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Chapter

Methane, Microbes and Models in Amazonian Floodplains: State of the Art and Perspectives

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Abstract

Amazon floodplain ecosystems include open water and intermittent flood forest and agricultural systems with different water types. They are a significant natural source of methane (CH₄) in the tropics. When soils are flooded and become anoxic, CH₄ is produced by methanogenesis, while microbially mediated aerobic and anaerobic oxidation of CH₄ serves as the primary biological sink of this greenhouse gas. Measurements of rates and controls on CH₄ production and emission in the Amazon basin mainly come from studies on individual wetlands and floodplain lakes. Similarly, microbial communities in those Amazon floodplain habitats have been studied on individual lakes based on sequence-specific DNA analysis. Existing biogeochemical ecosystem models of CH₄ from the Amazon floodplains focus on soil properties or involve factors such as pH, redox potentials, or substrates. None of these models incorporate appropriate seasonal inundation; neither the microbiota does it as a component. In this sense, our chapter will highlight how the important efforts already contributed to understand the CH₄ emission and its connections with abiotic and biotic factors in Amazon floodplains, as well as emphasize the need of encouraging cooperation and exchange of experience between research teams by using different approaches and scientific methods.

Keywords: methane emission, methanogenesis, methanotrophy, mathematical modeling

1. Introduction

The Amazon rainforest, well known for its vast biodiversity, is a unique ecosystem and plays an irrefutable role in the maintenance of global ecosystem services. The Amazon biome is one of the main contributors to the biogeochemical functioning of the terrestrial system [1]. A contributor to this functioning is the soil, which is considered one of the most complex and variable environmental compartments. The understanding of microbially mediated biogeochemical processes in this compartment is of particular interest in continental floodplains, where nutrient cycling is highly responsive for floating hydrology, and the gases produced in the soil may influence the global climate change [2].

Methane (CH₄) is one of the most important greenhouse gases (GHG). Amazonian wetlands are considered a significant source of CH₄ emissions. In addition to the positive emission of GHG such as CH₄, the wetlands provide a diverse range of vegetation that enables the sequestration of organic carbon.

Arguably, the most striking variation in the nature of the forests in the Amazon floodplains system is related to seasonal flooding. Variations in the level and flow of water, along with variations in temperature and sediment load, for example, are the most important factors to guide the structure and functioning of flood systems [3, 4]. The flood pulse, responsible for the change in soil saturation, makes those areas predisposed to the activity of the anaerobic microbial community. In the absence of electron acceptors, CH_4 is the final product of anaerobic decomposition of organic matter. The anaerobic oxidation of CH_4 may occur in the presence of some of these electron receptors (iron, manganese, and sulfate) and nitrogenous forms (nitrite and nitrate).

Given the recent recognition of the importance of Amazonian floodplains for the global dynamics of the CH_4 cycle, we emphasize the essential role of information from these systems as a key factor for the amelioration of CH_4 emission models. Thus, microbiota data combined with *in situ* observations can successfully lead to new approaches of CH_4 emission models for these ecosystems. This review first addresses the soil microbiota and the mechanisms related to them as part of the dynamics of the CH_4 cycle. The initial topics include microbial characteristics, mainly of saturated systems (e.g., anaerobic metabolism and interactions with metals). The chapter synthesizes studies that assessed possible consequences regarding changes in hydrology caused by climate change. Subsequently, a synthesis of the different integrated approaches is reported: biogeochemistry, isotope, and soil metagenomics, revealing the importance of interfacing different methodologies to develop a more trustworthy representation of that system. The chapter ends by identifying the knowledge on the emission models in Amazonian floodplains, as well as suggests the incorporation of new variables into those models.

2. Biogeochemical cycle of CH₄

Global biogeochemical cycles are mainly driven by microorganisms that feed on base compounds of carbon (C), such as CH_4 or carbon dioxide (CO_2) [5]. The CH_4 is the most abundant hydrocarbon in the atmosphere [6]. Due to its absorption characteristics, CH_4 manifests positive radiative forcing, being a GHG that contributes to the regulation of temperature on the surface of the planet. It is believed that CH_4 is responsible for 17% of global warming [7], taking into account the indirect chemical reactions of this gas with aerosols. The Global Warming Potential (GWP) of CH_4 is estimated to be 25 times higher than the GWP of CO_2 [8, 9] on a 100-year horizon.

The interest in estimates of CH₄ emission in tropical forests has grown in recent years, particularly in wetlands such as the Amazon basin [10–15] and Pantanal [16–18]. This is due to the fact that the largest natural sources of CH₄ are wetlands [19], contributing with 177–284 Tg CH₄ per year [7]. Humid areas are the largest and most uncertain sources of CH₄ to the atmosphere [20]. Remote sensing techniques employing visible, infrared and microwave observations offer varying degrees of success in providing quantitative estimates of wetlands and inundation

extent and monitoring natural and anthropogenic variations in these environments [21]. Another factor that may contribute to this uncertainty is the interannual variability of the water column associated to lakes and rivers, which directly influence the wetlands linked to them.

Wetlands have high C sequestration and store capacity, which justify the growing interest in studying the production and consumption of this gas in these ecosystems. The C sequestration refers to the removal of CO_2 from the atmosphere, transfer, and accumulation of that gas in the flooded areas as soil organic matter. That is, the sequestration of C in wetlands is related to the photosynthetic removal of CO_2 by producing organisms and its conversion into cellulose and other forms of C, and subsequently the transformation of waste into soil organic matter [22]. This ability to act on the C cycling, in addition to all other ecosystem services performed by those environments, makes them critical components in understanding local, regional, and global C stocks, capable of influencing the balance of CO_2 , CH_4 , and other GHG.

Floodplains are defined as environments that are seasonally flooded or saturated due to rising groundwater or surface water and remain like that for a certain period of the year or throughout the year [3]. According to Junk et al. [3], flooding of plains along rivers tends to occur as a single annual flood pulse that lasts months. In these plains, flooding can also lead to an increase in allochthonous inputs of C, making them essential to the food web and interesting to the scientific community.

The CH₄ is produced mainly by microorganisms belonging to the domain *Archaea* in the final stage of organic matter fermentation in anaerobic environments [23], which play a crucial role in the biodegradation of organic matter [24]. However, only a fraction of the produced CH₄ is emitted into the atmosphere. Microorganisms that oxidize CH₄, which are known as methanotrophic bacteria use the other part. There is no consensus in the literature on the percentage of CH₄ assimilated by these microorganisms. There are estimates that 10–100% of the CH₄ produced by anaerobic microorganisms are oxidized into CO₂ before reaching the atmosphere [25].

Part of the current understanding of the dynamics of CH_4 in wetlands is based on the premise that most of the oxidation of CH_4 occurs under aerobic conditions. However, recent studies indicate the action of several other electron acceptors (alternative to sulfate under aerobic conditions) in the anaerobic oxidation of CH_4 , including nitrate, nitrite, iron, and manganese [5, 26–32]. Studies also point to humic substances acting as a terminal acceptor for electrons in tropical flood areas [33]. In previous studies [32, 34], when attempting to justify the predominance of academic papers addressing the oxidation of CH_4 exclusively by aerobic means, taking into account the fact that sulfate has been, for a long time, the only electron acceptor involved in the oxidation of CH_4 in anoxic environments, the concentration of sulfate is generally too low in freshwater environments to play a role in the anaerobic oxidation of CH_4 . The contribution of anaerobic oxidation of CH_4 to the methanotrophic processes is not fully elucidated, but the increasing number of papers validating the information shows that this mechanism seems to be more common than previously thought.

In turn, methanogenesis occurs when energetically favorable electron acceptors such as oxygen, nitrate, sulfate, and iron are absent or have been depleted [35]. In the absence of oxygen, the complete decomposition of complex organic compounds requires syntrophic system interactions in individual steps in the global process [36]. A sequential action involves hydrolysis, acidogenesis, acetogenesis, and methanogenesis steps [37]. Therefore, the many microbial guilds involved in those processes include hydrolytic, syntrophic fermentative, acetogenic, and methanogenic microorganisms. Bacteria and fungi are responsible for breaking down complex molecules during hydrolysis, such as polysaccharides, proteins, and their forming units (amino acids, fatty acids, and alcohols) [38]. In the acidogenesis stage, fermentative microorganisms convert simple substrates into volatile fatty acids (VFA) (e.g., acetate, propionate, and butyrate), alcohols (e.g., ethanol and butanol), H₂, and CO₂ [39]. In acetogenesis, the VFA and alcohols produced, such as propionate, butyrate, and ethanol, are converted into acetate, H₂, and CO₂ by acetogenic bacteria [39]. Finally, methanogens convert acetate, H₂/CO₂, formate, and methylated compounds into CH₄.

3. The microbiota involved in the cycling of CH₄

The amount of CH_4 emitted from an ecosystem is the result of the balance between the production of CH_4 (methanogenesis) and the consumption (oxidation) of this gas (methanotrophy). Therefore, the emission of CH_4 into the atmosphere is determined by activity of methanogenic and methanotrophic microorganisms.

Methanogenic Archaea are widely ubiquitous in nature and have been detected in a wide range of environments, including freshwater sediments, hypersaline and rice lakes, anaerobic digesters, permafrost, and landfills, among others. They have a unique enzyme designed methyl-coenzyme M reductase (Mcr), which makes them specialized in producing CH₄ [39]. This group of microorganisms presents high diversity in morphology and physiological parameters [40].

The methanogenic microorganisms belong to the *Euryarchaeota* phylum and until recently were classified into seven orders (*Methanobacteriales, Methanocccales, Methanomicrobiales, Methanosarcinales, Methanocellales, Methanopyrales,* and *Methanomassiliicoccales*). The discovery of the genes involved in methanogenesis in *Bathyarchaeota* and subsequently *Verstraetearchaeota* led to a paradigm shift, demonstrating that the evolutionary origin of methanogenesis is prior to the phylum *Euryarchaeota* [41].

The metabolism of methanogenic *Archaea* gains energy by reducing C compounds (e.g., CO_2 , formate, acetate, methanol, ethanol, methylamines, and methyl sulfides) to CH_4 [23]. Thus, traditional methanogenic strains are widely characterized as hydrogenotrophic, acetoclastic, and methylotrophic based on the use of substrate. In most cases, the methane-producing pathways in the environment are determined by DNA sequencing of the corresponding methanogenic microorganisms [39]. The final step in all of these pathways is common and involves the conversion of methyl-S-CoM into CH_4 by methyl-coenzyme M reductase (Mcr) [42].

Taking into consideration the production pathway (**Figure 1**), hydrogenotrophic methanogenic microorganisms are known as H_2 oxidant, formate, or some simple alcohols and reduce CO_2 to CH_4 [43]. Most of the described methanogenic microorganisms are hydrogenotrophic. Acetoclastic methanogens divide acetate to form CH_4 and CO_2 . They are found in habitats where hydrogenotrophic methanogenic microorganisms reduce H_2 levels sufficiently to create the necessary conditions for the formation of high levels of acetate. Methylotrophic methanogenic microorganisms are common in sulfate-rich marine and hypersaline sediments, in which they use methylated compounds such as trimethylamine, dimethyl sulfate, and methanol [44]. In contrast, in sediments from freshwater environments, it is believed so far that methylotrophic methanogenesis is of little importance, although this is not what recent unpublished results have revealed for the floodable areas of the Amazon. However, the same reasoning used for anaerobic methanotrophy may be occurring in this case.

Methyl compounds, especially methanol, may play an underestimated role as contributors to the production of CH₄ in wetlands [44]. Although the use of methanol in the presence of hydrogen has been observed among methanogenic *Archaea*,



this substrate is rarely tested during the description of new species. This lack of information represents a serious obstacle to the analysis of metabolic abilities of methanogenic *Archaea* [45].

Meyer et al. [46] used a metagenomic approach to assess the relative abundance of genes involved in cycling CH₄ in forest and pasture soils in Western Amazon and they revealed that genes involved in methanogenesis from methylated compounds were significantly more abundant in the pasture. Soil methylotrophs call attention to the central role of these organisms in global methanol conversions, which mainly originate from plants [47] released from both living and decomposing plant material [48]. Soil microbiota is an essential component of plant decomposition and formation of organic matter. Thus, the understanding about these communities, as well as the one regarding decomposed material, is essential to elucidate the dynamics of these environments. The literature mentions that in tropical alluvial plains the predominant microbial pathways in methane production are acetoclastic and hydrogenotrophic [49, 50]. However, Alves [51], when evaluating the enrichment of primary and secondary forest and pasture samples in the Amazon, indicated a higher production of CH₄ by acetoclastic and methylotrophic pathways.

In flooded areas, known to have high methanogenic rates, methanotrophs are responsible for catalyzing the oxidation of CH_4 at the aerobic-anaerobic interfaces. Methanotrophic bacteria are able to use CH_4 as their sole source of C [52] and can be divided into four groups: Gammaproteobacteria (often referred as Type I or Type X); Alphaproteobacteria (formerly known as Type II); Verrucomicrobia; and NC10 phylum members [53].

Methanotrophic activity is only viable because of an enzyme known as monooxygenase methane (MMO), which acts in two distinct forms: particulate (pMMO), within an intracellular membrane, or soluble (sMMO), in the cytoplasm. Both convert CH_4 into the readily assimilated product, methanol [54].

The oxidations of CH_4 have proven to be an important sink for this gas produced by sediments in the Amazon, reducing the amount of CH_4 that reaches the atmosphere [8, 55].

The diversity of CH_4 metabolizers or metabolizing organisms tends to increase in the near future due to additional findings in surveys using a metagenomic approach and other increasingly robust approaches to the study of microbial diversity. This can be the currently ambiguous evolutionary history of this important metabolic function [23].

4. Influence of hydrology on tropical floodplains

Alluvial plains are among the most dynamic ecosystems, consisting of a mosaic of habitats with high spatial-temporal turnover rates [4, 56]. The complex interaction between the topography of the floodplain and the variation in river flow and sediment transport maintains a distinct gradient of lateral hydrological connectivity, which facilitates the coexistence of numerous aquatic, amphibian, and terrestrial species [4].

These sites exhibit highly heterogeneous stratigraphy produced by active river meanders and sediment deposition; dominant coarse-grained materials are interspersed with finer sediments, and organic matter is deposited, leading to distinct zones of oxic or anoxic conditions within the subsurface [57]. Regional variations in fresh water CH₄ emissions are important factors that should be considered to ensure reliable global estimates. The C stocks, as well as the different classes of organic matter, still need to be elucidated in order to decrease our limitations in building C cycling models in those environments. Hydrological variations are responsible for determining the intensity and duration of aerobic conditions. Changes in these conditions can increase or decrease the rates of decomposition of organic matter [58].

The Colombian wetlands were evaluated and showed that the studied ecosystems are valuable C sinks, and hydrogeomorphology acts as an important factor for the storage of C in these ecosystems [59]. Dalmagro et al. [18], when evaluating the largest tropical floodplain area in the world, Pantanal, revealed that they are potentially large C sinks and that the C balance was driven by the seasonal dynamics of precipitation and surface flooding that affected the anaerobic and aerobic phases of the soil. The assessment of the behavior of a freshwater flood area with a usual average flood period of 6 months per year, located in a park in the USA, showed that the environment become a source of CO_2 when it went through a prolonged flood

period (17 months). Such situations may occur more frequently in the future, as an intensification of rainfall is expected. Moreover, evidence suggests that the magnitude of wet and dry cycles can have significant effects on GHG emission [60].

Alluvial plains are environments adapted to variations in water level, and it seems that microbial communities can be adapted to these fluctuations and remain in a state of latency until the next flood. Hernández et al. [61] demonstrated that in Amazon forest soils the propensity to produce CH_4 (at the laboratory) was best observed in relation to the duration of the lag phase. Soils that were never flooded (dry forest) presented this phase for a longer time than sites that were permanently flooded. In a laboratory study that imposed different levels of flood frequency, differences in composition have also been observed, but an increase in diversity under conditions of higher water saturation has been reported [62].

Alluvial plains are among the most threatened ecosystems in the world because of anthropogenic activities, especially in developing countries, where high demand from agricultural areas drives deforestation. An additional threat to those ecosystems is the increase in terrestrial temperatures due to global warming, generating a cycle of change in water regime that may consequently alter the storage capacity of C in wetland ecosystems [63].

5. Sensitivity of floodplains to climate change

Current projections suggest that rates of GHG emission from floodplains will increase as global average temperatures continue to rise, and this is of particular importance in temperate and tropical systems. The metabolism of CH_4 in flooded areas is strongly influenced by environmental factors that have both spatial and temporal variability. The production and consumption of GHG are partially regulated by microbial processes, which are influenced by soil moisture and temperature [64]. In soils, the microbial production rate of CH_4 generally shows an exponential relationship with air temperature, with the peak rate corresponding to temperatures of 25°C (77 F) to 30°C (86 F) [65].

Wetlands are likely to become the main net sources of C under the effect of warming climatic conditions in decades [64]. Sanches et al. [66] determined the crucial factors related to the emission of CH_4 in lakes, on a large scale, observing emission patterns in different climate zones. The climate zones with the highest average air temperatures showed the highest emission rates.

Climate change in tropical wetlands is expected to cause an increase in temperature and a change in precipitation patterns, increasing the duration of the dry season, but also increasing the intensity of precipitation events. Given these predictions, the current and future balance of seasonally flooded tropical areas is still uncertain. A study conducted from 2014 to 2016 in the largest continuous wetland area in the world, the Brazilian Pantanal, demonstrated the response of CH₄ and CO₂ to the hydrological dynamics of this ecosystem [18]. Measurements revealed that CH_4 emission increased rapidly as soon as anaerobic conditions were established, with the highest CH₄ flow values having always been observed when soil redox potential values were less than –100 mV. In summary, the data indicated that the seasonally flooded rainforests of Pantanal are potentially large C sinks, but significant sources of CH₄ when anaerobic conditions dominate the soil (flood period). It is worth mentioning that the carried out measurements contemplate emission from tree trunks, soil flows, boiling, and diffusion from the water surface, since the methodology used was a 20 m (65.6 feet) high research tower, together with environmental sensors. A recent research suggests that CH₄ emission from tree branches are the dominant source of regional CH₄ emission to flooded tropical forest environments [11].

6. CH₄ emission in flooding areas: biogeochemistry, isotopic signature, and metagenomics

Understanding the level of sensitivity of flooding areas as a response to climate change also requires efforts to be better achieved. This demands more knowledge at all levels, ranging from single-cell ecophysiology to *in situ* and *ex situ* biogeochemical functioning. Thus, efforts to cultivate recalcitrant microorganisms, evaluations of the microbiota with independent methods of cultivation, and the combination of these approaches with isotopic determinations and physical and chemical characterization of soil and water are necessary to achieve an understanding of the processes mediated by microorganisms in these environments [67].

It is a challenge for researchers to design experiments and adopt methods that can detect C cycling in alluvial plains. One of the approaches used is the characterization of microbial communities in space and time from the sequencing of DNA or RNA and the construction of correlation matrices of relative abundances of microbial taxa or functional groups with environmental variables [68]. Regardless of the study method, the characterization needs to reflect the correct scale for the issue and should contain enough replicates to provide meaningful data [69].

Metagenomic studies indicate high functional redundancy in flooding areas. Although we know that microbial communities are diverse, DNA-based methods can artificially inflate functional redundancy estimates [69]. This fact is due to the DNA-based approach not being able to distinguish between dormant and active cells [70].

Different responses have been found when assessing the effect of increased salinity on the composition of the total (DNA) and active (RNA) microbial community in an anaerobic reactor [71]. The concentration and exposure time most strongly affected the microbial community, and especially the *Archaea* phylotypes at the RNA level, both in terms of global diversity and specific phylotypes.

The evaluation of the survival conditions of *Archaea* methanogenic under aerated conditions in floodplains with rice crops revealed the composition of the active community, indicating that unknown mechanisms maintain the stability of the community in these environments until 1 year after the start of drainage [72].

Stable isotopes have long been used as a tool to investigate environmental processes and their relationships with microorganisms, which can be established through metabolic pathways [73]. The merit of C isotopes lies in their relatively slow exchange rate for many minerals containing C and in relatively large fractionations, even at high temperatures. These two properties make C isotopes an excellent recorder of geological processes and allow a better understanding of C sources and related-volatile flows in geological time scales [74]. We are undergoing a reformulation of isotopic approaches based on the increase in genomic and transcriptomic databases, the latest technologies with improved instrumental and mass spectrometric data acquisition, processing, and evaluation [73]. For Coyotzi et al. [75], the incorporation of stable isotopes into the microbial biomass allows the recovery of labeled nucleic acids from active microorganisms. The combination of stable isotopes with metagenomics provides access to the genomes of microorganisms involved in metabolic processes of interest.

The CH₄ fluxes in terrestrial and aquatic environments have been evaluated in several ways, but in general, the monitoring of gas accumulation in flow chambers has been the predominant methodology to date. This methodology is conceptually simple and does not require expensive field equipment, but is laborious, based mainly on manual sampling [17].

7. Modeling of CH₄ emission

To improve the prediction of climate models, it is important to understand the mechanisms by which microorganisms regulate the flow of terrestrial GHG. This involves considering the complex interactions that occur between microorganisms and other biotic and abiotic factors in the environment. The potential to mitigate climate change by reducing GHG emission through the management of terrestrial microbial processes is a perspective of high importance for the future [18].

Despite this importance, however, tropical flood areas are poorly represented in global models to predict global CH₄ emission. A first step in the development of a process-based model of CH₄ emission from tropical flood areas for global applications was documented in 2014. To this end, the LPX-Bern Dynamic Global Vegetation Model (LPX) was slightly modified to represent the hydrology of the floodplain, vegetation, and associated CH₄ emission. The extent of tropical floodplains was prescribed using the production of the spatially explicit PCR-GLOBWB hydrology model. Several variables were introduced to this model, such as vegetation, ground cover (through remote sensing), not to mention that simulated CH_4 flow densities were evaluated against field observations and regional flow inventories. However, soil microbiota was not considered as a component in the modeling. Simulated CH₄ emissions at the Amazon basin scale were compared to simulations of previously performed models. Thus, it was found that this LPX model reproduces the average magnitude of the net flow densities of CH₄ observed for the Amazon basin. However, the model does not reproduce the temporal and spatial variability between sampling sites, considering that site information is too limited to attest or refute some resources of the model. At the Amazon basin scale, the results obtained with the promotion of this model highlighted the great uncertainty in the magnitude of CH₄ emission from floodable areas.

The sensitivity analysis provided clarification on the main drivers of CH_4 emission from the floodplain and their associated uncertainties. Due to an intrinsic limitation of the LPX to consider seasonality in floodplain extension, the model failed to reproduce the total dynamics of CH_4 emission, raising several scientific questions. Although this model includes more specific mechanisms for tropical floodplains, it was not possible to reduce the uncertainty in the magnitude of CH_4 emission from the Amazon basin, thus justifying the need for further research to restrict CH_4 emission and their temporal variability [15].

In the same year, Potter et al. [76] developed a new model that sought to seasonally estimate the carbon dynamics and CH_4 emission of floodable ecosystems in the Amazon. The Amazon wetland simulation model took into account three main components: (a) details of the type of vegetation in the wetlands and changes in the level of water, temperature, and dissolved oxygen; (b) primary production, mass accumulation, and decay of the litter layer in soils and sediments; and (c) routes for production and transport of CH_4 through the water column to the atmosphere.

The presented model is based on the input of the following data for simulations in a given flooded environment in the Amazon: latitude and longitude; vegetation types such as area cover fractions; daily surface temperature; solar irradiance flux; wind speed; precipitation; daily water depth; biomass production values for floating macrophytes; and satellite vegetation index data for flooded forest ecosystems. In order to improve the generality and use of this model, the incorporation of mechanical simulations of vertical mixing, horizontal exchanges, and various biogeochemical processes is necessary. In addition, the microbiota component is not directly reported.

In 2016 [77], when evaluating the atmospheric concentrations of CH_4 in the Amazon basin in 2010 and 2011, besides a 3D atmospheric chemical transport model (TOMCAT), two emission models in wetlands have been used [78–79] to reduce the uncertainty about CH₄ emission. The first set of wetland and rice paddy emission derived from the Bloom et al. method [79]. The method uses a satellite to evaluate the carbon variation available for methanogenesis, which leads to a more accurate representation of the timing of CH₄ emission. However, satellite data cannot distinguish between microbial CH₄ emission from natural wetlands and anthropogenic emission from rice cultivation. The second model [the Joint UK Land Environment Simulator (JULES), version 3.4.1 [78] simulates the Earth's land surface in terms of carbon, water, and energy variations and includes a methane flux in wetlands as a component, based on Gedney et al. [80]. The flow of CH4 is dependent on the available carbon substrate, the temperature, and the fraction considered wet. The estimates used through the two wetlands emission models are based on processes and showed similar behaviors when the atmospheric model is compared to observations, regardless of which model was used [77].

In the same year (2016), another research on CH₄ modeling was carried out, bringing to the fore the discussion of how beneficial the improvements in CH₄ models would be for terrestrial system models and for the additional simulation of climatecarbon cycle feedbacks. Over the past four decades, several empirical models have been developed to quantify the magnitude, investigate spatial and temporal variations, and understand the underlying mechanisms and environmental controls of CH₄ (CH₄ flows in terrestrial ecosystems). These CH₄ models are also used for the integration of multiple-scale CH₄ data, such as laboratory-based incubation and molecular analysis, field observational experiments, remote sensing, and aircraft-based measurements in various terrestrial ecosystems. The authors noted that there are large discrepancies between models in terms of representation of CH₄ processes and their environmental controls, and significant data, such as model incompatibilities, are partially attributed to different representations of landscape characterization and flood dynamics.

However, it should be noted that CH₄ models should represent more explicitly the mechanisms underlying the exchange of Earth-atmosphere CH₄, with emphasis on the improvement and validation of individual CH₄ processes over depth and horizontal space, and models capable of simulating CH₄ emissions at highly heterogeneous spatial and temporal scales, particularly in hotspots, should be developed; besides that, efforts should be made to develop benchmarking models (a modeling based on comparative analysis) that can be easily used for improvement, evaluation, and integration with data from molecular to global scales [81].

Widely applicable and robust prediction models should be developed from large data sets generated through collaboration with scientists around the world. To achieve high predictive accuracy, these data sets should cover a wide variety of information and variables at the most different scales of tropical floodplains within regions and globally.

8. Closing remarks

This chapter synthesizes the main progresses in scientific research applied to understanding the dynamics of CH₄ in tropical floodplains. Here, we focused on an integrative approach to the main aspects of the C cycle, describing methods based on observations on the Earth's surface. However, a better understanding of the methylotrophic methanogenesis and anaerobic oxidation of CH₄ still needs to be clarified for these environments. The next generation of models of CH₄ emission should take into account seasonal water level fluctuation and the methanogenic and methanotrophic activity associated with it. This bold goal can only be achieved

using a multianalytical approach based on a synergy of models, statistical methods for data integration, and scientific cooperation. This effort can help to create a unique design, in which not only the biosphere and the feedback of hydrological modeling but also the soil microbiota will be considered in the regional cycle of C.

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References

[1] Malhi Y, Roberts JT, Betts RA, Kileen TJ, Li W, Nobre CA. Cimate change, deforestation, and the fate of the Amazon. Science. 2008;**319**(5860):169-172. DOI: 10.1126/ Science.1146961

[2] Kotsyurbenko OR, Glagolev MV, Merkel AY, Sabrekov AF, Terentieva IE. Methanogenesis in soils, wetlands, and peat. In: Stams AJM, Sousa D, editors. Biogenesis of Hydrocarbons, Handbook of Hydrocarbon and Lipid Microbiology. Switzerland: Springer Nature; 2019. p. 1-18. DOI: 10.1007/978-3-319-53114-4_9-1

[3] Junk W, Bayley PB, Sparks RE. The flood pulse concept in riverfloodplain systems. In: Dodge DP, editor. Proceedings of the International Large River Symposium (LARS). Ottawa, Canada: Canadian Special Publication of Fisheries and Aquatic Sciences; 1989. pp. 110-127

[4] Tockner K, Pusch M, Borchardt D, Lorang MS. Multiple stressors in coupled river-floodplain ecosystems. Freshwater Biology.
2010;55(Suppl 1):135-151. DOI: 10.1111/j.1365-2427.2009.02371.x

[5] Raghoebarsing AA, Pol A, Van De Pas-Schoonen KT, AJP S, Ettwig KF, WIC R, et al. A microbial consortium couples anaerobic methane oxidation to denitrification. Nature. 2006;**440**(7086):918-921. DOI: 10.1038/ nature04617

[6] Caldwell SL, Laidler JR, Brewer EA, Eberly JEDO, Sandborgh SC. Critical review anaerobic oxidation of methane: Mechanisms, bioenergetics, and the ecology of associated microorganisms. Environmental Science & Technology. 2008;**42**(18):6791-6799. DOI: 10.1021/ es800120b

[7] IPCC (Intergovernmental Panel on Climate Change). Summary for

Policymakers. In: Stocker TF, Qin D, Plattner GK, Tignor M, Allen S, Boschung J, Midgley P, editors. Climate Change 2013: The Physical Science Basis. Cambridge: Cambridge University Press; 2013. p. 465-570

[8] Crutzen PJ, Lelieveld JHI. Human impacts on atmospheric chemistry. Annual Review of Earth and Planetary Sciences. 2001;**29**:17-45. DOI: 10.1146/ annurev.earth.29.1.17

[9] Forster P, Ramaswamy V, Artaxo P, et al. Changes in atmospheric constituents and in radiative forcing. In: Solomon S, Qin D, Manning M, Chen Z, et al., editors. Climate change 2007: The physical science basis. Contribution of working group I to the fourth assessment report of the intergovernmental panel on climate change. Cambridge: Cambridge University Press; 2007

[10] Engle D, Melack JM. Methane emissions from an Amazon floodplain lake: Enhanced release during episodic mixing and during falling water. Biogeochemistry. 2000;**51**(1):71-90. DOI: 10.1023/A:1006389124823

[11] Pangala SR, Enrich-Prast A,
Basso LS, Peixoto RB, Bastviken D,
Hornibrook ERC, et al. Large emissions
from floodplain trees close the
Amazon methane budget. Nature.
2017;552(7684):230-234. DOI: 10.1038/
nature24639

[12] Barbosa PM, Farjalla VF,
Melack JM, Amaral JHF, da Silva JS,
Forsberg BR. High rates of methane
oxidation in an Amazon floodplain
lake. Biogeochemistry. 2018;137(3):
351-365. DOI: 10.1007/s10533-0180425-2

[13] Sawakuchi HO, Bastviken D, Sawakuchi AO, Krusche AV, Ballester MVR, Richey JE. Methane

emissions from Amazonian rivers and their contribution to the global methane budget. Global Change Biology. 2014;**20**(9):2829-2840. DOI: 10.1111/ gcb.12646

[14] Melack JNM, Hess LL, Gastil M, Forsberg BRF, Hamilton SHK, Lima IBT. Regionalization of methane emissions in the Amazon basin with microwave remote sensing. Global Change Biology. 2004;**10**:530-544. DOI: 10.1111/j.1529-8817.2003.00763.x

[15] Ringeval B, Houweling S, Van Bodegom PM, Spahni R, Van Beek R, Joos F, et al. Methane emissions from floodplains in the Amazon basin: Challenges in developing a processbased model for global applications. Biogeosciences. 2014;**11**(6):1519-1558. DOI: 10.5194/bg-11-1519-2014

[16] Bastviken D, Santoro AL, Marotta H, Pinho LQ, Calheiros DF, Crill P, et al. Methane emissions from pantanal, South America, during the low water season: Toward more comprehensive sampling. Environmental Science & Technology. 2010;44(14):5450-5455. DOI: 10.1021/ es1005048

[17] Peixoto RB, Machado-Silva F,
Marotta H, Enrich-Prast A, Bastviken D.
Spatial versus day-to-day within-lake
variability in tropical floodplain lake
CH₄ emissions - developing optimized
approaches to representative flux
measurements. PLoS One. 2015;10(4):
1-11. DOI: 10.1371/journal.
pone.0123319

[18] Dalmagro HJ, Lathuillière MJ, Sallo F d S, Guerreiro MF, Pinto OB, de Arruda PHZ, et al. Streams with riparian forest buffers versus impoundments differ in discharge and DOM characteristics for pasture catchments in Southern Amazonia. Water. 2019;**11**(2):1-20. DOI: 10.1111/ gcb.14615 [19] Saunois M, Bousquet P, Poulter B, Peregon A, Ciais P, Canadell JG, et al. The global methane budget 2000 – 2012. Earth System Science Data. 2016;8:697-751. DOI: 10.5194/essd-8-697-2016

[20] Kirschke S et al. Three decades of global methane sources and sinks. Nature Geosciense. 2013;**6**(10):813-823. DOI: 10.1038/ngeo1955

[21] Prigent C, Papa F, Aires F, Rossow WB, Matthews E. Global inundation dynamics inferred from multiple satellite observations , 1993 – 2000. Journal of Geophysical Research-Atmospheres. 2007;**112**(D12107):1-13. DOI: 10.1029/2006JD007847

[22] Lolu AJ, Ahluwalia AS, Sidhu MC, Reshi ZA. Carbon sequestration potential of macrophytes and seasonal carbon input assessment into the Hokersar wetland, Kashmir. Wetlands.
2019;**39**(3):453-472. DOI: 10.1007/ s13157-018-1092-8

[23] Evans PN, Boyd JA, Leu AO, Woodcroft BJ, Parks DH, Hugenholtz P, et al. An evolving view of methane metabolism in the Archaea. Nature Reviews. Microbiology. 2019;**17**(4):219-232. DOI: 10.1038/s41579-018-0136-7

[24] Ghattas AK, Fischer F, Wick A, Ternes TA. Anaerobic biodegradation of (emerging) organic contaminants in the aquatic environment. Water Research. 2017;**116**:268-295. DOI: 10.1016/j. watres.2017.02.001

[25] Cronan CS. Ecosystem Biogeochemistry. Springer Textbooks in Earth Sciences, Geography and Environment. Switzerland: Springer Nature; 2018. 203p. DOI: 10.1007/978-3-319-66444-6

[26] Hu Z, Ma R. Distribution and characteristic of nitrite-dependent anaerobic methane oxidation bacteria by comparative analysis of wastewater treatment plants and agriculture fields in northern China. PeerJ. 2016;**4**:1-15. DOI: 10.7717/peerj.2766

[27] Schubert CJ, Vazquez F, Lösekann-Behrens T, Knittel K, Tonolla M, Boetius A. Evidence for anaerobic oxidation of methane in sediments of a freshwater system (Lago di Cadagno). FEMS Microbiology Ecology. 2011;**76**(1):26-38. DOI: 10.1111/j.1574-6941.2010.01036.x

[28] Zehnder AJ, Brock TD. Anaerobic methane oxidation: Occurrence and ecology. Applied and Environmental Microbiology. 1980;**39**(1):194-204

[29] Ettwig KF, Butler MK, Le Paslier D, Pelletier E, Mangenot S, Kuypers MMM, et al. Nitrite-driven anaerobic methane oxidation by oxygenic bacteria. Nature. 2010;**464**(7288):543-548. DOI: 10.1038/ nature08883

[30] Shen L, Ouyang L, Zhu Y, Trimmer M. Active pathways of anaerobic methane oxidation across contrasting riverbeds. The ISME Journal. 2019;**13**(3):752-766. DOI: 10.1038/s41396-018-0302-y

[31] Shi Y, Wang Z, He C, Zhang X, Sheng L, Ren X. Using 13 C isotopes to explore denitrification-dependent anaerobic methane oxidation in a paddy-peatland. Scientific Reports. 2017;7(40848):1-8. DOI: 10.1038/ srep40848

[32] Segarra KEA, Schubotz F, Samarkin V, Yoshinaga MY, Hinrichs K, Joye SB. High rates of anaerobic methane oxidation in freshwater wetlands reduce potential atmospheric methane emissions. Nature Communications. 2015;**6**:1-8. DOI: 10.1038/ncomms8477

[33] Valenzuela EI, Prieto-Davó A, López-Lozano NE, Hernández-Eligio A, Vega-Alvarado L, Juárez K, et al. Anaerobic methane oxidation driven by microbial reduction of natural organic matter in a tropical wetland. Applied and Environmental Microbiology. 2017;**83**(11):1-15. DOI: 10.1128/ AEM.00645-17

[34] Bridgham SD, Cadillo-Quiroz H, Keller JK, Zhuang Q. Methane emissions from wetlands: Biogeochemical, microbial, and modeling perspectives from local to global scales. Global Change Biology. 2013;**19**(5):1325-1346. DOI: 10.1111/gcb.12131

[35] Thauer RK, Kaster AK, Seedorf H,
Buckel W, Hedderich R. Methanogenic archaea: Ecologically relevant differences in energy conservation.
Nature Reviews. Microbiology.
2008;6(8):579-591. DOI: 10.1038/ nrmicro1931

[36] Schink B. Energetics of syntrophic cooperation in methanogenic degradation. Microbiology and Molecular Biology Reviews. 1997;**61**(2):262-280. DOI: 1092-2172/97/\$04.0010

[37] Batstone DJ, Keller J, Angelidaki I, Kalyuzhnyi SV, Pavlostathis SG, Rozzi A, et al. The IWA anaerobic digestion model No 1 (ADM1).
Water Science and Technology.
2002;45(10):65-73. DOI: 10.2166/ wst.2002.0292

[38] Nakayama CR, Penteado ED, Duarte RTD, Giachini AJ, Saia FT. Improved methanogenic communities for biogás production. In: Treichel H, Fongaro G, editors. Improving Biogas Production. Cham: Springer; 2019. pp. 69-98. DOI: 10.1007/978-3-030-10516-7_4

[39] Zhang Y, Ma A, Zhuang G, Zhuang X. The acetotrophic pathway dominates methane production in Zoige alpine wetland coexisting with hydrogenotrophic pathway. Scientific Reports. 2019;**9**(1):9141. DOI: 10.1038/ s41598-019-45590

[40] Enzmann F, Mayer F, Rother M, Holtmann D. Methanogens: Biochemical

background and biotechnological applications. AMB Express. 2018;**8**(1): 1-22. DOI: 10.1186/s13568-017-0531-x

[41] Berghuis BA, Brian F, Schulz F, Blainey PC, Woyke T, Quake SR. Hydrogenotrophic methanogenesis in archaeal phylum Verstraetearchaeota reveals the shared ancestry of all methanogens. Proceedings of the National Academy of Sciences of the United States of America (USA). 2019;**116**(11):5037-5044. DOI: 10.1073/pnas.1815631116

[42] Borrel G, O'Toole PW,
Harris HMB, Peyret P, Brugère JF,
Gribaldo S. Phylogenomic data support a seventh order of methylotrophic methanogens and provide insights into the evolution of methanogenesis.
Genome Biology and Evolution.
2013;5(10):1769-1780. DOI: 10.1093/
gbe/evt128

[43] Lyu Z, Shao N, Akinyemi T, Whitman WB. Methanogenesis. Current Biology. 2018;**28**(13):R727-R732. DOI: 10.1016/j.cub.2018.05.021

[44] Jiang Z, Xiao OT, Kuznetsov VL, Edwards PP. Turning carbon dioxide into fuel. Philosophical Transactions of the Royal Society A. 2010;**368**:3343-3364. DOI: 10.1098/rsta.2010.0119

[45] Jabłoński S, Rodowicz P, Łukaszewicz M. Methanogenic archaea database containing physiological and biochemical characteristics. International Journal of Systematic and Evolutionary Microbiology. 2015;**65**(2015):1360-1368. DOI: 10.1099/ ijs.0.000065

[46] Meyer KM, Klein AM, Rodrigues JLM, Tringe SG, Mirza BS, Tiedje JM, et al. Conversion of Amazon rainforest to agriculture alters community traits of methane-cycling organisms. Molecular Ecology. 2017;**26**(6):1547-1556. DOI: 10.1111/ ijlh.12426 [47] Stacheter A, Noll M, Lee CK, Selzer M, Glowik B, Ebertsch L, et al. Methanol oxidation by temperate soils and environmental determinants of associated methylotrophs. The ISME Journal. 2012;7(5):1051-1064. DOI: 10.1038/ismej.2012.167

[48] Morawe M, Hoeke H, Wissenbach DK, Lentendu G, Wubet T, Kröber E, et al. Acidotolerant bacteria and fungi as a sink of methanol-derived carbon in a deciduous forest soil. Frontiers in Microbiology. 2017;8(1361): 1-18. DOI: 10.3389/fmicb.2017.01361

[49] Conrad R, Noll M, Claus P, Klose M, Bastos WR, Enrich-Prast A. Stable carbon isotope discrimination and microbiology of methane formation in tropical anoxic lake sediments. Biogeosciences. 2011;8(3):795-814. DOI: 10.5194/bg-8-795-2011

[50] Conrad R, Ji Y, Noll M, Klose M, Claus P, Enrich-Prast A. Response of the methanogenic microbial communities in Amazonian oxbow lake sediments to desiccation stress. Environmental Microbiology. 2014;**16**(6):1682-1694. DOI: 10.1111/1462-2920.12267

[51] Alves KJ. Communities of methanogenic Archaea in different uses of Amazonian soils [dissertation]. Piracicaba: Luiz de Queiroz College of Agriculture (ESALQ); 2018

[52] Strong PJ, Xie S, Clarke WP.
Methane as a resource: Can the methanotrophs add value?
Environmental Science & Technology.
2015;49(7):4001-4018. DOI: 10.1021/ es504242n

[53] Kalyuzhhnaya MG, Xing X, editors. Methane Biocatalysis: Paving the Way to Sustainability. Switzerland: Springer International Publishing; 2018. 312p. DOI: 10.1007/978-3-319-74866-5

[54] Dalton H. The Leeuwenhoek lecture 2000: The natural and unnatural history of methane-oxidizing bacteria. Philosophical Transactions of the Royal Society B. 2005;**360**(1458):1207-1222. DOI: 10.1098/rstb.2005.1657

[55] Sawakuchi O, Ward ND, Borges CD, Tsai SIUM, Richey JE, Centen A, et al. Oxidative mitigation of aquatic methane emissions in large Amazonian rivers. Global Change Biology. 2016;**22**(3):1075-1085. DOI: 10.1111/ gcb.13169

[56] Stanford JA, Lorang MS, Hauer FR. The shifting habitat mosaic of river ecosystems. SIL Proceedings, 1922-2010. 2005;**29**(1):123-136. DOI: 10.1080/03680770.2005.11901979

[57] Boye K, Noël V, Tfaily M, et al.
Thermodynamically controlled preservation of organic carbon in floodplains. Nature Geoscience.
2017;10:415-419. DOI: 10.1038/ngeo2940

[58] Beringer J, Livesley SJ, Randle J, Hutley LB. Carbon dioxide fluxes dominate the greenhouse gas exchanges of a seasonal wetland in the wetdry tropics of Northern Australia. Agricultural and Forest Meteorology. 2013;**182-183**:239-247. DOI: 10.1016/j. agrformet.2013.06.008

[59] Pérez-rojas J, Moreno F, César J, Villa J. Catena soil organic carbon stocks in fluvial and isolated tropical wetlands from Colombia. Catena. 2019;**179**:139-148. DOI: 10.1016/j.catena.2019.04.006

[60] Zhao J, Malone SL, Oberbauer SF, Olivas PC, Schedlbauer JL, Staudhammer CL, et al. Intensified inundation shifts a freshwater wetland from a CO_2 sink to a source. Global Change Biology. 2019;**25**(10):3319-3333. DOI: 10.1111/gcb.14718

[61] Hernández M, Klose M, Claus P, Bastviken D, Marotta H, et al. Structure, function and resilience to desiccation of methanogenic microbial communities in temporarily inundated soils of the Amazon rainforest (Cunia reserve , Rondonia). Environmental Microbiology. 2019;**21**(5):1702-1717. DOI: 10.1111/1462-2920.14535

[62] Randle-Boggis RJ, Ashton PD,
Helgason T. Increasing flooding frequency alters soil microbial communities and functions under laboratory conditions.
MicrobiologyOpen. 2018;7(1):1-13. DOI: 10.1002/mbo3.548

[63] Mitsch WJ, Nahlik A, Wolski P, Bernal B, Zhang L, Ramberg L. Tropical wetlands: Seasonal hydrologic pulsing, carbon sequestration, and methane emissions. Wetlands Ecology and Management. 2010;**18**(5):573-586. DOI: 10.1007/s11273-009-9164-4

[64] Kayranli B, Scholz M, Mustafa A, Hedmark Å. Carbon storage and fluxes within freshwater wetlands: A critical review. Wetlands. 2010;**30**(1):111-124. DOI: 10.1007/s13157-009-0003-4

[65] Dunfield P, Knowles R, Dumont R, Moore TR. Methane production and consumption in temperate and subarctic peat soils: Response to temperature and pH. Soil Biology and Biochemistry. 1993;**25**(3):321-326. DOI: 10.1016/0038-0717(93)90130-4

[66] Sanches LF, Guenet B, Marinho CC, Barros N, de Assis Esteves F. Global regulation of methane emission from natural lakes. Scientific Reports. 2019;**9**(1):1-10. DOI: 10.1038/ s41598-018-36519-5

[67] Bodelier PLE, Dedysh SN. Microbiology of wetlands. Frontiers in Microbiology. 2013;**4**:1-4. DOI: 10.3389/ fmicb.2013.00079

[68] Boon E, Meehan CJ, Whidden C, Wong DHJ, Langille MGI, Beiko RG. Interactions in the microbiome: Communities of organisms and communities of genes. FEMS Microbiology

Reviews. 2014;**38**(1):90-118. DOI: 10.1111/1574-6976.12035

[69] Yarwood SA. The role of wetland microorganisms in plant-litter decomposition and soil organic matter formation: A critical review. FEMS Microbiology Ecology. 2018;**94**:1-17. DOI: 10.1093/femsec/fiy175

[70] Lennon JT, Jones SE. Microbial seed banks: The ecological and evolutionary implications of dormancy. Nature Reviews. Microbiology. 2011;**9**(2):119-130. DOI: 10.1038/nrmicro2504

[71] De Vrieze J, Regueiro L, Props R, Vilchez-Vargas R, Jáuregui R, Pieper DH, et al. Presence does not imply activity: DNA and RNA patterns differ in response to salt perturbation in anaerobic digestion. Biotechnology for Biofuels. 2016;**9**(244):1-13. DOI: 10.1186/s13068-016-0652-5

[72] Liu D, Nishida M, Takahashi T, Asakawa S. Transcription of mcrA gene decreases upon prolonged nonflooding period in a methanogenic archaeal community of a paddyupland rotational field soil. Microbial Ecology. 2018;75(3):1-10. DOI: 10.1007/ s00248-017-1063-2

[73] Adrian L, Marco-Uurrea E. Isotopes in geobiochemistry: Tracing metabolic pathways in microorganisms of environmental relevance with stable isotopes. Current Opinion in Biotechnology. 2016;41:19-25. DOI: 10.1016/j.copbio.2016.03.018

[74] Kueter N, Lilley MD, Schmidt MW, Bernasconi SM. Experimental carbonatite/graphite carbon isotope fractionation and carbonate/graphite geothermometry. Geochimica et Cosmochimica Acta. 2019;**253**:290-306. DOI: 10.1016/j.gca.2019.03.020

[75] Coyotzi S, Pratscher J, Murrell JC, Neufeld JD. Targeted metagenomics of active microbial populations with stable-isotope probing. Current Opinion in Biotechnology. 2016;**41**:1-8. DOI: 10.1016/j.copbio.2016.02.017

[76] Potter C, Melack JM, Engle D. Modeling methane emissions from Amazon floodplain ecosystems. Wetlands. 2014;**34**:501-511. DOI: 10.1007/s13157-014-0516-3

[77] Wilson C, Gloor M, Gatti LV, Miller JB, Monks SA, McNorton J, et al. Contribution of regional sources to atmospheric methane over the Amazon basin in 2010 and 2011. Global Biogeochem. 2016;**30**:400-420. DOI: 10.1002/2015GB005300

[78] Clark DB, Mercado LM, Sitch S, Jones CD, Gedney N, Best MJ, et al. The joint UK land environment simulator (JULES), model description – Part 2: Carbon fluxes and vegetation dynamics. Geoscientific Model Development. 2011;**4**:701-722. DOI: 10.5194/ gmd-4-701-2011

[79] Bloom AA, Palmer PI, Fraser A, Reay DS. Seasonal variability of tropical wetland CH_4 emissions: The role of the methanogen-available carbon pool. Biogeosciences. 2012;**9**(8):2821-2830. DOI: 10.5194/bg-9-2821-2012

[80] Gedney N, Cox PM, Huntingford C. Climate feedback from wetland methane emissions. Geophysical Research Letters. 2004;**31**:1-4. DOI: 10.1029/2004GL020919

[81] Xu X, Yuan F, Hanson PJ, Wullschleger SD, Thornton PE, Riley WJ, et al. Reviews and syntheses: Four decades of modeling methane cycling in terrestrial ecosystems. Biogeosciences. 2016;**13**(12):3735-3755. DOI: 10.5194/bg-13-3735-2016