

REVIEW ARTICLE

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Key Points:

- The key drivers of methane production and consumption are assessed for wetlands, marine and freshwaters, permafrost regions, and methane hydrates
- The balance of microbial controlled methane production and consumption are critical to methane climate feedbacks in all environments
- Wetlands and freshwater systems are likely to drive the methane climate feedback from natural settings in the coming century

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Methane Feedbacks to the Global Climate System in a Warmer World

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Abstract Methane (CH₄) is produced in many natural systems that are vulnerable to change under a warming climate, yet current CH₄ budgets, as well as future shifts in CH₄ emissions, have high uncertainties. Climate change has the potential to increase CH₄ emissions from critical systems such as wetlands, marine and freshwater systems, permafrost, and methane hydrates, through shifts in temperature, hydrology, vegetation, landscape disturbance, and sea level rise. Increased CH₄ emissions from these systems would in turn induce further climate change, resulting in a positive climate feedback. Here we synthesize biological, geochemical, and physically focused CH₄ climate feedback literature, bringing together the key findings of these disciplines. We discuss environment-specific feedback processes, including the microbial, physical, and geochemical interlinkages and the timescales on which they operate, and present the current state of knowledge of CH₄ climate feedbacks in the immediate and distant future. The important linkages between microbial activity and climate warming are discussed with the aim to better constrain the sensitivity of the CH₄ cycle to future climate predictions. We determine that wetlands will form the majority of the CH₄ climate feedback up to 2100. Beyond this timescale, CH₄ emissions from marine and freshwater systems and permafrost environments could become more important. Significant CH₄ emissions to the atmosphere from the dissociation of methane hydrates are not expected in the near future. Our key findings highlight the importance of quantifying whether CH₄ consumption can counterbalance CH₄ production under future climate scenarios.

Plain Language Summary Methane is a powerful greenhouse gas, second only to carbon dioxide in its importance to climate change. Methane production in natural environments is controlled by factors that are themselves influenced by climate. Increased methane production can warm the Earth, which can in turn cause methane to be produced at a faster rate - this is called a positive climate feedback. Here we describe the most important natural environments for methane production that have the potential to produce a positive climate feedback. We discuss how these feedbacks may develop in the coming centuries under predicted climate warming using a cross-disciplinary approach. We emphasize the importance of considering methane dynamics at all scales, especially its production and consumption and the role microorganisms play in both these processes, to our understanding of current and future global methane emissions. Marrying large-scale geophysical studies with site-scale biogeochemical and microbial studies will be key to this.

1. Methane in the Global Carbon Cycle

Methane (CH₄) is the most abundant reduced compound in the atmosphere and plays an important role in the Earth's carbon (C) cycle. This cycle consists of continuous transformations of C between the organic and inorganic pools in the atmosphere, terrestrial biosphere, hydrosphere, and geosphere. Atmospheric carbon dioxide (CO₂), the fully oxidized form of C, is fixed by the terrestrial and marine biosphere. During the decay of organic matter, C bound in this biomass can be converted to CH₄ depending on environmental conditions. CH₄ will eventually be oxidized back to CO₂, either in terrestrial and aquatic zones or in the atmosphere.

The fraction of the produced CH₄ that enters the atmosphere, where it acts as a powerful greenhouse gas (GHG), depends conceptually on three factors: the production rate, the rate of transport from the region of production/storage to the atmosphere, and the rate of consumption along this transport pathway

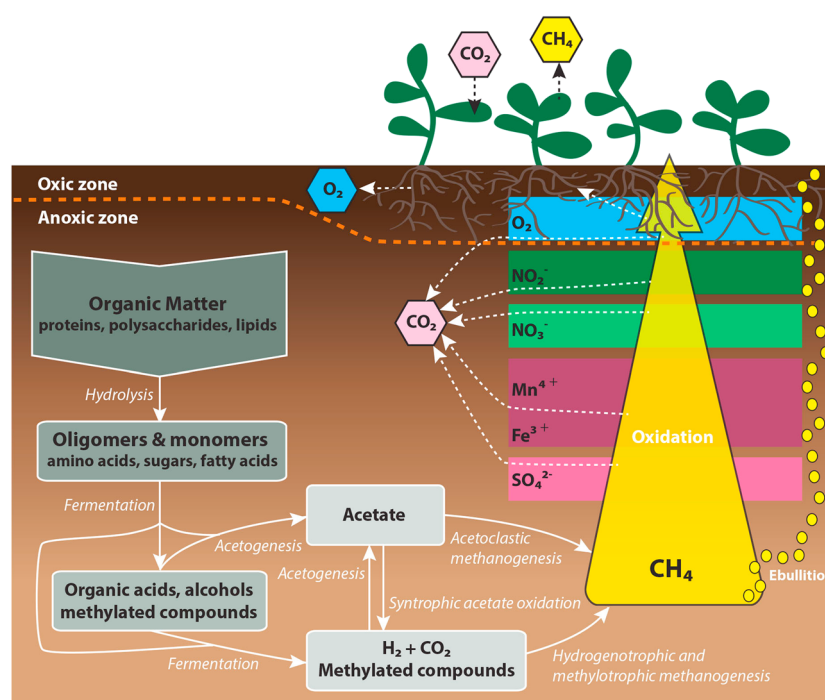


Figure 1. Conceptual illustration of CH_4 production and consumption prior to atmospheric release; all microbial conversion processes are shown in italics. Complex organic matter is degraded by microorganisms in anoxic environments by a multistep process including hydrolysis, fermentation, homoacetogenesis, and syntrophic acetate oxidation, leading to CO_2 and CH_4 as end products. The CH_4 diffuses upward through the soil/sediment layer where it can be oxidized by (an)aerobic methanotrophs. Here a theoretical distribution of available electron acceptors based on their electron potential is shown; the extent of the electron acceptor zones will vary between different environments. Part of this CH_4 can eventually reach the atmosphere. Some of the CH_4 can be released via plants or ebullition; note that these pathways of CH_4 release can also occur in aquatic environments (not shown). The vegetation represents vascular plants, which provide a direct pathway of vertical CH_4 release via aerenchyma.

(Figure 1). These factors lead to fluctuations in CH_4 emissions, which have affected atmospheric CH_4 concentrations over glacial-interglacial cycles (section 1.2). Fluctuations in CH_4 emissions can form strong positive feedbacks to current and future climate warming. The other key control on atmospheric CH_4 concentrations is its removal rate, primarily its reaction with the hydroxyl radical (OH ; see section 1.3), which approximately, but not perfectly, balances CH_4 emissions. Variations in the oxidation capacity of the atmosphere (primarily by OH) have a direct impact on CH_4 levels (McNorton, Chipperfield, et al., 2016; Rigby et al., 2017; Turner et al., 2017); these atmospheric feedbacks are not reviewed here.

In this review, we focus only on natural CH_4 emissions and how these will change under current and future warming. This includes the potential contribution of physical, geochemical, and biological feedbacks of CH_4 to the global climate system. We explore the role of environmental controls on CH_4 emissions and how these may change across a range of the most critical natural environments. The underlying concepts are first described (sections 1–3), before being discussed in the context of key source processes and regions: wetlands (section 4), marine and freshwater systems (section 5), permafrost regions (section 6), and methane hydrates (section 7). In particular, we focus on the role of microbial processes in CH_4 production and consumption and examine to what degree these hold the key to global CH_4 feedbacks in the future and over what timescales. Microbial processes are often treated as a “black box” in geophysical and geochemical studies; therefore, in section 2 we present the current state of knowledge regarding the primary microbial actors in the global CH_4 cycle as a reference point for those less familiar with the microbial literature. The final section (section 8) synthesizes the global CH_4 feedback and the timescales on which its different elements may operate; we also identify knowledge gaps and suggest pathways toward future research. We include a glossary at the end that defines the key terms used throughout this review.

1.1. Radiative Effects of Atmospheric Methane

CH_4 is a major anthropogenic GHG, second only to CO_2 (Myhre et al., 2013). It strongly absorbs infrared radiation in two fundamental bands at wavelengths of 3.3 μm and 7.7 μm , which are related to the stretching and

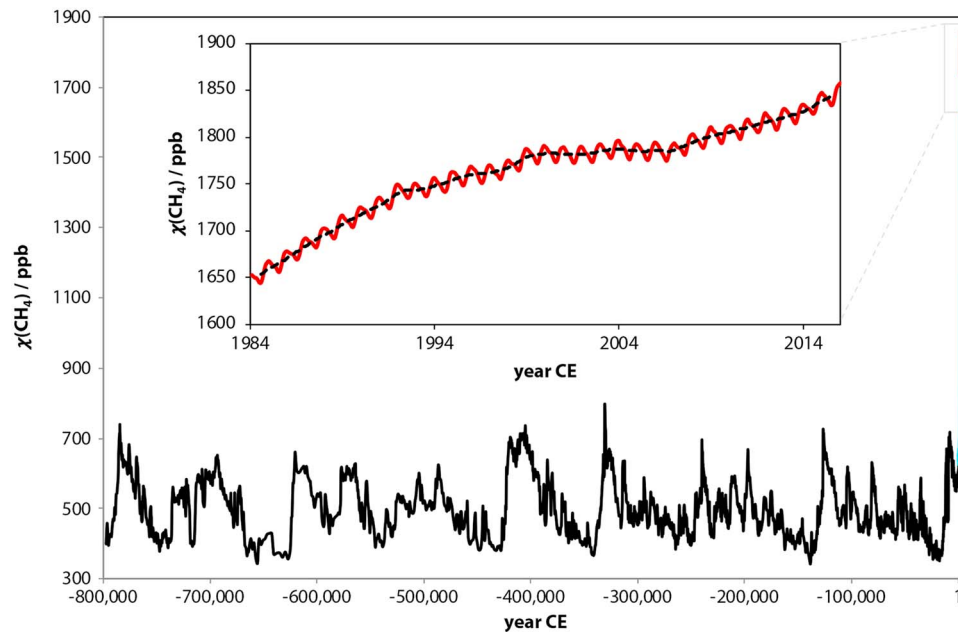


Figure 2. Past and recent variations in the atmospheric CH_4 concentrations, demonstrating both the sudden rise in recent history and the plateau between 1999 and 2006, the causes of which have been much discussed in recent publications (see section 1.3). The inset shows a magnification of the direct atmospheric measurements from 1984 to 2015, and the dashed black line is a 12 month running mean fit. Data sources: black—data set from the EPICA Dome C ice core record (data from IGBP PAGES/World Data Center for Paleoclimatology, Data Contribution Series # 2008-054) (Loulergue et al., 2008); blue—merged data set from the Law Dome ice core and firn measurements and Cape Grim atmospheric measurements (Etheridge et al., 1998; Ferretti et al., 2005; MacFarling Meure et al., 2006; Trudinger, 2002) (data from IGBP PAGES/World Data Center for Paleoclimatology, Data Contribution Series # 2010-070); and red—global average CH_4 mole fraction from direct atmospheric measurements (Tsutsumi et al., 2009) (data from World Date Center for Greenhouse Gases, WMO Greenhouse Gas Bulletin, No.12, 2016).

bending modes of the C–H bond. Although atmospheric concentrations of CH_4 are about 200 times lower than CO_2 , its global warming potential (GWP) is 28 over a 100 year time horizon and 84 over a 20 year time horizon (Myhre et al., 2013). It is important to consider the time horizon because of the relatively short lifetime of CH_4 in the atmosphere. The increase in atmospheric CH_4 concentrations since preindustrial times has resulted in a direct radiative forcing since 1750 of about 0.5 W/m^2 (Myhre et al., 2013). Estimates of the GWP of CH_4 are still evolving, with recent work suggesting that the radiative forcing of CH_4 from 1750 to 2011 may have been 25% higher than the 2013 Intergovernmental Panel on Climate Change (IPCC) estimates (Etminan et al., 2016).

CH_4 also affects the abundance of other important GHGs due to its important role in atmospheric chemistry (Fiore et al., 2002; Thompson & Cicerone, 1986). First, CH_4 oxidation leads to the photochemical formation of the greenhouse gas ozone (O_3). Second, in the stratosphere, CH_4 oxidation produces water vapor (H_2O), and the corresponding increase in stratospheric H_2O contributes to radiative forcing. Finally, after oxidation, the C atom from the original CH_4 molecule ends up in the form of the main anthropogenic greenhouse gas, carbon dioxide (CO_2) (Myhre et al., 2013). Taking these “climate-carbon feedbacks” into account, the GWP of CH_4 rises to 34 over a 100 year timeframe and 86 over a 20 year timeframe. The total change in radiative forcing since 1750 that can be attributed to CH_4 emissions is therefore about 1 W/m^2 at present (Myhre et al., 2013) or roughly 60% of the radiative forcing of CO_2 . Further details on the residence time of CH_4 and its radiative forcing can be found in the fifth assessment report of the IPCC (Myhre et al., 2013) and O’Connor et al. (2010).

1.2. Past Trends in Atmospheric Methane

Past atmospheric CH_4 concentrations have been reliably estimated from air trapped in polar firn and ice cores (Wolff & Spahni, 2007). The oldest available ice core record to date was drilled at the Dome C site in East Antarctica, covering the last 800,000 years with an average age resolution at its base of ± 550 years (Loulergue et al., 2008) (Figure 2). Recent trends in Late Holocene and Anthropocene CH_4 concentrations can be determined in ice cores drilled at locations with high accumulation rates on the polar ice sheets (MacFarling Meure et al., 2006), from firn ice (e.g., Battle et al., 1996; Sapart et al., 2013), or from high-

resolution ice cores in mountain glaciers outside the polar regions; these have much lower age uncertainty ranges, on the scale of decades (e.g., Hou et al., 2013). From these measurements, it is well established that throughout the middle to late Pleistocene, atmospheric CH₄ concentrations stayed within the range of 300–800 ppb (Figure 2). Milankovitch cycles were the main control on this variability in atmospheric CH₄ concentrations, with the dominant factor being the 100,000 year orbital cycle between 800,000 and 400,000 years ago (Loulergue et al., 2008). The 23,000 year orbital insolation cycle is more important from 400,000 to 5,000 years ago (Ruddiman, 2003). This correlation between CH₄ and 30°N summer solar insolation driven by orbital changes breaks up in the mid-Holocene, about 5,000 years ago (Ruddiman, 2003). This has been attributed to early human activities, in particular rice agriculture, impacting the global CH₄ budget (Fuller et al., 2011; Ruddiman, 2003; Ruddiman et al., 2008). However, Singarayer et al. (2011) suggest that the late Holocene CH₄ increase can be explained by orbitally induced changes of seasonal precipitation from the Southern Hemisphere tropics. Precise measurements of the inter-polar gradient of CH₄ over the late preindustrial Holocene (since about 800 B.C.E.) from air trapped in Greenland and Antarctic ice cores suggest that the increase of more than 100 ppb during this period has both natural and anthropogenic components (Mitchell et al., 2013).

With the onset of the industrial revolution in the late 1700s, the 300–800 ppb range of CH₄ concentrations documented for the last 800,000 years was disrupted by a dramatic anthropogenic-driven increase to more than 1800 ppb (see section 1.3 and Figure 2).

The glacial periods of the past 800,000 years were characterized by low atmospheric CH₄ concentrations, while higher concentrations were seen during interglacials (Past Interglacials Working Group of PAGES, 2016). In a direct comparison between Greenland and Antarctic ice cores, though, an asynchronous pattern can be observed in the δ¹⁸O records (used as a proxy for temperature) between warming and cooling events in both hemispheres. In the Northern Hemisphere, Dansgaard-Oeschger events are phases of rapid warming of 6–8°C occurring within a few decades (Long & Stoy, 2013), followed by drastic temperature drops (Brook et al., 2005; EPICA Community Members, 2006). In contrast, the Antarctic ice core data suggest the onset of cooling phases in the Southern Hemisphere during Northern Hemisphere Dansgaard-Oeschger warming events (Alley, 2000; Stenni et al., 2011). This out of phase shift of climate events in both polar regions is referred to as the bipolar seesaw phenomenon, which is well documented in δ¹⁸O time series. The ice core records of atmospheric CH₄ are in phase in both hemispheres, with an error range of a couple of hundred years (Barker et al., 2011). This reliable pattern is the reason why cross-hemispherical ice core comparisons of δ¹⁸O records are based on methane synchronization (Pedro et al., 2011).

Another characteristic of atmospheric CH₄ concentrations during interglacials in Antarctica is that they follow temperature trends in the Antarctic record much more closely than CO₂ concentrations, which tend to have a significant lag in their correlation with paleotemperatures (Severinghaus & Brook, 1999). Atmospheric CH₄ responded to Dansgaard-Oeschger warming events by increasing relatively quickly (within 100 years) (Brook et al., 1996; Flückiger et al., 2004), which has been attributed to increased emissions from Northern Hemisphere wetland CH₄ sources (Dällenbach et al., 2000; Wolff & Spahni, 2007). An inter-polar gradient between CH₄ concentrations in Greenland and Antarctic ice core records reflects the dominance of CH₄ sources in the Northern Hemisphere compared to the Southern Hemisphere (Dällenbach et al., 2000), which was likely due to higher CH₄ emission from northern wetlands in this case (Wolff & Spahni, 2007).

CH₄ sources can also be attributed using the isotopic composition of CH₄. For example, δ¹³C values of CH₄ recorded in Antarctic snow and ice in 1850 were lighter (−48.5‰) (Sowers et al., 2005) than current atmospheric CH₄ (−47.3‰) (Schaefer et al., 2016). This ¹³C enrichment of atmospheric CH₄ is the result of anthropogenic fossil fuel-derived CH₄ emissions with relatively high ¹³C content (Wolff & Spahni, 2007). Measurements of deuterium (²H) (Sowers, 2006) and radiocarbon (¹⁴C) (Petrenko et al., 2009, 2017) content of ice core CH₄ suggest that methane hydrates did not contribute to increased CH₄ emissions during the last glacial termination (24,000 to 8,000 years ago), including the rapid Younger Dryas-preboreal warming event (~11,600 years ago). This supports the conclusions from assessments of the potential future impacts of methane hydrate release under a warming climate (see section 7).

However, it is still debatable to what extent changes in atmospheric CH₄ levels were a driver of, or a response to, paleoclimate changes and if they were a major contributor to climate feedbacks. In addition, it has been

difficult to clearly attribute change in CH₄ observed from air trapped in ice cores to individual processes using isotope information because shifts in CH₄ emissions do not necessarily coincide with shifts in CH₄ sources (Möller et al., 2013). This is likely because different drivers of CH₄ release and its isotopic signature can change with time, and simultaneous shifts in sources (e.g., one source increasing while another decreases) do not necessarily result in a significant change in net CH₄ emissions to the atmosphere (Möller et al., 2013; Sowers, 2006). For example, the growth of ice sheets over boreal wetlands likely reduced high-latitude Northern Hemisphere emissions, while the expansion of tropical wetlands onto recently exposed continental shelves following sea level decline (due to water being locked up in the growing ice sheets) likely increased CH₄ emissions in the tropics. This may have shifted the isotopic composition ($\delta^{13}\text{C}$ and $\delta^2\text{H}$) of wetland-derived CH₄ during the last 160,000 years. However, the impacts of these and other drivers of the isotopic signature of CH₄ (such as the extent of methane oxidation following its production—see section 2.2—or the ratio of different metabolic pathways of C fixation in the plants that form the organic matter from which CH₄ is produced) on overall shifts in the isotopic composition of atmospheric CH₄ are poorly understood (Möller et al., 2013; Sowers, 2006; Wolff & Spahni, 2007).

Due to a lack of long-term CH₄ records, it is difficult to demonstrate that CH₄ has altered the global climate prior to CH₄ ice core records. Nevertheless, specific shifts in global climate have been linked to large-scale CH₄ release events by the use of indirect proxy information, most importantly the C isotopic composition in sedimentary records; this is based on atmospheric CH₄ being strongly depleted in ¹³C (e.g., Frieling et al., 2016). One such example is the global climate warming event of 5–8°C at the onset of the Paleocene-Eocene boundary, also known as the Paleocene-Eocene Thermal Maximum (PETM), which has been linked to the destabilization of CH₄ hydrates (Dickens et al., 1995, 1997) (section 7), although the causes of this warming period are much debated (Bowen et al., 2015; DeConto et al., 2012; Pagani et al., 2006). A shift in the $\delta^{13}\text{C}$ isotopic composition of organic C and carbonates in sedimentary records that cover this period suggests an increased release of CH₄ with a depleted $\delta^{13}\text{C}$ signature to the atmosphere to have been a possible driver of the high temperatures during the PETM (Bains et al., 2000). Due to the short atmospheric lifetime of CH₄, the warming associated with this event would have been caused by CO₂ that is formed from the oxidation of the large volume of released CH₄, rather than direct atmospheric loading of CH₄ (Bains et al., 2000). Therefore, the fundamental role of CH₄ as the direct driver of this warming event is not clear (Bowen et al., 2015; DeConto et al., 2012). The lack of a long-term CH₄ archive or an effective proxy makes direct links of CH₄ to past climate forcing difficult.

1.3. Recent Trends in Atmospheric Methane

The spatial and temporal evolution of atmospheric CH₄ has been monitored in great detail over the past decades by a large network of surface stations (Dlugokencky et al., 1998, 2003, 2009) and aircraft observations (e.g., Schuck et al., 2012) and has recently been augmented by satellites (Frankenberg et al., 2008; Jacob et al., 2016). This global observation network consists of 31 global stations and 400 regional stations providing in situ measurements, often with a suite of other trace gases (Ciais et al., 2014). These measurements are traditionally done with gas chromatography but are gradually being replaced by cavity ring-down spectroscopy. These stations provide the backbone of the analysis of global trends in CH₄. Total atmospheric column observations are provided by the Total Carbon Column Observing Network (TCCON), which is a network of ground-based Fourier Transform Spectrometers recording direct solar spectra in the near-infrared region. This can be converted into precise measurements of the total column concentration of CH₄, among other trace gases. The TCCON also provides a bridge to a new generation of satellites (Orbiting Carbon Observatory, or OCO-2, the Greenhouse Gases Observing Satellite, or GOSAT, and the Tropospheric Monitoring Instrument, or TROPOMI), which provide global coverage, operating in the infrared absorption bands of CH₄. These satellite measurements are less accurate than the in situ network but provide wider and more regular coverage.

Recent monitoring of atmospheric CH₄ has revealed several puzzling and unexpected temporal variations in atmospheric CH₄ concentrations (Figure 2). After a more than twofold increase over the industrial period, the growth rate of atmospheric CH₄ concentrations gradually declined during the 1990s, leading to relatively stable concentrations after 2000 (Dlugokencky et al., 1998, 2003, 2009). This was followed by a renewed increase since 2007 (Nisbet et al., 2014; Schaefer et al., 2016). The roles of both natural and anthropogenic sources, and variations in the atmospheric CH₄ sink, have been controversially discussed in a large number

of studies over the past years, primarily centering around debate over biogenic versus fossil CH₄ sources. These include the balancing of sources and sinks (Bousquet et al., 2006; Dlugokencky et al., 1994, 1998, 2003; Khalil & Rasmussen, 1993), and increases in anthropogenic CH₄ emissions (Bergamaschi et al., 2013; Bousquet et al., 2006; Dlugokencky et al., 2011; Franco et al., 2016; Schaefer et al., 2016; Turner et al., 2016), especially agriculture (Nisbet et al., 2016; Schaefer et al., 2016), or fossil fuel emissions (Worden et al., 2017). Short-term increases in Arctic emissions (Dlugokencky et al., 2009), and decreases (Monteil et al., 2011) and increases in wetland emissions (Bousquet et al., 2006, 2011; Schaefer et al., 2016), particularly the growth of tropical wetlands emissions (Bergamaschi et al., 2013; Bousquet et al., 2011; Dlugokencky et al., 1998, 2009; Nisbet et al., 2016; Pison et al., 2013), have also been suggested. Tropical wetlands are the most common natural source cited to explain the recent rise in atmospheric CH₄ concentrations and are also one of the least well-constrained natural CH₄ sources, primarily due to a lack of observational data on the extent of wetlands in the tropics (Melton et al., 2013). Most recently, wetlands were suggested to have responded in line with predicted climate change impacts on wetland CH₄ emissions, but this change in emissions likely did not play an important role in the increase of atmospheric CH₄ since 2007 (Poulter et al., 2017). So while some changes to natural CH₄ emissions may have been in response to climate warming, climate-related trends are not clear in most studies of recent atmospheric CH₄ dynamics. However, this topic is hotly debated and the science is rapidly evolving, with a recent study suggesting that decreased CH₄ emissions from biomass burning since 2007 could allow for the increases in both biogenic and anthropogenic fossil fuel CH₄ emissions posited in this debate (Worden et al., 2017).

In addition to source changes, variations in the abundance of the hydroxyl radical (OH) (Montzka et al., 2011) may have also contributed to the observed variations in the growth rate of atmospheric CH₄ (Dalsøren et al., 2016; Kirschke et al., 2013; McNorton, Chipperfield, et al., 2016; Monteil et al., 2011; Rigby et al., 2017; Turner et al., 2017). OH is responsible for about 90% of the removal of atmospheric CH₄. Its atmospheric concentration in the past has been affected by changes in CO, CH₄, and other hydrocarbons that consume OH and also by changes in NO_x, which recycles OH, and by changes in UV radiation and H₂O levels that produce OH (Bândă et al., 2016; Lelieveld et al., 2016; Naik et al., 2013). A recent analysis suggests that global mean OH increased by 46 ± 12% as a result of preindustrial to present-day increases in anthropogenic NO_x emissions (Naik et al., 2013). OH decreased by 17 ± 2%, 8 ± 2%, and 3 ± 3% due to the CH₄ burden, anthropogenic CO, and non-CH₄ volatile organic compound emissions, respectively (Naik et al., 2013). It is therefore probable that at least some of the variability in atmospheric CH₄ levels over the past decades is due to variations in atmospheric OH (Rigby et al., 2017; Turner et al., 2017). The reaction of CH₄ with OH and the formation of OH from water vapor are both temperature dependent and therefore will be affected by warming global temperatures (Voulgarakis et al., 2013). However, understanding the dynamics of OH at regional and global scales under future climate scenarios is highly challenging (McNorton, Chipperfield, et al., 2016; Rigby et al., 2017; Turner et al., 2017; Voulgarakis et al., 2013).

1.4. Globally Significant Methane Sources

CH₄ is emitted from a number of different natural and anthropogenic sources (Figure 3). The contribution of natural sources to global anthropogenic emissions since 1980 is estimated to be between 33 and 54%, while anthropogenic sources accounted for between 46 and 67% (Kirschke et al., 2013). Natural sources are dominated by wetlands, but there are also significant contributions from freshwater systems (Table 1); the latter include some recent high estimates that add to the uncertainty in the bottom-up budget (Saunois, Bousquet, et al., 2016). When CH₄ emission values from bottom-up studies (the focus of this review) are extrapolated and summed up, they result in unrealistically high and poorly spatially constrained best estimates for the total global CH₄ source (Table 1). Estimates of the total global CH₄ source derived from top-down studies, which are constrained by the observed global CH₄ burden, are generally considered more realistic, but they have only limited power in resolving contributions from individual source types and the underlying processes. There is some overlap between the high end of the top-down estimates and the low end of the bottom-up estimates (Table 1), but, in general, the available top-down estimates are much lower than bottom-up estimates.

Natural CH₄ sources include wetlands, freshwater systems, coastal sediments and oceans, methane hydrates, geological sources, and fauna, each of which may respond differently to a warming climate. The main anthropogenic sources are agriculture and waste, biomass burning, and fossil fuels. These include both methanogenic processes and infrastructural leakage of fossil CH₄. CH₄ from fossil fuel sources have recently been

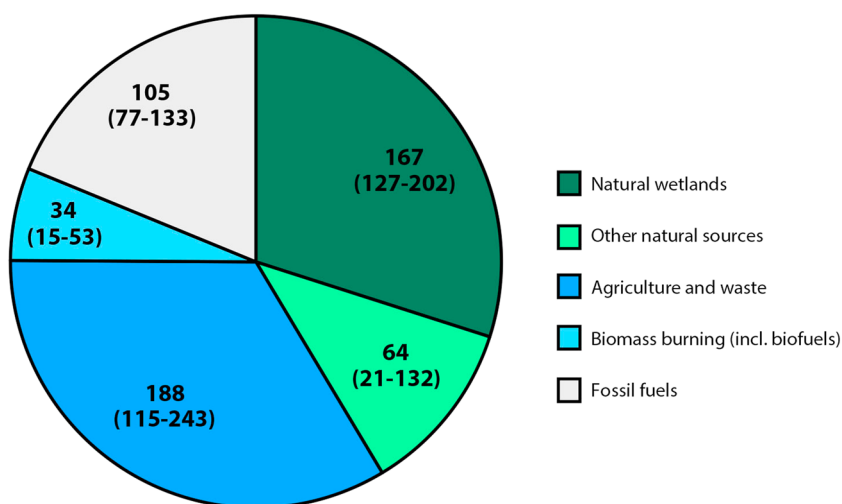


Figure 3. Overview of the main source categories of CH₄ emission to the atmosphere, based on the top-down budget for the period 2003–2012 from Saunio, Bousquet, et al. (2016); numbers are in Tg CH₄ yr⁻¹. The other natural environments discussed in this review are counted as “Other natural sources” in this figure. Of these, marine and freshwater CH₄ emissions account for 68%, wildfires 1.5%, permafrost 0.5%, and methane hydrates 0–1% of the 2003–2012 detailed bottom-up budget from Saunio, Bousquet, et al. (2016) (Table 1).

suggested to be a much larger component of the anthropogenic CH₄ budget, as much as 60% greater than previous estimates (Schwietzke et al., 2016). These anthropogenic sources are primarily influenced by population dynamics and land use change rather than climate change, although changes in climate, population, and land use are intrinsically linked.

In addition to separating CH₄ emissions into natural and anthropogenic sources, it is common to classify them by their formation mechanisms and/or conditions. The largest group of sources is of biogenic origin. Thermogenic sources are the main component of CH₄ in natural gas reservoirs, although biogenic CH₄ is present as well. Pyrogenic CH₄ from combustion processes also use biological material, but the production process is clearly distinct. The primary focus of this review is on biogenic and pyrogenic CH₄, as these sources are influenced by, and can form feedbacks to, climate systems. Thermogenic sources are unlikely to change under shifting climate regimes, with the notable exception of the destabilization of trapped thermogenic CH₄, for example CH₄ hydrates discussed in section 7.

An important requirement for most CH₄-forming processes is the absence of O₂, although there is some evidence for CH₄ production in oxic environments too (e.g., Keppler et al., 2006, 2009; Tang et al., 2016); however, these processes have been subject to sustained debate (e.g., Dueck et al., 2007; Nisbet et al., 2009). This includes mechanisms that are not driven by methanogenic archaea (e.g., Liu et al., 2015) or those that are governed by alternative pathways and nonoxygen sensitive enzymes (Tang et al., 2016), such as CH₄ production in freshwater lakes as a by-product of phosphorus metabolism rather than C or energy metabolism (Yao et al., 2016) or CH₄ production in oxygenated shallow marine waters by zooplankton (Schmale et al., 2017). There have been other recent indications of nonmicrobial CH₄ production, although only at very small levels insignificant in the context of the global CH₄ budget (Table 1) (Wang, Lerdau, & He, 2017). The presence of CH₄ in oxic zones in lakes is likely driven by the transport of dissolved CH₄ from CH₄ production areas, rather than aerobic, algae-related CH₄ production (Encinas Fernández et al., 2016). However, in marine environments, CH₄ production in fully oxygenated sulfate-rich zones (see section 2.2.2) has been directly attributed to bacterial degradation of dissolved organic matter in seawater (Repeta et al., 2016). The magnitude and significance of these mechanisms on a global scale are poorly constrained, but likely small.

There is considerable uncertainty in biogenic emissions (Melton et al., 2013; Schaefer et al., 2016) and in particular how natural CH₄ production and consumption processes will be affected by a combination of evolving environmental factors in response to climate change. For example, CH₄ release from thawing permafrost regions may be affected by temperature changes, not only driving unfrozen soil active layer deepening and

Table 1
Detailed Annual CH₄ Budget in Tg CH₄ yr⁻¹ (See Figure 3 and Associated Discussion), Adapted From Saunio, Bousquet, et al. (2016) (2003–2012); the Sink Values Are Based On Kirschke et al. (2013) (2000–2009)

	Bottom-Up	Top-Down
Total natural sources	384 (257–524)	231 (194–296)
Natural wetlands	185 (153–227)	167 (127–202)
Other natural sources	199 (104–297)	64 (21–132)
Other land sources	185 (99–272)	
Freshwaters	122 (60–180)	
Geological (onshore)	40 (30–56)	
Wild animals	10 (5–15)	
Termites	9 (3–15)	
Wildfires	3 (1–5)	
Permafrost soils (direct)	1 (0–1)	
Oceanic sources	14 (5–25)	
Geological (offshore)	12 (5–20)	
Other (including methane hydrates)	2 (0–5)	
Total anthropogenic sources	352 (340–360)	328 (259–370)
Agriculture and waste	195 (178–206)	188 (115–243)
Enteric fermentation and manure	106 (97–111)	
Landfills and waste	59 (52–63)	
Rice cultivation	30 (24–36)	
Fossil fuels	121 (114–133)	105 (77–133)
Coal mining	41 (26–50)	
Gas, oil, and industry	79 (69–88)	
Biomass and biofuel burning	30 (27–35)	34 (15–53)
Total sinks (Kirschke et al., 2013)		
Total chemical loss	604 (483–738)	518 (510–538)
Tropospheric OH	528 (454–617)	
Stratospheric loss	51 (16–84)	
Tropospheric Cl	25 (13–37)	
Soil uptake	28 (9–47)	32 (26–42)
Sum of sources	736 (567–884)	559 (453–666)
Sum of sinks	632 (492–785)	550 (536–580)

Note. Boldface is used in this table to highlight the total values for natural and anthropogenic methane sources and total sinks; the nonboldface values refer to values within these categories.

microbial activity (Bardgett et al., 2008) but also shifting precipitation patterns and altered hydrologic flow paths (Rawlins et al., 2010).

2. Microbial Controls on Methane Transformations

Microbes are the engines that drive Earth's biogeochemical cycles (Falkowski et al., 2008). Bacteria and Archaea carry out redox reactions (the successive transfer of electrons and protons between chemical elements) fundamental to the functioning of our biosphere. Earth's C cycle is controlled by transformations between the organic and inorganic pools, the majority of which are driven by this microbiological activity. However, the complexity of microbial community dynamics and functionality limits the inclusion of these analyses in geophysical and geochemical studies where they are often treated as a black box. We advocate that in order to fully understand the temporal and spatial variability of CH₄ emissions, the processes governing CH₄ production and consumption should be understood at all scales (see section 8.3). Therefore, in this section we describe the main microbial actors and their functions as a reference point for readers not familiar with the microbial literature in an effort to encourage more cross-field collaboration between the geosciences and microbial ecology.

2.1. Methane Production

Under aerobic conditions, even the most thermodynamically stable substrates can be rapidly oxidized directly to CO₂. In the absence of oxygen, degradation of organic matter often occurs stepwise in cooperation between different microbial functional groups. The initial degradation (hydrolysis; Figure 1) yields a variety of organic molecules (monomers and oligomers; Figure 1), which are then further converted into carboxylic acids, hydrogen, and CO₂ (Figure 1). Generally, methanogenesis is the final reaction in anaerobic degradation. So both CO₂ and CH₄ are the end products of organic matter degradation in the environment (Figure 1). It has been estimated that approximately 2% of CO₂ fixed in the biosphere annually is converted to, and released to, the atmosphere as CH₄ (Thauer et al., 2008).

Methanogenesis is a strictly anaerobic process catalyzed by specialized groups of archaea that convert CO₂ with H₂, methanol, methylamines, methylsulfides, or acetate into CH₄ (Figure 1) (Thauer et al., 2008). Hydrogenotrophic, methylotrophic, and acetoclastic methanogenic pathways share many genes and enzymes, most notably in the final step of CH₄ formation (Ferry, 1999).

Since their discovery, and until recently, methanogens were believed to be restricted to the phylum *Euryarchaeota* distributed over seven known orders: *Methanosarcinales*, *Methanomicrobiales*, *Methanopyrales*, *Methanocellales*, *Methanococcales*, *Methanobacteriales*, and *Methanomassiliicoccales*. The order *Methanosarcinales* is metabolically the most versatile, being able to utilize all substrates except formate (Kendall & Boone, 2006). The rest are restricted either to the reduction of CO₂ or single-carbon, methylated compounds using H₂ as the electron donor (Dridi et al., 2012; Fricke et al., 2006; Lang et al., 2015). Different modes of energy conservation by methanogens have been reviewed elsewhere (e.g., Ferry, 1999; Thauer et al., 2008; Welte & Deppenmeier, 2014).

Recently, a novel methanogenic metabolism has been proposed for thermophilic members of *Methermicoccus* genus (order *Methanosarcinales*), in which methoxylated aromatic compounds can be converted into CH₄ directly (Mayumi et al., 2016). This discovery could finally explain the origin of coal-bed methane as these compounds are natural constituents of coal and lignin material (Mayumi et al., 2016). Further, the concept of methanogens being from a single phylum has been challenged by the discovery of evidence for methanogenic pathways in archaea outside the euryarchaeal phylum (Evans

et al., 2015; Lang et al., 2015; Vanwonterghem et al., 2016). These novel, potentially methanogenic phyla, *Verstraetearchaeota* and *Bathyarchaeota* seem to be abundant in nature, and their contribution to CH₄ cycling in various ecosystems is unknown. These methanogens likely employ H₂-dependent metabolism of single-carbon methylated compounds such as methylsulfides, methanol, and methylamines, similar to the *Methanomassiliococcales* order mentioned above (Evans et al., 2015; Lang et al., 2015; Vanwonterghem et al., 2016). This substrate specialization may allow methanogens to coexist with sulfate-reducing bacteria (SRB), since SRB do not utilize single-carbon methylated compounds (Oremland & Polcin, 1982). In fact, the methanogens *Methanomassiliococcales* and *Bathyarchaeota* have been detected in sulfate methane transition zones around the globe (SMTZs—ecosystems where CH₄-dependent sulfate reduction is the predominant metabolic process) (Ruff et al., 2015). This suggests that CH₄ cycling in those ecosystems involves complex interactions between microbial production and consumption of CH₄.

2.2. Methane Consumption

2.2.1. Aerobic Oxidation of Methane

The production of CH₄ does not necessarily mean that it will ever reach the atmosphere where it can act as a GHG because CH₄ is subject to oxidation in many environments. In the natural environment, CH₄ produced in deeper anoxic layers diffuses through the sediment column toward the upper more oxidized zone (Figure 1). Here aerobic methane oxidizing bacteria (MOB) oxidize CH₄ to CO₂. The highly specialized mechanism of CH₄ oxidation is initiated by methane monooxygenase (Mmo), an enzyme which utilizes oxygen for the initial activation of CH₄ to methanol (Hanson & Hanson, 1996). The gene encoding for Mmo (*pmoA*) is commonly used as a biomarker for aerobic methanotrophy in the environment. Phylogenetically, MOB belong to three lineages: α -Proteobacteria, γ -Proteobacteria, and *Verrucomicrobia* (Hanson & Hanson, 1996; Op den Camp et al., 2009). The latter dominates only in high-temperature/low-pH conditions, such as volcanic regions (Op den Camp et al., 2009). Proteobacterial methanotrophs are ubiquitous and have been detected in a variety of habitats. Taxonomically, based on their difference in metabolism and morphology, proteobacterial methanotrophs have been divided into two groups: type I and type II. Type I methanotrophs belong to γ -Proteobacteria and are grouped in the family *Methylococcaceae*, which to date includes 18 genera (Bowman, 2011; Knief, 2015). They prevail in both terrestrial and marine CH₄-rich environments, utilizing CH₄ for both assimilation and energy generation (Hanson & Hanson, 1996). Type II methanotrophs are represented by α -Proteobacteria, including five known genera (Knief, 2015), which mostly thrive in terrestrial environments low in ambient CH₄ by utilizing even atmospheric concentrations (Bull et al., 2000; Holmes et al., 1999). They assimilate only about half of their C from CH₄, with the rest originating from CO₂ (Hanson & Hanson, 1996). Studies on the competition between members of type I and type II MOB have shown that CH₄, nitrogen, and copper availability can be crucial factors for success (Graham et al., 1993; Ho et al., 2013).

2.2.2. Anaerobic Oxidation of Methane

The thermodynamic stability of CH₄ was the reason that for decades O₂ was considered to be the only possible electron acceptor for CH₄ oxidation. The first indications for CH₄ oxidation under anaerobic conditions came from geochemical mass balance calculations that indicated the disappearance of CH₄ in anoxic marine environments where sulfate was the only available electron acceptor (Barnes & Goldberg, 1976; Panganiban et al., 1979; Reeburgh, 1976). Later, a combination of molecular and physiological studies provided strong indications for biologically driven sulfate-dependent anaerobic oxidation of methane (S-AOM). S-AOM is performed by anaerobic methanotrophic archaea (anaerobic methanotrophs—ANME) and sulfate-reducing bacteria, creating sulfate CH₄ transition zones in marine and brackish sediments (Knittel & Boetius, 2009). ANME are related to methanogens and employ a similar metabolism that operates in reverse, with reducing equivalents (molecules or electrons, directly) produced from the oxidation of CH₄ shuttled to sulfate-reducing bacteria (SRB) (Krüger et al., 2003). The type and process of this exchange has been investigated, but several theories still exist regarding either direct or indirect electron transfer between ANME/SRB partners (McGlynn et al., 2015; Milucka et al., 2012; Wegener et al., 2015).

The discovery that nitrogen oxides can also be used as electron acceptors for CH₄ oxidation (N-AOM) was made a decade ago, and until now, two groups of organisms have been identified in performing this process. N-AOM bacteria, *Methylomirabilis oxyfera*, use nitrite as the electron acceptor in an intra-aerobic pathway,

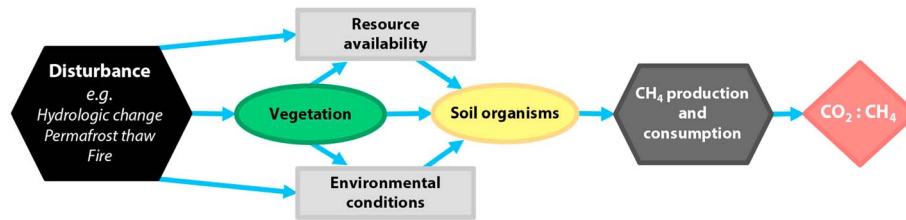


Figure 4. Schematic diagram of how environmental disturbance, forced by climate change, can alter the key processes governing the net release of CH₄ from natural CH₄ producing environments.

where nitric oxide is hypothesized to be dismutated to nitrogen and oxygen, with the latter then used by an *Mmo* (Ettwig et al., 2010, 2012). *M. oxyfera*-like bacteria thrive at oxic/anoxic interfaces where nitrogen oxides and CH₄ cooccur, as is the case in many freshwater sediments. Nevertheless, *M. oxyfera* have also been recently detected in brackish and even marine environments (Chen, Zhou, & Gu, 2014; Li-Dong et al., 2014; Padilla et al., 2016), indicating an adaptation to saline conditions and competition for CH₄ with S-AOM organisms. The other organisms shown to catalyze N-AOM are archaea related to methanogens, which utilize the methanogenic pathway in reverse (Haroon et al., 2013). This archaeon, *Methanoperedens nitroreducens*, is closely related to S-AOM performing ANME but uses nitrate as the terminal electron acceptor (Arshad et al., 2015; Haroon et al., 2013). *M. nitroreducens* have so far mostly been detected in freshwater habitats similar to those of *M. oxyfera*, where they coexist, as nitrite produced by *M. nitroreducens* can be used by *M. oxyfera* bacteria (Vaksmas et al., 2016; Welte et al., 2016).

Biogeochemical measurements and modeling also point to an iron-dependent CH₄ oxidation pathway in sediments that are rich in iron oxides and CH₄ (Crowe et al., 2011; Egger et al., 2015; Norði et al., 2013; Sivan et al., 2011). Recently, iron-reducing activity associated with CH₄ oxidation was shown under laboratory conditions for known ANME (Ettwig et al., 2016; Scheller et al., 2016). However, it still needs to be shown whether microorganisms can use this metabolism for growth.

3. Environmental Controls and Processes of Methane Emission

The microbially mediated processes of CH₄ production and consumption are controlled directly and indirectly by local environmental conditions. Environmental conditions have an effect on the pathway and rate of CH₄ production and emission, including the methanogenic population compositions present and their ability to function. Changes to environmental conditions can therefore alter local microbial communities and resultant CH₄ emissions. This was observed in warming permafrost where differences in soil substrate availability resulted in taxonomic shifts in methanogen communities, thereby affecting CH₄ emissions (Tveit et al., 2015). Similar effects have also been observed in marine environments (e.g., Yuan et al., 2014). Altered concentrations of CO₂ and CH₄, and also increasing temperature and drought, would determine the community composition and activity of methanotrophs (Horz et al., 2005; King, 1997; Knoblauch et al., 2008). These taxonomic shifts will in turn lead to community changes of metabolic partners, which could potentially cause a cascade effect through the whole microbial community and alter CH₄ dynamics. In terrestrial zones, elevated atmospheric CO₂ can increase primary production and organic C transfer to the rhizosphere (the soil zone influenced by microbial and plant root dynamics), increasing resource availability for methanogenesis (Figure 4) (Nazaries et al., 2013). Methanotrophy in these zones is thought to be less influenced by temperature and more by soil moisture, which controls oxygen availability (Nazaries et al., 2013).

3.1. Direct Methane Emission

Following its production, CH₄ can be transported vertically or laterally. The nature of the transport pathway (length, direction, and the presence of methanotrophs) determines the likelihood of CH₄ being consumed versus its eventual release to the atmosphere. CH₄ is readily transferred to the atmosphere directly via vertical transport through the soil zone (Borges et al., 2016; Olefeldt et al., 2013; Throckmorton et al., 2015). The lateral movement of CH₄ transports dissolved CH₄ via anoxic water bodies that are discharged into open waters where CH₄ can be emitted to the atmosphere (Abril & Borges, 2005; Dean et al., 2017; Street et al., 2016). This can only occur via diffusion and dissolution in moving water (except where confining sediment layers

redirect trapped CH₄ bubbles), whereas vertical transport can also occur as gas bubbles (ebullition). CH₄ can accumulate in concentrated gas pockets in waterlogged sediment, generally where gas diffusion is prevented by a confining layer, raising pore pressure until the bubbles are expelled (Baird et al., 2004; Glaser, 2004; Kellner et al., 2004; Tokida et al., 2007). Ebullition events can be triggered by either natural or artificial disturbance. Atmospheric pressure fluctuations play an important role in determining the timing and quantity of these emissions (Shakhova et al., 2014; Tokida et al., 2007), while tidal pressure acts as an important control on bubble release in shallow estuarine and marine environments (Chanton et al., 1989). Sea level rise and increased frequency of storm events associated with climate warming can affect the physical processes governing CH₄ release and therefore the magnitude of these emissions. In lakes, reservoirs and ponds, emissions of dissolved CH₄ can also be driven by hydrodynamic transport, whereby temperature gradients (primarily at nighttime) drive thermal convection causing relatively rapid upwelling of CH₄ from deeper water layers by both diffusion and advection (Poindexter et al., 2016). This process varies on a seasonal basis and could potentially be important on a global scale (Walter Anthony & MacIntyre, 2016).

3.2. Vegetation

The amount of CH₄ produced in a system depends on substrate availability. Vegetation can increase the availability of organic substrates for methanogenic communities by the exudation of acids and carbohydrates from root systems, the routing of oxygen into the soil zone, and by providing the accumulation of organic matter in the first place (Joabsson & Christensen, 2001) (Figure 1). Both the degree of soil water saturation and vegetation affect the activity of methanogens (Bubier et al., 1995; Dias et al., 2010), while soil moisture is an important determinant of vegetation composition (Figure 4) (Engelbrecht et al., 2007). In peatlands, there is also a symbiotic relationship between some vegetation species and methanotrophs (see section 4).

Soil saturation is often positively related with CH₄ emission because it reduces the aerobic zone where methanotrophic bacteria are active (e.g., Bubier, 1995; Goodrich et al., 2015; Hirano et al., 2009). Vascular plants themselves provide a direct pathway of vertical CH₄ release via aerenchyma (cortical oxygen-transporting gas spaces), which are common in plant species adapted to wetland conditions (Armstrong et al., 1991). This conductive plant tissue, for example, in sedges (*Carex* spp.), allows CH₄ produced in deep, anoxic layers to be transported directly to the surface without exposure to oxidizing layers (Chanton et al., 1989; Joabsson et al., 1999; Whiting & Chanton, 1993). This mechanism can also work in reverse, releasing oxygen from the roots into the rhizosphere, inhibiting CH₄ production by methanogenic archaea (Frenzel, 2000), as oxygen release stimulates CH₄ oxidation. Oxygen availability also alters the redox zonation around the roots (Van Der Nat & Middelburg, 1998). In water logged and aquatic systems, macrophytes can transport gases via passive (diffusive) or active (convective) systems. Passive transport is common over short flow paths, where plants utilize pressure gradients to transport gases through conductive tissue, but this mechanism is less effective over longer flow paths (Chanton, 2005). Recent measurements suggest that transport of CH₄ via tree stems also provides an important pathway for CH₄ emissions in forested tropical and temperate wetlands (Pangala et al., 2013, 2017, 2015).

CH₄ transport to the atmosphere via plant aerenchyma, bypassing the soil aerobic zone, is responsible for 55 to 85% of CH₄ emissions from peatlands, one of the most important ecosystem types with regards to global CH₄ emissions (Waddington et al., 1996). Vegetation composition, which is influenced by different environmental factors, is commonly used to model CH₄ emissions (Bubier, 1995; Bubier et al., 1995; Dias et al., 2010; Hendriks et al., 2007; Schrier-Uijl et al., 2010; van den Pol-van Dasselaar & Oenema, 1999; Whiting & Chanton, 1993). Soil saturation, or water table height, is also a good predictor of CH₄ emission, showing the same predictive power as species composition. However, water level shows high variability through time (Bubier, 1995; van den Pol-van Dasselaar & Oenema, 1999); therefore, subdaily measurements of water table levels are often required for accurate estimates of CH₄ emissions. In contrast, plant species composition is much more stable in time because it reflects integrated environmental factors over a longer period. Sampling only once a year can provide a good estimate of plant community composition.

3.3. Fire

Fire is a major terrestrial disturbance mechanism that can cause rapid alteration of local and regional vegetation and soil conditions (van der Werf et al., 2010). Under warmer climates, the frequency and intensity of burning is predicted to increase (e.g., Veraverbeke et al., 2017), impacting terrestrial C stores and indirectly

affecting landscape CH₄ fluxes. Fires can be a direct source of CH₄ emissions, although natural fires, in general, tend to have relatively high CO₂ and low CH₄ emissions (Akagi et al., 2014). The CH₄:CO₂ ratio can be slightly different depending on severity and fuel types and differs among ecosystems (Kasischke & Bruhwiler, 2002; van der Werf et al., 2010). For example, the CH₄:CO₂ emission ratio is higher in peatland fires (~0.01) compared to boreal forests (~0.004) and savannah/grassland (~0.001) (Kasischke & Bruhwiler, 2002; van der Werf et al., 2010). Peatland burning emitted on average 3.1 Tg CH₄ yr⁻¹ between 1990 and 2010, whereas savannas, grassland, and shrubland burning together emitted 5.6 Tg CH₄ yr⁻¹ (van der Werf et al., 2010). Although peatland fires release less CH₄ in total, per unit area they release significantly more CH₄ compared to savannas, approximately 3,700 and 80 g km⁻², respectively. Globally, fire is responsible for ~16 Tg of CH₄ emissions per year, with occasional peaks of up to 20 Tg CH₄ yr⁻¹ (Giglio et al., 2013; van der Werf et al., 2017). Isotopically ($\delta^{13}\text{C}$), the CH₄ produced during fires (pyrogenic CH₄) has an exceptionally high ¹³C content, being greater than 10‰ more enriched than CH₄ from other sources (Schwietzke et al., 2016). Therefore, even small changes in the contribution of pyrogenic sources to contemporary CH₄ emissions can affect the atmospheric $\delta^{13}\text{C}_{\text{CH}_4}$ value, providing an important constraint on pyrogenic CH₄ contributions to the recent CH₄ budget (Worden et al., 2017). $\delta^{13}\text{C}$ variations in CH₄ extracted from air trapped in polar ice cores have been explained by additions of pyrogenic CH₄ to the past atmosphere from both natural and early anthropogenic sources (Ferretti et al., 2005; Sapart et al., 2012).

Burning most severely affects the upper soil layers where soil organisms are abundant, increasing temperatures both during and after fire because burned soil is darker and therefore absorbs more solar radiation (Benscoter et al., 2011; Stoof et al., 2011) (Figure 4). The microbes that recolonize the soil are responsible for CH₄ fluxes following fires, but they are dependent on the remaining vegetation and resources such as soil organic matter that can be consumed during burning (Figure 4).

Sudden and gradual shifts in environmental conditions affect postfire CH₄ fluxes. For example, the destruction of aboveground cover and ash deposition cause soil temperatures to more rapidly increase during the day and decrease during the night, speeding up biological processes, stimulating decomposition and CH₄ release (Bissett & Parkinson, 1980; Hart et al., 2005); a similar effect occurs during the transition between seasons (Fisher et al., 2000). Ash deposition after fire was also found to increase methanogenesis, most likely due to its high nutrient release (Williams & Crawford, 1984). However, under dry conditions, consumption of CH₄ by methanotrophs results in the landscape becoming a CH₄ sink (Jauhiainen et al., 2008).

4. Wetlands

4.1. Wetlands as Organic Carbon Stores

A wetland is an area of land covered or saturated with fresh, brackish, or salt water permanently or temporarily (such as the Okavango Delta in Botswana), including marine areas where the water depth during low tide does not exceed 6 m (Navid, 1989). Wetlands can be natural (e.g., bogs and mangroves) or artificial (e.g., rice paddies) and are found across all climate zones (Ramsar, 2007). Wetlands provide a vital range of ecosystem services (Mitraet al., 2005; Mitsch & Gosselink, 2007) and play an important role in (terrestrial) C storage (Petrescu et al., 2015). Occupying only 4–6% of the Earth's land area (around 596–894 million ha), they sequester and retain C through permanent burial (Mitsch & Gosselink, 2007), storing between 400 and 500 Pg of C (Joosten & Couwenberg, 2008; Pageet al., 2011; Roulet, 2000)—approximately 20% of the global soil C pool (Lal, 2008).

Wetlands primarily sequester C through photosynthesis, storing C in plant biomass, and through the accumulation of organic matter in soils (peat) and also through the deposition of C-rich sediments in estuarine and mangrove environments. This C store is maintained by water logging, which limits the diffusion of oxygen into sediments. What little oxygen is present is rapidly used up by aerobic processes, creating anoxic conditions that slow down decomposition and facilitate the production of CH₄. As a result, wetlands are the largest single source of CH₄ emissions (Saunois, Bousquet, et al., 2016), contributing 150–225 Tg CH₄ yr⁻¹ (about one third of total global CH₄ emissions; Figure 3) (Bridgham et al., 2013; Kirschke et al., 2013; Saunois, Bousquet, et al., 2016). Of the total wetland CH₄ emissions, tropical wetlands account for 50–60%, northern (Boreal and Arctic) wetlands ~34%, and temperate wetlands ~5% (Bloom et al., 2010; Wanget al., 1996). In this section, we focus on terrestrial wetlands; mangrove and estuarine wetlands are considered in section 5.

4.2. Mechanisms of Methane Emission

CH₄ emissions from wetlands are difficult to predict (Bridgman et al., 2013; Ringeval et al., 2014), as they can vary by several orders of magnitude within and between sites depending on local and temporal (diurnal to seasonal) conditions, such as hydrology, vegetation, and climate (Turetsky et al., 2014). Both CH₄ production and consumption by microorganisms are controlled by (i) the water table, which determines the oxic and anoxic zones in the soil; (ii) the temperature of the soil, which affects the rates of microbiological processes; and (iii) substrate availability for microbial methanotrophy or methanogenesis (see sections 2 and 3 and Figure 4) (Walter & Heimann, 2000). Following production, one of the key mechanisms of CH₄ release from wetlands is plant-mediated transport, although ebullition can also be important. Diffusive fluxes (including hydrodynamic transport—see section 3.1) are generally considered less important (Poindexter et al., 2016) but can be significant in systems with large areas of open water (Billett & Moore, 2008). Here we consider only the role of small water bodies (ponds) in wetlands; larger bodies such as lakes are considered in section 5.

While the dominance of vascular plants has a significant positive relationship with CH₄ fluxes, substantial variation has been found between CH₄ emissions from various vegetation types likely due to methanotrophs associated with wetland plant species reducing net CH₄ fluxes. Methanotrophs in *Sphagnum* root systems can reduce diffusive CH₄ transport by up to 98% (Raghoebarsing et al., 2005; van Winden et al., 2012). The interplay of environmental conditions complicates the picture further. In *Carex*-dominated peatlands, lower CH₄ emissions were found compared to *Sphagnum*-dominated peatlands (Nilsson & Bohlin, 1993). This could be due to generally higher water tables in *Sphagnum* peatlands and also the lower availability of cellulose and hemicellulose in *Carex* peatlands (Bohlin et al., 1989; Nilsson & Bohlin, 1993). Methane transport via tree stems has recently been reported to be important in both tropical and temperate forested wetlands (Pangala et al., 2013, 2015). This pathway is responsible for up to 27% of the total seasonal ecosystem flux in temperate forested wetlands (Pangala et al., 2015) and is responsible for ~40% of total CH₄ emissions from wetlands in the Amazon (Pangala et al., 2017).

4.3. Regional Wetland Characteristics

Tropical wetlands dominate CH₄ emissions, but in comparison to northern wetlands, their biogeochemistry is poorly understood (Mitsch et al., 2010). While defined as being located between 23.45° north and south, the spatial extent of tropical wetlands is largely uncertain (Riley et al., 2011), and they are still being discovered (Dargie et al., 2017). Observational data suggest that these areas range between 2.8 and 6.0 × 10⁶ km², while models predict an area of 1.3 to 13.2 × 10⁶ km². This is primarily due to a lack of observational data (Melton et al., 2013), but uncertainties in distributions are even larger (Gumbricht et al., 2017; Sjögersten et al., 2014). Consequently, estimated CH₄ fluxes from tropical wetlands vary widely, from 85 ± 7 to 184 ± 11 Tg CH₄ yr⁻¹ (Melton et al., 2013).

Swamps (forested wetlands) and freshwater marshes (herbaceous and frequently inundated areas) are thought to be the most abundant wetland types in the tropics (Lehner & Döll, 2004; Mitsch & Gosselink, 2007). Both have common characteristics, such as high mean annual temperature with little seasonal variation and high precipitation, with the main input of organic matter coming from tropical rainforest vegetation. Soil types are highly variable in the tropics, but most are characterized by enhanced leaching, acidic conditions, and low nutrient availability (Moreira et al., 2011). Rice paddies are estimated to account for more than a quarter of tropical CH₄ emissions (Bloom et al., 2010). Increasing emissions from rice paddies and the expansion of tropical wetland areas are thought to have been important drivers of the recent rise in global atmospheric CH₄ (Figure 2) (Nisbet et al., 2016).

Northern and temperate wetlands are widely distributed in cold and temperate climates between 40° and 70°N and have an estimated annual CH₄ flux of 19 ± 7 g CH₄ m⁻² yr⁻¹ (Mitsch et al., 2013), roughly a quarter of the emissions from tropical wetlands. Northern and temperate wetland processes are also relevant to Southern Hemisphere temperate wetlands (e.g., Goodrich et al., 2015), which are less studied.

Peatlands are important wetlands in these areas, as well as in the tropics (Page et al., 2011; Evans et al., 2014). Peat soils are formed from partially decomposed plant material that has accumulated under anaerobic water-saturated conditions (Rydin & Jeglum, 2013). Peatlands can be divided into two main types: ombrotrophic (bogs) and minerotrophic (fen) peatlands. Bogs primarily receive water and nutrients from atmospheric deposition and precipitation and as a result tend to be nutrient poor. Fens also receive nutrients from the

surrounding aquifer and its catchment area, including anthropogenic inputs, so their nutrient status can range from oligotrophic to mesotrophic/eutrophic conditions (Abdalla et al., 2016; Clymo, 1983). CH₄ emissions from fens are slightly higher than those from bogs likely due to the greater presence of aerenchymatous plant roots (Corbett et al., 2015). Optimal water table heights for CH₄ production are generally below the peat surface in bogs, above the peat surface in nutrient-rich fens, and close to the peat surface in nutrient-poor fens (Abdalla et al., 2016; Turetsky et al., 2014).

Water table heights have historically been altered as humans seek to make use of otherwise waterlogged areas, usually by digging drainage ditches and extracting water. Wetland drainage causes oxygen intrusion into deeper soil layers, and the subsequent aerobic decomposition of organic matter and land subsidence leads to significant CO₂ emissions (Joosten, 2010; Leifeld et al., 2011; van der Akker et al., 2008), while CH₄ emissions generally decline (Moore & Dalva, 1993; Pelletier et al., 2007). Drained and degraded peatlands are net C sources (with reported net ecosystem exchange rates ranging from 80 to 880 g C m⁻² yr⁻¹) (Lamers et al., 2015), and the net flux of GHGs to the atmosphere directly impacts climate warming. As a mitigation action, many wetlands are being restored by rewetting (raising the water table back to previous levels prior to drainage) (Abdalla et al., 2016). Rewetting may lead to excessive CH₄ emission initially, when vegetation is flooded and dies off becoming available for methanogenesis (Augustin & Chojnicki, 2008). The evolution of CH₄ emission patterns following rewetting can vary depending on the previous land use (Abdalla et al., 2016), but rewetting is generally considered to reduce net GHG emissions in the long run (Joosten, 2015; Strack & Zuback, 2013). This may not remain the case if rising global temperatures drive CH₄ emissions higher.

4.4. Sensitivity and Drivers of Wetland Methane Climate Feedbacks

Global climate change is likely to have significant impacts on wetlands due to their susceptibility to temperature fluctuations, hydrology, and nutrient availability, which are expected to respond to rising atmospheric CO₂ concentrations (Erwin, 2009). Fires can also be important in wetland systems due to the high amounts of C stored in their soils, particularly in the tropics where fire frequencies are generally higher than in temperate and polar regions (see section 3.3) (van der Werf et al., 2010). For example, in a subtropical wetland marsh CH₄ emissions immediately following a fire increased by up to 50% (Levine et al., 1990).

Temperature is known to enhance archaeal CH₄ production and bacterial CH₄ oxidation (Frenzel & Karofeld, 2000; Kip et al., 2010; van Winden et al., 2012). In a global meta-analysis of CH₄ emissions and environmental parameters Yvon-Durocher et al. (2014) showed that CH₄ emissions are likely to increase relative to CO₂ emissions from wetlands under predicted global warming. Their analyses indicate that soil temperature increases between 0 to 30°C could correspond to a 57-fold increase in CH₄ emissions, depending on temperature optima of different microbes and their associated enzymes (Schipper et al., 2014). Although generalized across multiple ecosystems, and representing an unrealistic sustained temperature rise, this mirrors findings in permafrost settings (see section 6) (Conrad, 2002; Whalen, 2005). It is currently thought that CH₄ oxidation in wetlands can keep pace with increased CH₄ production as temperatures increase (Kip et al., 2010); however, CH₄ oxidation rates in soils are theoretically less temperature dependent than CH₄ production (Schipper et al., 2014). Anaerobic oxidation of CH₄ is also possible in freshwater wetlands and may be responsible for reducing the CH₄ emitted to the atmosphere by up to 50% (Segarra et al., 2015).

The influence of temperature on CH₄ emissions, however, is also strongly dependent on hydrologic conditions (Olefeldt et al., 2017). Mean precipitation in already dry midlatitude and subtropical regions is predicted to decline under warming scenarios, whereas in the wet midlatitudes and northern wetland regions it is predicted to increase (Collins et al., 2013). Extended droughts will lower water tables in wetlands and decrease CH₄ emissions but increase CO₂ emissions (Mitsch et al., 2010). Increased precipitation will raise water tables and even expand wetland areas thereby promoting C sequestration and also CH₄ emission. The balance between these two processes is critical in determining whether changes in wetlands are contributing to a positive or negative climate feedback. A rise in precipitation can also increase the rate of organic substrate leaching to deeper parts of the peat profile, leading to increased methanogenesis. CH₄ production rates at depth can be 2–4 times higher than in the top 1 m of peat, and this effect has been observed on decadal timescales (Glaser et al., 2016). Increased methanogenesis will put greater pressure on the oxidative capacity along the export pathway of this CH₄ whether vertically or laterally when dissolved in groundwater.

Wetlands are expected to become major net sources of C under warming climate conditions within decades (Kayranli et al., 2010). This may be balanced by increased plant production in response to higher atmospheric CO₂. When plant production and the accumulation of organic matter in peat soils occur at a higher rate than CO₂ and CH₄ emissions, the net climate feedback will become negative (Davidson & Janssens, 2006). The overall impact of climate change on wetland C storage and CH₄ emissions, however, remains uncertain as the response mechanisms are highly complex and vary from site to site. For example, plant-mediated transport will depend on changes in vegetation cover and constitutes a poorly understood feedback. Given that wetlands are the largest natural CH₄ source, understanding CH₄ dynamics in these systems is critical to the future of the global CH₄ budget. Protection, restoration, and sustainable management of wetlands can provide potential climate change mitigation benefits, but a better understanding of the mechanisms and magnitude of CH₄ emissions under shifting climate patterns is needed to determine the best management strategies.

5. Marine and Freshwater Systems

5.1. Aquatic Methane Dynamics

At present, freshwater systems (lakes, rivers, streams, and ponds) are estimated to be major sources of CH₄ to the atmosphere at the global scale with a combined flux of ~40 Tg CH₄ yr⁻¹, but with a large uncertainty range (8–73 Tg CH₄ yr⁻¹) (Kirschke et al., 2013); a more recent bottom-up inventory suggests that freshwater emission could be as high as 122 (80–160) Tg CH₄ yr⁻¹ (Saunois, Bousquet, et al., 2016). This uncertainty is largely due to recent freshwater studies that include (or exclude) ebullition, which have upscaling issues because of high temporal and spatial heterogeneity in flux densities, and uncertainty in inland water surface areas (Cole et al., 2007; Holgerson & Raymond, 2016). For instance, very small ponds contribute disproportionately to CH₄ emissions but are often excluded in global estimates, and their surface areas are poorly constrained (Downing et al., 2006; Holgerson & Raymond, 2016). A complicating factor is that very small ponds are sometimes included in the definition of wetlands with the risk that their associated CH₄ emissions are inappropriately attributed or accounted for twice in global emission assessments (Thornton, Wik, & Crill, 2016). Reservoirs created by dams in rivers are a special case of man-made freshwater systems that are often eutrophic and that contribute CH₄ to the atmosphere at an estimated rate of ~13 Tg CH₄ yr⁻¹ (Deemer et al., 2016).

Estuaries release ~7 Tg CH₄ yr⁻¹ to the atmosphere (Borges & Abril, 2011). CH₄ release from continental shelves and the open ocean is not well constrained, with estimates ranging from 1 to 20 Tg CH₄ yr⁻¹ (Borges et al., 2016). CH₄ emissions from mangrove forests, although extremely C rich and under threat from climate change and anthropogenic disturbance, are also poorly constrained (Donato et al., 2011; Valiela et al., 2001). C stocks in mangrove sediments could, in fact, increase in response to predicted precipitation increases in the tropics (Sanders et al., 2016).

Sediments of lakes, rivers, and coastal marine systems can accumulate large amounts of organic C-rich debris (Cole et al., 2007; Regnier et al., 2013). Degradation of this organic matter in the sediment in the presence of various electron acceptors typically leads to the development of a geochemical zonation. There are especially clear distinctions between oxic surface sediments, underlying sulfidic sediment layers where sulfide from SO₄²⁻ reduction accumulates (see section 2.1), and the methanic zone where CH₄ that formed through methanogenesis is present (Canfield & Thamdrup, 2009). This zonation is thought to be kinetically or energetically controlled through the differing abilities of the functional groups of microbes to compete for common substrates. The overall rate of anaerobic organic matter degradation is determined by the amount and quality (i.e., composition and age) of the organic matter (Arndt et al., 2013).

In general, rates of methanogenesis in freshwater sediments are higher than in marine sediments. This is mostly the result of a lower availability of SO₄²⁻ in freshwater sediments, which allows a larger proportion of the more easily degradable organic C to be converted to CH₄ (Borges & Abril, 2011; Capone & Kiene, 1988). The major pathways of methanogenesis in both types of environments differ: while hydrogenotrophic methanogenesis (from H₂/CO₂ and formate) is dominant in marine sediments, acetate fermentation is generally quantitatively more important in freshwater sediments (Whiticar et al., 1986). CH₄ may also be produced in oxic oligotrophic surface waters of the ocean (Reeburgh, 2007). This has been attributed to methylophilic methanogenesis using metabolites from phytoplankton or dissolved organic carbon as a C source

(Damm et al., 2010; Repeta et al., 2016); recent radiocarbon measurements have shown that dissolved CH₄ in the surface waters of the Beaufort Sea is modern, indicating that these processes are an important component of marine CH₄ emissions (Sparrow et al., 2018). Finally, upward seepage of CH₄ of microbial, thermogenic, or geothermal origin from the deep subsurface through the seafloor is a common feature in many oceanographic settings, especially on continental margins (Etiopie et al., 2008; Judd, 2003). This deep “geological” CH₄ flux is not sensitive to climate change (unless it is associated with permafrost thaw, see section 6.3, or methane hydrate dissociation, see section 7) but forms a relatively unknown background CH₄ flux against which it is difficult to measure changes in marine fluxes due to climate warming.

Most of the CH₄ produced in aquatic sediments (or formed in the deep subsurface) that is transported upward to the sediment surface through diffusion or seepage is oxidized to CO₂ by various methanotrophic pathways, allowing only a small proportion of the CH₄ to escape to the atmosphere (see section 2.2 and Figure 1) (Conrad, 2009; Reeburgh, 2007). In marine sediments, the anaerobic oxidation of CH₄ with SO₄²⁻ (S-AOM; see section 2.2.2) is particularly efficient and is thought to account for more than 90% of CH₄ removal (Knittel & Boetius, 2009; Reeburgh, 2007). In freshwater sediments, aerobic oxidation of CH₄ near the sediment-water interface and in the water column is typically the dominant removal process for CH₄, with a lesser role for SO₄²⁻ because of its lower availability (Borges & Abril, 2011). While AOM coupled to iron or manganese may significantly impact other biogeochemical cycles in aquatic sediments (e.g., phosphorus) (Rooze et al., 2016), rates of oxidation are estimated to be low and not major contributors to CH₄ removal (Egger et al., 2015; Sivan et al., 2011).

In some settings, dissolved CH₄ is present in sediments with abundant pore water SO₄²⁻, pointing toward inefficient oxidation of CH₄ with SO₄²⁻ (Egger et al., 2016; Iversen & Jørgensen, 1985; Jørgensen et al., 2001; Knab et al., 2009; Piker et al., 1998; Thang et al., 2013; Treude et al., 2005). The reasons for this slow microbial turnover of pore water CH₄ remain largely unknown. One suggestion may be that the CH₄ flux is so high that it overwhelms the microbial oxidation capacity (Boetius & Wenzhöfer, 2013; Orcutt et al., 2005). However, there are indications that in rapidly accumulating sediments the slow growth of CH₄ oxidizing communities prohibits the development of an efficient AOM barrier (Dale et al., 2008; Egger et al., 2016; Nauhaus et al., 2007; Thang et al., 2013). Rapid rates of sediment accumulation are common in coastal environments subjected to eutrophication and other human activities (e.g., dredging, sediment dumping, and increased river inputs of organic rich material) (Borges & Abril, 2011). The lack of an efficient oxidative barrier for CH₄ may contribute to increased CH₄ fluxes from such systems to the water column and the atmosphere. But given their relatively small area, these systems are likely not important sources of CH₄ at the global scale.

5.2. Mechanisms of Methane Emission

Differences in transport regimes for fluids, solutes, and gases play a critical role in controlling the efficiency of CH₄ removal in lakes, rivers, estuaries, and the ocean (see section 3.1) (e.g., Borges & Abril, 2011; Reeburgh, 2007). In all these environments, especially shallow waters, the total gas pressure can exceed the ambient hydrostatic pressure, resulting in the formation of CH₄ bubbles in the sediment (Maeck et al., 2013). Transport through ebullition is faster than through diffusion, although ebullition can also be highly episodic (Scandella et al., 2016), allowing CH₄ to bypass the geochemical barrier of oxygen and SO₄²⁻ (Figure 1) (DelSontro et al., 2010). In the intertidal zone in estuaries and in mangroves, CH₄ may also be transferred directly from sediments to the atmosphere (Borges & Abril, 2011). At low tide, this can take place through diffusion or ebullition (Martens & Val Klump, 1980) where, when tidal flats are vegetated, plants may act as both active and passive conduits of the CH₄ (Foster-Martinez & Variano, 2016; Van der Nat & Middelburg, 2000). Lateral tidal pumping, the flushing of CH₄ from intertidal sediments to the water by advective flow and subsequent diffusive transfer of the CH₄ to the atmosphere, contributes strongly to the high temporal and spatial variability in the CH₄ flux from estuarine waters to the atmosphere. Even at the same salinity, these fluxes range over several orders of magnitude (Borges & Abril, 2011; Middelburg et al., 2002). In general, more CH₄ escapes from aquatic systems to the atmosphere with decreasing salinity due to the combined effect of more CH₄ production near the sediment surface and less effective removal through oxidation due to lower SO₄²⁻ concentrations (Borges & Abril, 2011; Middelburg et al., 1996). In rivers and streams, CH₄ transfer to the atmosphere is driven primarily by water velocity, which is related to turbulence. This has been identified as a potentially significant outlet for terrestrially derived CH₄ on a global scale at 26.7 Tg CH₄ yr⁻¹ (Stanley et al., 2016).

5.3. Sensitivity of Marine and Freshwater Systems to Climate Change

Increased temperatures due to ongoing climate change are expected to increase CH₄ bubble formation in both marine and freshwaters because of a decrease in CH₄ solubility (Wever et al., 1998). As a consequence, more CH₄ could bypass the zones of aerobic and anaerobic oxidation, thereby enhancing the release of CH₄ to the atmosphere (Knittel & Boetius, 2009; Thornton et al., 2015). However, in marine settings, it is also possible for the oxidation potential of the sediment and water columns to match increased CH₄ release, such as that which occurred during the BP Deepwater Horizon CH₄ blowout in 2010 when there was a large CH₄ release from the seafloor (Kessler et al., 2011), but no subsequent emissions at the ocean surface were observed (Yvon-Lewis et al., 2011).

At least 50% of all lakes are located in boreal regions and northward, and climate change is currently leading to increased permafrost thaw (see section 6), warming of lake waters, and longer ice-free seasons, which together act toward enhancing CH₄ fluxes to the atmosphere. Longer ice-free periods could increase CH₄ emissions from northern freshwater systems by up to 50% by 2100 (Wik et al., 2016). Recent findings showed that spring ice out in these systems is associated with major CH₄ release from ice bubble storage and ebullition (Denfeld et al., 2016; Sepulveda-Jauregui et al., 2015). This highlights the need for measurements of fluxes in the shoulder (refreezing and thaw) seasons (Zona et al., 2016).

Declines in sea ice extent may also increase ocean surface CH₄ emissions in the Arctic (Kort et al., 2012; Parmentier et al., 2013). This may in part be due to increased CH₄ production in these ocean surface waters, as decreased sea ice cover can increase nutrient availability for methanogenesis (Damm et al., 2010). Shrinking ice cover has further been linked to increased terrestrial Arctic CH₄ emissions, as open ocean has a higher albedo than ice and may therefore cause higher temperatures in the region, which could enhance CH₄ production and subsequent emissions from tundra regions (Parmentier et al., 2013, 2015).

Thawing of subsea permafrost on the East Siberian Arctic Shelf (ESAS) has also been suggested to enhance CH₄ release to the atmosphere (Sapart et al., 2016; Shakhova et al., 2014; Shakhova, Semiletov, Leifer, et al., 2010). However, this conflicts with findings that subsea permafrost cores can contain insufficient CH₄ to fuel the fluxes reported (Overduin et al., 2015; Shakhova, Semiletov, Salyuk, et al., 2010; Thornton, Geibel, et al., 2016). It is also unlikely that CH₄ emissions from the ESAS are from shallow gas hydrates (see section 7) (Ruppel & Kessler, 2017), but geological sources (Shakhova, Semiletov, Leifer, et al., 2010), or the decay of old organic matter (Sapart et al., 2016) could play a role. The fate of CH₄ in the ESAS water column is still debated, although high rates of oxidation are to be expected preventing significant amounts of CH₄ released from the shelf from reaching the atmosphere (James et al., 2016; McGinnis et al., 2006; Ruppel & Kessler, 2017; Shakhova et al., 2014).

Mean global sea levels under the RCP8.5 emissions scenario could rise by up to 1.4 m by 2100, relative to pre-2000 mean sea levels (Carson et al., 2016). Increased coastal erosion by sea level rise, decreasing sea ice cover and permafrost thaw under global warming (see section 6), will increase the supply of potential substrate for methanogenesis in coastal sediments. Coastal erosion currently supplies ~15 Pg of previously stored “old” permafrost C to Siberian coastal sediments, which can be buried or fuel methanogenesis in the coastal shelf (Vonk et al., 2012). Sea level rise may also lead to submergence of current C-rich coastlines and thereby an expansion of the area in the coastal zone with sediments capable of high CH₄ production. Among present-day coastal environments, regions corresponding to drowned coastlines (i.e., drowned forests and peatlands) are often characterized by gas-rich sediments (Borges et al., 2016; Dale et al., 2008; Judd, 2003). The inflow of saline waters into current freshwater systems, however, will also increase the availability of SO₄²⁻ for AOM. It is yet to be shown whether the increase in methanotrophy will compensate for the CH₄ production from newly submerged C-rich coastal areas.

CH₄ fluxes from well-mixed estuaries and continental margins are highly sensitive to climate warming. For example, water column mixing may enhance downward transport of heat to the sediment and upward transport of CH₄ from the sediment to the surface waters, as demonstrated recently for the coastal zone of the North Sea (Borges et al., 2016). Given the seasonality in temperature in many coastal areas in temperate zones, the release of CH₄ to the atmosphere in such regions is expected to be highest in summer (e.g., Borges et al., 2016; Martens & Val Klump, 1980). Stratified coastal systems, in contrast, are unlikely to act as a major source of CH₄ to the atmosphere because most of the CH₄ is expected to be oxidized before it

reaches the surface waters (Borges & Abril, 2011). In particular, fjords (flooded valleys with steep slopes, formed by glacial activity) and fjärds (shallow flooded glacial depressions/valleys with gentle slopes), which are mostly located at relatively high latitudes and account for ~40% of the surface area in estuarine environments at the global scale (Laruelle et al., 2010), are generally stratified and likely not important as a source of CH₄ (Borges & Abril, 2011). On continental margins, slow exchange between surface and bottom waters is also mostly observed at relatively high latitudes (Reed & Harrison, 2016) but is not limited to specific types of shelves (Laruelle et al., 2010). Other systems may act as large CO₂ sinks, significantly offsetting the radiative forcing of the CH₄ released (e.g., Pohlman et al., 2017).

Changes in vegetation composition can also affect CH₄ fluxes in coastal areas. For example, shifts in mangrove forest species composition have been shown to increase CH₄ fluxes (Mozdzer & Megonigal, 2013), while relative methanotrophy rates in streams are higher in shaded reaches, so riparian vegetation dynamics play an important role here (Shelley et al., 2017).

Higher organic matter production rates in lakes, estuaries, and the coastal zone due to eutrophication may shift the biogeochemical zonation in sediments (Middelburg & Levin, 2009), which in some cases may also be accompanied by bottom-water hypoxia or anoxia (Kemp et al., 2009). Such shifts in the zones of CH₄ production and oxidation due to increased organic matter input can occur on timescales of years (Egger et al., 2015; Rooze et al., 2016) or seasons (Crill & Martens, 1983; Gelesh et al., 2016; Martens et al., 1986) and may increase the potential for release of CH₄ from sediments to overlying water and the atmosphere (Crill & Martens, 1983; Gelesh et al., 2016). High temporal resolution observations are needed to quantify CH₄ release to the atmosphere from seasonally hypoxic systems and to identify the key controlling factors (e.g., the role of wind and storms and the breakdown of stratification) (Gelesh et al., 2016; Townsend-Small et al., 2016). Both temperature-driven increased CH₄ emissions from northern freshwater lakes and from coastal waters have the potential to provide a positive feedback on a warming climate, with the former areas being quantitatively most important (Borges et al., 2016; Wik et al., 2016).

6. Permafrost

6.1. The Permafrost Carbon Pool

Permafrost is soil, sediment, or rock material that is permanently exposed to subzero temperatures for at least two consecutive years (Tarnocai et al., 2009). It is present beneath 24% (23×10^6 km²) of the Northern Hemisphere land surface and is a significant part of boreal, Arctic, and alpine ecosystems (Camill, 2005; Zhang et al., 1999). In the Southern Hemisphere, permafrost is mostly limited to a few alpine areas and is studied more in the context of geohazards than C storage. Permafrost soils contain ~50% of global terrestrial belowground organic C stocks (equivalent to 1,330–1,580 Pg C), which is roughly twice the amount of C currently present in the atmosphere as either CO₂ or CH₄ (Hugelius et al., 2014; Schuur et al., 2015; Tarnocai et al., 2009).

Polar ecosystems are warming faster than anywhere else on the globe (Christensen et al., 2013). Global climate models predict up to an 8°C rise in mean annual temperature in polar regions by 2100, compared to a global average of 1.4–5.8°C (Allan et al., 2014; Camill, 2005). Estimates of net CH₄ emissions from permafrost ecosystems are consistently between ~4–17 Tg CH₄ yr⁻¹ (or 1–7% of total annual natural CH₄ emissions) (Kirschke et al., 2013; Walter Anthony et al., 2016; Wik et al., 2016). Although at present these emissions are low on the global scale, they are predicted to rise due to permafrost thaw, which leads to increased substrate availability for methanogens and the potential release of trapped CH₄ (Blanc-Betes et al., 2016; Leibman et al., 2014; Lupascu et al., 2012; Schuur et al., 2015; Zona et al., 2016).

Permafrost ecosystems are currently considered a net C sink, taking into account CH₄ emissions and the CO₂ sink of tundra ecosystems (Kirschke et al., 2013; Parmentier et al., 2013; Schaefer et al., 2011). As a result of rising temperatures driving permafrost thaw, it is estimated that tundra ecosystems will shift toward a net C source by the mid-2020s (Schuur et al., 2015). Estimates of permafrost loss by the end of the 21st century have ranged from 20 to 70% (Lawrence et al., 2012; Schaefer et al., 2011; Schuur & Abbott, 2011; Wisser et al., 2011), but more recent conservative estimates are closer to 5–15% (Schuur et al., 2015), stabilizing at 60% of the current permafrost extent by 2300 if emission targets limit the global climate to 2°C of warming (Chadburn et al., 2017).

The exposure of frozen organic material can occur via gradual deepening (thawing) of the active (unfrozen) layer (Hinzman et al., 2013; Romanovsky & Osterkamp, 1997) and by abrupt thaw mechanisms that destabilize the land surface. The latter often occurs through the degradation of ice-rich material such as yedoma (Walter Anthony et al., 2014), causing slumping, subsidence, and/or rapid erosion (collectively named thermokarst) (Abbott & Jones, 2015; Schuur et al., 2015). Thermokarst processes can thaw large blocks of material (ranging in size from a few square meters to square kilometers) in periods of days to years but can further alter organic matter decomposition rates by perturbing local hydrological and soil conditions (Abbott & Jones, 2015). The relative importance of thermokarst processes versus gradual permafrost thaw depends on site-specific topography and threshold conditions (Schuur et al., 2015). Current estimates indicate that thermokarst is present in 20% of the permafrost region (Olefeldt et al., 2016) but is expected to increase with rising air temperatures.

Gradual and abrupt thaw can further be initiated or exacerbated by wildfire (see section 3.3), which is predicted to be a more common feature in permafrost ecosystems under a warming climate (Flannigan et al., 2005; Kasischke & Turetsky, 2006; Mack et al., 2011). Fire can burn off the insulating top layers of moss and soil causing an increase in vertical thaw (Myers-Smith et al., 2007; Schuur et al., 2008). It can also destabilize soil layers and structures resulting in thermokarst development (Schuur et al., 2008). After several forest fires in interior Alaska, soil CH₄ emissions increased by between 7 and 142%, indicating accelerated permafrost thaw and abundant microbial resources (Kim, 2003).

6.2. Permafrost Thaw and the Production of Methane

As permafrost ecosystems thaw, temperature, soil moisture, and substrate availability will on average increase, boosting in situ microbial activity (Blanc-Betes et al., 2016; Hofmann et al., 2016; Valentine et al., 1994) as old permafrost contains degradable organic C (Drake et al., 2015; Spencer et al., 2015). Methanogens are natural inhabitants of permafrost soils, and methanogenic activity has been measured at temperatures as low as -20°C (Rivkina et al., 2000). Acetate and hydrogen are considered the most significant substrates for CH₄ production in permafrost soils (see section 2) (Metje & Frenzel, 2007). Permafrost thaw is known to increase the relative diversity, abundance, and activity of methanogens within days to months (Allan et al., 2014; Mackelprang et al., 2011; Rooney-Varga et al., 2007). Further thaw progression and warming is often associated with a shift from acetoclastic to hydrogenotrophic methanogenesis (Allan et al., 2014; Barbier et al., 2012; Kotsyurbenko, 2005; Kotsyurbenko et al., 2007; Metje & Frenzel, 2007). This change could be due to changes in pH (Kotsyurbenko et al., 2007) or that hydrogenotrophic methanogens are often both cold and warm tolerant, whereas acetoclastic methanogens are more temperature restricted (Allan et al., 2014; Rooney-Varga et al., 2007). Methanogenesis rates in permafrost soils are stimulated by warming temperatures, with optimum ranges observed between 18 and 30°C (Chen et al., 2015; Metje & Frenzel, 2007; Tveit et al., 2015). Experimental temperature rises of 10°C have caused CH₄ production to increase by 2 orders of magnitude, with 30°C causing CH₄ production to increase by as much as 6 orders of magnitude (Metje & Frenzel, 2007; Rivkina et al., 2004; Tveit et al., 2015); short-term temperature rises of this magnitude above zero are possible during the Arctic growing season and could become more common as regional air temperatures increase (Parmentier et al., 2013; Schuur et al., 2015; Treat et al., 2015).

Aerobic methanotrophs can consume up to 90% of the CH₄ that is produced in permafrost soils (Popp et al., 2000). Permafrost soils are dominated by type I methanotrophs (see section 2) as these thrive at low temperatures (Khmelenina et al., 2002; Knoblauch et al., 2008; Wagner et al., 2005), while several studies found type II to dominate thawing permafrost (Barbier et al., 2012; Blaud et al., 2015; Knoblauch et al., 2008; Mackelprang et al., 2011). Further, *pmoA* (particulate methane monooxygenase; see section 2.2.1) gene copy numbers were higher in active layers than in permafrost indicating an increase in methanotroph population during thaw progression (Yergeau et al., 2010). Rising temperatures are likely to stimulate aerobic CH₄ oxidation (He et al., 2012b; Kip et al., 2010; Knoblauch et al., 2008; Metje & Frenzel, 2007). However, mesocosm experiments indicate that temperature-induced increases in CH₄ production cannot be fully compensated by methanotrophy, observing a drop of 98% to 50% oxidation efficiency from 5 to 25°C (van Winden et al., 2012), possibly due to lower CH₄ solubility at higher temperatures increasing the occurrence of ebullition over diffusion. The importance of anaerobic methanotrophs (see section 2.2) is not yet well explored at low temperatures, although this process could contribute to CH₄ consumption in permafrost soils (Kao-Kniffin et al., 2015).

While temperature is the main controlling factor for CH₄ production in permafrost soils, hydrology also plays a major role (Graham et al., 2012; Hofmann et al., 2016; Valentine et al., 1994; Wagner et al., 2007), with water table height positively correlated with CH₄ production (Blanc-Betes et al., 2016; Hofmann et al., 2016; Walter et al., 2001; Zhuang et al., 2004). The long-term in situ effect of hydrology is illustrated by an 18 year long snow accumulation study on Arctic tundra (Blanc-Betes et al., 2016), which showed that deeper snow cover caused both higher soil wetness and higher soil temperatures, resulting in a net CH₄ efflux. Climate change is expected to result in an increase in precipitation in the Arctic (Lawrence et al., 2012). This could have a positive effect on water table heights compared to temperate regions due to shallow active layers and generally mild topography in Arctic lowlands. Both the water table and the temperature therefore have an important controlling effect on CH₄ production (Wrona et al., 2016), which may be reflected in the methanogenic community abundance and activity.

6.3. Mechanisms of Methane Emission

CH₄ can be transported vertically or laterally via multiple pathways (see section 3.1). Thawed organic material can also be transported laterally via physical processes such as erosion and lateral transport by rivers (Dean et al., 2016; Drake et al., 2015; Tank et al., 2016) and subjected to microbial decomposition in the environment in which it settles (Vonk et al., 2012). Coastal permafrost zones are particularly vulnerable to erosion in response to sea level rise due to their high ground ice content (Günther et al., 2015; Vonk et al., 2012), and this has the potential to provide large amounts of organic material to shallow coastal zones (Tanski et al., 2016; Vonk et al., 2012), fueling CO₂ and CH₄ emissions (see section 5.3) (Fritz et al., 2017; Lantuit et al., 2013). Methanogenesis has been observed in unfrozen lake sediments (taliks) (Walter Anthony et al., 2014), and saturated streambeds and riparian zones (Street et al., 2016), each of which can include displaced thaw material. CH₄ concentrations in permafrost stream systems can be highly variable (e.g., Dean et al., 2016), but hot spots of CH₄ emissions have been observed in small creeks draining permafrost soils (Bussmann, 2013), and this CH₄ can then be transported to the ocean and/or emitted to the atmosphere (Stanley et al., 2016).

Little is known about microbial communities in aquatic sediments created by permafrost thaw. This is a significant knowledge gap since lake ebullition is the dominant form of CH₄ release from terrestrial permafrost zones (Bastviken et al., 2011; Kirschke et al., 2013; Wik et al., 2016). It is also not known whether lake area is expected to increase (Walter Anthony et al., 2016) or decrease (Smith et al., 2005; van Huissteden et al., 2011) and what effect this might have on future CH₄ emissions. Previous research shows the presence of active methanotrophs in these systems (He et al., 2012a). Methanotrophic activity in these systems responds positively to temperature increases (He et al., 2012a, 2012b), suggesting that this microbial CH₄ “filter” will continue to operate effectively as permafrost regions warm. These communities are sensitive to environmental conditions (He et al., 2012a) and will therefore be vulnerable to significant changes such as thermokarst development and shifts in vegetation cover. Further, as permafrost thaws, terrestrial CH₄-oxidizing communities can be transferred to lakes at increasing rates, potentially leading to a net increase in landscape-scale methanotrophy rates (Osudar et al., 2016).

Vegetation also plays an important role in CH₄ emissions from permafrost environments through the direct transfer of CH₄ from deeper soil layers to the surface (Bastviken et al., 2004), the stabilization and destabilization of permafrost ice complexes (Nauta et al., 2015), and via root exudates, providing substrate for methanogenesis (see section 3.2). Changes in vegetation due to climate change have already been observed in the form of shrubification (Elmendorf et al., 2012; Lantz et al., 2013) and shifts in the forest-tundra ecotone (Payette et al., 2001). It has been demonstrated that the removal of shrubs from a tundra ecosystem in north-east Siberia changed the landscape from a CH₄ sink to a CH₄ source (Nauta et al., 2015).

There are also geologic CH₄ stores trapped under some permafrost areas (Walter Anthony et al., 2012). These geologic CH₄ stores were produced millennia ago by microbial and thermogenic processes, then trapped under advancing ice sheets and permafrost, and as a result are generally radiocarbon dead (i.e., more than ~50,000 years old) (Etiope, 2012; Walter Anthony et al., 2012). Current fluxes to the atmosphere from these stores in permafrost regions are estimated to be around 2 Tg CH₄ yr⁻¹ (Kohnert et al., 2017; Walter Anthony et al., 2012). As ice sheets retreat and permafrost thaws under predicted climate warming, it is possible that CH₄ fluxes to the atmosphere from these stores may increase, contributing to the CH₄ climate feedback (Kohnert et al., 2017; Walter Anthony et al., 2012). However, the size of these stores, how long such

emissions could be sustained, and therefore their potential impact on the global climate are unknown, and it has been recently suggested that CH₄ emissions from such stores are unlikely to influence future climate (Petrenko et al., 2017).

6.4. Sensitivity of Permafrost Methane Fluxes to Climate Change

The direct quantification of CH₄ climate feedbacks is rare. An effective identifier of old C (i.e., C sequestered in organic matter prior to 1955) is radiocarbon (Dean et al., 2017). This has been applied to permafrost C stores that are converted to CH₄ and other forms of mobile C (Dean et al., 2018; Hilton et al., 2015; Raymond et al., 2007; Schell, 1983; Schuur et al., 2009; Walter Anthony et al., 2016). A recent study applied this method to estimate a direct permafrost CH₄ climate feedback of 0.1 to 0.3 Pg C via ebullition from thermokarst lake expansion in the Alaskan and Siberian yedoma region over the past 60 years (Walter Anthony et al., 2016). In contrast, dissolved CH₄ in lakes in yedoma permafrost systems in Alaska ranged from modern to old (3,300 years before present) in age (Elder et al., 2018) but did not contain the very old (~50,000 years and older) C that is found in yedoma permafrost C stores (Walter Anthony et al., 2016). In non-yedoma tundra systems, old permafrost C may be more likely to be released as CO₂ (Schuur et al., 2009) than CH₄, as old CH₄ derived from old permafrost was not observed in surface emissions despite considerable thaw occurring (Cooper et al., 2017). Further, if 10°C warming occurred, C release as CO₂ has been shown to have a larger effect on the overall permafrost carbon feedback than CH₄ (after taking into account the higher radiative forcing capacity of CH₄), due to higher rates of C release to the atmosphere under dry, oxic conditions (when CO₂ is released) than wet, oxygen-poor conditions (when CH₄ is released) (Schädel et al., 2016). However, whether permafrost regions release CO₂ or CH₄ is dependent on hydrology and whether these regions will become wetter or drier under future climate change is by and large unknown (Schädel et al., 2016; Schuur et al., 2015).

Recent modeling work suggests that the CH₄ climate feedback through to the year 2100 from permafrost regions may be relatively small compared to other feedbacks discussed in this review (see section 8.1) (Gao et al., 2013; Lawrence et al., 2015; Schaefer et al., 2014). However, these studies use models that likely do not adequately represent microbial responses in the Arctic. Modeling based on microbial dynamics predicts a much larger feedback from permafrost environments (30–90 Tg CH₄ yr⁻¹) (McCalley et al., 2014) than models lacking microbial activity (6–15 Tg CH₄ yr⁻¹) (Gao et al., 2013); incorporating deep C deposits and thermokarst activity into nonmicrobial models produces a slightly higher range (8–26 Tg CH₄ yr⁻¹) by 2100 (Schneider von Deimling et al., 2015). These large-scale physically based models also do not account for small-scale processes such as anoxic and oxic zones within soil pores that are temporally variable yet may play an important role in microbial CH₄ production and oxidation (Ebrahimi & Or, 2017) or local-scale processes such as thaw-induced land subsidence. These processes may be important at regional scales in balancing soil drying (promoting CH₄ oxidation) and soil wetting (promoting CH₄ production) (Helbig et al., 2016; Koven et al., 2015). The potential strength of the permafrost CH₄ feedback may be considered small through to 2100 but remains uncertain at these and longer timescales.

7. Methane Hydrates

Gas hydrates are solid, ice-like substances made of water cages stabilized by gas molecules through van der Waals-type (weak, charge-based) attraction. Since the main gas is CH₄, gas hydrates are often referred to as methane hydrates or clathrates: the general name for structured cage-like substances hosting gas molecules (Kvenvolden, 1993). Although the CH₄ can come from various sources, almost all is eventually derived from biologically produced organic matter. CH₄ is primarily microbially generated within or below the zone of occurrence, supplemented with thermogenic CH₄ produced at high temperatures at depth (Archer, 2007; Ruppel, 2011; Wallmann et al., 2012).

Methane hydrates have received much attention because of their potential as an energy resource and their possible role in submarine hazards, the global C cycle, and climate change (Archer et al., 2009; Boswell & Collett, 2011; Kvenvolden, 1993; Ruppel & Kessler, 2017). Recently, thorough reviews specifically dedicated to methane hydrate-climate interactions have been published and we refer the reader to these for a more complete literature coverage and detailed treatment and assessment (Mestdagh et al., 2017; Ruppel & Kessler, 2017).

7.1. Distribution and Size of Methane Hydrates

Methane hydrates form where thermodynamic conditions are favorable and where in situ CH_4 generation or external CH_4 supply is sufficient. Thermodynamic (pressure-temperature) conditions govern the gas hydrate stability zone (GHSZ), which provides a first-order prediction for minimum and maximum depth of methane hydrate occurrences in oceanic and permafrost sediments (Buffett & Archer, 2004; Hester & Brewer, 2009; Xu & Ruppel, 1999). In the ocean, the GHSZ typically starts at water depths of 300–600 m and extends down to a few hundred meters below the seafloor. In permafrost systems, the GHSZ starts shallower because of lower surface sediment temperatures (Hester & Brewer, 2009; Ruppel & Kessler, 2017). The actual occurrence of gas hydrates within the GHSZ depends on availability of CH_4 because CH_4 concentrations should exceed their solubility (Mestdagh et al., 2017; Xu & Ruppel, 1999). CH_4 availability is governed by local CH_4 generation (and, therefore, the availability of labile organic C), CH_4 losses (transport and consumption), and CH_4 supply from below by diffusion, advection, and bubble transport (Archer, 2007; Archer et al., 2009; Ruppel & Kessler, 2017; Wallmann et al., 2012; Xu & Ruppel, 1999).

Published estimates of the global methane hydrate inventory vary over orders of magnitude (100 to $>63,000$ Pg C) (Archer et al., 2009; Boswell & Collett, 2011; Buffett & Archer, 2004; Dickens, 2011; Milkov, 2004; Wallmann et al., 2012). Recent estimates vary from >455 Pg C (Wallmann et al., 2012) to 3,830 Pg C (Hunter et al., 2013), with other estimates in between: 550 (Piñero et al., 2013), 995 (Burwicz et al., 2011), 1146 (Kretschmer et al., 2015), 1500 (Boswell & Collett, 2011), 1800 (Johnson, 2011), and 2,630 Pg C (Yamamoto et al., 2014). This variability is due to our limited understanding of the governing factors, scarcity of data, and differences in upscaling procedures, that is, whether based on the volume of sediments within thermodynamic stability zone (GHSZ) or the actual volume of methane hydrate occurrence in sediments or based on more mechanistic approaches incorporating CH_4 production, consumption and transport, geothermal gradient information, and methane hydrate stability (Archer, 2007; Archer et al., 2009; Buffett & Archer, 2004; Dickens, 2011; Hunter et al., 2013; Piñero et al., 2013; Wallmann et al., 2012; Xu & Ruppel, 1999).

7.2. Sensitivity of Hydrates to Climate Change

The pressure and temperature dependence of gas hydrates implies that they may respond to global warming and associated changes in sea level. Increasing temperatures will eventually cause hydrate dissociation to gas and water, and if the liberated CH_4 is not microbially consumed and escapes from the sediments and enters the ocean or atmosphere, it may result in a positive feedback loop: warming causes CH_4 release, and more C in the atmosphere/ocean system causes more warming. This mechanism was identified more than two decades ago (Gornitz & Fung, 1994; Harvey & Huang, 1995; Kvenvolden, 1988) and has been recognized in geological records (Dickens, 2011; Dickens et al., 1995; Kennett et al., 2003; Sluijs et al., 2007). However, there is still very limited understanding, and much uncertainty and debate, about the rate and impact of hydrate dissociation on climate and the sensitivity of methane hydrates to climate change (Mestdagh et al., 2017; Ruppel & Kessler, 2017).

Climate warming will cause melting of ice sheets, thawing of Arctic permafrost, and warming of ocean (bottom) waters and accelerate sea level rise (Church et al., 2013). Ocean margin hydrates are more vulnerable to destabilization due to rising temperatures than stabilization due to sea level rise-induced pressure increases (Archer et al., 2009; Mestdagh et al., 2017). Warming of ocean bottom waters and surface sediments will eventually lead to warming of sediment within the GHSZ and thus to dissociation of hydrates, but only after hundreds to thousands of years. This delay is caused by the slow heat transfer within sediments, the heat consumption by the endothermic dissociation reaction, and the depth distribution of gas hydrates (Archer et al., 2009; Hunter et al., 2013; Mestdagh et al., 2017; Ruppel & Kessler, 2017; Xu & Ruppel, 1999).

Whether the CH_4 released by hydrate dissociation in subsurface sediments reaches the atmosphere is highly uncertain due to the presence of multiple sinks (Archer et al., 2009; Dickens, 2011; Hunter et al., 2013; Ruppel & Kessler, 2017). Within the GHSZ, CH_4 released at one depth may be incorporated into methane hydrates at another depth, and CH_4 may be physically trapped (in undersaturated pores or bubbles). By far the majority of CH_4 released upon hydrate dissociation will be consumed by methanotrophs in the sediments by anaerobic oxidation of methane (S-AOM; see section 2.2) (Boetius et al., 2000; Knittel & Boetius, 2009). Any CH_4 escaping microbial consumption in the S-AOM zone and diffusing upward will subsequently be subject to aerobic methanotrophic activity in oxygenated surface sediments. CH_4 release from sediments to bottom waters is therefore limited to seepage, pockmarks, and other areas of focused CH_4 release where this

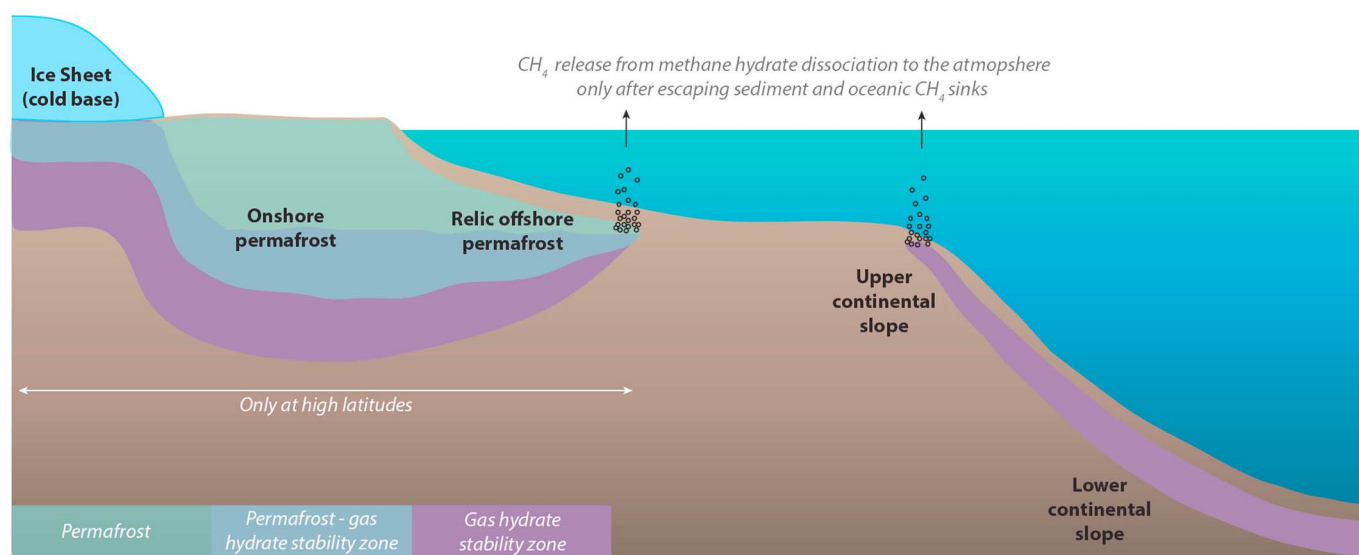


Figure 5. Conceptual diagram of methane hydrate reservoir and permafrost distribution based on Ruppel (2011), Ruppel and Kessler (2017), and Mestdagh et al. (2017). Five types of hydrate reservoirs are shown: subglacial hydrates, hydrates associated with onshore and offshore permafrost, and hydrates in upper and lower continental slopes. A sixth category, deep-sea hydrates, is not shown because of its low climate sensitivity (Ruppel & Kessler, 2017). Upper continental slope and relic offshore permafrost associated hydrates are most vulnerable to climate change and may dissociate, but almost all CH_4 liberated will be consumed in sediments and ocean before reaching the atmosphere. Note that the “gas hydrate stability zone” shows only potential methane hydrate occurrence.

microbial CH_4 filter is largely bypassed (Boetius & Wenzhöfer, 2013; James et al., 2016). CH_4 bubbles emitted from the sediment floor may ascend in the water column but will not make it to the sea-air interface at water depths more than tens of meters because of bubble-water gas exchange and oxidation (Archer et al., 2009; Hester & Brewer, 2009; James et al., 2016; McGinnis et al., 2006), as was seen following the 2010 BP Deepwater Horizon CH_4 blowout (see section 5.3). Similarly, CH_4 derived from permafrost-associated gas hydrates will be consumed by methanotrophs living at and near the surface of permafrost soils (see section 6.2) (He et al., 2012a). Accordingly, climate warming may cause gas hydration dissociation at depth, but with a delay of hundreds to thousands of years, and only a very small fraction of the CH_4 released will eventually reach the atmosphere (James et al., 2016; Ruppel & Kessler, 2017). Radiocarbon measurements of dissolved CH_4 in marine waters over the Beaufort Shelf in the U.S. demonstrated that CH_4 from thawing subsea permafrost and methane hydrates is not currently contributing to marine CH_4 emissions to the atmosphere (Sparrow et al., 2018).

In the context of climate change, it is instructive to divide hydrate reservoirs into five categories because of their differential susceptibility to climate change (Figure 5). This partitioning follows recent updates (Mestdagh et al., 2017; Ruppel & Kessler, 2017) on the original categories of Ruppel (2011); that is, subglacial hydrates have been added and deep-sea hydrates have been removed because the latter are relatively insensitive to climate change (Ruppel & Kessler, 2017). Subglacial hydrates in Antarctica are estimated to contain 80–400 Pg C (Wadham et al., 2012) but are likely not very sensitive to climate change over the next centuries (Ruppel & Kessler, 2017). Gas hydrates associated with onshore permafrost store are about 20 Pg C (Ruppel, 2015), but these are deeply buried and therefore will remain relatively stable under climate warming (Mestdagh et al., 2017; Ruppel & Kessler, 2017). Relic offshore permafrost-associated hydrates in the Arctic, formed from inundation of permafrost tundra, are likely more sensitive than onshore hydrates because the permafrost layer is thinner (Mestdagh et al., 2017; Ruppel, 2011). Hydrates in the upper continental slope are most vulnerable to climate change, while those in the lower continental slope (accounting for 95% of the total continental slope inventory) have low sensitivity because these hydrates are well within their thermodynamic stability zone, and bottom-water warming will be less in the deeper ocean during the coming decades (Kretschmer et al., 2015; Mestdagh et al., 2017; Ruppel, 2011; Ruppel & Kessler, 2017).

Kretschmer et al. (2015) combined Earth system model bottom-water temperature projections with a mechanistic hydrate occurrence model and found that upper continental slope sediments (water depth 300–700 m) and Arctic deposits were the most sensitive to warming. They calculated a within sediment

release of 473 Tg CH₄ for the next 100 years. On the one hand, this number may be too low because it is based on a conservative methane hydrate reservoir size (1,146 Pg C), but on the other hand, this model did not include microbial sinks within the sediments and thus substantially overestimates CH₄ release to the ocean-atmosphere system. This potential release of 4.73 Tg CH₄ yr⁻¹ is very small compared to the total anthropogenic CH₄ release of 335 Tg CH₄ yr⁻¹ (Kirschke et al., 2013), but consistent with present-day hydrate source of 2–6 Tg CH₄ yr⁻¹ used in contemporary global CH₄ budgets (Kirschke et al., 2013; Saunio, Bousquet, et al., 2016). However, there is no conclusive or direct evidence to attribute any significant atmospheric CH₄ to release from hydrates (Ruppel & Kessler, 2017).

7.3. Implications of Methane Hydrate Dissociation

Although only a minor fraction of the CH₄ released from hydrate dissociation upon global warming will eventually be emitted to the atmosphere, this CH₄ release can nevertheless have substantial impact on global climate and ocean chemistry on timescales of thousands of years (Archer et al., 2009). Sediment CH₄ release enhances substrate availability for aerobic methanotrophy in ocean waters and thus increases O₂ consumption. This process together with a warming-induced decreased solubility of O₂ and a reduction in ocean ventilation might lead to expanding ocean hypoxia (Yamamoto et al., 2014). Aerobic methanotrophy produces CO₂, which is estimated to increase atmospheric CO₂ concentrations by about 100 ppm for a total release of 1,600 Tg C over 13,000 years (Boudreau et al., 2015). This also adds about 0.4–0.5°C to the long-term impact of anthropogenic C on temperature (Archer et al., 2009), enhances ocean acidification (Biaostoch et al., 2011; Boudreau et al., 2015), and may interact with other carbon cycling processes (Ruppel & Kessler, 2017).

8. Assessing Global Climate Methane Feedbacks

8.1. Timeline of Methane Feedbacks

The global CH₄ climate feedback is ultimately controlled by the balance between microbial production and consumption and how both processes will evolve under changing environmental conditions. In Figure 6, we combine the information from the previous sections to compare the magnitude and timing of CH₄ production, consumption, and release from the different environments discussed in this review. The magnitudes of annual emission estimates are based on the high-end GHG emission IPCC scenario RCP8.5 (or similar), representing sustained high emissions (a common scenario in the modeling literature), while it is not yet clear which emissions trajectory we are currently following (Rockström et al., 2017; Saunio, Jackson, et al., 2016).

Microbial communities respond quickly to changing environmental conditions, with shifts in community composition and/or CH₄ emissions generally seen within a month (e.g., Treat et al., 2015). The time taken for methanogens to colonize areas where favorable CH₄ producing conditions have developed can be the critical factor (e.g., Bond-Lamberty et al., 2016; Schädel et al., 2016). The response of vegetation is considered to be slower, with 10–50% of global vegetation considered “highly vulnerable” to change under predicted future climate scenarios (Gonzalez et al., 2010). Global fire frequency is expected to increase (Collins et al., 2013; Stocks et al., 1998); at the same time fire occurrence may decrease as a result of anthropogenic land use changes (Andela & van der Werf, 2014; Knorr et al., 2016). These effects on fire regimes are variable in both frequency and severity. Fire will indirectly affect landscape CH₄ emissions and make future predictions challenging. For example, predictions of fire occurrence in the boreal North American biome until 2100 vary from +25 to +350% (Amiro et al., 2009; Bachelet et al., 2005; Balshi et al., 2009; Wotton et al., 2010).

We include anthropogenic CH₄ emissions in Figure 6 for context, and it is clear that these could remain the dominant source of emissions if we continue along a high-emission scenario (Riahi et al., 2011); recent work suggests that anthropogenic GHG emissions may be dropping below this trajectory, though (Saunio, Jackson, et al., 2016).

After anthropogenic emissions, wetlands will remain the most dominant natural CH₄ source to the atmosphere. Wetland CH₄ emissions are predicted to increase by 33–60% by the year 2100 (Figure 6). These values are based on the impact of expected increases in atmospheric CO₂ being the primary driver of wetland CH₄ feedbacks (Melton et al., 2013). However, these estimates do not include water level changes or direct temperature effects, which have a slight negative and a slight positive effect, respectively. A recent model

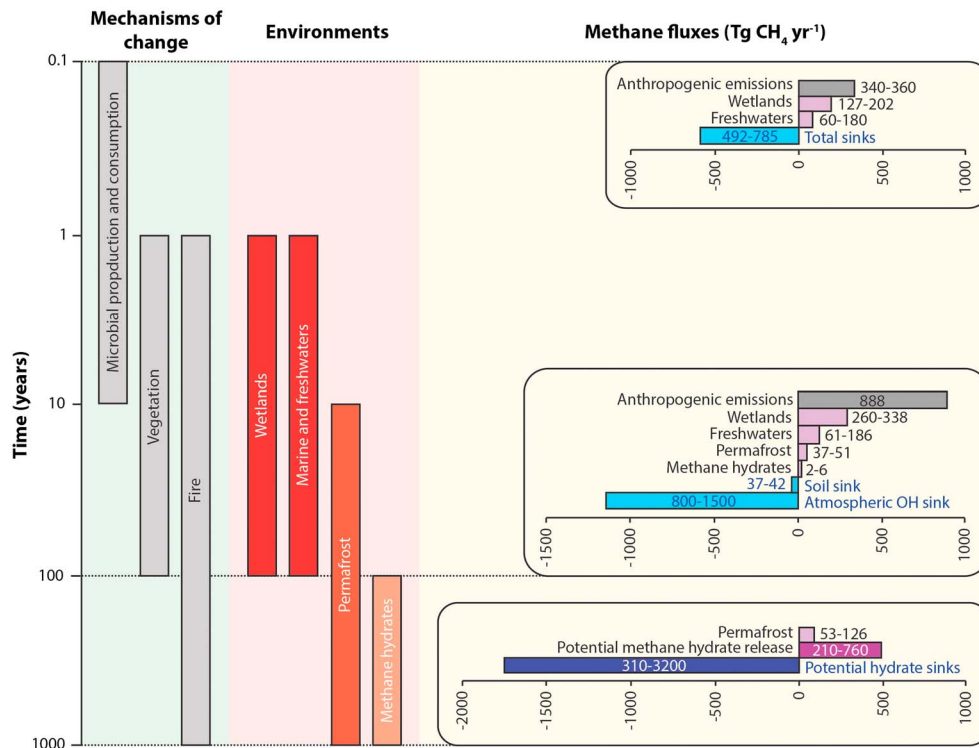


Figure 6. Estimated timescales of the potential CH₄ climate feedbacks discussed in this review; the timescale indicates the response time of the mechanisms of change to climate forcing and the immediacy of the impacts of these changes to CH₄ emissions from different environments. Present global CH₄ emissions (Kirschke et al., 2013; Saunois, Bousquet, et al., 2016) are included at the top right, followed by the potential future emission magnitudes along the timescale. The future emission magnitudes are based on estimates from a range of studies for each environment under RCP8.5 or similar scenarios; the RCP8.5 scenario 2100 anthropogenic CH₄ emissions are shown for reference (Riahi et al., 2011), but are not included beyond 2100 as we hope that anthropogenic emissions will have been curbed by then. Only potential CH₄ release from methane hydrates and oceanic sinks are shown beyond 2100 because their impact prior to this is considered minimal (see section 7); the estimated permafrost emissions up to 2300 are shown for context. The emission mechanism timescales are based on microbial production (Bond-Lamberty et al., 2016; Treat et al., 2015), microbial consumption (Kwon et al., 2016; Merbold et al., 2009; van Winden et al., 2012), vegetation change (Elmendorf et al., 2012; Gonzalez et al., 2010; Lantz et al., 2013; Nauta et al., 2015), and fire regime (Harris et al., 2016; Moritz et al., 2005). The 2100 emission estimates for each environment are based on wetlands (Melton et al., 2013; Zhang et al., 2017), freshwaters (Tan and Zhuang, 2015, and Wik et al., 2016, estimates for northern lakes—above 50°N, as a proxy for all lakes, estuaries, and coastal sediment emissions; see section 5—are added to current estimates of freshwater emissions in Saunois, Bousquet, et al., 2016), permafrost (Gao et al., 2013; Koven et al., 2015; Lawrence et al., 2015; McCalley et al., 2014; Schaefer et al., 2014), methane hydrates (Kretschmer et al., 2015; Ruppel & Kessler, 2017), soil sinks (Curry, 2007; Ridgwell et al., 1999), and the atmospheric OH sink (Voulgarakis et al., 2013). The 2300 emission estimates for permafrost are from Lawrence et al. (2015); the 2300 methane hydrate emission estimates show both the potential release of CH₄ from hydrates into marine sediments and the ocean (purple) (Kretschmer et al., 2015; Ruppel & Kessler, 2017), and the potential oceanic sink for this CH₄ (dark blue) (Ruppel & Kessler, 2017), indicating the low likelihood of a significant climate feedback from methane hydrate destabilization in the near to intermediate long term.

ensemble that incorporates temperature effects predicted a similar range of wetland CH₄ emissions by 2100 ($338 \pm 28 \text{ Tg CH}_4 \text{ yr}^{-1}$, RCP8.5) but a larger percentage increase relative to the ensemble's current predicted level of CH₄ emissions from wetlands (80–113%) (Zhang et al., 2017). We indicate an immediate feedback response from wetlands as rising precipitation increases wetland areas and the area of individual water bodies, which may already be occurring in the tropics (Nisbet et al., 2016), but this will be balanced between drought and increased water saturation (O'Connor et al., 2010). This does not necessarily suggest that the balance of CH₄ production versus consumption will shift in favor of increased production; it could simply represent the expansion of wetland areas, which are currently net CH₄ sources.

There is large uncertainty in current and future CH₄ emissions from freshwater systems, as can be seen in the range of values provided in Figure 6. We exclude marine sources here as current estimates of oceanic CH₄ emissions are low ($\sim 14 \text{ Tg CH}_4 \text{ yr}^{-1}$; Table 1) (Saunois, Bousquet, et al., 2016), and there are few predictions of future marine emissions. Emissions from freshwaters are predicted to increase primarily because of longer ice-free seasons in northern lakes (above 50°N) meaning longer periods of CH₄ production and emissions (Wik et al., 2016). Increased methanogenesis in northern lakes driven by rising temperatures may well be matched by methanotrophy in the sediment and water columns (He et al., 2012b).

We also exclude permafrost CH₄ emissions from the contemporary budget as conservative estimates render them relatively insignificant on current scales (Kirschke et al., 2013), while less conservative estimates (e.g., Walter Anthony et al., 2016; Wik et al., 2016) are not so easily accommodated in current regional top-down budgets (Sweeney et al., 2016; Thompson et al., 2017). However, CH₄ emission from permafrost environments will likely increase by 2100 and may become even more significant if warming continues through to 2300 and beyond (Figure 6). Several studies combine northern wetlands and permafrost areas into a single group (e.g., McNorton, Gloor, et al., 2016). Here we separate the wetland and permafrost regions (Figure 6), because permafrost thaw has the potential to be a longer-term feedback mechanism beyond 2100 (Figure 6), with a significantly larger soil C pool compared to wetlands. This so-called “permafrost carbon bomb” (Treat & Frolking, 2013) hypothesis, of both CO₂ and CH₄ release, has been highlighted as a significant process in past global climate shifts (e.g., DeConto et al., 2012).

In the contemporary CH₄ budget, we combine the soil sink with the total sinks term. In the 2100 budget, we use the same soil sink values as contemporary estimates but separate soils from the atmospheric OH sink because it is not yet known whether the soil sink will decrease (Blankinship et al., 2010) or increase (Lau et al., 2015) in response to climate change. The atmospheric OH sink, however, is intrinsically linked to atmospheric CH₄ concentrations and could decrease in conjunction with rising atmospheric CH₄ (Voulgarakis et al., 2013); however, lags in atmospheric OH response to fluctuations in CH₄ are a source of considerable uncertainty (McNorton, Chipperfield, et al., 2016; Rigby et al., 2017; Turner et al., 2017).

Methane hydrates are not expected to contribute significantly to global CH₄ emissions in the near or long-term future (Ruppel & Kessler, 2017). This is mainly due to the large CH₄ sinks present in sediments, ocean waters, and soils (in permafrost associated hydrates). To predict the potential climate feedback from methane hydrates beyond 2100, we provide a range of possible values of CH₄ release from hydrates to oceanic bottom waters (not the atmosphere) under future climate warming (the large range is a result of the uncertain size of this CH₄ reservoir; see section 7). We then include an estimate of the oceanic sink term (Ruppel & Kessler, 2017) to demonstrate that the potential magnitude of these sinks is much larger than the estimated CH₄ release from hydrates to ocean waters. This sink indicates that actual CH₄ emissions to the atmosphere resulting from methane hydrate dissociation are insignificant in the context of the contemporary and 2100 global CH₄ budgets (Figure 6). It is possible that in the long term (i.e., by 2300 and beyond; Figure 6), the CO₂ produced from the oxidation of CH₄ release from hydrates could have major consequences, including increased CO₂ concentrations in the atmosphere and ocean acidification (see section 7), but large CH₄ emissions to the atmosphere derived from methane hydrate dissociation are unlikely.

8.2. Combined Methane Climate Feedback Effect

The feedbacks discussed in this review operate in a net positive direction, and it is likely that they will act cumulatively and influence one another. The fastest occurring feedback effect could increase warming (including other non-CH₄ feedbacks), causing other feedbacks to take effect more quickly than expected (Figure 7). We indicate the potential timing and magnitude of these feedbacks in Figure 6 and how these could interact in Figure 7. Enhanced microbial and fire-induced pyrogenic CH₄ release could in the short term speed up climate feedback responses in wetland and marine and freshwater systems. This would in turn enhance the response of permafrost systems and the global CH₄ climate feedback (Figure 7).

Climate-driven environmental change impacts the global CH₄ cycle in many ways (Figure 7). For example, increasing temperatures regulate concentrations of reactive nitrogen species, oxygen, and organic C in soil pore water, altering primary production by plant communities, all of which regulate methanogenic activity (White et al., 2008). In contrast, in a series of boreal lakes, nutrient availability (particularly phosphorus) and microbial community interactions controlled methanogenesis (Denfeld et al., 2016). As shown in the previous sections, CH₄ production can also be offset as environmental conditions change. Sea level rise could drown coastal organic-rich soils, converting these areas to CH₄ sources, but can be counterbalanced by the simultaneous influx of SO₄²⁻ from seawater, which is utilized for AOM (see section 5).

Significant feedbacks are currently expected from the Arctic region, as temperatures are expected to rise at a higher rate in the region compared to the global mean (Christensen et al., 2013). But while field campaigns have indicated locally significant CH₄ emissions from Arctic lakes (Wik et al., 2016) or the East Siberian Arctic Shelf (Shakhova et al., 2014), there is to date no clear evidence that Arctic CH₄ emissions are increasing over

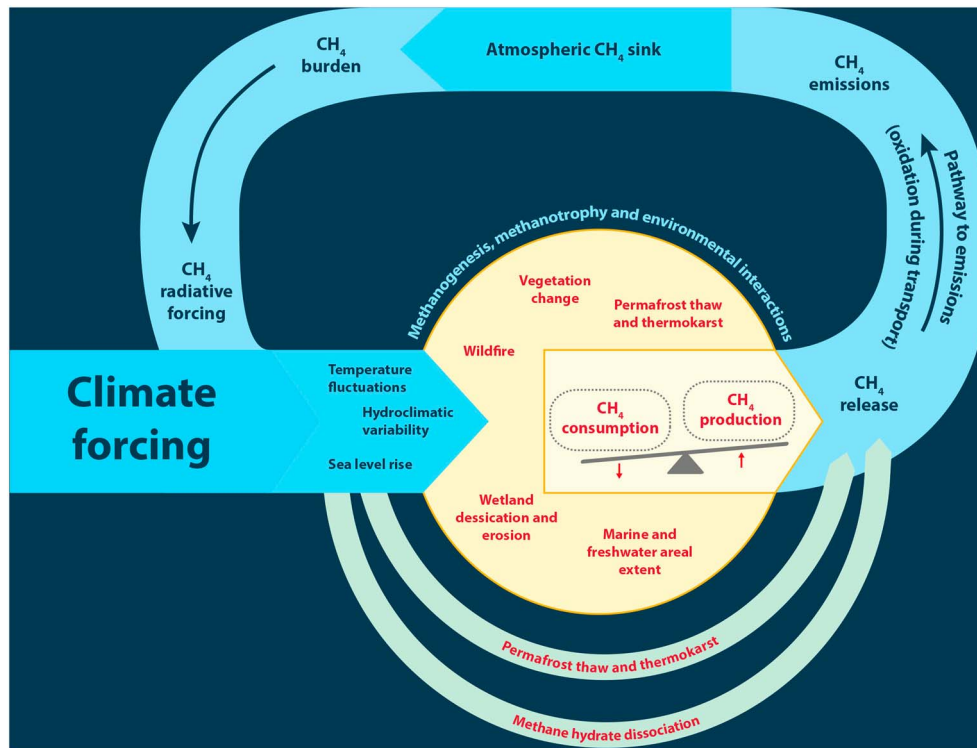


Figure 7. CH₄ climate feedback schematic showing how the feedback mechanisms discussed in this review relate to each other: each feedback mechanism (within the yellow circle) is forced by climate change, altering CH₄ emissions to the atmosphere. Direct CH₄ feedbacks are indicated with green arrows, and indirect feedbacks are within the yellow circle. After production, CH₄ is exposed to oxidation before being emitted to the atmosphere where it is then consumed by the atmospheric CH₄ sink. The amount of CH₄ in the atmosphere is known as the atmospheric CH₄ burden and, prior to its oxidation in the atmosphere, causes radiative forcing (the greenhouse effect) that feeds back to the overall climate forcing (completing the positive CH₄ climate feedback loop shown in light blue).

time. In fact, atmospheric measurements at long-term monitoring stations show no significant increase of Arctic CH₄ emissions (Bergamaschi et al., 2013; Bruhwiler et al., 2014; Dlugokencky et al., 2009; Sweeney et al., 2016). This suggests that at present, Arctic emission increases are negligible or small in absolute terms (Tg CH₄ yr⁻¹). It is possible that the additional CH₄ that could be produced at higher temperatures is removed before reaching the atmosphere and/or that the oxidative capacity of sinks also increases in line with production. For example, Fisher et al. (2011) observed seepage of thermogenic (not related to climate change) CH₄ from the seafloor off the coast of Spitsbergen, but no corresponding increase in the atmosphere. Further, these regions are also CO₂ sinks, with CO₂ uptake providing a negative radiative forcing 231 times greater than the positive forcing of CH₄ emissions to the atmosphere (Pohlman et al., 2017). The main drivers of CH₄ emissions and their sensitivity to climate change have largely been identified for specific environments, demonstrating that the combined environmental controls on net CH₄ emissions cannot be easily generalized for different ecosystems, and must be resolved individually. Quantifying combined feedbacks is highly challenging and requires the use of sophisticated Earth System Models (ESMs). However, environment-specific controls on microbial activity and net CH₄ fluxes mean that the incorporation of the global CH₄ climate feedback into ESMs is a major challenge (Ebrahimi & Or, 2017; Wieder et al., 2013; Xu et al., 2014).

8.3. Limitations and Future Directions

The interconnected nature of the feedbacks discussed in this review, and their mismatched timelines, makes complete understanding of their interactions complex and reliable predictions difficult (Khalil & Rasmussen, 1993). We have focused here on CH₄ climate feedbacks from a bottom-up perspective, that is, based on observations at the Earth's surface. However, there is considerable disagreement between the global CH₄ budgets derived from these observations and those derived from atmospheric, or top-down, approaches (Table 1). The gradual decrease of the growth rate of atmospheric CH₄ in the 1990s toward the relatively constant levels in 2000–2007 has been interpreted as an indication for a new steady state where global

emissions did not increase over this entire period (Dlugokencky et al., 2003). This leaves little room for increasing emissions from natural feedbacks on the global scale, unless they are offset by decreasing anthropogenic emissions, or an increased sink term.

The renewed increase in atmospheric CH₄ since 2007 is evidence of a new global-scale imbalance between sources and sinks. Increased emissions from the feedbacks discussed in this review would increase this imbalance in the future, but it is unclear how the atmospheric OH sink will respond to these additional emissions. Given the many uncertainties in the global CH₄ budget and the potential major feedbacks, continued and expanded monitoring of the evolution of atmospheric CH₄ is required to provide high-quality top-down constraints on the source-sink imbalance. However, to substantially advance our process understanding of the global CH₄ cycle and predictions of future CH₄ levels, it is increasingly important to reconcile top-down and bottom-up budgets, particularly as bottom-up observations themselves require careful multidisciplinary efforts incorporating geochemical, physical, and biological observations.

This can be done by comparing bottom-up estimates with top-down budgets on a study by study basis (e.g., Pangala et al., 2017). Such comparisons would be made easier by a study intercomparison project and a regularly updated and openly available database of both global and regional top-down and bottom-up CH₄ budgets to serve as a reference point for researchers putting together bottom-up CH₄ emission estimates (e.g., Saunio, Bousquet, et al., 2016). However, top-down studies are necessarily large scale and global in scope, while bottom-up studies tend to be process and location specific, making direct comparisons between top-down bottom-up studies challenging. Intercomparison projects of the observational networks (see section 1.3) on which top-down studies are based would help improve top-down estimates for smaller regions, as would expanding atmospheric observation networks; the latter would also help reduce uncertainties in top-down estimates, in general. From a bottom-up perspective, better constraint of CH₄ production, consumption, and emission variability across multiple scales, from microbial to regional, would help improve understanding of how this variability contributes to the larger-scale CH₄ budgets. This includes assessing the response of both CH₄ production and consumption to environmental shifts under predicted climate change and how this varies across scales. Further, there is to some degree a focus on discovering new CH₄ sources in the literature, but future research should also consider new CH₄ sinks (e.g., Brankovits et al., 2017; Waring et al., 2017) as this may improve the sink terms in current global CH₄ budgets. These efforts require not only increased long-term monitoring of sources and sinks of CH₄ but also in situ manipulation experiments aimed at providing insight into the relative sensitivity of production versus consumption processes in the source-to-atmosphere pathways. This remains the key uncertainty in bottom-up budgets.

Glossary

Bacteria and Archaea Single-celled microorganisms (microbes) that thrive across diverse environments and form the basis of many biogeochemical reactions on Earth. Archaea are key CH₄ producers.

Bottom-up Referring to CH₄ budgets and inventories estimated from observations and modeling at the Earth surface, including process-specific measurements and models.

Earth System Models Models that integrate biological, physical, and chemical interactions between the atmosphere, ocean, land, ice, and biosphere to predict global and regional responses to future climate change scenarios.

Ebullition The release of gas bubbles that have been building up in soil or sediment.

Electron Acceptors A compound that can incorporate the electrons released during oxidation (in this case the oxidation of CH₄). Alternative electron acceptors in the context of CH₄ oxidation refer to electron acceptors other than O₂.

Eutrophic Nutrient conditions that support high levels of biological productivity.

Freshwater Systems In this review, we refer to inland waters (lakes, rivers, and streams), as freshwater systems following Saunio, Bousquet, et al. (2016), and to distinguish among marine, estuarine, and freshwater systems. In general, the terms inland waters and freshwater systems are interchangeable, except that inland waters can also include saline (salty) lakes and rivers, whereas freshwater systems by definition cannot.

Global Warming Potential The climate impact of different forcing agents can be compared via this metric, which compares the radiative forcing, over a certain time horizon, caused by the emission of 1 kg of a certain forcing agent, to the forcing caused by the emission of 1 kg of CO₂.

Macrophytes Emerged, submerged or floating-leaf aquatic plants that are large enough to be seen by the naked eye.

Mesotrophic Nutrient conditions that support intermediate levels of biological productivity.

Metabolites Substances necessary for metabolism, performing roles such as promoting or inhibiting certain biological processes.

Methanogenesis (Carried out by **methanogens**) The production of CH_4 , which is possible via several pathways: **Hydrogenotrophic** pathway—via the metabolism of hydrogen; **Methylotrophic** pathway—via the metabolism of single- or multi-carbon compounds; **Acetoclastic**—utilizing acetic acid.

Methanotrophy (Carried out by **methanotrophs**) The conversion of CH_4 to CO_2 , which can occur in the presence of several different **electron acceptors** (Figure 1).

Milankovitch Cycles Repetitive orbital variations of the earth which influence the amount of solar radiation reaching the planet. The three relevant planetary movements are eccentricity (the shape of earth's orbit around the Sun, resulting in a $\sim 100,000$ year cycle), obliquity (the varying angle between Earth's rotational axis and its orbital rotation plane, $\sim 41,000$ year cycle), and precession (variation of the orientation of Earth's rotational axis, $\sim 26,000$ year cycle).

Monomers and Oligomers A molecule that may join with other molecules to form oligomers (consisting of a few units) or polymers (unlimited units).

Oligotrophic Nutrient-poor conditions that support limited levels of biological productivity.

Phytoplankton Aquatic micro-organisms that obtain their energy via photosynthesis.

Positive Climate Feedback A mechanism of climate warming that is positively influenced by climate itself. As warming increases, so too will the magnitude of the mechanism, forming a positive feedback loop.

RCP8.5 Representative Concentration Pathways (RCPs) are atmospheric greenhouse gas concentration trajectories used by the Intergovernmental Panel on Climate Change to describe potential ranges of radiative forcing based on possible greenhouse gas emission scenarios. RCP8.5 is the highest pathway leading to a radiative forcing of $+8.5 \text{ W m}^{-2}$ by 2100 relative to pre-industrial times.

Shrubification The expansion of landscape areas covered in shrubs.

Sphagnum A genus of mosses found in wetlands that play an important role in the control of acidification and water retention and contribute significantly to terrestrial organic carbon storage in wetland ecosystems.

Thermophile (Thermophilic) An organism which can flourish in high-temperature environments, for example, deep subsurface and volcanic zones.

Thermokarst Features caused by the rapid destabilization of permafrost soils via ice melting that results in slumping, subsidence, erosion, and/or general surface collapse.

Top-Down

Referring to CH_4 budgets and inventories estimated from atmospheric observations.

Vascular Plants Plants that include xylem for the conduction of water and minerals through the plant and phloem for the conduction of photosynthesis products.

Yedoma Ice-rich and organic carbon-rich silty sediments deposited in the late Pleistocene in areas that were not glaciated during this period, found predominantly in North Siberia, and also Alaska and Northwestern Canada.

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