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Perspective

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Viability of enhancing methanotrophy in terrestrial ecosystems exposed to low concentrations of methane

Eric A. Davidson [1,2] ✉, Danielle R. Monteverde [2] & Jeremy D. Semrau[3]

Methane is a potent but relatively short-lived greenhouse gas, with anthropogenic and natural sources and rapidly increasing atmospheric concentrations. Hence, it is an important target for reducing emissions and increasing sinks, as doing so could notably reduce rates of climate change in the near-term. This includes potentially enhancing methanotrophy, a microbial process of methane oxidation that occurs broadly in aquatic environments, in soils and on foliar and bark surfaces. Methanotrophy can be an important sink where it intercepts relatively high concentrations of methane produced from within soils or water bodies, but when methanotrophs are exposed to only ambient atmospheric methane concentrations (about 2 ppm), methane oxidation occurs at very slow rates. Here we present an assessment of possible strategies – including introduction of exogenous microbes to soils and plant tissues, improved tillage and nutrient management in agriculture, and reforestation – to enhance rates of methanotrophy for removal of atmospheric methane, where the low concentration constrains the energy available to support methanotrophic growth.

The urgent need to reduce methane (CH_4) emissions and to remove CH_4 from the atmosphere has sparked interest in a variety of abiotic catalytic processes for removing atmospheric CH_4 and in the biotechnology potential to increase rates of methanotrophy (microbial CH_4 oxidation) in a variety of engineered and natural systems[1–4]. Some progress has been made in the application of engineered methanotrophy systems to environments with elevated CH_4 concentrations, such as animal barns, landfill covers, wastewater treatment, and coal mine vents[5–8]. Those are highly engineered environments where the resulting introduction and management of methanotrophs may reduce net CH_4 emissions from these CH_4-rich environments[5]. Here we address the potential for enhanced methanotrophy in environments that generally experience only ambient atmospheric CH_4 concentrations (~2 ppm), such as many upland forest and agricultural soils and surfaces of tree bark and leaves, where successfully introducing cultures of microbial communities that contain natural or engineered methanotrophs remains more challenging. Nevertheless, the widespread occurrence of methanotrophy in natural soils, albeit typically at low rates of CH_4 oxidation that account for only 5-10% of the total global atmospheric CH_4 sink[9], makes for an intriguing target for biotechnical approaches to increase overall atmospheric CH_4 removal rates. We describe why the introduction of methanotrophs to natural environments may have limited value, but better understanding of the multiple factors that limit methanotrophic communities could enable management practices that maximize native methanotrophic activity in a variety of terrestrial and aquatic ecosystems.

A basis for effective manipulation of microbial communities in situ

Historic and recent developments in medicine and agriculture have demonstrated that human intervention in the microbial content of various environments, ranging from the human gut to agricultural soils, can have beneficial impacts[10–13]. These results provide encouragement that perhaps similar tools could be used to help solve other vexing problems, such as climate change caused by the accumulation of greenhouse gases in the atmosphere. However, these past successes required major interventions and careful application. For instance, manipulation of the human gut microbiome can require bowel cleansing to remove the pre-existing community prior to introduction of the preferred community in order to enable long-term changes in the microbial community[10,11]. Further, the use of plant growth-promoting rhizobia to enhance crop productivity can be successful in the short term, such as one growing season, but typically fails to provide long-term benefits[14], and thus must be continuously re-applied.

Efforts to augment populations of methanotrophs in soils and on plant leaf and bark surfaces via introduction of exogenous microbes are based on the assumptions that: (1) there are viable empty niches for additional methanotrophs; (2) introduced methanotrophs will compete and/or shift

[1]Appalachian Laboratory, University of Maryland Center for Environmental Science, Frostburg, MD, 21532, USA. [2]Spark Climate Solutions, Covina, CA, 91723, USA. [3]Department of Civil and Environmental Engineering, University of Michigan, Ann Arbor, MI, 48109-2125, USA. ✉e-mail: edavidson@umces.edu

the existing native soil microbial community structure towards one that is more dominated by methanotrophic activity; and (3) the conditions in those environments will be conducive to the survival and growth of the introduced organisms. However, these assumptions have not been rigorously assessed, and the efficacy of methanotrophic augmentation is unclear.

An ecological and evolutionary perspective of CH_4 oxidation under low CH_4 concentrations

Methanotrophs are nearly ubiquitous because CH_4 is present in most terrestrial and aquatic ecosystems, both natural and anthropogenic. They have also been found and shown to grow, albeit slowly, in the atmosphere[15–17]. It should come as no surprise that the physiological diversity of methanotrophy is quite broad, with these intriguing microbes having evolved many different mechanisms to release the energy inherent in the C-H bond of CH_4, including coupling microbial CH_4 oxidation to the reduction of oxygen, sulfate, nitrate, nitrite, manganese and iron oxides[1,18].

Energy limitation

Despite this fascinating diversity of methanotrophs, there is a serious biophysical barrier that often limits methanotrophic activity. Especially in upland soils and plant surfaces, where the main or perhaps only source of CH_4 is from the atmosphere (presently at about 2 ppm), the supply of CH_4 is often the limiting factor controlling the overall rate of CH_4 oxidation[19–21]. Although microbial consumption of methane at atmospheric concentrations has been well-documented, it is clear that energy yields are low, i.e., oxidation of atmospheric methane to carbon dioxide yields anywhere between 0.28 to 0.6 kJ C-mol^{-1} hr^{-1}, depending on the methanotrophic strain[22]. This would appear to be lower than previously understood requirements for cell maintenance of aerobic bacteria (i.e. 5.7 kJ C-mol^{-1} hr^{-1} at 25 °C[23]), and as such it is uncertain how methanotrophy is viable at atmospheric concentrations of methane. It should be stressed, however, that required maintenance energy is a complex matter and is non-linearly dependent on growth and death rates, growth yield, and endogenous metabolism, and so it may be possible that these low energy yields are sufficient to enable methanotrophic survival[24]. In any event, it is reasonable to conclude that methanotrophy at 2 ppm methane is likely to be energy and carbon-limited. In contrast, methanotrophs have been found to prosper in soil microsites close to methanogenesis, where CH_4 concentrations are elevated[25], or where they intercept CH_4 diffusing from plant roots[26].

Further evidence that CH_4 concentration, and hence energy supply, is often limiting the rate of methanotrophy comes from observations of correlations of methanotrophy with soil temperature and moisture. Most soil microbial processes are inhibited by very dry conditions, but methanotrophy has been shown to be negatively correlated with soil moisture, i.e., higher rates of CH_4 oxidation occur at lower soil moisture contents[25,27,28]. This relationship is explained by the effects of soil water on the diffusion of atmospheric CH_4 into the soil. Diffusion of gases through water is five orders of magnitude slower than diffusion of gases through air, and CH_4 is also sparingly soluble in water. When water occupies the tortuous pores spaces between soil particles, gaseous diffusion is slower, resulting in concentrations of CH_4 within the soil atmosphere that are substantially lower than the 2ppm CH_4 in the air above the soil[27,28]. Another hint is that methanotrophy often tends to show a stronger correlation with soil moisture than with temperature[19,25,29]. All enzymatic processes are temperature-dependent, but when the CH_4 substrate supply is inhibited by diffusional constraints of soil gases, then the apparent temperature dependence of the enzymatic process is suppressed, which is commonly observed for methanotrophy in soils.

Adaptations to variations in CH_4 concentration and energy

Methanotrophs often experience a wide range of CH_4 concentrations, and as a consequence, there is ample evidence of methanotrophic adaptation to varying availability of CH_4. For example, in wetland areas of boreal forests, where CH_4 is produced by methanogenic archaea in the subsoil and then diffuses upward to the soil surface, soil methanotrophs are exposed to elevated concentrations of CH_4 and are found to have higher apparent Michaelis–Menten half saturation constants (K_M) compared to methanotrophs in upland forest soils exposed only to atmospheric CH_4 concentrations[20]. That is, these microbes exhibit an apparent lower affinity for CH_4, presumably because the presence of CH_4 at relatively high concentration does not confer a selective advantage to maintaining a strong binding mechanism sensitive to low concentrations. In addition, with greater CH_4 availability, the enzymatic systems used by these methanotrophs typically have faster turnovers (higher V_{max}), increasing specific CH_4 oxidation rates. As a result, such populations remove more CH_4 per unit time as compared to populations in upland soils where the only source of CH_4 is the overlying atmosphere.

In contrast, at low CH_4 concentrations, such as the upland boreal forest soil, successful methanotrophs typically exhibit a high substrate affinity, i.e., a low K_M, but also commonly have a low V_{max}[20]. In other words, there is simply less energy available to support growth when methanotrophs must depend on atmospheric CH_4 as their main energy source, meaning that they must develop strategies to capture enough energy and carbon to eke out a living where CH_4 is sparingly available. Intriguingly, these microbes that are adapted to low CH_4 concentrations also exhibit a higher specific affinity towards methane at low concentrations, i.e., a higher value of V_{max}/K_m, indicating that enzyme activity initially increases rapidly with increasing substrate concentration (the steep initial curve for the blue line in Fig. 1) and then levels off as the lower V_{max} is approached at higher concentrations[22,30]. Where there are higher concentrations of CH_4, such as in a wetland, rice paddy, or landfill cover, the overlying soil naturally supports populations of

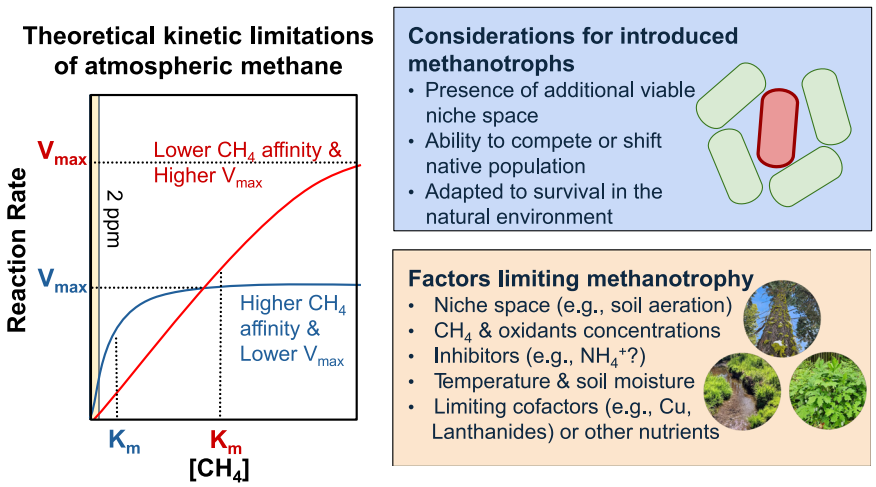

Fig. 1 | Theoretical Michaelis–Menten curves for a high affinity methanotroph (e.g., upland forest) and low affinity methanotroph (e.g., bog). The relevant V_{max} and K_m values are shown for high affinity and low affinity methanotrophs in relation to atmospheric methane concentrations (2ppm).

methanotrophs that are adapted to those conditions, and as such, have no need to bind methane tightly (i.e., have high K_m values). Instead, their strategy is to have high V_{max} values, enabling them to have correspondingly much higher growth rates at high concentrations[21,31], resulting in the red line in Fig. 1 crossing over the blue line as concentrations increase.

Another example of a native community responding to varying CH_4 concentrations comes from the oceanographic realm. Researchers studying the Deepwater Horizon oil spill found that a huge bloom of methanotrophic bacteria, which were minor components of the community prior to the spill, quickly expanded to consume nearly all of the released CH_4 within the water column with "no measurable CH_4 loss to the atmosphere"[32]. Such rapid response of methanotrophic populations has also been found in terrestrial systems. For example, at the aerobic-anaerobic interface of saturated rice paddy soils, methanotrophs can feast on the high concentrations of CH_4 produced via methanogenesis by coupling it to oxygen (O_2) reduction. When the rice paddy is drained, methanogenesis is inhibited, and CH_4 concentrations accordingly decrease, but the methanotroph communities can quickly adapt to continue to oxidize CH_4 at atmospheric levels, albeit at much lower rates. They then revert back to high CH_4 consumption when the soils are re-flooded[33].

The lesson here is that native microbial communities are diverse and well poised to respond to changing availability of an energy source such as CH_4 when it becomes kinetically and thermodynamically viable. Extant populations of microorganisms found in oceans, on plant surfaces, and in soils are already well adapted to their environments through years to millennia (or more) of evolution.

Can humans improve on the methanotroph communities already present?

Adding methanotrophs to environments

Unfortunately, it may not be feasible to select for organisms with specific CH_4 affinities greater than the CH_4 affinities of natural communities already adapted to using atmospheric concentrations. That is, the inherent energetic limitations for growth at atmospheric or lower soil CH_4 concentrations are unlikely to be overcome. The reason that methanotrophs are not more abundant in low-CH_4 environments is that, even with the advantage of high specific affinity and low maintenance energy requirement, they cannot carry out the oxidation reaction at high enough rates to grow and colonize more surfaces. For example, although the methanotroph *Methylocapsa gorgona* can oxidize CH_4 at atmospheric concentrations, its doubling time when doing so is on the order of a month[34]. Such rates are extremely slow, especially when compared to some methanotrophs that can double on the order of hours at high concentrations of CH_4[35]. Substrate limitation on rates of methanotrophy and growth of methanotrophic populations applies to both native and exogenous methanotrophs and would also apply to potential bioengineered organisms.

Manipulating the abundance of organisms carrying out methanotrophy at 2 ppm concentrations also has limited potential because of lack of evidence of the persistence of added organisms. Applications of additional methanotrophs could possibly provide a temporary increase in the capacity to oxidize atmospheric CH_4 for as long as the added organisms survive with this limited energy source, but repeated applications would be economically viable only if they could be done inexpensively, perhaps concurrent with other management activities such as alternative wetting drying cycles as done in rice paddy management to inhibit methanogenesis.

Furthermore, if a microorganism is not abundant in a natural or quasi-natural environment (recognizing that human disturbance of some sort is pervasive in all ecosystems), there is probably an evolutionary or ecological explanation of the barriers to its expansion. For example, microbial communities are known to be dynamic and experience high rates of turnover, sometimes on the scale of days[36] as they adapt to changes in their niche space. As a result, introducing a foreign or bioengineered species or community at one time point does not ensure that it will persist through multiple turnovers of the population, especially if the introduced organisms were not already well adapted to the specific physio-chemical properties of environmental niches[37]. Indeed, failure of sustained survival commonly contributes to the inefficacy of microbial inoculants to enhance crop productivity in the field[38,39].

While enhancing methanotrophy at high concentrations is beyond the scope of the focus here on ambient concentrations, we do not wish to leave the impression that all efforts to enhance methanotrophy would be infeasible. Indeed, as described in the introduction, there may be good opportunities to enhance methanotrophy in natural and engineered environments where CH_4 concentrations are at least periodically elevated. In wetlands, rice paddies, and landcover soils, the extant populations are already relatively abundant and well adapted to periodically concentrated CH_4 conditions, with higher K_M, higher V_{max}, and faster growth rates. Nevertheless, it might be possible to develop consortia that could oxidize an even larger fraction of the CH_4 that is intercepted by methanotrophs in these relatively high-CH_4 concentration environments, assuming that there is room for further optimization of their ability to utilize the energy present at the higher CH_4 concentrations they experience due to proximity to a CH_4 source. Similarly, bioreactors in CH_4-rich environments would need methanotroph populations possessing optimized kinetic characteristics.

Outlook for possible interventions at atmospheric concentrations

Our knowledge of factors limiting CH_4 oxidation is incomplete, so it is conceivable that other factors besides the CH_4 and O_2 substrates (or other oxidants, such as sulfate and nitrate) could be limiting in some circumstances. One of the most prevalent enzymes used by methanotrophs, the particulate CH_4 monooxygenase, requires copper for its activity, with whole-cell activity increasing with copper availability[40–42]. If copper were more limiting to methanotrophs than the supply of CH_4, then it is possible that copper amendments could allow the existing methanotrophic population to achieve higher reaction rates at their ambient CH_4 concentrations.

In addition, the second step in the central methane oxidation pathway – the oxidation of methanol by the methanol dehydrogenase – is dependent on the availability of lanthanides. It is tempting to speculate that methanotrophy could be enhanced through the provision of these rare earth elements, but experimental data is limited and equivocal on this issue. One study suggests that in situ methane oxidation is driven by the use of lanthanides[43] while another found that the addition of lanthanum inhibited methanotrophy[44]. Therefore, while copper/lanthanide amendments could possibly be effective in some circumstances to enable the extant population to increase CH_4 oxidation rates and grow somewhat better, the magnitude of responses to such amendments in situ has yet to be clearly demonstrated. In these cases as well, however, it is not the organisms themselves that are limiting, but rather one or more of the essential resources for the organisms to obtain energy from CH_4 and grow.

Rates of uptake of atmospheric CH_4 are often lower in agricultural soils compared to untilled native soils[45]. In agricultural soils, nitrogen in the form of ammonium is often a competitive inhibitor of CH_4 oxidation, although there are also reports of no effect or stimulation of CH_4 oxidation, especially in rice paddy soils[46,47]. Soil compaction from poor management can restrict the diffusion of atmospheric CH_4 and O_2 into the soil. Hence, agricultural management practices related to fertilization and tillage can influence rates of methanotrophy. There is no clear evidence that the communities of methanotrophs would be deficient if more favorable conditions were provided through better soil management, so we believe that the best ways to enhance methanotrophy in agricultural soils would be to improve soil aeration and to manage nitrogen (and perhaps copper and lanthanides) more efficiently.

It may be possible to restore the surface areas upon which methanotrophs previously grew. We know that methanotrophs are present on the bark of many trees, albeit growing slowly and with low rates of CH_4 oxidation, similar to rates in upland soils[26,48,49]. In addition to the many other negative environmental and socioeconomic impacts of deforestation, it also results in a large reduction in bark area that can host methanotrophs, as well as less aerated soils[50]. The croplands and pasture lands that replace forests

can still host methanotrophs in soils, but no longer on the previously abundant surfaces of the trees that were removed. Reforestation could be an effective way of increasing the abundance of methanotrophs by re-establishing the area of bark surfaces within which methanotrophy can occur, as well as improving soil aeration[50]. The effect on the global CH_4 budget is likely to be modest at best, due to inherently low rates of atmospheric CH_4 oxidation at bark surfaces, and there are many other ecological and socio-economic advantages of reforestation, such as increased biodiversity, soil conservation, and carbon storage, that may be stronger motivating factors for reforestation than the modest gain in atmospheric CH_4 uptake. Nevertheless, a modest increase in methanotrophy with reforestation of previously cleared forests could be a co-benefit that should not be neglected. Because methanotrophs are nearly ubiquitous in environments where CH_4 exists, it is unclear whether adding methanotrophs to bark and foliar surfaces of regrowing forests would speed up their colonization sufficiently to be cost-effective where payments for CH_4 destruction serviced are available.

Less is known about what limits colonization of leaf surfaces by methanotrophs. Correlations of CH_4 uptake with photosynthetically active radiation and stomatal conductance suggests that the site of CH_4 oxidation, when it occurs, is within the leaf[26,51]. Measurable rates of CH_4 oxidation have been demonstrated on or in the foliage of certain plant taxa, such as duckweed[52] and sphagnum moss[53], where they intercept CH_4 produced within their ecosystems. We speculate that there may be other factors, such as UV radiation or leaf exudates, that inhibit robust colonization by methanotrophs on leaves, but this topic warrants additional research.

Conclusions

Although introduction of exogenous methanotrophs to enhance rates of CH_4 oxidation in environments with ambient atmospheric CH_4 concentration may not offer great promise because of inherent energetic limitations, efforts to understand better the multiple factors that limit methanotrophic communities could enable management practices that maximize native methanotrophic activity in a variety of terrestrial and aquatic ecosystems. Improved knowledge of limitations of methanotrophy could also help identify opportunities where ecosystem conservation or restoration could maintain or increase natural CH_4 sinks. Finally, such knowledge would also enable improved predictions of how natural CH_4 sinks are likely to respond to anthropogenically-driven, rising atmospheric CH_4 concentrations.

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Author contributions

E. Davidson conceived of the manuscript topic. E. Davidson, D. Monteverde, and J. Semrau contributed equally to writing and editing.

Competing interests

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Additional information

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Correspondence and requests for materials should be addressed to Eric A. Davidson.

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