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Review Article

Regulation of Atmospheric Methane Levels by Microorganisms: Could Methanotrophs Play a Role in Mitigating Climate Change?

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Abstract

Global warming refers to the long-term increase in the Earth's surface temperature, which can lead to significant and wide spread impacts on the planet. These effects include rising sea levels, changes in precipitation patterns, and more frequent and severe natural disasters. Atmospheric levels of methane (CH_4) have risen by over 150% since the pre-industrial era, with agriculture and livestock production being major contributors. This review aims to explore the effect of climate change on methanotrophic microorganisms and the potential of managing microbial communities to reduce CH_4 emissions, thereby mitigating CH_4 emissions as part of broader climate change strategies. While methanogens are CH_4-producing bacteria, methanotrophic bacteria can utilise CH_4 as a source of energy source and can consume large amounts of CH_4 directly from both the atmosphere and soils. Many factors influence the balance of microbes acting as a sink or consumers of greenhouse gasses including changes in terrestrial and marine environments. Temperature, CO_2 levels and precipitation have all been shown to have a profound effect on the ecology of methanogens, driving positive feedback which exacerbates the rate of climate change. Reducing CH_4 emissions is an important aspect of mitigating the impacts of climate change, and it may be theoretically possible to mitigate a considerable portion of global CH_4 emissions by managing microbial communities in various environments by reviewing land use and farming management practices. Examples of these practices include the reforestation of native woodlands, altering the management of organic materials in rice paddies and the reduction of CH_4 release from ruminant livestock utilizing additives to animal feeds such as red seaweed or hormonal products such as bovine somatotropin. Although efforts to mitigate CH_4-induced climate change effects are ongoing, further research is required to better elucidate the mechanisms involved in methanogenesis and the potential for reducing CH_4 emissions through targeted interventions.

Keywords: Global warming; Greenhouse gases; Methane; Methanotrophs

Introduction

Long-term increases in the surface temperature of the earth, universally described as global warming, are primarily instigated by the emission of greenhouse gasses because of human activities. Thermal energy is trapped by greenhouse gasses in the atmosphere by the absorption of infrared radiation. Global warming manifests itself in a myriad of ways and scientists have predicted mass loss of biodiversity, increased air pollution, rising sea levels and regular extreme weather events if the trajectory of climate change continues its current course. Rising temperatures are already resulting in more heatwaves and extreme weather events, such as hurricanes and wildfires, while glaciers and ice sheets are melting at an alarming rate, threatening low-lying areas because of rising sea levels (Bolan *et al.* 2024). Climate change can also have a significant impact on human health, including greater incidence of heat-related illnesses and the increased spread of infectious diseases, while ocean acidification is threatening marine ecosystems and the livelihoods of individuals who depend on these sensitive environments.

The leading cause of the Earth's rapidly changing climate is elevated emissions of gasses such as methane (CH_4), carbon dioxide (CO_2) and nitrous oxide (N_2O) (Bhatti *et al*. 2024). Although the planet's terrestrial and marine environments sequester large quantities of greenhouse gasses from the atmosphere through photosynthesis and other processes, emissions far outweigh the amounts these natural carbon sinks can absorb, leading to the dramatic increases in atmospheric concentrations of greenhouse gasses observed in recent decades (Nayak *et al.* 2022).

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Microbes have been key drivers in determining atmospheric concentrations of greenhouse gasses ever since the evolution of marine cyanobacteria in the ocean more than 3.5 billion years ago (Schopf and Packer 1987). Microbes play an important role in both the release and uptake of greenhouse gases such as N_2O, CO_2 and CH_4 in the atmosphere. Some microbes, such as denitrifiers, can consume N_2O, reducing its concentration in the atmosphere. In addition, microbes are also involved in carbon cycling, as they decompose dead organic materials and release CO_2 back into the atmosphere (Wu *et al.* 2024). In soil, microbes also help to regulate the balance of CO_2 in the atmosphere by absorbing it through photosynthesis and releasing it back into the atmosphere through respiration. Other microbes, such as methanogens, produce CH_4 as a by-product of their metabolic processes, contributing to the increase of atmospheric CH_4 levels. Methanotrophic microbes can however oxidize CH_4 under both aerobic and anaerobic conditions, effectively removing CH_4 from both the atmosphere and soil (Guerrero-Cruz *et al.* 2021). By reducing CH_4 emissions, methanotrophs help lower the concentration of this potent greenhouse gas in the atmosphere, which may help offset CH_4 emissions from various natural and human-made sources, including wetlands, oceans, soils, and landfill sites. Methanotrophs can therefore act as natural CH_4 sinks, breaking down CH_4 before it reaches the atmosphere and thus playing a vital role in mitigating climate change by reducing a major greenhouse gas. In addition, the metabolism of CH_4 by methanotrophs converts it into CO_2 and biomass, which can become part of the soil carbon pool, contributing to long-term carbon storage.

Microbes are responsible for both the production and consumption of greenhouse gases, so microbial activities are likely to be significantly influenced by a changing climate. This review aims to evaluate the effect of climate change on methanotrophy and the potential of managing microbial communities to reduce CH_4 emissions, thus mitigating the effects of climate change.

Methane levels and climate change

CH_4 is a potent greenhouse gas that plays a significant role in climate change. Levels of CH_4 in the atmosphere have significantly increased since preindustrial times, with levels reaching 1,892 ppb in 2020 as measured by the Earth System Research Laboratory of the NOAA. Since 2007, globally averaged atmospheric CH_4 concentrations have been increasing at an accelerating rate, with concentrations of CH_4 in the earth's atmosphere rising by a record amount in 2020, despite a dip in emissions of carbon during the COVID-19 pandemic (Peng *et al.* 2022). This study found that the global average concentration of methane increased by 15.19 ppb in 2020, with a further record increase of 18.12 ppb in 2021.

Sources of methane in the atmosphere

Sources of CH_4 in the atmosphere are varied, but they all involve either the decomposition of organic matter by microbes or the release of CH_4 from fossil fuels. CH_4 is believed to be responsible for between 20 – 30% of global warming, with significant CH_4 emissions being released by microorganisms (Singh *et al.* 2010). Methanogenic bacteria play a vital role in global carbon cycling owing to their unique ability to generate CH_4. According to the Global Carbon Project, methanogens produce CH_4 (approximately 250 million tons per year) in natural environments such as sediments, wetlands and oceans. These environmental sources are however surpassed by CH_4 emissions emanating from artificial environments (approximately 320 million tons of CH_4 annually) including livestock farms, landfills, rice cultivation and biogas and wastewater facilities (Gålfalk *et al.* 2016). Fires and burning of other biomass types, such as burning wood or agricultural waste, can also produce significant amounts of CH_4. Methane release is primarily *via* the combustion of fossil fuels or other practices such as venting and flaring. Apart from CH_4 emissions from fossil fuel extractions, all these artificial sources of CH_4 are predominantly driven by microorganisms. Fig. 1 shows the relative contributions of the different sources mentioned above to global anthropogenic CH_4 emissions.

Regarding agricultural CH_4 emissions, ruminant animals are the most significant source of CH_4, resulting in much higher carbon footprints for meat production (19 – 48 times greater) than crop foods (Ripple *et al.* 2014). Cows and other ruminants generate CH_4 as part of their digestive process, which is then released through flatulence and belching. Depending on the breed, a single cow can emit between 151-497 g of CH_4 per day (Broucek 2014). In ruminants, the majority of methanogenesis occurs in the rumen which is a large fermentative chamber (Patra 2012), where methanogens use CO_2 and hydrogen to generate CH_4. Rice paddies also contribute substantially to the release of CH_4 from agriculture, despite only covering approximately 10% of cultivatable farmland. Since rice is the staple food for at least half of the world's inhabitants, predictions indicate that CH_4 emissions due to rice production could double by the end of this century (Groenigen *et al.* 2013).

Production of CH_4 by methanogenic bacteria

There are over 50 described species of methanogenic bacteria, and all known methanogens are members of the archaeal phylum Euryarchaeota. Methanogenesis involves the synthesis of CH_4 which is carried out by this group of microorganisms. The methanogens, which are coccoid or rod-shaped, are a unique group of anaerobic microbes which occur in various environments such as oceans, swamps,

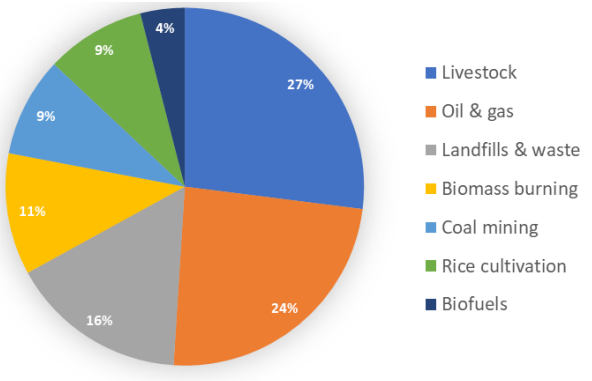

Fig. 1: Global anthropogenic CH_4 emission contributions (adapted from Hammandhu and Sakthi 2017)

cultivated rice fields, sewage digestors and the intestinal tracts of ruminant animals. Methanogenesis relies on substrates such as CO_2, hydrogen, acetate, formic acid, methylamines and methanol, which are produced as the end products of the breakdown of biological materials by other fungal and bacterial species in the adjacent microbial communities.

Since methanogens are anaerobic organisms, they do not use oxygen for respiration, with carbon being the final electron acceptor in methanogenesis. The substrate utilised for CH_4 production dictates CH_4 production by one of three major pathways. For the hydrogenotrophic pathway, CO_2 is utilised as the source of carbon with the primary electron donor being hydrogen (Hungate 1967). Hydrogenotrophic methanogenesis occurs *via* a seven-step pathway, in which reduced cofactors and H_2 are utilized to reduce CO_2 to CH_4 (Kurth *et al.* 2020). Second, CH_4 can be produced from acetate *via* the acetoclastic pathway (Lakhani *et al.* 2017). Acetoclastic methanogenesis, only performed by *Methanosaeta* and *Methanosarcina*, involves the cleavage of acetate, with the reduction of the methyl group of acetate to CH_4 and the oxidation of the carboxyl group to CO_2 (Kurade *et al.* 2019). Finally, methylotrophic methanogens can utilise methanol and methylamines that are produced in the rumen (Lakhani *et al.* 2017). Methyl-coenzyme M reductase (MCR), an important catalyser in the biological process of methanogenesis, is responsible for the final step in this reaction, catalysing the reduction of methyl-coenzyme M (methyl-CoM) to CH_4 and coenzyme M (CoM) (Chen *et al.* 2020a). In turn, the generation of CH_4 releases adenosine triphosphate for numerous other cellular activities.

CH_4 uptake by methanotrophic bacteria

Methanotrophic bacteria can consume large amounts of CH_4 directly from both the atmosphere and soil. Methanotrophs have been isolated from various habitats such as soils, rice paddies, landfills, groundwater and seawater, peat bogs and hot springs and are grouped according to a variety of morphological and physiological characteristics (Whittenbury *et al.* 1970). During the oxidation process, CH_4 is converted into methanol by the methane monooxygenase (MMO) enzyme, whereafter the methanol is further oxidised into formaldehyde. Two iso-enzymes of MMO occur, those being soluble MMO (sMMO) and particulate or membrane-bound MMO (pMMO) (Semrau *et al.* 2010). In the gamma-proteobacterial methanotrophs, formaldehyde may be oxidised to formate by the cyclic ribulose monophosphate pathway, whereas the serine cycle is exploited for formaldehyde assimilation by the alpha-proteobacterial methanotrophs. By oxidising CH_4 to CO_2 for energy, verrucomicrobial methanotrophs utilise the classical Calvin-Benson-Bassham (CBB) cycle (Khadem *et al.* 2011). Fig. 2 shows the classification of methanotrophs based on their physiology.

While some soil environments can act as sources of CH_4, soils can also act as effective sinks for CH_4 (Reay 2003). High concentrations of CH_4 typically observed in wetland ecosystems are generated due to the anaerobic breakdown of organic materials. In these environments, the CH_4 is predominantly utilised by methanotrophs as a carbon source, with two distinct types of methanotrophs being observed. First, low-affinity methanotrophs which can flourish at higher CH_4 concentrations (> 40 mg. kg^{-1}), often observed in waterlogged soils and sediments, can consume a significant quantity of the CH_4 generated in these soils before the CH_4 has a chance to escape into the atmosphere. Low-affinity methanotrophs catalyse CH_4 oxidation in areas such as the zone surrounding the oxygen-liberating roots of wetland plant species and in oxygenated surface soil layers (Conrad 2007). It has been estimated that > 80% of endogenous CH_4 produced in anaerobic soil environments is absorbed by methanotrophs before it can escape into the atmosphere (Conrad and Rothfuss 1991; Frenzel *et al.* 1992). Second, high-affinity methanotrophs, in contrast, which are adapted to grow at CH_4 concentrations of < 1.8 mg. kg^{-1}, tend to be most active in the top few centimetres of these waterlogged areas, making use of the atmospheric CH_4 diffusing into the soil from the surface (Schopf and Packer 1987). For CH_4 that has already been released into the atmosphere, these high-affinity methanotrophs may serve as a CH_4 sink, removing approximately 30 million tons of CH_4 annually from the air (IPCC 2023).

The water content of soil tends to be a key factor as to whether soil acts as a source or a sink of CH_4. In well-drained soils, the aerobic conditions required by methanotrophs prevail, resulting in CH_4 uptake and a net CH_4 sink. When soils become waterlogged, the availability of oxygen falls and the balance shifts from methanotrophs to methanogens, with the soil becoming a net source of CH_4. Harriss *et al.* (1982) observed that whereas swamp soils under waterlogged conditions operate as a net source of CH_4, during the drought season, high-affinity CH_4 oxidation activity resulted in the direct consumption of atmospheric CH_4. The shift between different environments acting as either a CH_4 source or sink has additionally been observed in tidal wetlands with shifting water levels (Kelley *et al.*

Table 1: Summary of the effect of climate change on methanotrophy

Climate fluctuation parameter	Effect on CH_4	References
Elevated temperatures	Significant rise in net CH_4 emissions from wetlands and permafrost	(Friborg *et al.* 1997; Zhuang *et al.* 2004; McCalley *et al.* 2014; Arndt *et al.* 2019)
Elevated temperatures	Altered soil microbial methanogenesis	(Inglett *et al.* 2012; Yvon-Durocher *et al.* 2014)
Elevated temperatures	Rise in anaerobic CH_4 respiration rate in soils	(Dean *et al.* 2018)
Elevated temperatures	Decreased methanogenic respiration rates of CH_4 in wetland soils	(Chen *et al.* 2020b)
Elevated temperatures	Enhanced CH_4 emissions in forest soils but not in floodplains	(Gontijo *et al.* 2024)
Elevated temperatures	Aerobic methanotrophic could potentially lessen emissions of CH_4 emissions	(Roldán *et al.* 2022)
Increased precipitation	Significantly increase in CH_4 release (30%)	(Neumann *et al.* 2019)
Flooding conditions	Elevated emissions of CH_4 from floodplain soils	(Gontijo *et al.* 2024)
Elevated CO_2 levels	Significant reduction (70%) of the abundance of methanotrophic bacteria	(Kolb *et al.* 2005)
Elevated CO_2 levels	Substantial reduction (30%) in CH_4 consumption by soil microbes	(Phillips *et al.* 2001)
Elevated CO_2 levels	Increase in CH_4 release from rice paddies in the shorter term, although reduced production of CH_4 in the longer term	(Tian *et al.* 2024)
Raised temperatures and elevated CO_2 concentrations	Increase in methanogenesis with higher CO_2 concentrations and concomitant elevated temperatures.	(Wang *et al.* 2024)

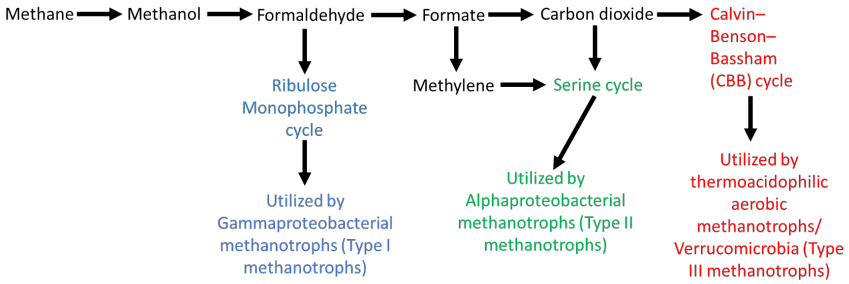

Fig. 2: Methanotrophs and methanotrophic metabolism for utilizing CH_4

1995), tropical peatlands (Melling *et al.* 2005) and rice paddies (Cai *et al*. 2016). Cai *et al.* (2016) observed that high-affinity CH_4 oxidation in rice paddies was rapidly induced during the low-affinity oxidation of high CH_4 levels. This high-affinity activity was, however, gradually lost over two weeks but was able to be repetitively resumed when the soil was flushed again with higher CH_4 levels.

The effect of climate change on methanotrophy

Although the capture of CH_4 by methanotrophs is the largest terrestrial sink for this greenhouse gas, CH_4 is only second to CO_2 as the most important greenhouse gas concerning climate change. Understanding the responses of microorganism-mediated CH_4 variations to climate fluctuations is therefore vital to accurately predict future CH_4 emissions. A summary of the effect of various climate change parameters on methanotrophy, reported in this review, is presented in Table 1.

Environments above 45 degrees latitude have undergone more significant environmental changes from global warming compared to those at lower latitudes, experiencing higher average air temperatures, increased precipitation, and permafrost thawing (Vitt *et al*. 2000). Ice cores obtained from the Antarctic and Greenland indicate that changes in atmospheric CO_2 and CH_4 levels are strongly linked to historical temperature variations (Petit *et al.* 1999; Monnin *et al*. 2001), which implies an association between temperature and the sources of these gasses. Studies carried out in high-latitude soils from the northern hemisphere indicated that global warming may cause a significant rise in net CH_4 emissions from both wetlands and permafrost in this region (Zhuang *et al.* 2004), as well as from Arctic tundra ecosystems (Arndt *et al.* 2019). Significant emissions of CH_4 have also been observed owing to permafrost thaw in Northern Sweden, associated with a switch from hydrogenotrophic methanogenesis, during the early months of thawing, to partly acetoclastic methanogenesis later in fully thawed marshy areas (McCalley *et al.* 2014). The resultant higher CH_4 release could elevate atmospheric CH_4 levels, leading to significant positive feedback for the worldwide climate. In addition, earlier spring thaws in arctic environments have been correlated to elevated CH_4 emissions which have been detected earlier in the year (Friborg *et al.* 1997). Although higher temperatures associated with global warming could potentially increase the activities of both methanogenic and methanotrophic bacteria, it is still unclear how this may influence net global CH_4 emissions.

Temperature appears to have a profound effect on the ecology of methanogens and various studies have demonstrated that soil microbial methanogenesis is greatly influenced by temperature (Inglett *et al.* 2012; Yvon-Durocher *et al.* 2014) indicating that anaerobic CH_4

respiration rate in soils is likely to increase sharply as global temperatures rise (Dean *et al.* 2018). In semi-arid regions, soil moisture is influenced by evapotranspiration due to elevated temperatures, suggesting that CH_4 fluctuations can be driven by temperature changes (Dijkstra *et al.* 2011). Chen *et al.* (2020a) have carried out a study using anaerobic wetland soils in the Tibetan plateau to assess whether methanogenesis by microbes displays a compensatory reaction to changes in temperature. The results indicated that methanogenic respiration rates of CH_4 increased with cooling while decreasing with experimental warming, which was largely explained by alterations in the composition of methanogenic species in the microbial populations. This aligns with long-term studies on aerobic soils, which suggest that a compensatory response from the microbial community can significantly mitigate the effects of temperature variations on soil CO_2 respiration rates in various environments (Chen *et al*. 2020b). This is in agreement with long-term studies on aerobic soils which indicate that counteractive responses of bacterial communities can significantly diminish the effect of changes in temperature on CO_2 respiration rates in environments such as grasslands and forests (Crowther *et al.* 2016; Dacal *et al.* 2019). In a study investigating CH_4 cycling under various climate change scenarios, soils from two Amazon floodplains and an upland forest in the Amazon basin were subjected to a 3°C temperature increase and flooding using a microcosm experiment (Gontijo *et al.* 2024). Although CH_4 fluxes were not affected by the elevated temperatures in the floodplains, prolonged flooding of the forest soils at elevated temperatures (30°C) enhanced CH_4 emissions, highlighting the variability of CH_4 release from different soil types under different environmental conditions (Gontijo *et al.* 2024). From the evaluation of freshwater lake sediments in Antarctica, it appeared however that aerobic methanotrophic species could potentially lessen emissions of CH_4 in climate-sensitive areas such as the polar regions when they are exposed to higher temperatures (Roldán *et al*. 2022). In evaluating the effects of temperature on methanotrophic communities, an important consideration may be methanotroph physiology, since physiological adjustments have been observed in the genus *Methylobacter*, leading to thermal acclimation and shifts in CH_4 consumption (Tveit *et al*. 2023).

Changes in precipitation can be directly related to global warming, where elevated temperatures can result in faster evaporation and surface drying, in turn increasing the duration of droughts (Trenberth 2011; Feng *et al*. 2019). Altered rainfall patterns can have both direct and indirect effects on CH_4 production. Aspects including the type of ecosystem, the activity of methanogenic bacteria, and the characteristics of the soil can all affect the magnitude of these effects. Drier conditions could promote oxygen availability, leading to more favourable conditions for methanotrophs with a consequent reduction in net CH_4 emissions. Conversely, excessive rainfall in other areas could lead to greater expanses of waterlogged environments which would favour methanogenesis and net CH_4 emissions. In northern latitudes such as Alaska, where soil and air temperatures are often mismatched, it has been shown that rainfall can act as a significant conveyor of thermal energy into soils (Neumann *et al.* 2019). In this study, a thawing wetland was rapidly warmed by spring rainwater entering the soils, which significantly elevated CH_4 release by approximately 30% (Neumann *et al.* 2019). It is anticipated that Northern latitudes may receive more precipitation in the future (Bintanja and Andry 2017) and by heating soils and elevating CH_4 emissions, it has been postulated that global warming related to permafrost thaw could be augmented by higher precipitation levels (Neumann *et al*. 2019). An investigation on the effect of flooding of different soil samples from the Amazon basin demonstrated CH_4 emissions from floodplain soils in response to flooding conditions, while non-flooding conditions encouraged CH_4 uptake. In contrast, soils from an upland forest in the same area demonstrated a reduced capability to act as a CH_4 sink when exposed to dry and warm conditions (Gontijo *et al*. 2024).

As with CH_4, average atmospheric concentrations of CO_2 have been rapidly increasing and are currently around 415 mg. kg^{-1}, largely as a result of burning of fossil fuels. The UK Met Office has predicted that if the build-up of CO_2 continues at current rates, CO_2 concentrations in that atmosphere will have passed 560 mg. kg^{-1} by 2060. This is significant in relation to CH_4 in that the abundance of methanotrophic bacteria of both the *Methylosinus* group (class *Alphaproteobacteria*) and the *Methylosarcina/Methylobacter* group (class *Gammaproteobacteria*) group were shown to be significantly reduced (by 70%) in samples of soil from locations with a CO_2-enriched atmosphere (Kolb *et al.* 2005). In addition, a substantial reduction in CH_4 consumption by soil microbes has been observed when CO_2 levels are elevated (Phillips *et al.* 2001). Data from the study indicated a 30% decrease in CH_4 consumption in woodland soils, related to increasing atmospheric CO_2 levels, which would substantially reduce the sink strength of these environments leading to positive feedback on the greenhouse effect. This phenomenon could be explained by data showing that soil moisture strongly predicted variability in CH_4 uptake by soil microbes (McLain *et al.* 2002), where CH_4 sink ability is probably inhibited by moisture-restricted dissemination of both CH_4 and O_2 into the soils. Interestingly, Zhuang *et al.* (2004) have also observed that root exudate alterations, connected to climate-induced augmentation of plant growth, can likewise elevate CH_4 release due to these exudates enhancing the bioavailability of carbon and thus consequently enhancing methanogenesis. Although it appears that elevated CO_2 levels increase the release of CH_4 from rice paddies in the shorter term, the effect of elevated CO_2 levels on CH_4 emissions can change over time, indicating the flexibility of CH_4-emitting microbes (Tian *et al*. 2024). In this regard, Yu

Table 2: Summary of the effectiveness of various strategies to mitigate CH_4 emissions

Strategy to reduce CH_4 emissions	Effectiveness of strategy	References
Regeneration of natural forests following land-use change	More than a hundred years for the CH_4 sink potency of forested soils to recover	(Smith *et al*. 2000)
Soil aeration of agricultural soils	Boost methanotrophic activity and CH_4 uptake	(Davidson *et al*. 2024)
Reforestation of native woodlands	Around 50 years required after reforestation before significant increases in CH_4-oxidation occurs	(Nazaries *et al.* 2011)
Reestablishing degraded land back to native vegetation	Little effect on CH_4 flux	(McDaniel *et al*. 2019)
Short-term draining practices in rice paddies carried out numerous times	A large flush of CH_4 directly following each drainage, followed by a rapid reduction in CH_4 flux	(Yagi *et al.* 1997)
Keeping the soil dry during the non-growing season in rice paddies	Substantial decreases in CH_4 emissions	(Cai *et al*. 2000; Xu *et al*. 2003)
Addition of organic fertilisers such as straw and pig manure to rice paddies	Increased CH_4 emissions	(Bossio *et al.* 1999)
Addition of pig slurry to rice paddies before seeding followed by nitrogen-rich topdressing	No increase in CH_4 emissions, therefore, may be a good option for replacing artificial fertilisers without compromising sustainability	(Moreno-García *et al*. 2020)
Addition of ammonium sulphate fertilizer to rice paddies	Inhibits methanogenesis by promoting the increase of sulphate-reducing bacteria	(Neue 1997)
Nutritional interventions for livestock include concentrates, supplementation of oils to the diet and optimising protein intake	Can reduce CH_4 emissions but add to feed costs	(MacHmüller *et al*. 2000; Clark *et al*. 2023)
Halogenated compounds added to cattle feed inhibit methanogenic bacteria	Effects of adding these compounds are only transitory	(Nevel and Demeyer 1992)
Propionate precursors (fumarate or malate) added to cattle feed	Large quantities are required to be effective	(Newbold *et al*. 2005)
Addition of red seaweed (*Asparagopsis taxiformis*) to cattle feed	Reduction of enteric CH_4 generation by over 80%	(Roque *et al*. 2021)

et al. (2022) observed that long-term (> 10 years) CH_4 release from rice paddies declined due to the enhancement of CH_4 oxidation, in addition to reduced production of CH_4. Further studies using a multifactorial approach across different ecosystems to consider the synergistic or antagonistic effect of all these variables such as temperature, precipitation and CO_2 concentrations on microorganism-mediated CH_4 flux are however required. In this regard, (Wang *et al.* 2024) evaluated CH_4 fluxes from rice paddies under conditions of both raised temperatures and elevated CO_2 concentrations and observed an increase in methanogenesis with higher CO_2 concentrations, which was especially noticeable with concomitant elevated temperatures.

Managing microbial communities to reduce CH_4 emissions

Reducing CH_4 emissions is an important aspect of lessening the impacts of global warming. Since methanotrophs are responsible for the biological oxidation of CH_4 both directly from the atmosphere and from the soil, it may be theoretically conceivable to mitigate a substantial share of global CH_4 discharge by managing these microbial communities in various environments. Table 2 provides a summary of the effectiveness of various strategies to mitigate CH_4 emissions by managing microbial communities.

Worldwide, previous solutions to the ongoing task of producing additional food have been to transform natural environments into agroecosystems, although concerns regarding the sustainability of these practices are now being raised. These concerns include questions regarding increases in soil greenhouse gas release due to changes in land use. Calculations have shown that the global soil CH_4 sink has declined by approximately 71% due to the transformation of natural soils for agricultural use, indicating the significant effect of land use change on greenhouse gas emissions (Smith *et al*. 2000). Soil compaction by livestock or agricultural machinery drives CH_4 flux towards becoming a net source of CH_4, by decreasing soil macropore sites and exacerbating soil anoxia (Sitaula *et al*. 2000; Liu *et al.* 2007). Methane oxidising bacteria are stratified in soils depending on the CH_4:O_2 ratio (Reim *et al*. 2012) and after disturbance of soils due to compaction or tillage, it may take a long time for the spatial distribution of the methane oxidising bacteria community to re-establish. A study has estimated that it could take more than a hundred years for the CH_4 sink potency of forested soils in Northern Europe to recover from disruption because of land-use change (Smith *et al.* 2000). Methane oxidising bacteria populations appear to recover over time in afforested soils owing to decreased compaction, improved water-filled pore space and lower concentrations of ammonium (Hiltbrunner *et al*. 2012). Davidson *et al*. (2024) have suggested that soil aeration is one of the best ways to boost methanotrophic activity in agricultural soils.

Changes in land use management have been shown to influence CH_4 oxidation by altering the composition of the methanotrophic community (Ojima *et al.* 1993). In addition, land use change has been shown to elevate CH_4 variability while reducing the strength of the CH_4 sink in upland topsoil (Nazaries *et al.* 2011). About 30–50% of the terrestrial CH_4 sink consumed by methanotrophs occurs in temperate forest soils (Ojima *et al*. 1993) but logging and deforestation alter these forest soils from a net absorber of CH_4 to a net emitter (Keller *et al*. 1990; Zerva and Mencuccini 2005). In a study by Nazaries *et al*. (2011) on volcanic soils in New Zealand, CH_4 oxidation was determined following the reforestation of native woodlands after being burnt. Their results indicated

that the establishment of a methanotrophic community is required before significant increases in CH_4-oxidation rates could occur and that around 47 years may be required after reforestation to reestablish a stable community of methanotrophic organisms comparable to that of an established native forest. These results suggest microbial control of CH_4 changes and identify the requirement to account for this response to afforestation and reforestation in predictions of CH_4 emissions (Nazaries *et al.* 2011). A meta-analysis conducted by McDaniel *et al.* (2019) proposes that reestablishing degraded land back to native vegetation would however have little effect on CH_4 and N_2O flux.

In flooded soils such as rice paddies, the breakdown of organic matter in waterlogged rice paddies generates CH_4 where oxygen transfer in saturated soils increases methanogen activity (Lakhani *et al.* 2017). Although temporary draining methods carried out numerous times during the immersion of rice paddies produced a large flush of CH_4 directly following each drainage, a rapid reduction in CH_4 flux followed this (Yagi *et al.* 1996). These results demonstrate that CH_4 emissions from rice paddies can be significantly lowered using short-term draining practices and that a key strategy for mitigating CH_4 emissions from these fields is the enhancement of water management practices. In addition, keeping the soil dry during the non-growing season substantially decreases emissions of CH_4 from cultivated wetland rice soils (Cai *et al*. 2000; Xu *et al.* 2003). During the development of practices to lessen CH_4 release from rice paddies and other similar environments, it is also important to consider that practices focussing on mitigating CH_4 release can result in increases in the release of other greenhouse gasses such as N_2O (Lagomarsino *et al.* 2016), although N_2O does have a much lower GWP than CH_4.

Another promising option to reduce CH_4 release from rice paddies is to alter the management of organic materials by stimulating aerobic decomposition by composting into the soil during the non-growing season when the fields are drained (Yagi *et al.* 1997). The types of fertilisers used in paddies can also influence CH_4 emissions where CH_4 emission is significantly higher in paddies fertilized with organic manures compared to those treated with chemical fertilisers (Traore *et al.* 1999). The addition of organic fertilisers such as straw and pig manure has been shown to increase CH_4 emissions owing to the additional carbon input (Bossio *et al.* 1999). Moreno-García *et al.* (2020) applied pig slurry as an alternative to mineral fertilisers to rice paddies in Northern Spain and observed that the addition of large amounts of pig slurry before rice seeding in soils with lower organic matter content amplified CH_4 release when compared to mineral fertilization. Conversely, the addition of pig slurry before seeding followed by nitrogen-rich topdressing to complement the crop needs did not result in increased CH_4 emissions. These data led the authors to conclude that organic fertilisers such as pig slurry may be a good option for replacing artificial fertilisers without compromising the sustainability of growth in rice fields.

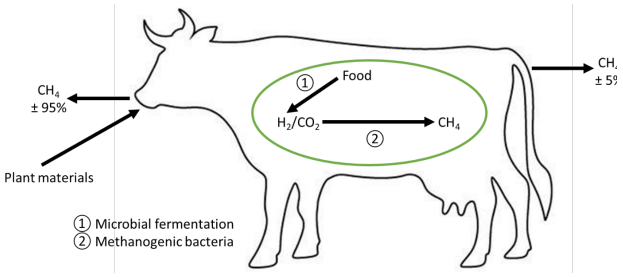

Fig. 3: Methane production in ruminants by methanogenic bacteria

Although greater fertilization with nitrogen has also been shown to inhibit CH_4 uptake by impeding the activity of methanotrophs (Wang and Ineson 2003), the inhibition of methanogenesis using fertilisers such as ammonium sulphate promotes the increase of sulphate-reducing bacteria at the expense of methanogenic species (Neue 1997). Taken together, these data suggest that the application of different types of fertilisers to rice paddies can substantially influence CH_4 emissions from these environments, although further studies on the replacement of chemical fertilisers with organic fertilisers are still required.

With regards to ruminant livestock, emissions of CH_4 are largely from the breakdown of organic materials anaerobically *via* bio-methanogenesis, where the CH_4 produced in the rumen is absorbed across the intestinal wall into the blood and moved to the lungs where it is expelled. In ruminants, methanogens utilise H_2 and CO_2 to produce CH_4 as shown in Fig. 3.

Methane release from ruminants decreases nutrient utilization efficiency, making it important to manipulate the rumen microbial environment to lower emissions of CH_4, serving the dual purpose of augmenting the productivity of the animals while also reducing CH_4 impact on global warming. The management of the ruminal hydrogen pathways has been shown to provide the potential to control or manipulate ruminant CH_4 emissions (Tseten *et al*. 2022). Nutritional intervention strategies to reduce CH_4 emissions from livestock include using concentrates, supplementation of oils to the diet (MacHmüller *et al.* 2000), optimising protein intake (Clark *et al.* 2023) and improving pasture quality. The addition of dietary additives that affect methanogenic bacteria in the rumen has also been proposed as a possible agent to reduce CH_4 emissions.

Halogenated compounds inhibit methanogenic bacteria (Nevel and Demeyer 1992), but often their effects are only transitory and while a decrease in CH_4 emissions has been observed with probiotics such as yeast cultures, these are often only non-significant reductions (McGinn *et al*. 2004). Propionate precursors such as fumarate or malate serve as alternate hydrogen acceptors and cut down CH_4 generation (Newbold *et al*. 2005), but large quantities are required to obtain a notable response, making this an expensive option. The addition of red seaweed (*Asparagopsis taxiformis*) to cattle feed was shown to

reduce enteric CH_4 generation by over 80%, suggesting that this is a potential additive to animal feeds that could substantially reduce the carbon footprint of cattle (Roque *et al.* 2021). Red seaweed contains structural analogues of CH_4 called bromoform, which inhibits the generation of CH_4 by inhibiting the final stage of methyl relocation by the MCR complex. Finally, hormonal products such as bovine somatotropin can reduce CH_4 emissions through effects on animal metabolism. Cattle breeding programmes focused on host genetic factors that alter microbial responses are potential strategies for reducing CH_4 emissions from cattle. The goal would be to develop livestock that maintains microbial communities emitting less CH_4 without compromising the animals' well-being and productivity. Since concentrations are too low for economical capture, CH_4 capture from ruminant housing is not, however, deemed a feasible option to reduce CH_4 emissions from livestock.

Other potential benefits of methanotrophs

Due to the abundance of excess CH_4 in certain environments and industries, the conversion of CH_4 into high-value end products has gained significant attention. While landfill sites are significant sources of CH_4 production, across the world, many sites now routinely gather CH_4, which can then either be used for on-site electricity generation, or the CH_4 can be piped directly into the local gas supply network, providing the benefit of reduced CH_4 emissions while also avoiding the use of fossil fuels. Adding cover soils to landfill sites is an effective technique for enhancing CH_4 removal since this provides soil for methanotrophic microbes to flourish (Nisbet-Jones *et al*. 2022). The anaerobic digestion of various organic materials and wastes can exploit methanogenesis for CH_4 harvesting, avoiding the release of gasses such as N_2O and CH_4 that occur when these materials are applied to soils He *et al*. (2023) identified the methanotroph *Methylotuvimicrobium buryatense* as a good candidate for CH_4 removal at emission sites such as anaerobic digestors, gas wells and landfills since this species demonstrates rapid CH_4 uptake, even at low CH_4 concentrations.

Methanotrophs could also be employed for the bioconversion of CH_4 into bioplastics, methanol, ectoines, exopolysaccharides and single-cell proteins (Zappi *et al.* 2020; Guerrero-Cruz *et al*. 2021), in addition to being used to produce useful compounds such as vitamin B12, biopolymers, organic acids and short-chain fatty acids using CH_4 as the carbon source (Strong *et al*. 2015; Comer *et al.* 2017). The production of single-cell proteins from methanotrophs, utilized for animal feed in agriculture, is possible using CH_4 from natural gas (Wang *et al*. 2020). As an added advantage to reducing CH_4 emissions from rice paddies, it has also been shown that certain methanotrophs, including genera such as *Methylobacter*, *Methylomonas* and *Methylocucumis* can be utilized as bio-inoculants for rice agriculture, significantly reducing nitrogenous fertilizer requirements (Cao *et al*. 2022; Mohite *et al*. 2023).

Methanotrophic bacteria offer significant potential for remediating polluted locations (Ahmadi and Lackner 2024), and are known to degrade chlorinated and halogenated hydrocarbons (Lee *et al*. 2006; Le *et al.* 2021) and persistent organic pollutants such as pentachlorophenol and trichloroethylene (Fenibo *et al*. 2023) which act as major aquatic contaminants. Since the oxidative degradation of persistent organic pollutants by methanotrophs only generates very low levels of toxic intermediates, this is a substantially more sustainable approach to treating contaminated water sources, compared to reductive dehalogenation pathways utilized by other microbes (Dutta *et al.* 2022).

Conclusions

The effects of climate change are complex and far-reaching, affecting nearly every aspect of life on Earth. Immediate action is therefore necessary to reduce the emissions of greenhouse gasses before they become irreversible. Global warming is widely recognized as the leading environmental challenge currently facing the world, and mitigating its effects is a priority for many countries. The advancement of innovative approaches to lower CH_4 release from all key emitting sources is required, and a significant opportunity exists to reduce the rate of the warming of the planet by the middle of this century. A study by Ocko *et al*. (2021) has estimated that implementing these mitigation strategies to reduce CH_4 emissions could slow down the rate of warming by approximately 30% and potentially avoid 0.25^{o}C of additional global-mean warming by 2050. The Climate and Clean Air Coalition (https://www.ccacoalition.org/) claims immediate and long-lasting benefits for climate, agriculture, and human health by reducing CH_4 emissions by 45% by 2030. Mitigation efforts at this level could potentially prevent 255,000 deaths from cardiovascular and respiratory diseases, 26 million tons of crop losses, the loss of 73 billion work hours as a result of heat exposure and 775,000 asthma-related hospital visits every year, which would equate to a global saving of approximately US$ 470 billion annually.

Studies on microorganisms and their role in climate change are limited, even though potential changes in microbial biodiversity and processes could play a crucial role in modulating emissions of many greenhouse gasses. Although microorganisms in some instances contribute negatively to climate change, they correspondingly have the potential to make an immense contribution to mitigation efforts. Many factors influence the balance of microbes acting as a sink or consumer of greenhouse gasses. As discussed in this review, temperature, CO_2 levels and precipitation have all been shown to have a profound effect on the ecology of methanogens, although it may be

theoretically possible to mitigate a considerable portion of global CH_4 emissions by managing microbial communities in various environments by reviewing land use and farming management practices. Recommendations include improving conditions for methanotrophic activity, such as oxygenation in wetlands, to increase CH_4 uptake, managing water levels or adding organic amendments to rice paddies to reduce CH_4 emissions and including methanotrophic biofilters on landfills to oxidize CH_4 as it escapes from decomposing organic matter. Future research thrusts in this area could include the design of genetically engineered methanotrophs, using CRISPR or other synthetic biology techniques, to increase their CH_4 uptake rate or expand their environmental tolerance, making them more effective in diverse conditions or using advanced molecular and bioinformatics tools to profile methanotroph communities, and explore how these organisms adapt to environmental changes. In addition, the feasibility of deploying methanotrophs in specific environments to reduce CH_4 emissions still needs to be assessed, considering the scalability and potential environmental risks of such an intervention.

Therefore, although microbes offer significant prospects for alleviating many of these human-induced issues, further multifactorial studies assessing environmentally relevant conditions are still required to further elucidate these processes since what we have currently learnt in this field is incomplete and often very difficult to interpret. An ongoing effort is therefore needed to overtly incorporate microorganisms in future technology and policy developments.

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Author Contributions

SMT conceptualised, designed, and wrote the manuscript. TER revised and finalised the manuscript. Both authors read and approved the final manuscript.

Conflict of Interest

No potential conflict of interest was reported by the authors.

Data Availability

No new data were generated during this study.

Ethics Approval

Not applicable.

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