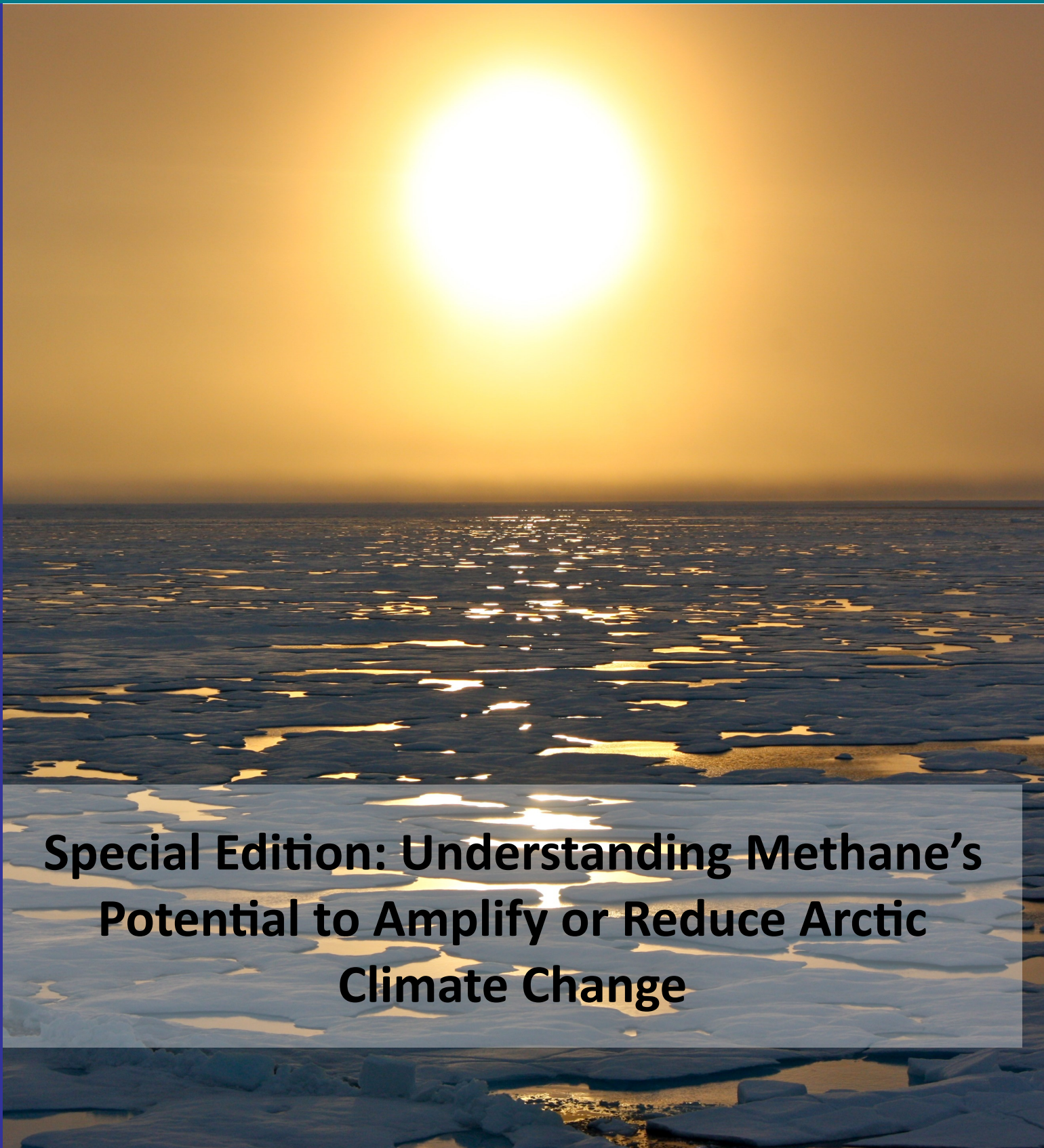




CLIMATE ALERT

A Publication of the Climate Institute | *Protecting the balance between climate and life on Earth*



Special Edition: Understanding Methane's Potential to Amplify or Reduce Arctic Climate Change



A MESSAGE FROM THE CHIEF SCIENTIST *METHANE—THE OTHER CARBON-CONTAINING GREENHOUSE GAS*



Commentary by
Michael MacCracken

With good reason, significant attention is being devoted to sharply cutting emissions of carbon dioxide (CO₂). In general, emissions result from combustion of coal, oil, and natural gas (together, fossil fuels) to provide energy and, somewhat less importantly, from clearing of land for agriculture, wood products, and communities. Using fossil fuels in particular transfers carbon that has been tied up underground for tens of millions of years to the coupled atmosphere-upper ocean-living biosphere system, which leads to an uptick in the atmospheric concentration. As a significant fraction of this will persist for millennia, and somewhat less for much longer, its implications are concerning.

Just this March, the CO₂ concentration at the Mauna Loa Observatory in Hawai'i reached 400 ppm, up over 40% above its preindustrial baseline. Stabilizing the atmospheric concentration, much less bringing it back down, will require essentially cutting emissions to zero. The longer this takes, the higher the elevated CO₂ concentration will be, the longer it will persist, and the greater the climate change and associated impacts will be. On first sight, the intensifying impacts would seem to be large enough to merit strong near-term steps to cut emissions. However, the fact that fossil fuels provide roughly 80% of the energy providing food, energy, and other services for the 7 billion people on the planet means that the use of fossil fuels cannot simply be ended. In order to do that,

we first need to find an alternative means for securing the services that fossil energy has been providing and more, given the continuing growth in the global population.

The global average temperature is now up about 0.9°C over its preindustrial average and projected to rise further with the onset of the strong El Niño that appears to be emerging. Furthermore, the rate of sea level rise is accelerating due both to additional melting of the Greenland and Antarctic ice sheets and greater uptake. Coupled with the likelihood and intensity of extreme weather increasing, the rate the world's nations are proposing to cut emissions is so modest that it will not lead to a slowing of the rate of warming until well into the second half of this century. By that time, the increase in global average temperature is projected to be over 2°C and still rising. This means that we will be headed to well above the level of temperature increase that international leaders have agreed will cause, based on solid scientific results, quite disruptive impacts on the environment and society.

So what, if anything, can be done? To simplify the analyses for the negotiation process, the warming effects of the emissions of non-CO₂ species have been combined together to create a CO₂-equivalent (CO₂e) concentration based on the relative strengths of their warming influences, integrated over a 100-year period. This approach to approximating how climate models treat the full chemistry and warming influences of each individual gas was adopted a quarter of a century ago, when there were expectations that

nations would by now be well along in cutting their emissions. Unfortunately, that has not been the case. In the search for emissions pathways that could contribute to a near-term slowing of the overall greenhouse warming influence, we now have to go back and separate out the distinct roles and lifetimes of each individual greenhouse gas and type of warming or cooling aerosol. Continuing to use the hundred-year Global Warming Potential (GWP-100) would be obscuring potentially effective policy options.

Recognition of this emerged almost a decade ago in leading elements of the scientific community at the NASA Goddard Institute for Space Studies and a bit later in our studies here at the Climate Institute (see <http://www.climate.org/topics/climate-change/maccracken-proposal-north-south-framework.html>). The benefits of a plausible set of actions were further studied in detail in a 2011 international assessment sponsored by the United Nations Environment Programme and World Meteorological Organization (published as Shindell, et al., *Science*, volume 335, pages 183-189, 2012). These studies all made it very clear that achievable reductions in emissions of methane, black carbon and the precursors of tropospheric ozone, all species that have a relatively short atmospheric lifetime, could reduce the projected warming by ~0.5°C, which is about half of the projected warming from the present out to 2050. This would be a very important contribution to slowing the pace of global warming while at the same time providing a number of benefits for human health, energy efficiency, and cleaner



air. Recognizing the importance of such efforts, Secretary of State Hillary Clinton with UNEP and representatives of five other nations launched the Climate and Clean Air Coalition (<http://www.ccacoalition.org>) in 2012; it is now a growing international effort to pursue reductions in the emissions of these species.

For the past several years, the Climate Institute has been encouraging efforts that will cut emissions of these short-lived species. The most far-reaching has been our contribution to the development of a new methodology for life cycle analysis (see <http://www.leonardoacademy.org/programs/standards/life-cycle.html>). This methodology would accurately account for the effectiveness of cutting emissions of methane, black carbon, and other species contributing to climate change in limiting global warming, as well as more fully treat related environmental and health-related influences. We also published a special edition of *Climate Alert* (<http://www.climate.org/publications/Climate%20Alerts/Autumn2009.html>) on black carbon, and coordinated with Rotec on their efforts to install black carbon controls on jeepneys in Manila and trucks in Xian. We furthermore participated in the development by the international Gold Standard Foundation in the establishment of a methodology for accrediting emissions reductions from clean stove replacement programs in India and other nations.

With this issue of *Climate Alert* we focus our attention on methane. There are a number of very important and effective actions that can be taken to limit emissions from human

activities. Some include tightening up emissions from oil and gas operations (as EPA is working on with new rules), capturing emissions from waste disposal and sewage sites, and reducing emissions from the agricultural sector (e.g., from feed lots, chicken and pig operations, etc.). Even taking these actions, the atmospheric methane concentration seems likely to remain roughly 1000 ppb above its preindustrial level of about 750 ppb, and could become even higher if thawing of permafrost and clathrates leads to an increase in natural emissions. With the per mass effectiveness of methane as a global warming agent being as much as a factor of 100 times that for CO₂ over a 20-year period, exploring possible options for pulling the methane concentration down is worthy of exploration. As a basis for such analysis, it is vital to understand the natural sources and sinks of methane and the processes and factors that influence them.

This is what Lyle Zimmerman and Brooke Labonte cover in the accompanying article in this issue. A biologist with undergraduate and masters degrees from Stanford and a Ph. D from MIT, Dr. Zimmerman established and led his own research group at the UK MRC National Institute for Medical Research in London. An Arctic Fellow with the Climate Institute, he has led the Climate Institute's study of the methane cycle and especially the role of methanotrophs (methane consuming bacteria and archaea) in limiting damage from both human-generated and naturally occurring methane emissions. His co-

author Brooke Labonte, a Climate Institute Arctic Intern, is a recent graduate of Ryerson University in Toronto, Ontario, where she studied Geographic Analysis and Environment and Urban Sustainability. Their article highlights the importance of the methane cycle in present and future climate and the many uncertainties in our understanding of this cycle, especially the role of methanotrophs, and recommends research to fill these gaps in our understanding.



CLIMATE CHANGE AND THE MICROBIAL METHANE BANQUET

BY LYLE ZIMMERMAN & BROOKE LABONTE



- Methane is a powerful greenhouse gas, second only to CO₂ in importance, with increasing production from human activities as well as imminent releases from thaw of vast Arctic deposits
- Methane's brief atmospheric lifetime makes it especially important for addressing warming in the critical next few decades.
- Specialized microorganisms dominate the global methane cycle.
- Key classes of microbes that consume vast quantities of methane remain unidentified and virtually unstudied.

Overview

A sudden increase in atmospheric methane presents one of climate change's more frightening possible tipping points. As the principal component of natural gas, methane is increasingly replacing coal and petroleum as an energy source, but its participation in the global carbon cycle reaches far beyond its role as a fossil fuel. Second in importance only to the much more abundant CO₂ as a climate-warming greenhouse gas, methane (CH₄) currently contributes ~14%¹ of man-made atmospheric 'radiative forcing' (greenhouse warming). Ubiquitous microbes are ultimately responsible for both creating and consuming most of this powerful greenhouse gas, but science is only just beginning to identify and understand the basic biology of these vital-

ly important microorganisms.

Methane is terrifying not only due to increasing industrial and agricultural emissions, which have nearly tripled atmospheric methane concentration since 1750, but also because of the potential for enormous releases from natural carbon reservoirs beneath Arctic permafrost where warming is occurring most quickly. The prospect of retreating ice belching a globe-altering dose of this potent greenhouse agent has been highlighted by the sudden appearance of deep craters on the Yamal peninsula in Siberia, probably from subterranean methane build-up, and the observation of fields of methane bubbles off the Siberian coast and in arctic lakes.

Methane's physical properties and atmospheric variations throughout Earth's climatic history are fairly well documented. However, relatively little is known about the microbial organisms and processes that are responsible for ~85% of global methane production and ~60% of its consumption.

These specialized methane-making and -consuming single-celled life forms are found nearly everywhere in Earth's waters and sediments/soils. Better understanding of their complex ecologies and response to climate change and other anthropogenic pressures is badly needed. Whether or not these microbial ecologies can be harnessed for climate mitigation, learning more about them is essential for avoiding poor decisions that might inadvertently exacerbate warming.

The Deepwater Horizon Bacterial Buffet

2010 saw an eye-opening demonstration of the microbial response to methane in the Gulf of Mexico. The largest oil spill in history occurred about 1500 meters below the surface as the Deepwater Horizon drilling rig blew out. In addition to oil, about a half million tons of natural gas, mostly methane, was released on the seafloor. If that methane had all bubbled up to the atmosphere, it would have added about 1% to the annual global production in a single dose.

Fortunately, fossil fuel companies aren't alone in noticing that methane can be an energy source, and evolution has had a head start of a few billion years. Recent research has shown that methane-eating microbes (methanotrophs) are virtually ubiquitous both on land and in the sea. They are even capable of removing methane from the atmosphere at very low concentrations- literally eating it out of the air- as well as consuming enormous amounts seeping from marine sediments and even abrupt well blowouts like the Deepwater Horizon spill.

Under pressure at depth, methane rising from the Deepwater Horizon wellhead dissolved in seawater, with very little immediately reaching the atmosphere (**Figure 1A**). Instead, the dissolved gas appears to have triggered dense local blooms of specialized methane-eating bacteria. These bacterial plumes spent several months gorging on this methane buffet and then mysteriously disappeared, leaving behind a trail of nutrient and oxygen depletion in the local waters (**Figure 1B**) signifying high rates of bacterial metabolism in the presence of a concentrated methane food source (**Figure 1C**) {Kessler et al., 2010, Shiller & Joung 2012}.

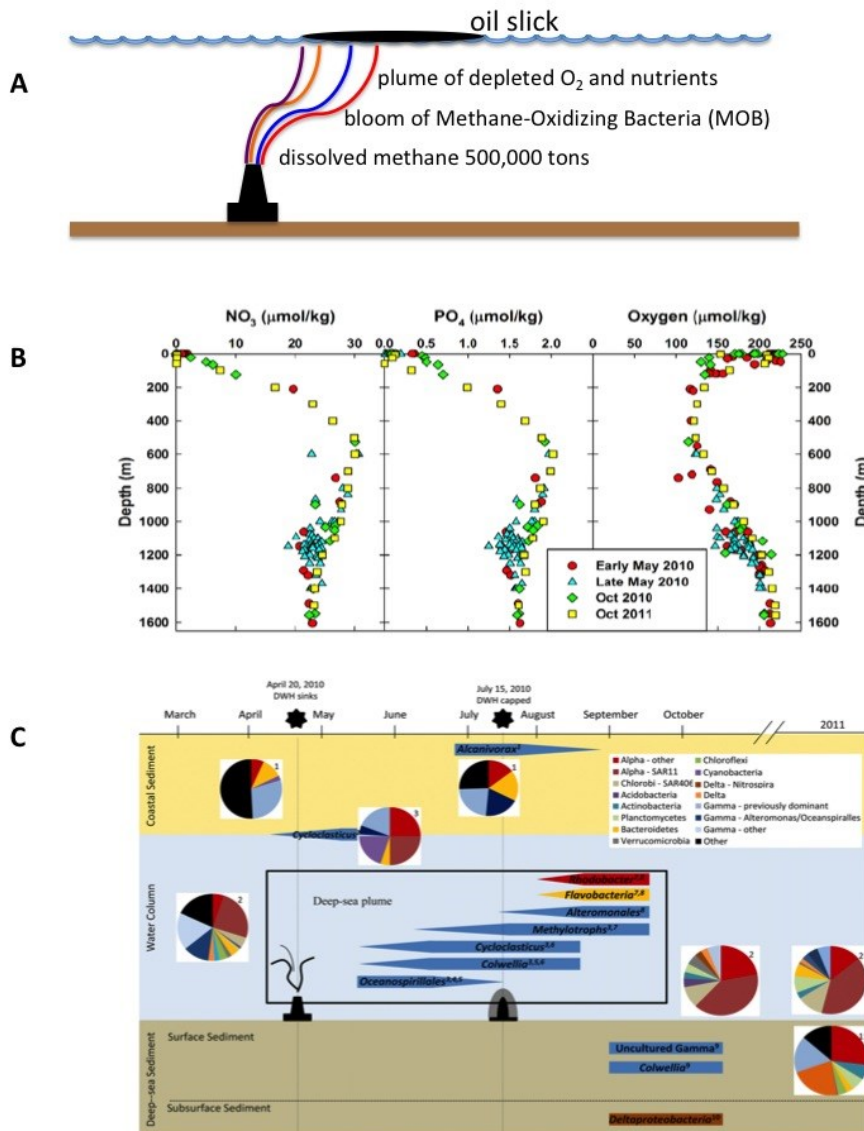


Figure 1. Marine bacteria consumed much of the methane released by the 2011 Deepwater horizon well blowout event

Notably, this natural gas banquet was left unfinished, with above-normal methane levels persisting for at least the following year (Crespo-Medina et al., 2014). Researchers speculate that these intense microbial blooms may have petered out after using up dissolved oxygen in the local seawater, or depleting the nitrate or trace met-

als required for the specialized metabolism of methane. The plume of methanotrophic bacteria could also have been devoured by other microorganisms as part of the oceanic food chain, or even plundered by oceanic viruses.

While methane-eating bacteria were first described more than a century ago, the explosive growth and

voracity of the methanotrophic response to the Deepwater Horizon spill took scientists by surprise. Known and unknown bacterial species were metabolizing methane at rates 10,000 times higher than previously observed for the Gulf of Mexico, which has abundant naturally occurring seafloor oil and gas seeps and associated microbial communities. The striking capacity of microbes to cope with sudden methane releases—and the unknown factors that may limit this capacity—may have a huge role to play in a warming Earth.

Key Questions For Current Research

What do we know, and more importantly, what *don't* we know about how methanotrophic microbes respond to potential methane releases in the warming Arctic and elsewhere?

What *are* these methane-consuming organisms (and the related microbes that produce methane)? How do they function biochemically and ecologically in various environments, and what factors limit their methane-consuming activity?

How will climate change affect or constrain the microbially-mediated global methane cycle?

Are there ways we can help methanotrophic microbes consume gas more efficiently to reduce dangerous methane build-up in the atmosphere?

Bugs, Sources, and Sinks: Methanogens and Methanotrophs in the Global Methane Cycle

Methane (CH₄, a single carbon atom tightly bound to 4 hydrogen atoms) is a naturally-occurring greenhouse gas. All gases with more than three atoms

can absorb and re-emit infrared radiation, contributing to the atmosphere's warming greenhouse effect. Methane's carbon originally derives from photosynthetic sequestration of atmospheric CO₂ by plants. Most methane is the end product of microbial breakdown of organic material in the absence of oxygen, although some is also produced without microbial activity, by thermal cracking of hydrocarbons. Much of this production is consumed by other microbes before reaching the atmosphere (**Figure 2 Overview**); the microbial methane cycle is the focus of this article.

Once methane makes it to the atmosphere, nearly all of it is oxidized and destroyed within a decade by photochemically-produced OH⁻ radicals, forming CO₂ and water vapor. In an indirect forcing from methane, both of these oxidation products also contribute greenhouse effects, and the resulting CO₂ persists, at least in part, for many thousands of years. In the long run, the sum of this indirect forcing from methane-derived CO₂ therefore contributes more warming than direct forcing from methane itself. However, on decadal scales decreasing methane emissions has great potential for slowing the pace of global warming.

Counterintuitively, methane's potency as a greenhouse gas derives in part from its relative scarcity. Greenhouse gas molecules like CO₂ and methane both prevent heat from radiating back out to space and cause the lower atmosphere to retain it in a roughly similar way. How-

ever, CO₂ is so abundant in the atmosphere that it already traps most of the radiation at the wavelengths that it interacts with. This blocking can't get more intense at the peak spectrum, although increasing CO₂ concentration slightly broadens the absorption span and causes warming to occur at lower, warmer levels of the atmosphere. In contrast, because methane is present at a much lower concentration in the atmosphere, each incremental increase has a greater warming effect, since there is headroom at its unsaturated peak

The global balance of natural production and consumption of methane is dominated by only three groups of microorganisms:

1. the anaerobic methane-producing (methanogenic) Archaea, bacteria-like organisms found in sediments beneath the seabed, under fresh-water lakes and wetlands, and deep in oxygen-free soils;
2. their close relatives, the vitally important but virtually unknown anaerobic methanotrophic Archaea (**ANME**), microorganisms that consume methane in the absence of oxygen, particularly in marine sediments. ANME consume >90% of ocean methane (7-25% of global production), but have yet to be cultured in laboratories.
3. methane-oxidizing bacteria (**MOB**), ubiquitous soil and water bacteria that consume methane using oxygen.

These three groups of organisms determine the rate at which methane is produced, how much of it is consumed before reaching the atmosphere, and are even responsible for harvesting a significant portion directly from the air.

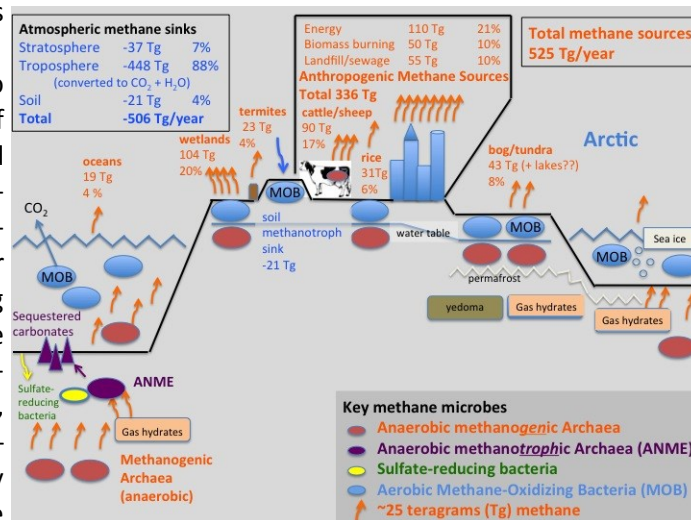


Figure 2. Global methane cycle overview

spectrum to efficiently absorb more radiation.

Since methane is a short-lived yet powerful greenhouse gas, and its concentration in the atmosphere is close to a steady state (production and destruction nearly balanced), relatively small changes in emissions have the potential to change atmospheric concentrations and quickly affect climate. This is where methanotrophic microbes play critical roles.

The Anaerobic Archaea: Methanogenesis and Methanotrophy

Single-celled organisms of the domain Archaea are one of the six kingdoms of life (along with animals, plants, fungi, protists, and bacteria). Formerly considered a subset of bacteria, genomic ancestry analysis now groups them as distant relatives (**Figure 3**). They consist of the extremophiles (organisms surviving in

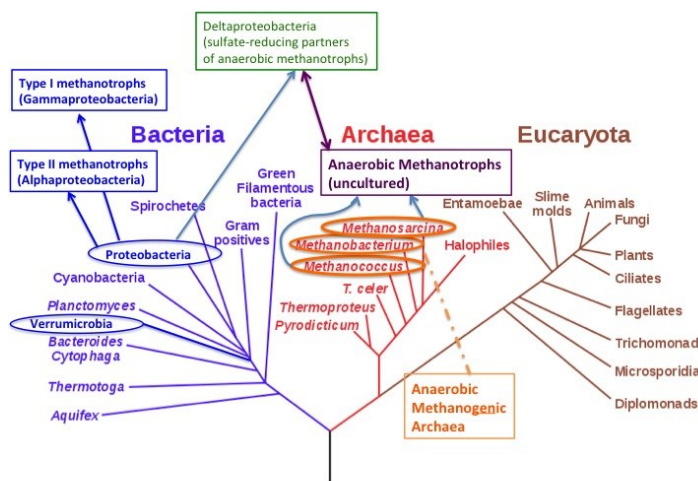


Figure 3. Tree of Life highlighting methane-consuming and methane-producing microbes

hot springs, deep sea thermal vents, and acidic or alkaline conditions) and the anaerobic methanotrophs (ANME) and methanogens. Methanogenic Archaea are responsible for producing most global methane. Neither methanogenic Archaea nor ANME can grow in the presence of oxygen, although they can survive as dormant seed populations.

Archaeal methanogens produce methane virtually wherever there is organic material to digest in the absence of oxygen- in sediments hundreds of meters beneath the seafloor, in lake bottoms and the saturated soils of wetlands and ricefields, as well as in the guts of termites and ruminant animals such as cattle and sheep (and to a lesser degree in other animals, including humans).

The key enzyme in the final step of methane formation during microbial fermentation, methyl-coenzyme M reductase (encoded by the *mcrA* gene), is also central to the metabolism of the methane-producing methanogens' close relatives, the methane

-consuming ANME, which are principally known from seafloor sediments {Knittel & Boetius 2009}. These anaerobic methanotrophs run the same *mcrA* enzymatic reaction in reverse to obtain energy, usually using sulfate from seawater as an

electron acceptor to oxidize methane. Many ANME live in

close proximity with obligate partner sulfate-reducing bacteria (Figures 3 & 4a).

Hence, oceanic methane is produced by methanogenic Archaea in deeper marine sediments (up to 800 m beneath the sea floor) where neither oxygen nor sulfate is present. Then, as methane filters upward through to shallower sulfate-penetrated sediments (from millimetres to 200 m beneath the sea floor), more than 90% is consumed by ANME (corresponding to ~7-25% of total global methane production).

ANME were virtually unknown until the last few decades; indeed, metabolizing methane in the absence of oxygen had been thought to be bioenergetically impossible until their discovery. These organisms have still not been cultured in the laboratory, so much remains mysterious about their identity, basic biology, biochemistry and genomics. They grow extremely slowly (doubling times of weeks to months), and incorporate very little of methane's carbon into

their own biomass (in contrast to the aerobic methanotrophs).

From the perspective of greenhouse gas mitigation, ANME do exhibit an extremely useful feature. While their aerobic counterparts, the methane oxidizing bacteria (MOB, found in aerated soil and water, see below) can absorb up to about half of metabolized methane carbon into their own cellular structures, they also 'exhale' CO₂, converting a short-lived but powerful greenhouse gas into a weaker but much longer-lived one that also acidifies ocean waters.

In contrast, many ANME convert carbon from methane into carbonate, which reacts with calcium in seawater and precipitates as solid calcium carbonate rock on the sea floor (Figure 4B). Where methane venting and anaerobic methanotrophy have been ongoing, large plates of microbially-

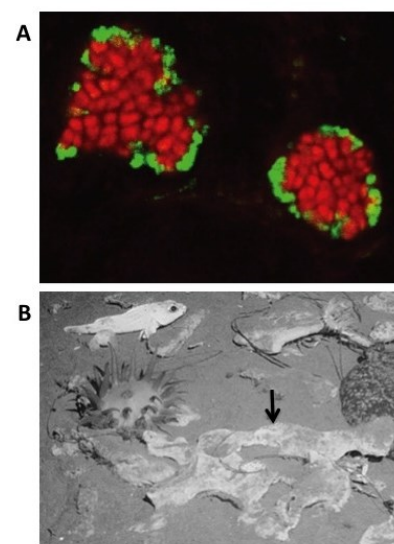


Figure 4. Anaerobic methanotrophs consume >90% of oceanic methane

derived calcium carbonate can be seen on the ocean bottom, permanently sequestering methane carbon away from the atmosphere rather than con-



verting it into CO₂.

They're Everywhere: Aerobic Methane-Oxidizing Bacteria

Even though the ANME filter out more than 90% of the methane produced under the sea floor, substantial amounts of dissolved gas still escape into the sea, and anaerobic methanogens also produce methane in various terrestrial environments. Once in the water column, sufficient oxygen may be present for consumption by aerobic methanotrophic bacteria.

In contrast to the anaerobic methanogens and ANME Archaea, aerobic methanotrophs or methane-oxidizing bacteria (MOB) are members of several different families of conventional bacteria in the phylum Proteobacteria and the more recently-described phylum Verrucomicrobia (**Figure 3**). All of these aerobic methanotrophs base their metabolism on the enzyme methane monooxygenase (MMO) to oxidize methane (CH₄) to methanol (CH₃OH) from which energy and carbon are then harvested for cellular use. The MMO gene is a valuable tool for researchers, who can focus on this sequence to identify and analyse methane-consuming bacteria among complex water or soil microbial ecologies. The subtypes of MMO genes and their association with cellular membrane structures are used to divide MOB into Type I and Type II subgroups.

To attack the methane molecule, with its exceptionally tight carbon-hydrogen bonds, the MMO enzyme requires cofactors like iron and copper. Depletion of these or other nu-

trients like nitrates can limit methane consumption, but the principal constraints on methanotrophy are usually oxygen concentration and the availability of methane itself.

One of the features shared by nearly all methanotrophs is that they are highly specialized for growth only on methane and methanol ('obligate methylotrophy'), although some exceptions with a bit more dietary flexibility ('facultative methanotrophs') have recently been discovered. While methanotrophic bacteria exist nearly everywhere as 'seed populations' in the world's oceans and aerated soils, and their growth and ability to metabolize methane is not restricted by cold, they only bloom to greater density when methane concentrations are elevated.

Aerobic MOB can grow much more quickly than their anaerobic counterparts, and incorporate much more of the ingested methane carbon into their own cell structures. Measured ratios of (CO₂ produced)/(methane consumed) range between 0.16 to 0.4 (Borjesson et al. 2001), with the remainder converted into biomass. This high ratio of biomass production allows MOB to form successful symbiotic relationships with other organisms, particularly mussels, where methane concentrations are high, such as seafloor seeps. MOB biomass also enters the food chain through predation by other microorganisms. Depending on the food chain, some of this methane-derived bacterial biomass will also sequester carbon, at least temporarily.

Methane Hydrates, the Clathrate Gun Hypothesis, and the Microbial Silencer

'Tipping points' occur when one relatively stable state gradually accumulates a series of small changes until it becomes unstable, and then transitions rapidly to a very different stable state (rather than undergoing gradual and reversible changes between states). Such geologically sudden changes are known to have happened at various points in Earth's history, even without the virtually instantaneous atmospheric injection of fossil carbon over the last century. Methanotrophic microbes, particularly in the world's oceans, have played a vital role in buffering or recovering from at least some of these events.

One potential tipping point trigger is rapid thawing of the vast amounts of water-methane ice thought to exist at or beneath the ocean floor at low temperature and high pressure in solid form. Known as methane hydrates, or clathrates, these are thought to be largely formed from methane accumulated from biological processes (methanogenic microbes), although in the Gulf of Mexico and Siberian gas fields, clathrate methane is also derived from thermal activity.

While methane hydrates take the form of icy-looking lumps beneath the seabed, even in solid form they are lighter than water and float upwards if freed from deposits. Once above the depth limit of the 'gas hydrate stability zone' (GHSZ), they turn into methane bubbles, which in turn may dissolve in seawater or equilibrate with other sea water gases before reaching the atmosphere. The GHSZ is determined by a combination of pressure and temperature in ocean depths, with a lower boundary around 2000 meters below



the seabed limited by geothermal heat. At the other end, clathrates can exist up to around 300 meters beneath sea level along continental margins, but can be present at depths as shallow as 150 meters underwater in cold polar seas. Clathrates can also be stabilized at even shallower depths by overlying solid lids such as permafrost.

The total store of clathrates remains uncertain. Estimates derive mostly from seismic mapping using high-energy sonar and modelling, but in any case the amounts are vast--in the general neighbourhood of 5 trillion tons of methane. The atmosphere currently contains about 3 billion tons of methane, so even release of a tenth of the clathrate methane in a short period would have an effect on the Earth's radiation budget equivalent to increasing CO₂ tenfold (Archer 2007). The 'clathrate gun hypothesis' suggests that sudden warming in the geological past may have been triggered by such sudden releases ('methane excursions'), perhaps as a result of asteroid impacts or other physical events like submarine landslides destabilizing clathrate deposits.

Did the 'clathrate gun' go off to end recent glacial periods? Warm eras virtually always show higher levels of atmospheric methane. However, this can be an effect of warming driven by other factors rather than a cause; for instance, warmer climates often lead to large increases in methane-producing wetlands.

Methane produced by wetlands can be distinguished from marine clathrates by isotopic analysis of deuterium/hydrogen ratios. Isotope studies of ice cores from Greenland show

that large clathrate releases were probably not responsible for the sharp warming at the end of two recent cold periods-- the Older and Younger Dryas, ~14,000 and 11,500 years ago, respectively (Sowers 2006).

Furthermore, most of the global hydrate reserve is sufficiently insulated from the Earth's surface climate that large releases in response to anthropogenic climate change are likely to be slow. Modelling by Archer and others indicates human-induced warming could instigate large-scale methane releases from hydrates beneath deep temperate oceans, but these releases would occur over thousands of years. These studies suggest that the comparative slowness of clathrate breakdown would allow marine methanotrophs to consume much of the methane before it reaches the atmosphere, and that direct radiative forcing from clathrate methane will therefore probably not be a major climate driver.

However, a chronic global increase in MOB activity will have major effects on warming seas, which contain decreasing amounts of dissolved oxygen. Aerobic methanotroph metabolism would consume even more oxygen, exacerbating hypoxia from warming. CO₂ produced by MOB likewise contributes to ocean acidification. The scale of the contribution from the poorly-understood ANME, which can sequester methane carbon as carbonate rock, remains an open question.

Meanwhile, Somewhere North of Siberia... More Bacteria

The shallow, cold Arctic Ocean may be an exception to the relative resistance of undersea clathrates to anthropogenic climate change. Here, clathrate deposits can exist much closer to the surface, kept in place both by cold water temperatures, which raise the GHSZ closer to the surface, and offshore permafrost.

This solid permafrost lid formed when sea level was ~120 meters lower during the ice age, but has been gradually thawing shorewards with sea level rise following the last glacial maximum 20,000 years ago. Intense plumes of methane bubbles rising from the seabed ('flares') have been detected by sonar. In deeper waters, these bubbles both dissolve and exchange gases with seawater (reducing the methane content in bubbles). ANME in seabed sediments and MOB in the water column are both present in the Arctic, and the rate at which they consume methane is virtually unaffected by cold temperatures.

While methane dissolved in deep water can still surface and escape into the atmosphere by gas exchange, several unique properties of the Arctic Ocean limit this. Ice cover can block surface gas exchange, and many large rivers pour into the Arctic, creating a buoyant fresh water barrier floating on denser saltier water and preventing methane-saturated water mixing from below. Modelling studies indicate that MOB can oxidize available dissolved methane completely over ~50 years, with deep water eventually returning to the Atlantic (Elliot et al 2011).

However, the ability of ice and freshened surface waters to block methane-saturated deep water from atmos-



pheric exchange is finite. Rapid Arctic warming is forcing ice cover to retreat quickly, and increased storm frequency causes more mixing and dilution of the freshwater layer, allowing more methane to escape (Shakhova et al 2014). Better understanding of the factors that truncated the Deepwater Horizon methanotroph bloom is also needed. Could MOB depletion of oxygen and trace metals (iron/copper) also eventually limit the methanotroph response in the Arctic? How might the rest of the polar sea food chain respond to sustained methanotroph blooms?

Parts of the Arctic Ocean (in particular the East Siberian Sea) are so shallow that methane bubbles from the seabed can arrive at the surface relatively intact. While it is clear that methane releases are ongoing, in particular where the edge of the undersea permafrost 'lid' is thawing, at present much of this seems to be in response to post-ice age sea level rise rather than anthropogenic warming (Portnov et al., 2013, Portnov et al., 2014). Isotopic studies of atmospheric methane over northern Europe also show that clathrate methane has yet to make a major contribution, with most of the methane that makes it to the atmosphere over Northern Europe appearing to derive from gas fields or wetlands (Fisher et al., 2011).

Several studies have modelled how projected warming over the next century may affect releases of clathrate methane by lowering the GHSZ boundary in the Arctic Ocean (Biaostoch et al., 2011; Elliot et al., 2011). Models suggest that most of the methane that dissolves in saturated sediment could be consumed

by ANME, with the carbon retained within the seafloor, and most of the remainder digested by MOB in the water column. These analyses conclude that clathrate methane released due to anthropogenic warming is not likely to be a major contributor to global warming over the next 100 years.

However, these initial studies do predict that increased bacterial metabolism from rising clathrate methane could significantly deplete oxygen and lower pH in the Arctic basin, to the detriment of the ocean ecosystem. Since these are relatively early modelling studies of complex processes at the intersection of oceanography, geology and biology, the scientific understanding of these interactions may change quickly.

The Microbial Methane Cycle in Soil and Freshwater Sediments

Like marine methanotrophic bacteria, aerobic soil methanotrophs are nearly all highly specialized to use only methane/methanol as a source of energy and carbon. These bacteria are present, at least as 'seed' populations, in virtually all the world's terrestrial soils (including your back garden), but different soil environments support very different bacterial communities and methane-consuming capacities.

Soils and sediments with high concentrations of methane (up to ~100 ppm), such as wetlands, ricefields and landfill, tend to support dense populations of 'low-affinity oxidizers'. These include most of the MOB species that have been successfully cultured in the laboratory and about which we understand most. Although

they bind methane with low affinity, they thrive in conditions where concentrations are relatively high and consume large amounts of methane before it can reach the atmosphere.

Eating Thin Air: Upland Soil Methanotrophs

The other functional category of MOB species is the 'high affinity oxidizers', which provide the 'soil sink' for atmospheric methane. Other MOB and ANME capture and oxidize CH₄ where it is present in higher concentrations within soil on its way up from localized sources. Methane is present in the atmosphere at very low concentrations (less than 2ppmv), but high-affinity oxidizers in soil are thought to consume upwards of 20-60 million tons of atmospheric methane annually, making up 4-15% of the global methane sink).

The activity of these high-affinity MOB can be detected in most of the world's soils using molecular and biochemical methods, but these organisms have yet to be identified or cultured as pure populations in the laboratory, and their identity remains mysterious. While they are able to harvest methane at very low concentrations, they appear to grow very slowly, surrounded by thousands of varieties of other soil bacteria, possibly relying on some for metabolic services analogous to the symbiotic partnership between ANME and sulfate-reducing bacteria. Identifying the responsible high-affinity organisms for intensive study is one of the holy grails of methanotroph studies.

Although high affinity methanotrophs appear to be ubiquitous in soils, not all soils are equal. The key factor for methanotrophy in many

soils seems to be water saturation, although availability of cofactors like copper or iron and nitrogen exposure can also be important. Saturation reduces oxygen availability, which both limits aerobic methanotrophy and encourages anaerobic methanogenesis.

Thus, forest soils, well-drained by tree roots, are excellent methane consumers. Disturbed or irrigated agricultural soils perform much more poorly. According to one calculation, the conversion of natural soils to agricultural use has reduced the global methane soil sink by 71% (Smith et al., 2000). Consideration of this vital atmospheric service needs to be incorporated in land-use management and planning.

Future of Terrestrial Methanotrophy

A number of studies have addressed how the microbial methane cycle may be affected by a more carbon-rich atmosphere and warming climate (Nazaries et al., 2013; Turetsky et al., 2014). Wetlands constitute by far the largest natural source of atmospheric methane, and are expected to increase in extent with warming, both in the tropics and at higher latitudes. The activity of methane-producing Archaea is strongly dependent on water table level and temperature (in contrast to MOB methane-consuming activity, which is relatively temperature-insensitive).

The water table affects the balance of methanogenesis and methanotrophy primarily by affecting the boundary of oxygen availability beneath which anaerobic methanogenic microbes thrive on organic matter.

particularly those underlain by permafrost, are increasingly becoming recognized as critical. These soils often contain very high concentrations of carbon because of the differences in the balance of plant growth and microbial degradation.

Although plants grow slowly in arctic and subarctic conditions, much of the organic material created is buried and sequestered in permafrost, where virtually no microbial breakdown occurs. High-latitude terrain has therefore been acting as a vast carbon storage reservoir for tens of thousands of years, with permafrost carbon estimates running above 1,700 petagrams (1.7 trillion tons, or about twice the current total atmospheric carbon).

This is changing rapidly as the Arctic warms (Figure 5). Current estimates predict release of ~170 billion tons of carbon from permafrost thaw by 2100 (MacDougall et al. 2012), putting a substantial dent in the Earth's remaining cumulative emissions budget of 440 billion tons of manmade CO₂ for staying under a 2°C temperature rise. Much of the high Arctic consists of bog or muskeg, a thin layer 'active zone' of seasonally-thawed saturated soil overlying permafrost. Warming tends to increase the thickness of this thawed active zone, releasing greater amounts of stored organic material for anaerobic fermentation and methane production by methanogenic Archaea, or, depending largely on water saturation, MOB ac-

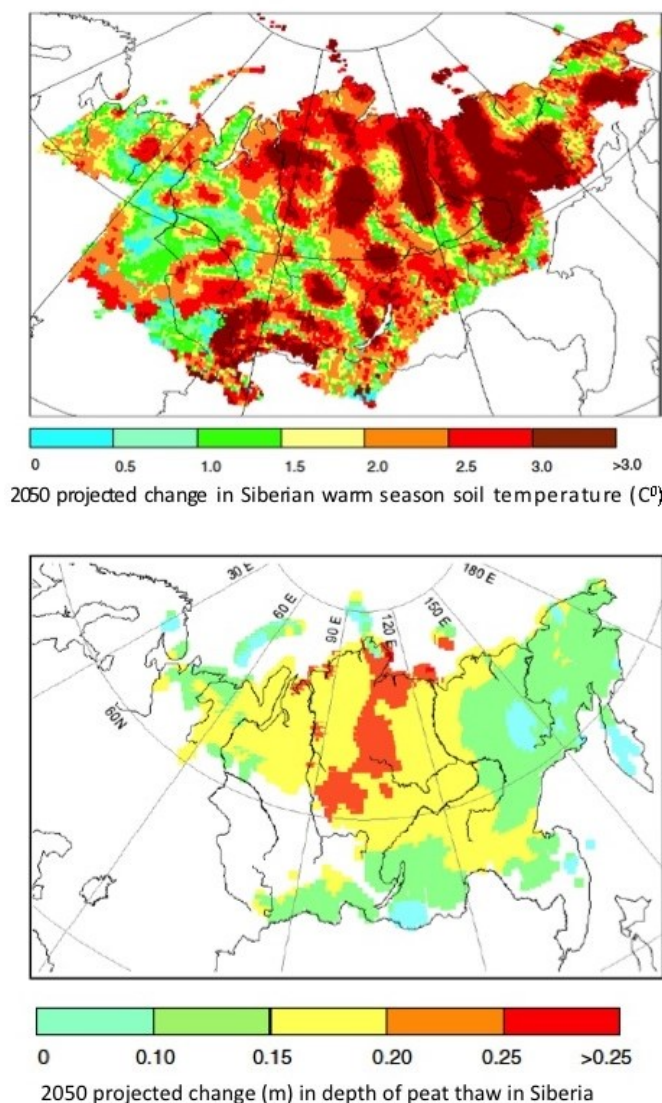


Figure 5. Projected peat thaw in Siberia

While tropical and subtropical wetlands have long been assumed to be the largest natural sources of atmospheric methane, high-latitude soils,



tivity producing CO₂.

Many analyses of global warming have assumed that arctic environments would act as a larger atmospheric carbon sink in the future, by virtue of enjoying a longer growing season and becoming more photosynthetically productive. However, other studies suggest that any gains in Arctic carbon storage from a longer growing season may be more than offset by increased greenhouse forcing from methane emissions. Thus, high latitude wetlands can act as both a net carbon sink, and a net source of greenhouse gases (Friborg et al., 2003).

How Arctic warming affects wetland extent and soil saturation is key for the methanogenesis/methanotrophy balance. The hydrology and landscape changes induced by permafrost thaw are too complex to cover here (Walter et al., 2014). Thawing results in a variety of surface structures like taliks, wetlands and thermokarst lakes, but can also lead to drainage of surface water/soils if a permafrost basement is punctured. Strategies for permafrost stabilization with methanotroph benefits are discussed below.

Managing microbes for methane mitigation

Human activities now produce the majority of atmospheric methane. Methanotrophs are vital for limiting emissions from human sources such as landfill, sewage treatment and agriculture. Other sources, such as those from fossil fuel extraction, transport and industry, are not generally accessible to microbial mitigation before they reach the atmos-

phere. One exception may be methane in coal mine ventilation, a major emissions source in many countries. At laboratory scale, open bioreactors containing methanotroph cultures can remove 70-90% of methane at concentrations typical of coal mine atmospheres (Jiang et al 2010).

Methanotrophic bacteria are already widely employed in various bioremediation processes, particularly for breaking down toxic halogenated hydrocarbons in chemical waste ponds. However, obtaining a sufficiently dense bloom of methanotrophs to oxidize these toxic compounds usually involves providing extra methane as well as oxygen, so these applications may not actually reduce emissions.

Landfills and sewage treatment facilities are also major methane sources, contributing ~55 million tons annually, or around 10% of atmospheric methane. These facilities have long intentionally utilized endogenous MOB, and research to further optimize methanotroph activity is ongoing. The same considerations as in wetlands often apply, with oxygen often a limiting factor. Forced air sources can greatly increase methane consumption and reduce emissions, but the the combination of oxygen with high landfill methane concentrations can introduce unacceptable explosion risks (Lopez et al., 2013).

Restoring Ecologies for Optimal Methane Mitigation

The basic biology of methanotrophs still holds many mysteries. Key categories of organisms, like ANME and high-affinity MOB, have yet to be

identified as species or grown in culture, limiting the application of the most powerful biochemical and genomic research tools. Laboratory engineering and large-scale deployment to combat future methane releases seems a distant prospect, or worse, a study in unforeseen consequences more suited to a Hollywood disaster movie. Attempts to artificially modify soil or water microbes for introduction into biomes near the base of environmental food chains should be treated with extreme caution.

In practice, field applications of engineered methanotrophs are likely to remain very limited. Nearly all existing methanotrophs are 'obligate methylotrophs', meaning they can only grow on methane or another single-carbon compound, methanol. Large quantities of some species might be grown under laboratory conditions, but released into the environment in the absence of enriched methane sources they would be outcompeted by other soil bacteria, and would be unlikely to respond to increases more ably than endogenous methanotrophs already present as seed populations virtually everywhere.

While the anaerobic methanotrophs (ANME) found in marine sediments play a vital role in the global methane cycle, and have the attractive ability to permanently sequester methane's carbon in the form of carbonate precipitates rather than releasing a portion as CO₂, they also have several properties that are likely to make them difficult to deploy. ANME have thus far been impossible to culture in the laboratory, and often exist in obligate relationships with other microbial species or communities such as sulfate-reducing bacteria, greatly complicating manipulations. Their extremely slow growth



rates, with doubling times of weeks to months (compared to ~20 minutes for many bacteria) also makes for ponderous engineering prospects.

Learning more about methanotrophic microbes remains vitally important despite the barriers to direct deployment for climate mitigation. Understanding the ecology of naturally-occurring methanotrophs will be essential for predicting greenhouse forcings from anticipated clathrate methane releases as oceans warm. Knowledge of methanotroph ecology will also be key for assigning values to ecosystem services from particular habitats and minimizing costly future mistakes. As mentioned above, more than half of the global capacity of the high-affinity soil sink for atmospheric methane has been lost by agricultural conversion of previously undisturbed land, particularly forests. Methane mitigation provides one more reason to aggressively combat deforestation.

Understanding and tweaking the workings of methanotrophs and methanogens in major anthropogenic sources like landfills and rice fields could also provide very large reductions in methane emissions. The very large emissions from non-managed natural sources might also be mitigated, with potential increased removal of methane directly from the atmosphere. An intriguing prospect of achieving this through addressing an ancient human environmental impact is discussed below.

Ricefields

Rice production, typically in semi-artificial wetland environments, is an important part of the food supply,

and demand is expected to rise by 65% over the next two decades with the world's rising population. Ricefields annually emit between 6% and 19% of total anthropogenic methane, but the amount produced varies widely with regional conditions and practices.

Studies have shown that one such practice, intermittent drainage of paddies, can reduce methane production by 40-48% without decreasing rice yields (Ma & Lu, 2010, Ma et al., 2013). Intermittent drainage achieves at least two things: it tips the balance away from establishing anaerobic methanogens in saturated soil and towards aerobic methanotrophs in aerated soil. Exposure to air also regenerates iron and sulfate ions from reduced forms, allowing other anaerobic bacteria to compete with methanogens for key substrates.

Ruminant farming

Domestic cattle, sheep and goats are a major anthropogenic source of methane, contributing about 90 million tons per year or ~17% of the global atmospheric source (wild ruminants are a small factor, contributing only about another million tons). Ruminant methane emissions result from an ancient symbiosis with anaerobic gut microbes, which are an essential part of the ruminant digestive strategy.

While methanogenic Archaea dominate in the guts of ruminants, some wild herbivores such as kangaroos possess similar gut anatomy but produce little or no methane, with digestion services provided by other classes of anaerobic bacteria leading to alternative end products such as ace-

tate. Some of these non-methanogenic kangaroo gut acetogens are already known to be present at low levels among the gut flora of domestic cattle (Godwin et al., 2014). Theoretically, methane emissions from cattle, goats and sheep might be driven down by encouraging the prevalence of these naturally-occurring gut acetogen bacteria at the expense of methanogenic Archaea. Understanding why these microbes succeed in kangaroo could eventually provide strategies for adapting domestic ruminant digestion.

Reforestation

Aerobic methanotrophic bacteria exist virtually ubiquitously as seed populations in almost all soils and waters, both fresh and salt. Their capacity to convert methane to biomass or CO₂ is limited by the availability of their energy/carbon source (methane or methanol), oxygen, nitrate and trace nutrients such as iron or copper.

In many terrestrial environments, the level of the water table is the critical factor determining the balance between methane production (by anaerobic methanogenic Archaea) and methane consumption/oxidation by aerobic methanotrophs. Saturated wetland soils host anaerobic methanogens; drier aerated soils contain methanotrophs. There is a hierarchy among different soil ecosystems, with upland forest soils capable of the largest amount of methane oxidation.

Non-saturated soils contain bacterial communities that not only oxidize methane released by underlying organic fermentation, but actually consume methane directly from air and are responsible for about 4% of the annual atmospheric methane budget. Differ-



ent soil ecotypes provide this service with different efficiency; boreal and temperate forests and upland grasslands are the most effective (Dalal et al., 2008). Remarkably, deforested areas can recover optimal atmospheric methane oxidation capabilities within a few decades following reforestation (Nazaries et al., 2011). Methane mitigation can be added to the long list of valuable carbon sequestration and ecosystem services provided by forests.

Breaking Bubbles

As described above, methane released at depth dissolves in the water column, and can be efficiently oxidized by methanotrophic bacteria. However, in shallow Arctic seas and lakes, large bubbles can escape directly to the atmosphere, evading oxidation by methanotrophs. In localized regions of high bubble release, it may be possible to encourage greater solvation in the water column by simple physical methods. Covering sediment with a screen or other porous material to reduce the size of bubbles will increase the surface-to-volume ratio and encourage dissolution, increasing availability for methanotrophic digestion (Stolaroff et al., 2012).

Reverse Geoengineering the Mammoth Steppe

Wetlands are the largest natural sources of methane, but in many regions they also provide essential habitat and ecosystem services. Simple ditching to drain wetlands may also be counterproductive, as ditches themselves can be highly meth-

anogenic environments.

Are there other avenues for encouraging methanotrophy or reducing methanogenesis from wetlands without increasing the human footprint on valuable natural areas? Researchers in northeast Siberia are evaluating a radical strategy whose principal goal is keeping sub-tundra permafrost carbon frozen by restoring an ancient ecosystem. As a side effect, their program could tilt the balance away from methanogenesis and towards methane consumption.

In the rapidly warming Arctic, there is deep concern about methane releases from organic material in thawing permafrost loess/yedoma (organic-rich soils with high ice content), as well as terrestrial gas hydrate deposits trapped beneath a destabilized permafrost 'lid', the likely cause of last summer's crater appearances on the Yamal peninsula. The degree to which thawed organic material produces methane, and in turn how much methane is consumed before reaching the atmosphere, depends largely on the water table. Permafrost-underlain terrain undergoes complex transitions with gradual thawing, producing thermokarst and thaw lakes and associated wetland which can also drain when the 'floor' of underlying ice layers disappears (Walter et al., 2014).

In much of the high arctic in both Siberia and Canada, permafrost is overlain by muskeg or bog. However, this appears to be a relatively recent geological feature. Up until about 14,000 years ago, during both colder ice age stadial periods as well as warmer interglacial periods, the Siberian steppe was highly productive grassland (the 'Mammoth Steppe'),

with large herbivore densities comparable to contemporary African savannahs (Zimov et al., 2012). The change from grassland to today's relatively unproductive moss-covered boggy wetland and taiga forest coincided with the disappearance of large herbivores such as mammoths and woolly rhino as well as the decline or local extirpation of extant species like musk oxen and bison.

The cause of the Pleistocene large herbivore extinctions remains controversial. Rapid warming at the end of the ice age contributed to changes in diet and habitat, but many researchers argue that overhunting by humans arriving on the steppes with new technologies was a critical factor. Regardless of the cause of the extinctions, their disappearance has been associated with the ensuing steppe-tundra transition (Zimov et al., 1995), with reduced grazing pressure leading to prevalence of mossy wetland and boggy muskeg sparse low forest.

If late Pleistocene overhunting was indeed the cause of large herbivore extinctions, then high arctic muskeg/bog is an early but large-scale feature of the human planetary footprint. In 1989, the Zimov group, based at the Northeast Science Station in Chersky, began a long-term, large-scale 'Pleistocene Park' experiment to see if this footprint can be removed (Zimov 2005), but not by cloning mammoths. In a 6 square mile enclosure in one of the coldest regions on Earth, they have begun reintroducing extant cold-adapted large herbivores like Yakut horses, musk oxen, reindeer, moose, wood bison and wapiti (elk) to see if the productive grassland steppe can be restored. Preliminary results are mixed, with poaching and adaptation-related herbivore mortality, but con-

version to well-drained, highly productive grassland occurred surprisingly quickly (Zimov et al., 2012).

The principal goal of this project is not to create a nature reserve, but is a serious attempt to test a form of reverse geoengineering for combating warming. By restoring the Pleistocene grassland steppe state from Holocene bog/muskeg, they hope to address one of the most pressing problems in contemporary climate change: carbon (and methane) emission from thawing permafrost. Light-coloured grassland has a much higher albedo than dark mossy bog or scrub taiga, reflecting more solar radiation in summer. In winter, herbivores disturb snow cover while foraging, allowing deeper penetration of cold and permafrost reinforcement (Figure 6).

The effects on microbial methane ecology are also robust. Stabilizing permafrost at shallower soil depths reduces both the bank of organic material available to methanogenic archaea and the volume of their saturated soil niche. Methanogens also produce methane much more slowly at colder temperatures in contrast to MOB, whose metabolism is relatively insensitive to cold. Draining tundra soils has been experimentally shown to reduce methane and CO₂ output (Merbold et al., 2009). Grass roots penetrate much more deeply than those of bog mosses, and have the

effect of drying out soil, creating a larger niche for methane oxidizing bacteria.

The ‘Pleistocene rewilding’ aspect of the experiment remains controversial, but the scientific analysis being applied is rigorous. In principle, the strategy could be applied to large areas of northeast Asia and North

greenhouse gas. Recent progress in understanding aspects of the biological methane cycle underlines how much we still don’t know.

Research priorities include:

- Identification and laboratory culture of high affinity methanotrophic bacteria from soil. Isolation and culture will allow biochemical and genomic analysis to understand how these organisms capture and consume methane at atmospheric concentrations.
- Identification and laboratory culture of anaerobic methanotrophic Archaea from marine sediments. Anaerobic methanotrophy remains virtually a black box despite its importance in the global methane cycle. Laboratory culture will allow detailed analysis of biochemical mechanisms and the limitations on growth and carbon sequestration.
- Quantifying anaerobic methanotroph activity *in situ* in marine sediments, in particular their ability to permanently sequester methane hydrate-derived carbon, and understanding the complex relationships they have with other microorganisms.
- Identifying factors limiting aerobic and anaerobic methanotroph growth and metabolism in marine and soil ecologies, particularly in the Arctic
- Quantifying soil methanotrophy in different ecosystem types for optimal land-use planning, especially in the Arctic
- Continuing to identify aerobic methanotrophs from different bacterial lineages, particularly fac-

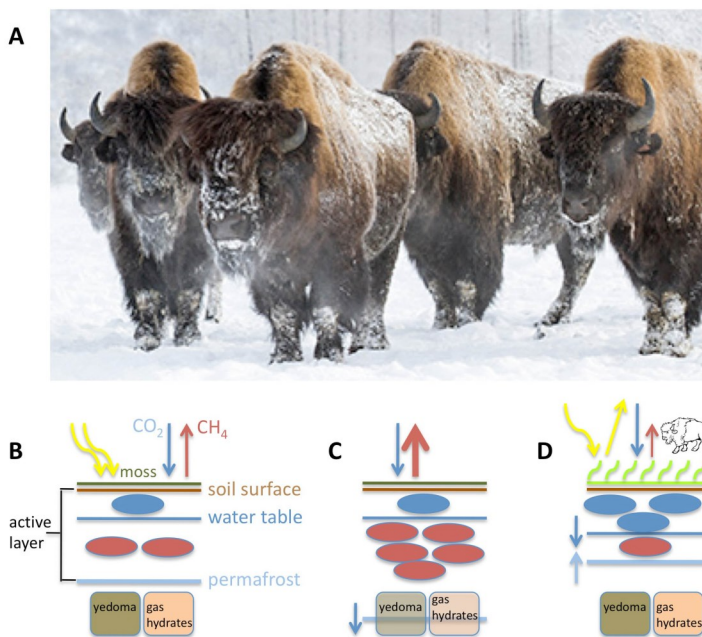


Figure 6. Restoration of the Mammoth Steppe: Can large herbivore reintroductions stabilize permafrost and reduce methane emissions?

America. Coincidentally, in April 2015 Alaska saw the reintroduction of the first wild Wood Bison herd in over a century, a subspecies that had neared extinction in North America. The scale of risk from thawing permafrost carbon demands ambitious approaches.

Conclusion

Methane-consuming microbes manage much of the global budget of the Earth’s second-most important



ultative methanotrophs, which can use alternative energy/carbon sources in addition to methane/methanol. The role of these organisms in the global methane budget remains unknown, and they may be more suitable for bioremediation and mitigation applications than obligate methanotrophs.

Footnote

1. Comparing effects of different greenhouse gases is complicated by their differing atmospheric lifespans (~9 years for methane versus centuries-to-millennia for CO₂). This calculation is based on a given quantity of methane having ~30 times stronger warming influence over a 100-year span than CO₂. Its relative influence is about 80 times stronger on a 20-year basis, so cutting its emissions is especially critical to slowing warming over the next few decades (IPCC, 2013).

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*Front cover image: Arctic sunset, taken by Kathryn Hansen, NASA
Back cover image: Polar bears, taken by Jessica Robertson, US Geological Survey*

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