chanton et al., 1989; Tokida et al., 2007) of the CH_4 produced in the soil that is emitted to the atmosphere. The plant-mediated transport includes diffusive and advective (associated with gas or liquid flow) transports, soil diffusion includes soil gaseous diffusion and advection and aqueous diffusion and advection.

Environmental factors affecting CH_4 processes have many direct and indirect controls. The dominant direct factors controlling methanogenesis and methanotrophy in most ecosystems include

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oxygen availability, dissolved organic carbon concentration, soil pH, soil temperature, soil moisture, nitrate and other reducers, ferric iron, microbial community structure, active microbial biomass, wind speed (Askaer et al. 2011), plant root structure (Nouchi et al. 1990), etc. Indirect factors include soil texture and mineralogy, vegetation, air temperature, soil fauna, nitrogen input, irrigation, agricultural practices, sulfate reduction, and carbon quality, etc. (Banger et al., 2012; Bridgham et al., 2013; Hanson and Hanson, 1996; Higgins et al., 1981; Mer and Roger, 2001). The complicated effects induced by a few key factors on CH_4 processes have been mathematically described and incorporated in many CH_4 models; for example, direct factors such as soil temperature, moisture, oxygen availability, soil pH, and soil redox potential (Grant, 1998; Riley et al., 2011; Tian et al., 2010; Zhuang et al., 2004). The indirect factors such as nitrogen input (Banger et al., 2012), irrigation (Wassmann et al., 2000), and agricultural practices were not reviewed in this study as their impacts are indirect and were modeled through impacts on vegetation and hydrology (Li, 2000a; Ren et al., 2011; Xu et al., 2010).

3. Model Representation of CH_4 Processes

[Insert Figure 1 here]

[Insert Figure 2 here]

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

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WHyMe incorporate Walter CH_4 module (Walter and Heimann, 2000; Walter et al., 1996; Wania et al., 2009) while LPJ-WSL incorporates the CH_4 module from Christensen et al (Christensen et al., 1996).

The number of CH_4 models has steadily increased since the 1980s (Figs. 1 & 2): 1 in the 1980s, 11 in the 1990s, 14 in the 2000s, and 14 for 2010-2015. This increase in model developments is driven by many factors, including a desire to understand the contribution of CH_4 processes to regional CH_4 budget (Fig. 1). For instance, the Lovley's model was built to understand the CH_4 production and sulfate reduction in freshwater sediment (Lovley and Klug, 1986); while all models published in the 2010s are applicable for CH_4 budget quantification, particularly at regional scale. This rapid increase in CH_4 model development indicates a growing effort to analyze CH_4 cycling and quantify CH_4 budgets across spatial scales. Meanwhile, the key mechanisms represented in the models have increased at a slower pace (Fig. 2). The most important changes are representation of vertically-resolved processes within the soil and regional model simulation. For example, the percentage of the newly developed models with vertically-resolved CH_4 biogeochemistry has increased from 54% before 2000 to ~79% in the recent decade (2010-2015). The proportion of models with regional simulation capability (producing spatial map of CH_4 fluxes with inputs of spatial map of driving forces) has doubled from ~50% before the 2010s to almost 100% afterwards (Fig. 2).

[Insert Tables 1, 2, and 3 here]

The majority of these models were designed to simulate land-surface exchange in saturated ecosystems (primarily natural wetlands and rice paddies) (Huang et al., 1998b; Li, 2000a; Walter et al., 1996) (Table 1). Not all of the models explicitly represented the belowground mechanistic processes for CH_4 production and consumption and the primary carbon biogeochemical processes (Christensen et al., 1996; Ding and Wang, 1996). The land-atmosphere CH_4 exchange is a net balance of many processes including production, oxidation, and transport, which are represented in models with different complexities (Table 2). Some models are quite complicated, while some are relatively simple. The obvious tradeoff in modeling CH_4 cycling is to represent mechanisms as accurately as possible while managing complexity (Evans et al., 2013), and ensuring that additional complexity enhances predictability (Tang and Zhuang, 2008).

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3.1 CH_4 Model Classification

[Insert Figure 3 here]

[Insert Figure 4 here]

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

3.2 Methanogenesis

Models make use of four types of modeling frameworks (Table 3) to relate methanogenesis to substrate requirements. Similar to Eqs (1) – (4) in Table 3, there are four model algorithms to represent methanogenesis: (1) empirical association between methanogenesis and environmental condition,

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including temperature and water table; (2) empirical correlation of methanogenesis with biological variables (particularly heterotrophic respiration and soil organic matter); (3) methanogenesis as a function of concentration of substrate (DOC); and (4) a suite of mechanistic processes simulated for methanogenesis.

Representation of the substrate for methanogenesis may be a key aspect of simulating CH_4 cycling in terrestrial ecosystems (Bellisario et al., 1999); however, more than half of the models examined do not explicitly simulate substrates for methanogenesis. We note, however, that explicit representation of substrates and their effects on methanogenesis requires additional model parameters, and therefore degrees of freedom in the model, which can lead to increased equifinality (Tang and Zhuang, 2008). The optimum complexity level for methanogenesis and consumption models remains to be determined.

The first model algorithm correlates methanogenesis with environmental factors and ignores substrate production and its influence on methanogenesis [Eq. (1)] (Table 3). This group includes Christensen's model (Christensen et al., 1996), which simulates the net flux of CH_4 based on fraction of saturated soil column and soil temperature, and the IAP-RAS model (Mokhov et al., 2007), which calculates methanogenesis as an empirical equation of soil temperature. This group has a role in site-specific interpolation of observations for scaling over time at a given site, but does not explicitly represent carbon or acetate substrate. The second model algorithm directly links methanogenesis with heterotrophic respiration or soil organic matter content, but does not explicitly represent carbon or acetate substrate availability [Eq. (2)]; examples are the LPJ model family (Hodson et al., 2011; Spahni et al., 2011; Wania et al., 2010, 2009) and CLM4Me (Riley et al., 2011). The third model algorithm simulates dissolved organic carbon (DOC) or different pools of soil organic carbon, which are treated as a substrate pool influencing CH_4 production [Eq. (3)]; examples are the MEM model (Cao et al., 1995; Cao et al., 1998) and DLEM (Tian et al., 2010). The fourth model algorithm considers the primary substrates for methanogenesis, that is, acetate and single-carbon compounds [Eq. (4)]; examples are Kettunen's model (Kettunen, 2003), Segers' model (Segers and Kengen, 1998; Segers and Leffelaar,

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2001a, b; Segers et al., 2001), van Bodegom's model (van Bodegom et al., 2000; van Bodegom et al., 2001), and the *ecosys* model (Grant, 1998).

Methanogenesis is a fundamental process for CH_4 cycling, and a majority of models simulate methanogenesis in either implicit or explicit ways (Tables 2 & 3). For example, 32 models (i.e. Cartoon model, CASA, CH4MOD, Christensen model, CLM4Me, Ding model, DLEM, DNDC, DOS-TEM, ecosys, Gong model, HH model, IAP-RAS, Kettunen model, Lovley model, LPJ-Brn, LPJ-WHyMe, LPJ-WSL, Martens model, MEM, MERES, ORCHIDEE, SDGVM, Segers model, TCF, TEM, TRIPLEX-GHG, UW-VIC, van Bodegom model, VISIT, Walter model, and Xu model) simulate methanogenesis as one individual process. As a comparison, only three out of 40 CH_4 models reviewed explicitly simulate two methanogenesis pathways (acetoclastic methanogenesis and hydrogenotrophic methanogenesis) (Table 3). As mentioned earlier, it is well-recognized that there are two dominant methanogenesis pathways and their relative combination changes significantly across environmental gradients, for example, along the soil profile (Falz et al., 1999) and across landscape types (McCalley et al., 2014). This lack of representation of two methanogenesis mechanisms might have caused dramatic bias in simulating CH_4 flux temporally and spatially and needs to be addressed in future model improvements.

Michaelis-Menten-like equations, widely used for simulating CH_4 production and oxidation, consider substrates limiting factors (Segers and Kengen, 1998). A few CH_4 models in the third category of methanogenesis models (linking methanogenesis with a substrate) use the Michaelis-Menten-like equation to compute methanogenesis and methanotrophy rates (Eqs. 3, 5, & 6). For example, DLEM simulates methanogenesis as a function of DOC concentration and other environmental controls, and Michaelis-Menten-like functions were used to compute methanogenesis on the basis of DOC as substrate.

3.3 Methanotrophy

Methanotrophy is another important process for simulating the land-atmosphere exchange of CH_4 (Table 2). Aerobic and anaerobic methanotrophy occurs in different locations in the soil profile, and affect both methanogenesis in the profile and CH_4 diffusing in from the atmosphere. For example,

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the oxidation of atmospheric CH_4, rhizosphere and bulk soil oxidation, and oxidation during CH_4 transport from soil to the atmosphere have been measured and modeled (Tables 1 & 2). Anaerobic CH_4 oxidation has been measured (Blazewicz et al., 2012) and has been proposed to be incorporated into ecosystem models (Gauthier et al., 2015).

It has been confirmed that the aerobic oxidation of CH_4 produced in the soil profile and aerobic oxidation of atmospheric CH_4 play a major role in CH_4 consumption in the system, and that anaerobic oxidation of CH_4 is a minor contributor. Currently, no models explicitly simulate the anaerobic oxidation of CH_4 in soil, although a few recent studies highlighted the importance of this process (Blazewicz et al., 2012; Caldwell et al., 2008; Conrad, 2009; Smemo and Yavitt, 2011; Valentine and Reeburgh, 2000). The key reasons for this omission are that the process has not been mathematically described, the key parameters are uncertain (Gauthier et al., 2015), and the biochemical mechanism is not fully understood.

Methanotrophy has been simulated with dual Monod Michaelis-Menten-like equations with CH_4 and oxygen as limiting factors (Table 3). Recent work has shown that the Michaelis-Menten approach may be inaccurate when representing multi-substrate, multi-consumer networks, and that a new approach (called Equilibrium Chemistry Approximation, ECA) can ameliorate this problem (Tang and Riley 2013, 2015; Zhu et al., 2016). Although the ECA approach has not been applied for simulations of CH_4 emissions, CH_4 dynamics are inherently multi-consumer, including transformations associated with methanogens, heterotrophs, ebullition, advection, diffusion, and aerenchyma transport, even if only one substrate is considered.

3.4. CH_4 within the Soil/Water Profile

CH_4 produced in the soil profile or below the water table is not transported immediately into the atmosphere. The time required for CH_4 to migrate from deep soil profile to the atmosphere ranges from minutes to days (depending on temperature, water, soil texture, and emissivity of plant roots), or even a season if the surface is frozen. The majority of current CH_4 models assume that CH_4 transport to the atmosphere occurs immediately after CH_4 is produced, and a portion is oxidized (Tian et al., 2010; Fan

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et al., 2013); for models simulating CH_4 flux over minutes to days, the lack of modeled transport may produce unrealistic simulations.

Some models do simulate CH_4 dynamics within the soil and water profile (e.g., *ecosys*, CLM4Me), which produces a lag between methanogenesis and emission, allowing for oxidation to be explicitly represented during transport, and is valuable for simulating the seasonality of CH_4 flux (Table 2). For example, the recently observed CH_4 burst in the spring season in some field experiments confirms that the storage of CH_4 produced in winter can produce a strong emission outburst (Song et al., 2012). Without understanding the mechanism of CH_4 storage beneath the soil surface, this phenomenon will be difficult to simulate. In most of the models considering CH_4 storage, the CH_4 is treated as a simple gas pool, under the water table, which will be transported to the atmosphere through several transport pathways.

3.5. CH_4 Transport from Soil to the Atmosphere

The transport of CH_4 produced and stored in soil column is the bottleneck for CH_4 leaving the system; therefore, this process is an important control on the instantaneous land-surface CH_4 flux. Several important pathways of CH_4 transport to the atmosphere are identified: plant-mediated diffusive and advective transport, aqueous and gaseous diffusion, and ebullition (Beckett et al., 2001; Chanton, 2005; Mer and Roger, 2001; Whiting and Chanton, 1996). Model simulation of these transport pathways uses direct control of simulated land surface CH_4 flux, with CH_4 transport simulation considered in a manner similar to Eq. (7) (Table 3).

The majority (83%) of the current models simulate at least one transport pathway. Specifically, 70% of the models simulate CH_4 transport via aerenchyma, 80% simulate gaseous diffusive transport, and 60% simulate ebullition transport (Table 1). More than 50% of models simulated these three transport pathways. Some models simulate explicitly the aqueous and gaseous diffusion of CH_4 (Riley et al., 2011), while most models do not simulate advective transport. Many models simulate diffusion and plant-mediated transport in very simple ways. For model improvement in this area, three issues remain as challenges:

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(1) Most models treat transport implicitly; for example, the diffusion processes is treated simply as an excessive release of CH_4 when its concentration exceeds a threshold (Tian et al., 2010). This treatment prevents the model from simulating the lag between methanogenesis and its final release to the atmosphere, which has been confirmed to be the key mechanism for hot-moment and hot-spot of CH_4 flux (Song et al., 2012) and for oxidation during transport.

(2) The parameters for plant species capable of transporting gas (i.e., *aerenchyma*) are poorly constrained (Riley et al. 2011), although plant-mediated transport has been identified as the dominant pathway for CH_4 emission in some natural wetlands (Aulakh et al., 2000; Colmer, 2003).

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

3.6. Environmental Controls on CH_4 Processes

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Although a suite of environmental factors affects various CH_4 processes, many of these factors are not explicitly simulated in many models. These factors include soil temperature, soil moisture, substrate, soil pH, soil redox potential, and oxygen availability. Many other factors not directly incorporated in the models, could indirectly affect CH_4 cycling. For example, nitrogen fertilizer affects methanogenesis through its stimulating impacts on ecosystem productivity, which in turn affects DOC, soil moisture and soil temperature (Xu et al., 2010). The CLM4Me model simulates permafrost and its effects on CH_4 dynamics, and has a simple relationship for soil pH impacts on methanogenesis (Riley et al., 2011). Wania et al. (2013) reviewed a number of active CH_4 models for their representation of CH_4 production area. In this review, we specifically focus on temperature, moisture, and pH because these factors directly affect CH_4 processes in all environments, and they have been explicitly simulated in the many of the models.

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

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10 in Table 4), and (3) Arrhenius type function (Eq. 11 in Table 3). Of these three model representations of temperature dependence, the Q_{10} equation is the most common mathematical description. However, the parameters for these empirical functions vary widely across the models (Table 4). Actual temperature responses may diverge significantly from the models at low temperatures, close to the freezing point of water, and high temperatures, close to the denaturation point of enzymes.

[Insert Table 4 here]

Soil moisture is another important factor controlling CH_4 processes, because water limits O_2 diffusion from the air through the soil column and because microbes can become stressed at low matric potential. CH_4 is produced typically under conditions with a low reduction potential, which is normally associated with long-term inundation. Although methanogenesis occurs solely under reducing conditions (methanogenesis within plant biomass under aerobic condition has never been simulated although it has been reported in experiments (Keppler et al., 2006)), methanotrophy occurs under drier, aerobic conditions. A low water content can also limit microbial activity in frozen soils or soils with high osmolarity (Watanabe and Ito, 2008). Therefore, soil moisture has different impacts on different CH_4 processes. Four types of model representation are used to simulate moisture's effects on CH_4 processes (Eqs. 13-16 in Table 3).

(1) Methanogenesis occurs only in the saturated zone and an exponential function for soil moisture is used to control methanotrophy (e.g., CLM4Me);

(2) Linear function for moisture impacts (e.g., CLASS use linear function for moisture impact on methanotrophy) (Curry, 2007);

(3) Reciprocal responsive curves for moisture impacts on methanogenesis and methanotrophy (e.g., DLEM) (Tian et al., 2010);

(4) A bell-shaped curve for methanogenesis (e.g., TEM uses a function similar to Eq. (16) for moisture impacts) (Zhuang et al., 2004).

Soil pH is another important factor that has been included in a number of CH_4 models (Cao et al., 1995; Zhuang et al., 2004). Methanogens and methanotrophs depend on proton and sodium ion translocation for energy conservation, thus they are directly affected by pH. The pH impacts on CH_4

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processes are simulated as a bell-shaped curve although the mathematical functions used to describe pH impacts are different (Eq. 17a, 17b, and 17c). Moreover, even when the same functions were used in different models, they were associated with different parameter values, indicating slightly different response functions; for example, the MEM model sets pH_{min} (minimum pH value for CH_4 processes being active), pH_{opt} (optimal pH value for CH_4 processes being most active), and pH_{max} (minimum pH value for CH_4 processes being active) values of 5.5, 7.5, and 9 (Cao et al., 1995). This set of parameter values was adopted in the TEM model (Zhuang et al., 2004), whereas the DLEM model uses values of 4, 7, and 10 (Tian et al., 2010). The CLM4Me model uses a different function while keeping the impact curve at the same shape, but its peak has an optimal pH of 6.2 (Meng et al., 2012). It should be noted that while pH has been confirmed to significantly affect CH_4 production (Xu et al., 2015), the simulation of pH dynamics caused by organic acid in soils remains a key challenge for the incorporation of this phenomenon.

For the other environmental factors, model representation is still in its infancy; however, several models consider oxygen availability as an electron acceptor for methanotrophy (e.g., Beckett model, Cartoon model, CLM4Me, *ecosys*, Kettunen model, MERES, Segers model, van Bodegom model, De Visscher model, and Xu model). In addition, only a few models simulate the impacts of the electron acceptor (i.e. nitrate, sulfate, etc.) on CH_4 processes (Table 2). For example, the van Bodegom model simulates iron biogeochemistry, and the Lovley model, Marten model, and van Bodegom model all simulate sulfate as the electron acceptor and its impacts on methanogenesis and methanotrophy (Lovley and Klug, 1986; Martens et al., 1998; van Bodegom et al., 2001). Explicitly representing these processes enables future coupling of CH_4 cycling to processes that are regionally significant, such as iron reduction on the Alaskan North Slope (Miller et al., 2015). These models have the potential advantage of more accurately simulating biogeochemical processes of carbon and ions, although large uncertainties still exist because of the lack of data for constraining model parameters.

3.7. CH_4 implementation in ESMs

The importance of CH_4 flux in simulating climate dynamics has been well recognized (IPCC 2013; Ringeval et al., 2011); yet few ESMs have implemented a CH_4 module (Ringeval et al., 2011;

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Riley et al., 2011; Xu et al., 2014; Hopcroft et al., 2011; Eliseev et al., 2008). While these models have been claimed to be coupled within ESMs, truly fully coupled simulations within ESMs to evaluate CH_4 dynamic impacts on global climate system are rare (Eliseev et al., 2008; Hopcroft et al., 2011). For example, the SDGVM has been coupled within Fast Met Office UK Universities Simulator (FAMOUS), a coupled general circulation model, to study the association between terrestrial CH_4 fluxes with rapid climate fluctuation during the last glacial period (Hopcroft et al., 2011). IAP-RAP model was used to simulate terrestrial CH_4 flux and its contributions to atmospheric CH_4 concentrations and further on climate change. The quasi-coupling between ORCHIDEE_WET with an ocean-atmosphere general circulation model was used to theoretically evaluate terrestrial CH_4 dynamics on climate system (Ringeval et al., 2011). The CLM application within CESM framework has both CLM4Me and CLM-Microbe module for CH_4 dynamics, but none of them have been applied for a fully coupled simulation to evaluate CH_4-climate feedback. It should be a key research effort for CLM community in next five years to complete this coupling. All previous coupled ESM simulations have concluded that changes in terrestrial CH_4 flux has small impacts on climate change, while they also pointed out that large uncertainties exist. Given the importance of CH_4 as a greenhouse gas and uncertainties in current ESMs in simulating permafrost carbon and CH_4 flux, more efforts should be invested to implement CH_4 module in ESMs and further evaluate the CH_4-climate feedback under different climate scenarios.

3.8 Summary

Through the four decades of modeling CH_4 cycling in terrestrial ecosystems, consensus has been reached on several fronts. First, CH_4 cycling includes a suite of complicated processes, and both the simple and complex models are able to estimate land-surface CH_4 flux to a certain level of confidence, although models of different complexity do provide different results (Tang et al., 2010). Second, although a number of CH_4 models have been developed, several gaps remain that need new model representations (e.g., dynamic linkage between inundation dynamics and the CH_4 module (Melton et al., 2013), anaerobic oxidation of CH_4 (Gauthier et al., 2015)).

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Two recent CH_4 model-model inter-comparison projects raised several important points (Bohn et al., 2015; Melton et al., 2013): (1) the distribution of the inundation area is important for accurately simulating global CH_4 emissions, but was poorly represented in CH_4 models; (2) the modeled response of land-surface CH_4 emission to elevated CO_2 is likely biased as a number of global change factors were missing, which indicates the need for modeling with multiple global environmental factors; and (3) the need for comparison with high-frequency observational data is identified as an important task for future model-model inter-comparison. These lessons will be helpful for, and likely addressed during, model improvements and applications of more mechanistic CH_4 models.

Although the primary individual CH_4 processes have been studied and quantified at a certain level of confidence, only a few modeling studies have reported these individual processes as previously discussed. For example three pathways of CH_4 transports were represented in Kettunen, 2003 and Walter et al., 1996, but none of those modeled results have been evaluated against observational results for those individual processes. One reason is that measurements rarely distinguish among individual processes; another reason is that the majority of CH_4 models do not explicitly represent all processes (Table 2). However, a number of studies report significant shifts in the processes contributing to the surface CH_4 flux along environmental gradients or across biomes (Conrad, 2009; Krumholz et al., 1995; McCalley et al., 2014). Projecting CH_4 fluxes into future changing climate conditions requires not only accurate simulations of CH_4 processes, but also shifts among the various processes. In addition, CO_2 flux has been evaluated within the Earth System Modeling framework, but only a few studies have evaluated the CH_4 flux and its contribution to climate dynamics. Given the much higher warming potential and relatively faster rate of increase of atmospheric CH_4, fully coupled simulations are needed to represent the feedbacks between terrestrial CH_4 exchanges and climate. We note that a few recent studies reported a relatively small climate warming-methane feedback from global wetlands and permafrost (Gao et al., 2013; Gedney et al., 2004; Riley et al., 2011). A fully mechanistic CH_4 model that accounts for all the important features is critically needed. In addition, a modeling framework to integrate multiple sources of data, such as microbial community structure and functional activities, ecosystem-level measurements, and global scale satellite measurements of gas concentration and flux is needed with these mechanistic CH_4 models.

4. Needs for Mechanistic Methane Models

During the last few years, the scientific community has continued to improve and optimize models to better simulate methanogenesis, methanotrophy, CH_4 transport, and their environmental and biological controls (Xu et al., 2015; Zhu. Q. et al., 2014). A number of emerging tasks have been identified, and progress in these directions is expected. First, linking genomic data with large-scale CH_4 flux measurements will be an important, while challenging, task for the entire community; for example, some work has been carried out in this direction (De Haas et al., 2011; Larsen et al., 2012). An effort has been initialized to develop a new microbial functional group-based CH_4 model, which has the advantages of linking genomic information for each individual process with the four microbial functional groups (Xu et al., 2015). Second, data-data and model-model comparisons are another important effort for model comparison and improvement. One ongoing encouraging feature that all recently developed CH_4 models possess is the capability for regional simulations as well as the possibility to be run at the site level (Riley et al., 2011; Zhu. Q. et al., 2014).

Third, microbial processes need to be considered for incorporation into ecosystem models for simulating carbon cycling and CH_4 processes (DeLong et al., 2011; Xu et al., 2014). Although a few models explicitly simulate the microbial mechanisms of CH_4 cycling (Arah and Stephen, 1998; Grant, 1998; Li, 2000a; Segers and Kengen, 1998), none of them have been used for regional- or global-scale estimation of microbial contributions to the CH_4 budget. A reasonable experimental design and a well-validated microbial functional group-based CH_4 model should be combined to enhance our capability to apply models to estimate a regional CH_4 budget and to investigate the combination of microbial and environmental contributions to the land surface CH_4 flux (DeLong et al., 2011). Fourth, incorporating well-validated CH_4 modules into Earth System Modeling frameworks will allow a fully coupled simulation that provides a holistic understanding of the CH_4 processes, with its connections to many other processes and mechanisms in the atmosphere. Several recently developed models fall in the framework of Earth System Models (Riley et al., 2011; Ringeval et al., 2010), which provide a

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foundation for this application in a relatively easy way. This effort will likely contribute not only to the CH_4 modeling community, but also to the entire global change science community (Koven et al., 2011). The iron and sulfate biogeochemistry that has been implicitly simulated in a few models (Table 2), but was not included in any of the recently developed models because that effort will likely be achieved over the long term, owing to poor understanding of the mechanisms and the lack of observational data.

[Insert Figure 5 here]

Based on the above-mentioned needs and model features as well as the mechanisms for the CH_4 models, the next generation of CH_4 models will likely include several important features (Fig. 5). The models should (1) be embedded in an Earth System Model, (2) consider the vertical distribution of thermal, hydrological, and biogeochemical transport and processes, (3) represent mechanistic processes for microbial CH_4 production, consumption, and transport, and (4) support data assimilation and a model benchmarking system as auxiliary components.

5. Challenges for Developing Mechanistic CH_4 Models

Knowledge Gaps - Modeling CH_4 cycling is a dynamic process. As new mechanisms are identified the modeling community should ensure that the mechanisms are well studied and mathematically described, as has occurred over the past decades (Conrad, 1989; McCalley et al., 2014; Schütz et al., 1989; Xu et al., 2015). However, a number of knowledge gaps need to be filled before a full modeling framework of CH_4 processes within terrestrial ecosystems can be achieved. The first gap is either confirmation or rejection of a few recently observed CH_4 mechanisms; these mechanisms need to be fully vetted before being considered for incorporation into a model. The first most well-known mechanism still under debate is aerobic CH_4 production within plant tissue (Beerling et al., 2008; Keppler et al., 2006). Since its first report in 2006 (Keppler et al., 2006), a few studies have confirmed the mechanism in multiple plant species (Wang et al., 2007). While its existence in nature is still under debate (Dueck et al., 2007), this mechanism will likely not be incorporated into an ecosystem model before solid evidence is presented and consensus is reached. The second new mechanism is fungi as a microbial group carrying out CH_4 production (Lenhart et al., 2012). More field- or lab-based experiments are needed to investigate this mechanism and its contribution to the global CH_4 budget,

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probably through a data model integration approach. Third, the aerobic production of methane from the cleavage of methylphosphonate has been demonstrated in marine systems (Karl et al., 2008), but the significance of this process in terrestrial systems is unknown. Forth, the large CH_4 emission from rivers and small ponds are still not fully understood (Holgerson and Raymond, 2016; Martinson et al., 2010), which will likely be a direction for future model improvement.

Another knowledge gap is the missing comprehensive understanding of spatial and temporal variations in CH_4 flux; particularly, the "hot spots" and "hot moments" of observed CH_4 flux are still not completely understood (Becker et al., 2008; Mastepanov et al., 2008; Song et al., 2012). The traditional static chamber method of measuring CH_4 emissions could underestimate the CH_4 flux because sparse sampling is unlikely to detect these foci or pulses of unusually high emissions. Better methods are also needed to measure CH_4 cycling during the shoulder seasons in the Arctic and subarctic when fluxes may be most variable (Zona et al. 2016). These knowledge gaps are key hurdles for CH_4 model development efforts. No model has yet been tested for simulating hot spots or hot moments over large spatial or long temporal scales. However, the high range (usually of factor 1-10) of the observed CH_4 flux might cause regional budgets to vary substantially (Song et al., 2012); therefore, mechanistic model representations of these mechanisms are highly needed.

Modeling Challenges - Better simulation of CH_4 cycling in terrestrial ecosystems requires improvement in the model structure to represent mechanistic CH_4 processes. First is the challenge to simulate the vertical profile of soil biogeochemical processes and validate such models with observational results. Although some models have a capability for vertical distribution of carbon and nitrogen (Koven et al., 2013; Tang et al. 2013; Mau et al., 2013), a better framework for CH_4 and extension to cover the majority of CH_4 models are needed. This vertical distribution of biogeochemistry is necessary for simulating the vertical distribution of CH_4 processes and CH_4 transport through the soil profile before reaching the atmosphere. A second challenge is incorporating tracer capability. Isotopic tracers (^{13}C, ^{14}C) have been widely used for quantifying the carbon flow and partitioning among individual CH_4 processes (Conrad, 2005; Conrad and Claus, 2005), but for ecosystem models this capability has not been represented even though it is very important to understanding CH_4 processes

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and integrating field observational data. A third challenge is to simulate microbial functional groups. Microbial processes are carried out by different functional groups of microbes (Lenhart et al., 2012; McCalley et al., 2014). Therefore, model comparison with individual processes requires representing the microbial population sizes (or active biomass) for specific functional groups (Tveit et al., 2015). This goal has proved more difficult than representing plant functional types or traits in models, because not all microbial taxonomic groups have ecologically coherent functions (Philippot et al., 2010). A fourth challenge is to simulate the lateral transport of dissolved and particulate biogeochemical variables that are necessary to better simulate the storage and transport of CH_4 within heterogeneous landscapes (Weller et al., 1995). A fifth challenge is modeling CH_4 flux across spatial scales. Although a few studies have been used to demonstrate the approach for simulating CH_4 budget at plot scale and eddy covariance domain scale (Zhang et al., 2012), a mechanistic framework to link CH_4 processes at distinct scales is still lacking while highly valuable. Finally, a sixth challenge is accurate simulation of CH_4 within human-managed ecosystems. Human management practices are always hard to simulate and predict, and their impacts on CH_4 processes are challenging (Li et al., 2005).

Data Needs - First, a comprehensive dataset of field measurements of CH_4 fluxes across various landscape types is needed to effectively validate the CH_4 models. Although a number of datasets have been compiled (Aronson and Helliker, 2010; Chen et al., 2012; Liu and Greaver, 2009; Mosier et al., 1997; Yvon-Durocher et al., 2014), some landscape types are still not fully covered. Meanwhile, high-frequency field observational data are also needed, particularly long-term observational data in some less-studied ecosystems; for example Arctic tundra ecosystems have been considered as an important contributor to global CH_4 budget in the changing climate (IPCC, 2013; Koven et al., 2011), however, long-term dataset of CH_4 flux is lacking. It is well-known that inter-annual variation of climate may turn an ecosystem from a CH_4 sink to a CH_4 source (Nauta et al., 2015; Shoemaker et al., 2014); therefore, a long-term observational dataset that covers these temporal shifts in CH_4 flux and its associated ecosystem information would improve our understanding of the processes and our representation of them in CH_4 models. Second, microbial community shifts and their role in CH_4 processes are important, although information is incomplete for model representation of this mechanism

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(McCalley et al., 2014; Schimel and Gulledge, 1998). Although a number of studies have reported the microbial community structure and its potential association with changes in CH_4 processes (Monday et al., 2014; Schimel, 1995; Wagner et al., 2005), none of this progress has been documented in a mathematical manner suitable for a modeling representation.

Third, a comprehensive dataset of all primary CH_4 processes within an individual ecosystem would be valuable for model optimization and validation. Although some datasets exist, no study has investigated all primary individual CH_4 processes within the same plot over the long term. Given the substantial spatial heterogeneity of CH_4 processes, this lack of process representation may cause bias in CH_4 simulations at regional scale. It should be noted that land surface net CH_4 flux is a measurable ecosystem-level process, whereas many individual CH_4 processes are difficult to accurately measure. Therefore, designing field- or lab-based-experiments suitable for measuring these processes is a fundamental need. For example, the anaerobic oxidation of CH_4 has been identified as a critical process for some ecosystem types, but no comprehensive dataset on it is available for model development or improvement.

Last but not least, high quality spatial data as driving forces and validation data for CH_4 models are critical for model development as well (Melton et al., 2013; Wania et al., 2013). Spatial distribution and dynamics of wetland area probably are the most important data need for CH_4 models (Wania et al., 2013). Spatial distribution of soil temperature, moisture, and texture are fundamental information because they serve as direct or indirectly environmental control on CH_4 processes. Recently launched Soil Moisture Active Passive (SMAP) satellite could be used as an important data source for soil moisture for driving CH_4 model (Entekhabi et al., 2010). It has been identified that soil texture and pH are important for simulating CH_4 processes (Xu et al., 2015). In addition, the atmospheric CH_4 concentration data from satellite could be used as important benchmark for model validation purposes, for example Scanning Imaging Absorption spectrometer for Atmospheric ChartographY (SCIAMACHY) (Frankenberg et al., 2005) and Greenhouse gas Observing SATellite (GOSAT) (Yokota et al., 2009).

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Data-Model Integration - Model development and data collection are two important, but historically independent scientific approaches; the integration between model development and data collection is much stronger for advancing science (De Kauwe et al., 2014; Luo et al., 2012; Peng et al., 2011). Although data-model integration is recognized as very important for understanding and predicting CH_4 processes and some progress has been made, integrating experiments and models presents multiple challenges, particularly, 1) the methods for integrating data with the models are not well developed for CH_4 cycling; 2) the metrics for evaluating data-model integration are not consistent in the scientific community; and 3) the regular communication between data scientists and modelers on various aspects of CH_4 processes and their model representation is lacking.

Methods for data-model integration have been recently created, for example, Kalman Filter (Gao et al., 2011), Bayesian (Ogle and Barber, 2008; Ricciuto et al., 2008; Schleip et al., 2009; Van Oijen et al., 2005), and Markov Chain Monte Carlo (Casella and Robert, 2005). However, no studies have evaluated these methods for integrating CH_4 data with models. In addition, the metric for evaluating the data-model integration is still not well developed. A very helpful strategy for data-model integration is to solicit timely input from modelers when designing a field experiment. A good example of this is the U.S. Department of Energy-sponsored project Next Generation Ecosystem Experiments - Arctic (ngee-arctic.ornl.gov), which was planned with inputs from field scientists, data scientists, and modelers. Another successful example is the U.S. DOE-sponsored project, Spruce and Peatland Responses Under Climatic and Environmental Change (SPRUCE) (mnspruce.ornl.gov), in which the experiment design for data-model integration created an opportunity for modeling needs to be adopted by the field scientists. A modeling framework that focuses on model parameterization and validation ability is under development at Oak Ridge National Laboratory; building model optimization algorithm into an ESM framework will enable more effective parameterization of newly developed CH_4 modules within CLM at site, regional, and global scales (Ricciuto et al, personal communication).

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6. Concluding Remarks

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CH_4 dynamics in terrestrial ecosystems have been intensively studied, and model representation of CH_4 cycling has evolved as new knowledge becomes available. This is inherently a slow process.

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Currently, the primary mechanisms for CH_4 processes in terrestrial ecosystems are implicitly represented in many, but not all, terrestrial ecosystem models. Development of CH_4 models began in the late 1980s, and the pace of growth has been fast since the 1990s. Model development shifted from theoretical analysis in the 1980s and 1990s to being more applied in the 2000s and 2010s, expressed as being more focused on regional CH_4 budget quantification and integration with multiple sources of observational data. Although some current CH_4 models consider most of the relevant mechanisms, none of them consider all the processes for methanogenesis, methanotrophy, CH_4 transport, and their primary environmental controls. Further, evidence demonstrating that incorporating all of these processes would lead to more accurate prediction is needed. Incorporating sophisticated parameter assimilation, uncertainty quantification, equifinality quantification, and metrics of the benefits associated with increased model complexity would also facilitate scientific discovery.

The CH_4 models for accurate projection of land-climate feedback in the next few decades should: (1) use mechanistic formulations for primary CH_4 processes, (2) be embedded in Earth System Models for the global evaluation of terrestrial-climate feedback associated with CH_4 fluxes, (3) have the capacity to integrate multiple sources of data, which makes the model not only a prediction tool but also an integrative tool, and (4) be developed in association with model benchmarking frameworks. These four characteristics pave the way for examining CH_4 processes and flux in the context of global change. These improvements for CH_4 modeling would be beneficial for ESMs and further simulation of climate-carbon cycle feedbacks.

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Table 1. Terrestrial ecosystem models for CH_4 cycling and the model representation of three pathways of CH_4 transport (models are in alphabetical order; author's last name is used if the model name is not available)

Model	Aerenchynma	Diffusion	Ebullition	References
Beckett model	Yes	Yes	No	(Beckett et al., 2001)
Cartoon model	Yes	Yes	Yes	(Arah and Stephen, 1998; Arah and Kirk, 2000)
CASA	Yes	Yes	Yes	(Potter, 1997; Potter et al., 1996)
CH4MOD	Yes	Yes	Yes	(Huang et al., 1998b; Huang et al., 2004; Li et al., 2012)
Christensen model	No	No	No	(Christensen et al., 1996)
CLASS	No	Yes	No	(Curry, 2009; Curry, 2007)
CLM4Me	Yes	Yes	Yes	(Riley et al., 2011)
CLM-Microbe	Yes	Yes	Yes	(Xu et al., 2015; Xu et al., 2014)
DAYCENT	No	Yes	No	(Del Grosso et al., 2002; Del Grosso et al., 2009; Del Grosso et al., 2000)
Ding model	Yes	No	No	(Ding and Wang, 1996)
DLEM	Yes	Yes	Yes	(Tian et al., 2010; Xu and Tian, 2012)
DNDC	Yes	Yes	Yes	(Li, 2000b)
DOS-TEM	Yes	Yes	Yes	(Fan et al., 2013)
ecosys	No	Yes	Yes	(Grant, 2001, 1998)
Gong model	Yes	Yes	Yes	(Gong et al., 2013)
HH model	Yes	Yes	Yes	(Cresto-Aleina et al., 2015)
IAP-RAS	No	No	No	(Eliseev et al., 2008; Mokhov et al., 2007)

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Kettunen model	Yes	Yes	Yes	(Kettunen, 2003)
Lovley model	No	No	No	(Lovley and Klug, 1986)
LPJ-Bern	Yes	Yes	Yes	(Spahni et al., 2011)
LPJ-WHyMe	Yes	Yes	Yes	(Wania et al., 2010, 2009)
LPJ-WSL	No	No	No	(Hodson et al., 2011)
Martens model	Yes	Yes	Yes	(Martens et al., 1998)
MEM	No	No	No	(Cao et al., 1995; Cao et al., 1998)
MERES	Yes	Yes	No	(Matthews et al., 2000)
Nouchi model	Yes	Yes	No	(Hosono and Nouchi, 1997; Nouchi et al., 1994)
ORCHIDEE	Yes	Yes	Yes	(Ringeval et al., 2010; Ringeval et al., 2011)
Ridgwell model	No	Yes	No	(Ridgwell et al., 1999)
SDGVM	No	No	No	(Hopcroft et al., 2011)
Segers model	Yes	Yes	Yes	(Segers and Kengen, 1998; Segers and Leffelaar, 2001a, b; Segers et al., 2001)
Tagesson model	No	No	No	(Tagesson et al., 2013)
TCF	Yes	Yes	Yes	(Watts et al., 2014)
TEM	Yes	Yes	Yes	(Zhuang et al., 2004)
TRIPLEX-GHG	Yes	Yes	Yes	(Zhu Q. et al., 2014)
UW-VIC	Yes	Yes	Yes	(Bohn and Lettenmaier, 2010; Bohn et al., 2007)
van Bodegom model	Yes	Yes	Yes	(van Bodegom et al., 2000; Van Bodegom et al., 2001)
VISIT	Yes	Yes	Yes	(Inatomi et al., 2010; Ito and Inatomi, 2012)

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De Visscher model	No	Yes	No	(De Visscher and Van Cleemput, 2003)
Walter model	Yes	Yes	Yes	(Walter and Heimann, 2000; Walter et al., 1996)
Xu model	Yes	Yes	Yes	(Xu et al., 2007)

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

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

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biogeochemistry	DOS-TEM, *ecosys*, Gong model, HH model, IAP-RAS, Kettunen model, Lovley model, LPJ-Bern, LPJ-WHyMe, LPJ-WSL, Martens model, MERES, ORCHIDEE, Ridgwell model, SDGVM, Seger model, TRIPLEX-GHG, UW-VIC, VISIT, De Visscher model, Walter model, Xu model
Regional-scale, capacity for up-scaling	CASA, CH4MOD, Christensen model, CLASS, CLM4Me, CLM-Microbe, DAYCENT, DLEM, *ecosys*, Gong model, HH model, IAP-RAS, LPJ-Bern, LPJ-WHyMe, LPJ-WSL, Martens model, MEM, MERES, ORCHIDEE, Ridgwell model, SDGVM, Tagesson model, TCF, TEM, TRIPLEX-GHG, UW-VIC, VISIT, Walter model

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Table 3. The mathematical equations used to described the CH_4 processes used in representative models (P_{CH4} is the CH_4 production rate; $Oxid_{CH4}$ is the CH_4 oxidation rate; T_{CH4} is the CH_4 transport rate; D_{CH4} is the CH_4 diffusion rate; some parameter may have been changed from original publication to keep relatively consistent in this table)

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

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	6	$Oxid_{CH_4} = V \times \left(\frac{[CH_4]}{K_{CH_4} + [CH_4]}\right)\left(\frac{[O_2]}{K_{O_2} + [O_2]}\right) \times f(T, W)$	Oxidation as a function of CH_4 and O_2 concentration, temperature and moisture	Cartoon model, CLM4Me, CLM-Microbe, Kettunen model
CH_4 transport	7	$T_{CH_4} = V * ([CH_4] - \overline{[CH_4]})$	*V* is the parameter for distance, diffusion coefficient, etc.; $[CH_4]$ is the concentration of CH_4 in the soil/water profile (dissolvability for DLEM, 0 for DNDC); and $\overline{[CH_4]}$ is the threshold of CH_4 concentration above which CH_4 will be transported to the atmosphere via either of the three transport pathways	DLEM, DNDC, Walter model
	8a	$A = \frac{C(z) - C_a}{r_L z / D + r_a} pT\rho_r$	*Aerenchyma transport*	CLM4Me
	8b	Moves to first unsaturated layer and then released to gaseous phase	*Ebullition*	CLM4Me
	8c	$D_{CH_4} = D \times \frac{\Delta[CH_4]}{\Delta z}$	Diffusion of CH_4 was simulated following Fick's law; CLM4Me separate aqueous and gaseous diffusion	CLM4Me, CLM-Microbe, *ecosys*, Ridgwell model, TRIPLEX-GHG; Sergers model
Temperature effects	9	$f(T) = a \times T + b$ $f(T) = a \times T^2 + b \times T + c$ $f(T) = b \times e^{0.2424 \times T}$	Linear regression on temperature or degree days; DNDC simulate temperature impact on production not on oxidation	DAYCENT, DNDC, IAP-RAS, LPJ family
	10	$f(T) = Q_{10}^{\frac{(T - T_{ref})}{10}}$	Q_{10} equations; T_{ref} is the reference temperature	CH4MOD, CLM-Microbe,

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				CLM4Me, DLEM, VISIT, Kettunen model
	11a	$V_T = V^0 \times \exp\left(\frac{\Delta E}{R}\left[\frac{1}{T^0} - \frac{1}{T}\right]\right)$	Arrhenius equation	Cartoon model, Ding model
	11 b	$f_T = \frac{T_s \times \exp\left(A - \frac{H_a}{R \times T_s}\right)}{\left[1 + \exp\left(\frac{H_{dl} - S \times T_s}{R \times T_s}\right) + \exp(S\times \right.}$	Modified Arrhenius equation; T_s is soil temperature at K; A is the parameter for $f_T = 1.0$ at $T_s = 303.16$ K; H_a is the energy of activation (J mol^{-1}); R is universal gas constant (J mol^{-1} K^{-1}); H_{dl} and H_{dh} are energy of low and high temperature deactivation (J mol^{-1})	*ecosys*
Moisture effects on methanogenesis and methanotrophy	12	No moisture effect is simulated, rather inundation area is simulated	No equation, while a temporal and spatial variation of inundation and saturation impacts	CASA
	13	$F_\vartheta = e^{-P/P_c}$	Water stress for oxidation, where P is soil moisture and Pe= -2.4×10^5 mm	CLM4Me
	14	$f(SM) = \begin{cases} 1, \\ \left[1 - \frac{log_{10}\varphi - log_{10}(0.2)}{log_{10}(100) - log_{10}(0.2)}\right]^\beta \\ 0, \end{cases}$	β is an arbitrary constant, ϕ is the soil water potential	CLASS
	15	$f_{prod}(SM) = \left(\frac{SM - SM_{fc}}{SM_{sat} - SM_{fc}}\right)^2 \times 0.368 \times e^{\left(\frac{SM - SM_{fc}}{SM_{sat} - SM_{fc}}\right)}$ $f_{oxid}(SM) = 1 - f_{prod}(SM)$	Different impacts on CH_4 production and consumption; SM: soil moisture; SM_{fc}: field capacity; SM_{sat}: saturation soil moisture	DLEM

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

Table 4. Temperature dependence of CH_4 processes in various models (blank indicates the Q_{10} function is not used; all temperatures are expressed as °C, 273.15 was used for unit conversion)

Model	Q_{10}	Reference temperature (°C)	Note	Sources
CASA			Based on a linear equation with temperature	(Potter, 1997)
DAYCENT			Linear equation y = 0.209 * T + 0.845	(Del Grosso et al., 2000)
LPJ family LPJ-Bern LPJ-WHyMe LPJ-WSL			Linear function was used for temperature impacts on diffusion	(Hodson et al., 2011; Spahni et al., 2011; Wania, 2007)
Christensen's model	2	2	For temperature > 0, the temperature impact is set to zero when < 0	(Christensen and Cox, 1995)
CH4MOD	3	30	T=30 for 30 < T ≤ 40	(Huang et al., 1998b)
CLM4Me	2	2	Parameters for baseline simulation	(Riley et al., 2011)
CLM-Microbe	1.5	13.5		(Xu et al., 2015)
DLEM	2.5	30	For a temperature range of [-5, 30]; temperature impact is set to zero when < -5 or > 30	(Tian et al., 2010)
Kettunenn's model	4.0 for production, 2.0 for oxidation	10	Standard Q_{10} function	(Kettunen, 2003)
ORCHIDEE	Abisko site, 2.6; Michigan site, 3.2; Panama site, 1.2	Mean annual temperature	Q_{10} function with different parameters across biomes	(Ringeval et al., 2010)

TEM	Alpine tundra: wetland, 3.5; upland, 0.8. Wet tundra: wetland, 2.2; upland, 1.1. Boreal forest: wetland, 1.9; upland, 1.5	Alpine tundra: wetland, -3.0; upland, 8.0. Wet tundra: wetland, -5.5; upland, 8.0. Boreal forest: wetland, 1.0; upland, 7.0	Q_{10} function with different parameters across biomes	(Zhuang et al., 2004)
TRIPLEX-GHG	1.7-16 for production, 1.4-2.4 for oxidation	25 for optimal, 45 for highest temperature	Modified Q_{10} equation	(Zhu et al., 2014a)
VISIT		Mean annual temperature		(Ito and Inatomi, 2012)
Walter's model	2	Ombrotrophic bog, 12; poor fen, 6.5; oligotrophic pine fen, 3.5; Arctic tundra, 0; swamp, 27	Q_{10} function with different parameters across biomes	(Walter and Heimann, 2000)
Cartoon model model		10	Arrhenius equation	(Arah and Stephen, 1998)
ecosys		30	Modified Arrhenius equation	(Grant et al., 1993)

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Figure legend

Figure 1. The published CH_4 models and modeling trends in terms of applicability and mechanistic representation of CH_4 cycling processes at decadal-scale and the envisioned CH_4 model capability

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

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

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

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

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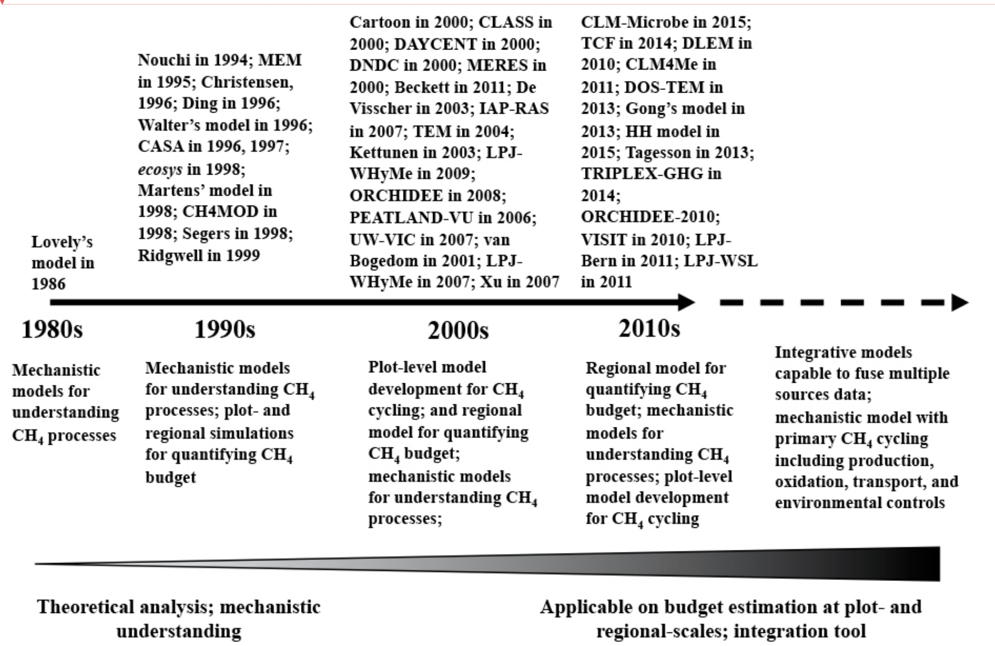

Fig. 1.

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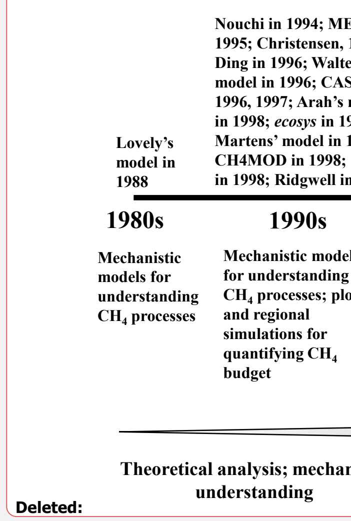

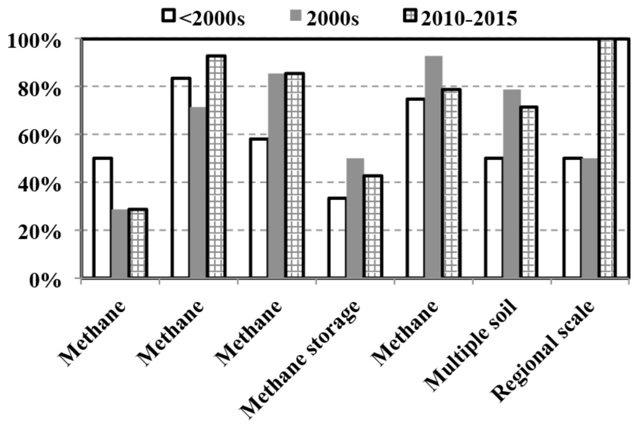

Fig. 2.

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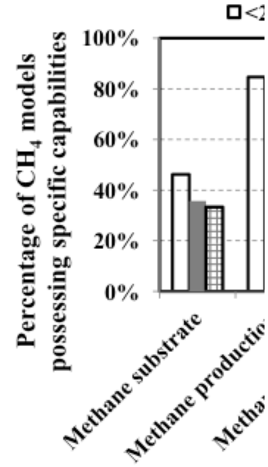

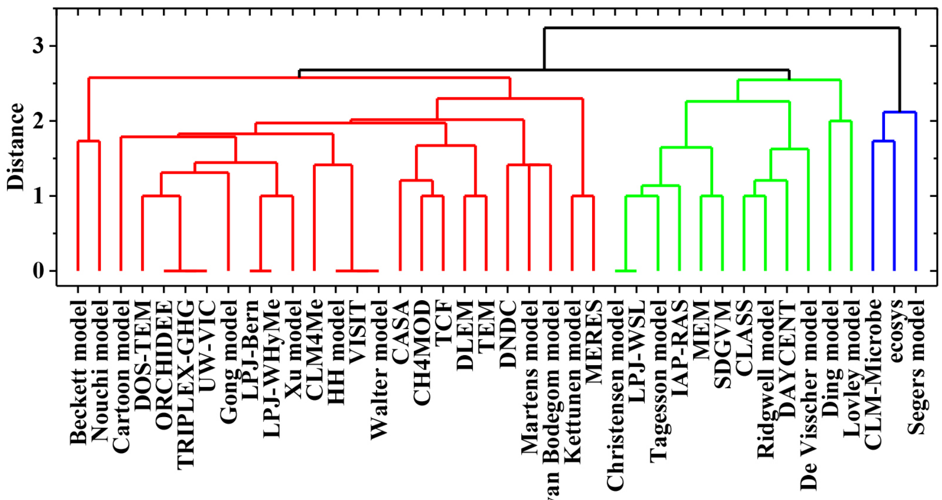
Distance
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2
3
Beckett model
Nouchi model
Cartoon model
DOS-TEM
ORCHIDEE
TRIPLEX-GHG
UW-VIC
Gong model
LPJ-Bern
LPJ-WHyMe
Xu model
CLM4Me
HH model
VISIT
Walter model
CASA
CH4MOD
TCF
DLEM
TEM
DNDC
Martens model
van Bodegom model
Kettunen model
MERES
Christensen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

Fig. 3

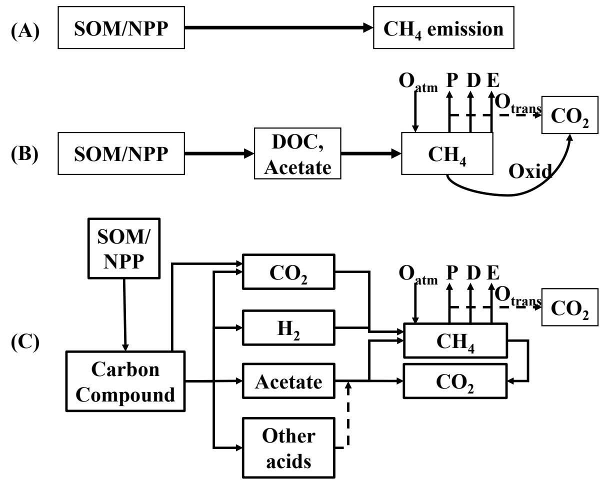

Fig. 4.

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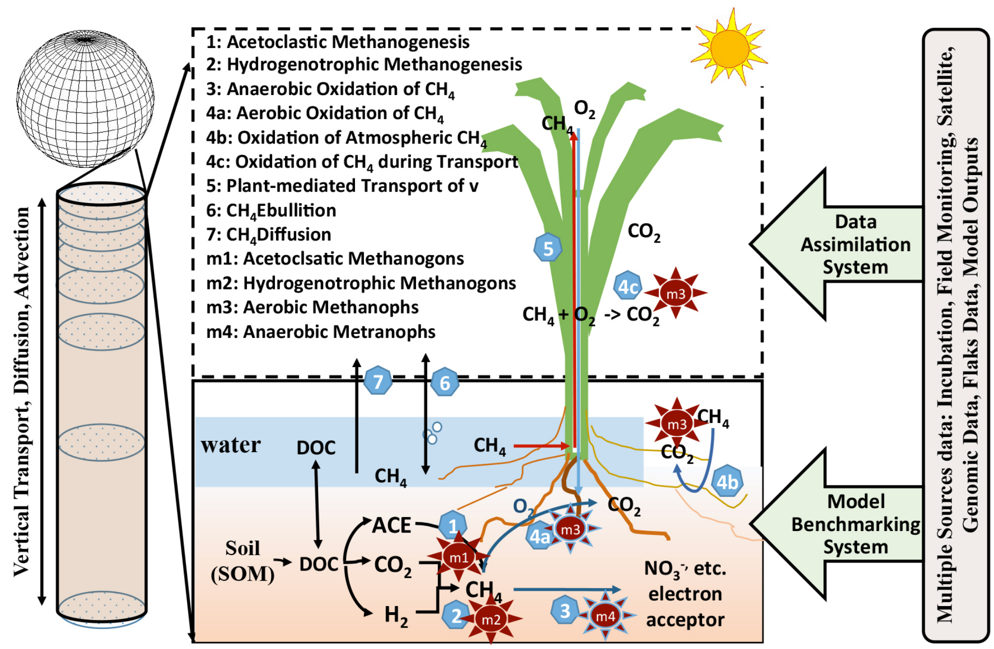

Fig. 5

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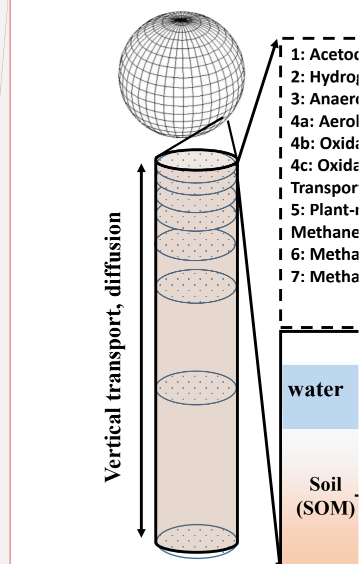

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