Microorganisms and climate change: terrestrial feedbacks and mitigation options

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Abstract | Microbial processes have a central role in the global fluxes of the key biogenic greenhouse gases (carbon dioxide, methane and nitrous oxide) and are likely to respond rapidly to climate change. Whether changes in microbial processes lead to a net positive or negative feedback for greenhouse gas emissions is unclear. To improve the prediction of climate models, it is important to understand the mechanisms by which microorganisms regulate terrestrial greenhouse gas flux. This involves consideration of the complex interactions that occur between microorganisms and other biotic and abiotic factors. The potential to mitigate climate change by reducing greenhouse gas emissions through managing terrestrial microbial processes is a tantalizing prospect for the future.

Radiative forcing
A measure of the influence that a factor has in altering the balance of incoming and outgoing energy in the Earth–atmosphere system. It is an index of the importance of the factor as a potential climate change mechanism.

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From the first molecules of oxygen produced by marine cyanobacteria ~3.5 billion years ago[1] to the methanogens luxuriating in the warm, carbon-rich swamps of the Carboniferous period[2], microbial processes have long been key drivers of, and responders to, climate change. It is widely accepted that microorganisms have played a key part in determining the atmospheric concentrations of greenhouse gases, including carbon dioxide (CO_2), methane (CH_4) and nitrous oxide (N_2O) (which have the greatest impact on radiative forcing), throughout much of Earth's history. What is more open to debate is the part that they will play in the coming decades and centuries, the climate feedbacks that will be important, and how humankind might harness microbial processes to manage climate change. The feedback responses of microorganisms to climate change in terms of greenhouse gas flux may either amplify (positive feedback) or reduce (negative feedback) the rate of climate change. With the twenty-first century projected to experience some of the most rapid climatic changes in our planet's history, and with biogenic fluxes of the main anthropogenic greenhouse gases being tied integrally to microorganisms, improving our understanding of microbial processes has never been so important.

In terrestrial ecosystems, the response of plant communities and symbiotic microorganisms, such as mycorrhizal fungi and nitrogen-fixing bacteria, to climate change is well understood, both in terms of physiology and community structure[3–9]. However, the response of the heterotrophic microbial communities in soils to climate change, including warming and altered precipitation, is less clear. This is a crucial factor, as it determines the nature and extent of terrestrial-ecosystem feedback responses. However, understanding the responses of microbial communities to climate change is complicated by the vast and largely unexplored diversity of microbiota found in the terrestrial environment, for which only a few examples of food webs have been fully constructed[10]. Also, different terrestrial ecosystems comprise different microbial communities, and this is further compounded by effects of land use, other disturbances (such as management practices) and different biogeographical patterns (distribution of microbial communities over space and time)[11,12].

In this Review, we examine the direct and indirect effects of climate change on terrestrial microbial communities and the biogeochemical processes that they underpin. We discuss the multifactorial and multidirectional interactions and feedbacks between above-ground and below-ground communities, as well as soil abiotic properties and their importance in feedback responses to climate change. We also argue that using new, sophisticated molecular and biochemical tools to better understand microbial responses can improve the prediction of feedback responses to climate change in terms of greenhouse gas emissions. Finally, we address the effects of soil nutrient cycling and the feedback response of net greenhouse gas fluxes, and explore ways in which terrestrial microorganisms could be exploited for the mitigation of anthropogenic climate change.

Microbial control of greenhouse gas emissions

Understanding the physiology and dynamics of microbial communities is essential if we are to increase our knowledge of the control mechanisms involved in greenhouse gas fluxes[13,14]. This topic has received little attention owing to the assumption that microbial community structure has little relevance to large-scale ecosystem models[15], and to the lack of theoretical background and technologies to measure the vast diversity of microbial communities in natural environments and determine their link to ecosystem functioning. Nevertheless, recent advances in molecular techniques and their application to the characterization of so-called uncultivable microorganisms has started to provide an improved understanding of microbial control of greenhouse gas emissions[14].

Carbon dioxide. In the global carbon cycle, annual emissions of CO_2 from the burning of fossil fuels are dwarfed by the natural fluxes of CO_2 to and from the land, oceans and atmosphere. Current levels of atmospheric CO_2 depends largely on the balance between photosynthesis and respiration. In oceans, photosynthesis is primarily carried out by phytoplankton, whereas autotrophic and heterotrophic respiration return much of the carbon taken up during photosynthesis to the dissolved inorganic carbon pool[16,17]. For terrestrial ecosystems, the uptake of CO_2 from the atmosphere by net primary production is dominated by higher plants, but microorganisms contribute greatly to net carbon exchange through the processes of decomposition and heterotrophic respiration (FIG. 1a), as well as indirectly, through their role as plant symbionts or pathogens and by modifying nutrient availability in the soil[18].

Approximately 120 billion tonnes of carbon are taken up each year by primary production on land[19], and ~119 billion tonnes of carbon are emitted, half by autotrophic (mainly plant) respiration and half by heterotrophic soil microorganisms[20]. Together, the land and oceans constitute a net sink of ~3 billion tonnes of carbon each year, effectively absorbing about 40% of current CO_2 emissions from fossil fuel use.

In addition, 1 billion to 2 billion tonnes of carbon are added to the atmosphere each year[21] through changes in land use (predominantly tropical deforestation). Furthermore, because soils store ~2,000 billion tonnes of organic carbon, their disturbance by agriculture and other land uses can greatly stimulate the rates of organic matter decomposition and net emissions of CO_2 to the atmosphere[22]. For example, deep ploughing or drainage of organic, carbon-rich soils is known to stimulate rates of decomposition and respiration, because it gives microorganisms greater access to both buried organic carbon and oxygen[23]. Through such cultivation and disturbance, soils are estimated to have already lost 40 billion to 90 billion tonnes of carbon since human intervention began[24]. Although these responses are mediated by microbial activity, it is generally thought that changes in the structure and diversity of terrestrial microbial communities will have little effect on CO_2 production at the ecosystem level because, unlike CH_4 and N_2O production, CO_2 production results from numerous microbial processes. However, recent findings have challenged this assumption by providing evidence of a direct link between CO_2 fluxes and changes in the structure and physiology of the microbial community[14,25].

Methane. Global emissions of CH_4 are arguably even more directly controlled by microorganisms than emissions of CO_2. Natural emissions (~250 million tonnes of CH_4 per year) are dominated by microbial methanogenesis, a process that is carried out by a group of anaerobic archaea in wetlands, oceans, rumens and termite guts. However, these natural sources are exceeded by emissions from human activities (mainly rice cultivation, landfill, fossil fuel extraction and livestock farming) (~320 million tonnes of CH_4 per year), which, aside from some emissions from fossil fuel extraction,

Figure 1 | **Greenhouse gas fluxes. a** | In terrestrial ecosystems, atmospheric carbon dioxide (CO_2) is fixed into sugars by the autotrophic (mainly plant) communities in the presence of daylight. Plants release a great portion of fixed carbon back to the atmosphere through autotrophic respiration. Along with the release of a substantial portion of newly fixed carbon through their roots, plant litters form a main source of energy for soil heterotrophs, including microorganisms and animals; this carbon pool is respired back to the atmosphere through heterotrophic respiration. A smaller amount of organic carbon remains unused and is stored in the soil. Some organic carbon is also used by some microorganisms for energy, but at a slower rate. CO_2 is also released into the atmosphere by anthropogenic activites such as fossil fuel burning (not shown). **b** | The methane (CH_4) cycle involves the conversion of organic residues (sugars) into CH_4 by methanogenesis, which is mainly carried out by a specialized group of archaea, called methanogens, under anoxic conditions. However, most CH_4 produced in soils is immediately oxidized by methanotrophs, which use CH_4 as a source of energy. This is mainly an aerobic process, and the availability of oxygen is a rate-limiting step. Methanotrophs also oxidize some atmospheric CH_4. The CO_2 produced by methane oxidation then enters into the CO_2 cycle (part **a**). **c** | The substrates for nitrous oxide (N_2O) production, ammonium (NH_4^+) and nitrate (NO_3^-), enter soils in various forms. Atmospheric dinitrogen (N_2) can be deposited in the soil following fixation by soil microorganisms and is subsequently converted to NH_4^+; alternatively, reactive forms (mainly NO_3 and NH_3) can be deposited in precipitation or as dry deposition. Sources of N_2O, including fixed N_2, can also be released from organic residues from plants and animals, animal waste and nitrogen fertilizers. The major source of anthropogenic substrate is agricultural application of nitrogen fertilizers and manure. In soil, a considerable amount of NH_4^+ is used by plants and microorganisms, and the remaining portion is transformed into NO_3^- by NH_3-oxidizing bacteria and archaea through nitrification. Most NO_3^- is converted into N_2 via various nitrogen oxides (including N_2O) by denitrification processes (carried out by denitrifying bacteria), and these then escape in the atmosphere. Some nitrate is leached into the groundwater, and some is used by plants. CH_3COOH, acetic acid; $C_6H_{12}O_6$, glucose; H_2, hydrogen gas; H_2O, water; NO_2^-, nitrite; O_2, oxygen gas.

Heterotrophic
Of an organism: able to use organic compounds as nutrients to produce energy for growth.

Autotrophic
Of an organism: able to synthesize organic carbon from the fixation of inorganic carbon (for example, by photosynthesis or chemosynthesis).

Dissolved inorganic carbon pool
The sum of inorganic carbon in solution.

Net primary production
The part of the total energy fixed by autotrophic organisms that remains after the losses through autotrophic respiration.

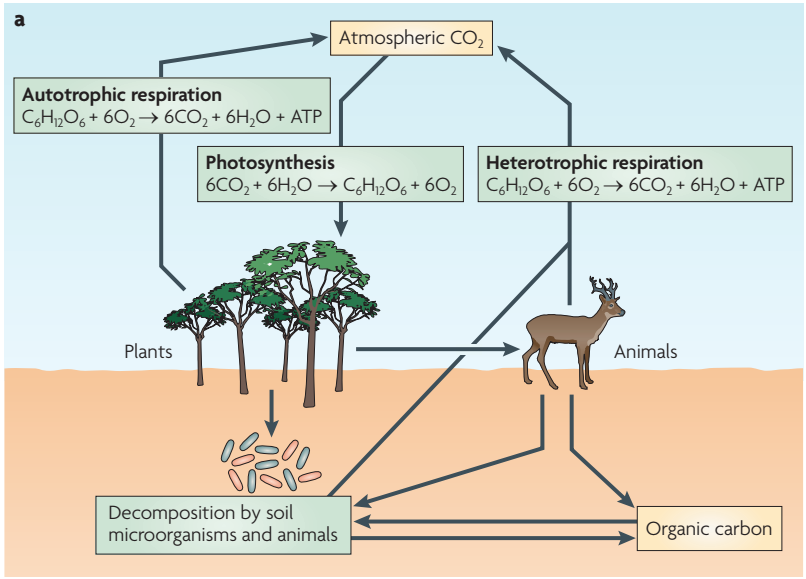
Methanogenesis
The process by which methane is produced by microorganisms (mainly archaea).

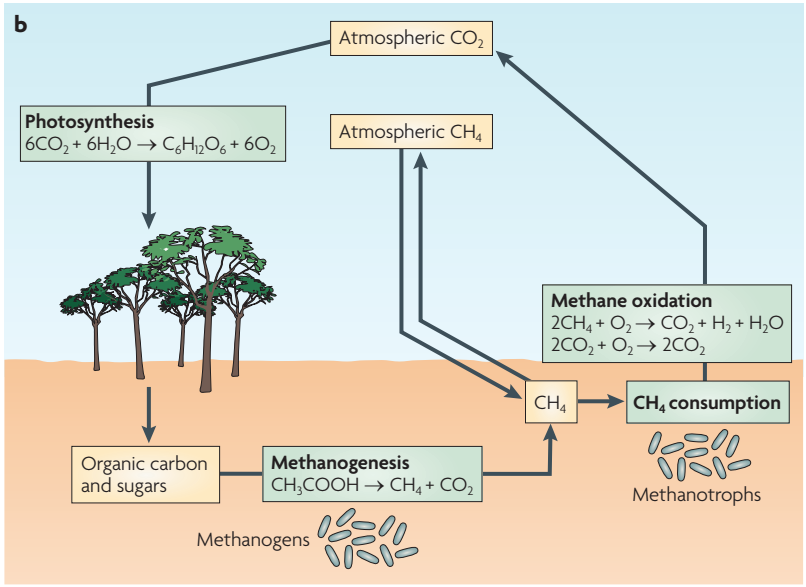
Methanotrophic
Of an organism: able to use methane as a nutrient to produce energy for growth.

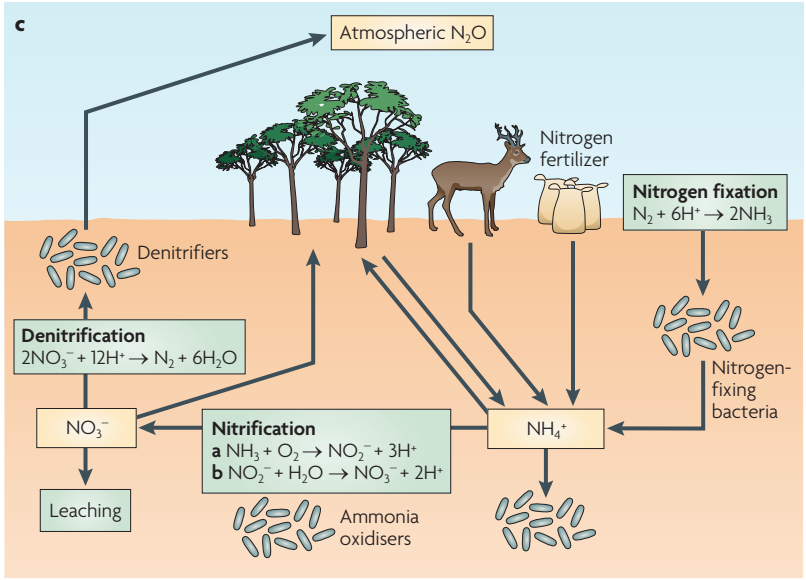
Nitrification
The conversion of NH_3 into a more oxidized form such as nitrate or nitrite.

Denitrification
The reduction of oxidized forms of nitrogen to N_2O and dinitrogen.

Reactive nitrogen
Nitrogen in a form that can undergo biological transformations, such as nitrite and nitrate.







are also predominately driven by microorganisms[21]. Methanotrophic bacteria serve as a crucial buffer to the huge amounts of CH_4 produced in some of these environments (FIG. 1b). The so-called 'low-affinity' methanotrophs (active only at a CH_4 concentration of >40 parts per million; also called type I methanotrophs), which mainly belong to the class Gammaproteobacteria, can often consume a large proportion of the CH_4 produced in soils before it escapes to the atmosphere[26]. For CH_4 already in the atmosphere, methanotrophic bacteria may also act as a net CH_4 sink. The so-called 'high-affinity' methanotrophs (active at a CH_4 concentration of <12 parts per million), which mainly belong to the class Alphaproteobacteria (also known as type II methanotrophs), remove approximately 30 million tonnes CH_4 from the atmosphere each year[21].

Nitrous oxide. Similarly to CO_2 and CH_4 emissions, global N_2O emissions have a predominantly microbial basis. Natural and anthropogenic sources are dominated by emissions from soils, primarily as a result of microbial nitrification and denitrification[21] (FIG. 1c). For each tonne of reactive nitrogen (mainly fertilizer) deposited on the Earth's surface, either naturally or deliberately, 10–50 kg are emitted as N_2O[27,28]. Several studies have been carried out to distinguish the relative contributions of nitrification and denitrification to net N_2O flux, although little is known about the degree of microbial control of these processes at the ecosystem level. Most N_2O produced by nitrification is a result of the activity of autotrophic ammonia (NH_3)-oxidizing bacteria belonging to the class Betaproteobacteria)[29]. However, recent studies suggest that some archaea also have an important role in nitrification[30], although their relative contribution to this process is still debated.

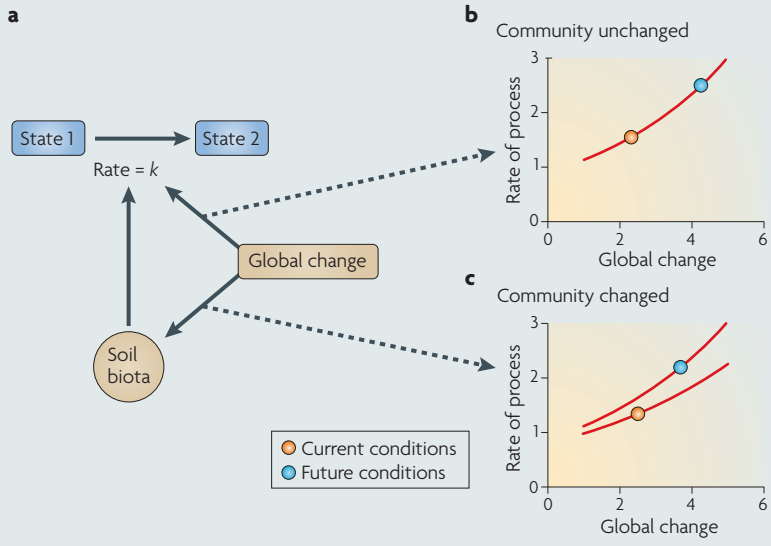
By contrast, denitrification is a multistep process in which each step is mediated by a specific group of microorganisms that have the enzymes necessary to catalyse that particular step. The production of N_2O is typically the result of incomplete denitrification. Denitrifying activity is distributed among phylogenetically diverse bacterial populations, although each denitrifying enzyme catalysing a specific step in the process (for example, nitrate reductase) is highly conserved genetically[31]. A recent study provided direct evidence of a strong link between denitrifying bacterial communities and the rate of N_2O emissions from soils[32].

Effect of climate change and feedback responses

Previous research on climate change and feedback responses has focused on measuring biogeochemical processes, and this information has been used to develop predictive climate models. Because our understanding of the microbial response to climate change remains limited, and the representation of the process in predictive models is basic, we ignore potentially important effects that terrestrial microorganisms might have on climate change. To improve our understanding of climate change and feedback responses by terrestrial microorganisms, we need to expand the predictive climate models to include information on the structure, physiology and

Box 1 | **Microorganisms, process rates and climate models**

The relationship between global changes (altered temperature, carbon dioxide (CO_2) levels and precipitation) and the rate of processes such as denitrification and respiration can change according to the response of microbial communities. For example, a soil process (such as the decomposition of organic carbon) converts a component from state 1 to state 2 at a rate *k*, and it is assumed that the process is mediated by the soil biota present (see the figure, part **a**). In the first scenario (see the figure, part **b**), global change directly influences the functioning of existing microbial communities without altering the community structure. This may cause a shift in the process rate, but its behaviour and controls remain unchanged. However, as in the second scenario (see the figure, part **c**), a shift in microbial community structure caused by global change could also alter the fundamental control mechanism of the process. Most ecosystem models and all climate models that include a description of microbial processes use first-order rate kinetics, which assume that the microbial population is sufficient to carry out the function (for example, decomposition) and that the rate of the process is modified by environmental factors such as temperature and moisture. This approach works well within the parameterized limits of the model, and process rates largely follow trajectories that are mimicked well by such formulations. What is not known, however, is what happens if the climate changes beyond the parameterized limits. For example, if the structure of the microbial community changes in such a way that the function also changes, a discontinuity in the response may occur and the response could move to a different trajectory (see the figure, part **c**). Such threshold effects cannot be represented in the current structure of ecosystem and coupled-climate models. Understanding these potential threshold effects and identifying the systems and processes for which they are likely to be of greatest importance remain key challenges for microbiology.



biogeographical patterns of microbial communities, as well as the functional links between microorganisms and plant communities.

There is substantial evidence to suggest that climate change will have both direct and indirect effects on terrestrial microbial communities and their functions. The effects of increased CO_2 levels on microbial communities are often indirect, as they are mediated by cascading effects on plant metabolism, growth and diversity, and the associated changes in soil physicochemical properties such as soil moisture and resource quality (carbon to nitrogen ratio)[33]. The main direct effects of climate change on soil microorganisms are likely to be caused by changes in temperature and moisture content. These factors can affect processes such as greenhouse gas flux in two ways: by modifying the physiology of existing microbial populations and/or by changing the structure of the microbial community. For example, at higher temperatures, most microorganisms grow and use substrates at faster rates, so the rate at which processes such as respiration occur may change; however, the control mechanism remains the same. In the second scenario, in which climate change facilitates a shift in microbial-community structure, the process rates and the mechanism of control might change, because the new microbial community will have different physiologies[13] (BOX 1). In extreme cases, this may result in the loss of a particular process (caused by, for example, the loss of an entire functional group, such as denitrifiers or methanogens) and/or the prominence of a previously insignificant process (caused by, for example, a shift in community composition to one with higher physiological capabilities in organic carbon decomposition; BOX 1)[13,34]. Below we discuss the greenhouse gas fluxes that result from microbial feedback responses to changes in climate and atmospheric composition, including increased CO_2 and temperature, and altered precipitation.

Carbon dioxide. It is generally accepted that increased levels of CO_2 quantitatively and qualitatively alter the release of labile sugars, organic acids and amino acids from plant roots[35], and this can stimulate microbial growth and activity. This can then change the CO_2 flux depending on the availability of nutrients (such as nitrogen)[4,36–38] (FIG. 2). In the long term, it is argued that the increase in microbial biomass as a result of increased carbon release by the roots can lead to immobilization of soil nitrogen, thereby limiting the nitrogen available for plants and creating a negative feedback that constrains future increases in plant growth[36]. This, in turn, may lead to an increased soil carbon to nitrogen ratio, which favours higher fungal dominance and diversity[18,39,40]. Fungi generally have higher carbon assimilation efficiencies (that is, they store more carbon than they metabolize) than bacteria, and fungal cell walls mainly consist of carbon polymers (chitin and melatin) that are much more resistant to decomposition than those in bacterial cell membranes and walls (phospholipids and peptidoglycan). As a result, in ecosystems dominated by fungi, soil respiration rates are typically low, which increases the potential for carbon sequestration[40]. This scenario is likely to occur only when nitrogen is a growth-limiting factor, such as in temperate forests[41,42]. However, several studies have shown that increased levels of atmospheric CO_2 can lead to substantial increases in soil respiration[43–46], and that, in general, below-ground responses to increased CO_2 are often greater than above-ground responses in the same systems[46]. Conversely, in some cases, because soil microorganisms preferentially use labile carbon over complex carbon, rates of litter decomposition will slow down, which in turn may lower CO_2 emissions by respiration and favour carbon sequestration in the soil. Change in the quality and quantity of carbon supplied by plants can also influence the feedback response by directly affecting the physiology and structure of the soil microbial community[27,47].

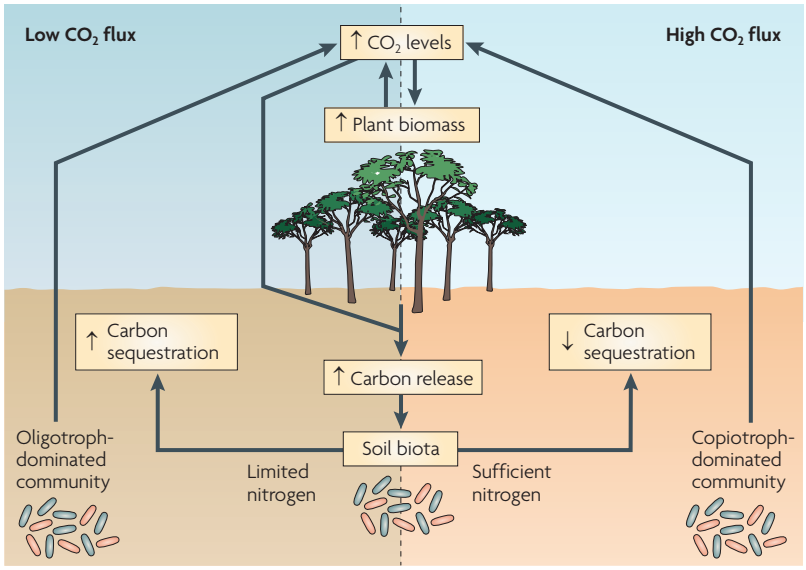


Figure 2 | **A simplistic conceptual model to illustrate complex feedbacks caused by climate change.** Increased levels of carbon dioxide (CO_2) result in a higher plant biomass and a higher rhizodeposition of carbon, which increases microbial biomass and activity in the short term. However, in the long term, limitation of mineral nutrients such as nitrogen may constrain this response. Such mineral limitation will affect the dominance of oligotrophic and copiotrophic microorganisms in a given ecosystem, which in turn may influence CO_2 flux.

The average global surface temperature is predicted to increase by between 1.1 and 6.4 °C by 2100 (REF. 21), and this might also have an effect on soil carbon sequestration by potentially accelerating heterotrophic microbial activity. The sensitivity of stable and labile fractions of soil organic carbon to temperature change is thought to vary greatly. For example, increased thaw rates and depths in high-latitude permafrost render the large stocks of organic carbon in these soils (400 Petagrams (Pg); that is, 4,000 million tonnes) vulnerable to increased decomposition rates[48]. Without the balancing effect of organic carbon input from above-ground primary production, this could result in a large and uncontrollable positive-feedback effect[49].

Overall, increased temperature has been directly linked to increased soil respiration, and a global average temperature increase of 2 °C is predicted to increase soil carbon release by 10 Pg, mainly owing to increases in microbial activity[50–52]. This is thought to be because the increased temperature will stimulate the use of labile carbon; however, recalcitrant carbon is diverse and complex in structure, so its temperature sensitivity is uncertain. This scenario is further complicated by the role of environmental constraints in organic carbon decomposition, including physical and chemical protection against enzymatic activity, and the impact of drought, floods and temperature on enzymatic activity and on the availability of oxygen[52]. Moreover, these environmental constraints are themselves affected by climate change. Therefore, predicting the effect of temperature increases on carbon stock has been difficult. In some cases, increased temperature may lead to a loss of soil organic carbon, especially in temperate ecosystems[53,54]. Indeed, a recent study shows that even subtle warming (by approximately 1 °C) can increase the ecosystem respiration rates in a subarctic peatland, particularly in the subsurface layers[55]. This is indicative of a large and long-lasting positive feedback of the organic carbon stored in northern peatlands to the global climate system, although the mechanism of this response remains unclear[56].

Because different microbial groups have distinct optimal temperature ranges for growth and activity, increased temperature can affect the composition of the microbial community, which in some cases could reduce the release of soil organic carbon owing to the loss of acclimatized microbial groups[57]. For example, an increase in temperature in a high-latitude ecosystem resulted in an up to 50% decrease in bacterial and fungal abundance and soil respiration, as well as a phylogenetic shift in the fungal community[58], suggesting that increased temperature does not always lead to enhanced carbon loss to the atmosphere. To complicate matters further, these changes in respiration could be caused by shifts in the composition and activities of microbial communities or by changes in the quality and quantity of soil organic carbon[59,60]. Specifically, there is evidence that warming of soils leads to a decreased relative abundance of fungi and to changes in bacterial community structure in arctic ecosystems[61], but the long-term reduction in soil respiration due to warming could also be caused by the sequential removal of easily decomposable organic carbon that results from an initial stimulation of decomposition. It is also possible that some soil organic carbon is physically and chemically protected from microbial decomposition[59,62]. Because there are so many variables, the estimation of carbon loss by climate change is unreliable[63], and reducing this uncertainty will be a major advancement.

Another key determinant of the terrestrial microbial community structure and the decomposition rate of soil organic carbon is soil moisture, which will be affected by the 20% increase or decrease in precipitation rate that has been predicted by the Intergovernmental Panel on Climate Change[21]. Microbial communities respond to moisture levels directly, because they require water for physiological activities, and indirectly, owing to the effect of changing soil moisture on gas diffusion rates and oxygen availability. The effect of changing precipitation on the feedback responses of soil microorganisms to climate change may therefore be due to the direct effect on microbial physiology and community structure. Long periods of drier conditions may limit microbial growth and decomposition[64] and may consequently have a negative-feedback effect on carbon fluxes in some ecosystems. However, soil drying may increase oxygen availability and enhance carbon cycling in wetlands and peatlands, thereby having a positive-feedback effect on CO_2 fluxes[65].

It is important to note that feedback responses caused by altered temperature and moisture will differ between different ecosystems and regions. For example, increasing temperature is likely to have a more pronounced effect in alpine, arctic and temperate regions because microbial growth is often limited by temperature in

Permafrost
Soil that remains permanently frozen.

Recalcitrant carbon
A form of carbon that is resistant to microbial decomposition owing to its chemical structure and composition.

Peatland
An area dominated by deep organic soils.

these ecosystems. Conversely, increased drought conditions may have a stronger effect in tropical regions, as this may cause large changes in root growth and substantial reductions in microbial biomass or shifts in microbial community structure[66,67]. Therefore, the challenge is to quantify the feedback effects of climate change on greenhouse gas flux at both the ecosystem and regional scales and then to integrate this information to produce more robust predictions on a global scale.

Methane. CH_4 is the second most important anthropogenic greenhouse gas in terms of total climate forcing, and microbial utilization (methanotrophy) is the largest terrestrial sink. Therefore, to better predict CH_4 emissions, it will be essential to understand the response of CH_4 flux to climate change.

The responses of microorganism-mediated CH_4 fluxes to changes in climate and atmospheric composition are as uncertain as those of CO_2 fluxes. Recent analyses suggest that climate warming, particularly at high latitudes, may lead to a substantial increase in net CH_4 emissions from permafrosts and wetlands, which will serve as a notable positive feedback to global climate warming[68]. Although warmer conditions might be expected to increase the activities of both methanogens and methanotrophs when other factors are not limiting, it is by no means clear whether this response would be balanced and how it might affect net CH_4 emissions globally. Similarly, increased net primary production and altered water table depths and soil water contents, which are likely to occur following climate warming in some ecosystems such as arctic tundra, could enhance methanogenesis and net CH_4 emissions, whereas reduced precipitation and drying of soils in other areas could promote oxygen availability (and therefore CH_4 oxidation) and so reduce net CH_4 emissions[69].

Several studies have shown that increased CO_2 levels lead to a substantial decrease (up to 30%) in CH_4 uptake by soil microorganisms and to an increased CH_4 efflux[70,71]. However, the mechanism by which CH_4 uptake is decreased remains unknown. In some studies, plant-mediated increases in soil moisture explain reductions in CH_4 consumption[72,73], whereas in others studies, reduced CH_4 oxidation has been found to occur without concomitant increases in soil moisture[74]. Increased CO_2 levels may affect CH_4 emissions indirectly through their effects on microbial activity and physiology, and it is possible that plant-mediated increases in soil moisture in the presence of increased CO_2 levels in the soil will lead to more anoxic conditions, thereby increasing methanogenesis and reducing methanotrophy. However, higher temperature and reduced moisture are thought to increase net CH_4 uptake by terrestrial ecosystems, as they invariably increase gas diffusion rates and microbial access to oxygen and atmospheric CH_4.

Most experimental designs to date have tested the impact of one climate variable (for example, increased temperature) on CH_4 flux, but for better prediction we need to investigate microbial responses in multifactorial experimental designs in which many interacting climatic variables can be tested. In one such study, both increased temperature and CO_2 levels were tested simultaneously, and it was reported that the stimulatory effect of increased CO_2 levels on CH_4 flux was offset by increasing temperature[75]. This finding is in agreement with an early report stating that increased temperature enhanced CH_4 uptake, whereas increased CO_2 levels decreased it, and it was suggested that the effect of both treatments was indirect and mediated through their impact on soil moisture[72].

Increased CO_2 levels have been reported to reduce the abundance of methanotrophs by up to 70% (REF. 76), so the feedback response of CH_4 flux could also be caused by a shift in functional microbial communities. Indeed, previous studies have shown that CH_4 fluxes that occur owing to changes in land use are related to changes in the composition[77,78] and abundance[79,80] of the methanotroph community. It is possible that changes in CH_4 flux that are due to increased CO_2 levels or temperature are also related to changes in the abundance and community structure of methanotrophs, but this requires further investigation. Some studies have also found that the abundance of type II methanotrophs declined in response to increasing precipitation and temperature[81,82]. However, a recent study in a permafrost tundra area observed the opposite effect of increased temperature on these microorganisms[83], which may suggest that the methanotrophic communities of different ecosystems respond differently to altered temperature and precipitation. Although the available data suggest a substantial response of the microorganism-mediated CH_4 flux rate to projected changes in climate and atmospheric compositions, further study of the temperature sensitivity of different groups of methanogens and methanotrophs, and its interaction with moisture and CO_2 levels across different ecosystems, is essential to more accurately predict future terrestrial CH_4 fluxes.

Nitrous oxide. The direct effects of changes in climate and atmospheric composition on microorganism-mediated fluxes of N_2O may be less pronounced than the effects on CO_2 and CH_4 fluxes, with global emissions being primarily dependent on the supply of reactive nitrogen (such as NH_3 and nitrogen oxides (NO_x)). Together with industrialization and rising emissions of NO_x from fossil fuel burning, the intensification of agriculture and associated NH_3 emissions has led to a threefold to fivefold increase in the release of reactive nitrogen over the past century[21]. Such increased availability of reactive nitrogen in terrestrial ecosystems is likely to result in enhanced nitrification and denitrification and, therefore, enhanced N_2O production[84], but again, the type and extent of interaction with climate change remains poorly understood.

Some studies have reported a decrease in denitrification activity at increased levels of CO_2 (REFS. 85,86), whereas others reported no effect[87,88]. Moreover, some studies reported an increased N_2O emission under increased CO_2 levels, but only when excess mineral nitrogen was available[70,89]. This may suggest that when reactive nitrogen availability is low an ecosystem will show reduced N_2O emission under increased CO_2 levels,

Water table
The level at which the groundwater pressure is the same as the atmospheric pressure.

Box 2 | **Classification of bacteria on the basis of carbon mineralization**

Owing to our inability to culture most microorganisms, functional classification of bacterial communities has not been possible. However, recent findings suggest that microorganisms can be classified into oligotrophs and copiotrophs. For example, a combined experimental and meta-analysis study carried out on the rates of organic carbon mineralization found that the phylum Acidobacteria exhibits oligotrophy, whereas the class Betaproteobacteria and the phylum Bacteroidetes follow copiotrophic lifestyles[103]. A second study provided further evidence that bacterial community composition influences heterotrophic respiration and that changes in bacterial community composition can potentially influence soil carbon storage[121]. This study reported that the class Gammaproteobacteria and phylum Firmicutes become dominant at the expense of the Acidobacteria in rain forest soils and are responsible for enhanced mineralization of dissolved organic carbon and, therefore, for increased soil respiration. These two studies, along with others[122], suggest that soils dominated by oligotrophs (such as the Acidobacteria) may have low carbon turnover and, consequently, low carbon dioxide emission and higher carbon sequestration.

Culturing oligotrophs from the natural environment is a long-standing problem. A recent study[123] showed that the trophic structure of microorganisms in marine systems is reflected in their genomic contents and can be used as a proxy for uncultured microorganisms. This indicates that we can classify uncultivable microorganisms into trophic groups on the basis of their genome structure. Based on this study, a model was developed that allows us to define the types of bacteria that specific ocean niches can sustain. Such a system could and should be used for defining microorganisms in a terrestrial ecosystem. Use of such information in the future may improve the predictions made by climate models.

whereas the reverse will be true for an ecosystem with high reactive nitrogen availability. There is little information available on the microbial basis of such changes in N_2O flux, but shifts in the structure of NH_3-oxidizing bacterial communities and decreases in their abundance under increased CO_2 levels have been observed[90].

There are also contradicting reports on the temperature sensitivity of nitrifying and denitrifying microbial communities[91]. One analysis of previous studies[85] concluded that projected increases in temperature would not greatly affect nitrifying or denitrifying enzymes. However, other studies have found that the proportion of the total N_2O flux that is associated with nitrification decreases at higher temperatures, and this was linked to a change in structure of the NH_3-oxidizing bacterial community[92]. Future research on this topic should therefore focus on assessing N_2O production by nitrifying and denitrifying microorganisms in response to a changing availability of reactive nitrogen, and on its interactions with changes in climate and atmospheric composition.

Microbial communities and mitigation options

The manipulation of terrestrial ecosystems offers a potentially powerful means by which to mitigate anthropogenic climate change. Below, we discuss strategies that could be used to manage microbial communities in the soil so that they contribute towards mitigating climate change.

Managing microbial communities to reduce carbon dioxide emissions. Currently, soils contain about 2,000 Pg of organic carbon, which is twice the amount of carbon in the atmosphere and three times the quantity found in vegetation[21,93]. The capacity of different land types (for example, woodland, pasture and arable land) to store carbon differs, and it has been suggested that land use can be managed to sequester a further 1 Pg of carbon per year in soils[93,94]; this potential has received considerable scientific attention[95–98]. However, this may not be easily achievable on a global scale owing to the complex biological mechanisms that control the incorporation of organic carbon into soil, as well as the influence of changing abiotic factors, such as moisture, temperature, land use and nitrogen enrichment, which also affect soil carbon pools[97,99]. Forest soils are considered to be especially effective at storing carbon, in part because of a high abundance of fungi in the soil relative to bacteria, which favours carbon sequestration (see above)[67,98,100,101].

To manage the soil microbial communities to increase carbon sequestration, it will be important to understand their ecology and function. This is a challenge in itself, because of our inability to characterize the species diversity and function of soil microbial communities and our lack of theoretical principles in microbial ecology, such as the definition of a species and the factors driving community formation and structure [102]. Nevertheless, there is some evidence that bacteria can be categorized on the basis of their carbon mineralization capacity and can be divided into copiotrophic (characterized by high growth rates on labile carbon and dominant in nutrient-rich environments) and oligotrophic (slow-growing and dominant in nutrient-limited ecosystems) species[103]. It has been suggested that the Acidobacteria are oligotrophic, whereas the Proteobacteria and the Actinobacteria form copiotrophic communities (BOX 2). It can be argued that manipulating land use (for example, changing from arable land to forestry) and land management practices (for example, using low-nitrogen-input agriculture) may promote the growth of oligotrophic communities. However, the ecological strategies of other dominant microbial taxa need to be understood. It is true that not all taxa in a phylum will be either copiotrophic or oligotrophic[57], and thus phyla alone may not be a predictor of carbon loss from the soil[103]. It is therefore essential that we use rapidly developing technologies such as high-throughput sequencing to better understand soil microbial diversity. Moreover, emerging technologies such as metagenomics, metatranscriptomics, metaproteomics and stable-isotope probing (SIP) must be used to examine the physiological abilities and roles of individual taxa in a given ecosystem (BOX 3). Only then can we begin to predict whether a particular soil is a net carbon emitter or sink based on microbial ecology. This approach can be further expanded by combining metagenomics with SIP to find out the specific function of a microbial population in a community. Future work should attempt to use this approach to differentiate between populations that use labile carbon and those that promote carbon sequestration.

In agriculture, the often large losses of soil organic carbon owing to cultivation can be reduced by low- and no-tillage practices, which favour soil communities dominated by fungi[101]. Such agroecosystems prevent the increase in microbial decomposition and respiration

Arable land
Land that is used for growing crops.

Mineralization
The conversion of organic carbon into inorganic forms, mainly CO_2.

Box 3 | **Advances in linking microbial communities to ecosystem function**

Recent developments in molecular and genomic methods provide a golden opportunity to assign ecological roles to different microbial taxa. 'Meta-omic' techniques have greatly advanced this area of science. Metagenomics involves the direct isolation of DNA from environmental samples, its cloning into a vector and its transfer into a surrogate host. Subsequent sequencing of all inserts provides information on the type, diversity and functional ability of the microorganism. Although covering all genomes will have logistical and cost constraints, metagenomics is useful if the aim of a study is to know the composition and functional potential of a microbial community[124,125]. The presence of genes is only an indicator of functional potential, and several genes are never expressed in a microbial system. This problem can be overcome by first extracting RNA from the sample and then constructing cDNA before sequencing (called metatranscriptomics). This approach is now further improved by direct sequencing of RNA, which removes bias associated with the synthesis of cDNA from RNA[126]. Metaproteomics, which involves the direct extraction of proteins from the environment and their analysis by mass spectrometry, has also greatly progressed recently. However, to fully use this approach to link a microbial community with its ecological function, protein databases need to be expanded.

Stable-isotope probing (SIP) is the most widely used method of microbial-community analysis and involves tracking the incorporation of stable-isotope atoms from a particular substrate into microbial cell components (such as DNA and RNA)[127]. SIP–metagenomics is already providing new information on uncultivable microorganisms that oxidize methane or degrade pollutants[128]. In this case, DNA from microorganisms that use labelled substrate is separated from other microbial DNA before cloning. This ensures that most of the clones contain inserts originating from the microorganisms that provide targeted functions, and therefore reduces the number of clones to be screened to a manageable level.

that comes from ploughing and disturbance[22], and it has been proposed that widespread adoption of this practice could lead to sequestration of up to 55 Pg of organic carbon in surface soil[104]. However, there are also possible trade-offs, as low- or no-tillage agriculture has been found, in some cases, to enhance emissions of N_2O from soil (owing to increased rates of denitrification that are due to anaerobic conditions in compacted soils), thereby offsetting some of the benefits of increased soil carbon storage[23]. The conversion of croplands to permanent grassland, which causes a build-up of organic matter at the soil surface[105,106], could also increase carbon sequestration. Furthermore, the plant functional diversity on degraded or agriculturally improved soils[54,96,107,108] could be manipulated to manage the levels of carbon released in the soil. Concomitant application of nitrogen-based fertilizers could, in some cases, enhance soil carbon storage by increasing plant production and by suppressing microbial decomposition of recalcitrant organic matter[109,110].

There is contradictory evidence about the effects of nitrogen enrichment on soil carbon stocks, and therefore it is not possible to make sweeping statements about how soil carbon sinks will respond to nitrogen enrichment[99]. Moreover, to realize the real potential of soils to sequester carbon in the long term, we need to further our understanding of the interactions between different climatic (temperature, moisture level and water table level), soil (pH, moisture content and structure) and biotic (bacterial, fungal and archaeal soil fauna, and plants and their consumers) properties that influence soil carbon cycling, which is currently limited.

Grassland
Land that has grass as the dominant vegetation.

Managing microbial communities to reduce methane emissions. Our understanding of the microbiology of greenhouse gas cycling is more complete for CH_4 than for CO_2 or N_2O, as the pathway is simple and specialized microorganisms are involved. However, many of the above uncertainties also apply to the management of terrestrial CH_4 fluxes. Because most atmospheric CH_4 is produced by microorganisms, it is theoretically feasible to control a substantial proportion of CH_4 emissions from terrestrial ecosystems by managing microbial community structure and processes. The biological oxidation of CH_4 by methanotrophs accounts for only ~5% of the global sink of atmospheric CH_4 (~30 million tonnes per year)[111] and may therefore seem less important. However, methanotrophs are also responsible for the oxidation of up to 90% of the CH_4 produced in soil before it can escape to the atmosphere[112]. It is well established that conversion of arable land or grassland to forest results in a substantial reduction in CH_4 flux[113,114], and it is evident that both the type and abundance of methanotrophs are important for predicting CH_4 flux[77,79,115]. However, no current climate model considers this finding, so future research must focus on incorporating these data and interactions to improve predictions of CH_4 fluxes across various ecosystems. This knowledge can also be applied to the reduction of CH_4 emissions by changing land use and management. In rice cultivation, for example, methanotrophs have long played a crucial part in absorbing a proportion of the CH_4 produced and, as a result, improved management of flooding frequency and duration could reduce net emissions by increasing oxygen availability in soils[116]. There is also great potential to make effective use of inhibitors of methanogenesis, such as ammonium sulphate fertilizers, in managed systems to promote the growth of sulphate reducers at the expense of methanogens[117]. To reduce methane emissions from ruminant livestock, strategies include improving feed quality and directly inhibiting methanogen communities in the rumen using antibiotics, vaccines and alternative electron acceptors[22].

Managing microbial communities to reduce N_2O emissions. A major source of anthropogenic N_2O emission is the use of nitrogen fertilizers in agriculture. As a substantial proportion of applied fertilizers is emitted in the form of N_2O, better targeted fertilizer applications, which reduce the availability of nitrogen to microorganisms, can substantially decrease N_2O emissions. Potential strategies include reducing the amount of fertilizer and applying it at an appropriate time (when crop demand for nitrogen is high and leaching-loss rates are low), using slow-release fertilizers, and avoiding nitrogen forms that are likely to produce large emissions or leaching losses (such as nitrate in wet soil). Similarly, improved land drainage and better management practices to limit anaerobic conditions in soils (for example, land compaction and excessive wetness) could reduce denitrification rates and, thus, N_2O emissions. Finally, for the mitigation of N_2O fluxes from agriculture, the use of nitrification inhibitors in fertilizers to limit nitrate production and subsequent leaching or denitrification

Box 4 | **Microorganisms as a source of biofuels**

Perhaps the most enticing and controversial area of microbial climate engineering is the substitution of fossil fuel energy sources with biofuels. As strong sources of methane (CH_4) production, landfill sites are increasingly being used for heat and electricity generation. Numerous large-scale sites across the developed world now routinely collect the CH_4 produced and either pipe it directly into the gas supply network or use it on-site for electricity generation and space heating. Such use of landfill CH_4 provides the double climate benefit of avoided CH_4 emissions and substitution of fossil fuels[129]. An extension of this technology is the use of anaerobic digestion of manure, sewage and other organic wastes to maximize methanogenesis for methane collection and use. Such optimized systems also help to avoid the more diffuse emissions of nitrous oxide (N_2O) and CH_4 to the atmosphere that occur when such wastes are applied directly to soils[130].

For liquid biofuels generated from agricultural crop and residue feedstocks, microorganisms are again at the heart of current efforts to increase production and reduce fossil fuel use[28,131]. Suggested solutions to some of these problems include the use of cellulosic crop and forest residues as the feedstock for biofuel production: recent advances include the discovery of a fungus that can convert woody material into biodiesel[132] and the production of ethanol by a modified *Escherichia coli*[133]. Such discoveries have prompted further optimism that extant or engineered microorganisms can be used to improve the net climate benefits of biofuels[134]. Similarly, the production of algal biomass under controlled conditions and its subsequent conversion to biodiesel or ethanol also helps to avoid the land-use changes, food price increases and N_2O penalties that are associated with many first-generation biofuels such as corn ethanol[135].

losses is now a well-established strategy[23]. These and similar microorganism-mediated strategies (BOX 4) have great potential to reduce greenhouse gas emissions from the land use and agricultural sectors.

Conclusions and perspectives

There is consensus among scientists that global climate change is happening and that the increases in global average temperatures since 1900 can be largely attributed to human activities. However, there remains much uncertainty about predictions of future greenhouse gas emissions and the response of these emissions to further changes in the global climate and atmospheric composition. To help tackle this uncertainty, there is a need to better understand terrestrial microbial feedback responses and the potential to manage microbial systems for the mitigation of climate change. There is an urgent need to improve the mechanistic understanding of microbial control of greenhouse gas emissions and the interactions between the different abiotic and biotic components that regulate them. This understanding will help to remove large uncertainties about the prediction of feedback responses of microorganisms to climate change and will enable the knowledge to be incorporated into future models of climate change and terrestrial feedbacks.

It is currently difficult to know whether changes in processes that are associated with climate change are brought about by the effect of climate change on soil microbial communities, by changes in soil abiotic factors or by interactions between the two. Moreover, it is unclear how microorganisms respond to climate change and therefore what their potential is to influence climate feedbacks across ecosystems and along environmental gradients. Another issue that needs to be taken into consideration is that, to date, most studies have focused on one greenhouse gas, whereas evidence suggests that microorganism-mediated fluxes of different greenhouse gases respond differently to climate change. For example, it is assumed that conservation of peatland will enhance carbon sequestration, but this may also increase CH_4 fluxes, so the effect on net greenhouse gas flux is still unclear.

On the basis of the above information, we propose several topics of research that need to be prioritized to develop microorganism-mediated approaches to mitigate climate change. First, we need to better understand and quantify microbial responses to climate change to comprehend future ecosystem functioning. Second, we need to classify microbial taxa in terms of their functional and physiological capabilities and to link this information to the level of ecosystem function. Third, we need to improve our mechanistic understanding of microbial control of greenhouse gas emissions and microbial responses to simultaneous climatic factors, such as warming, altered precipitation and increased CO_2 levels, across different ecosystems. Fourth, we need to develop a framework

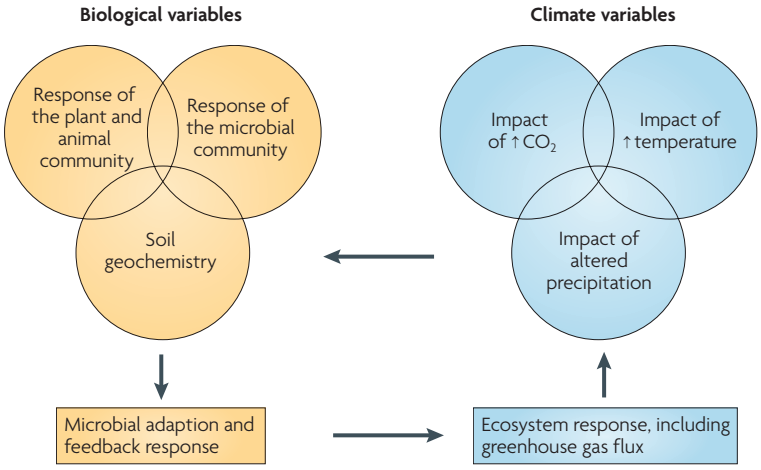


Figure 3 | **A proposed framework for future research on climate change and ecological responses.** It is important to understand the responses of individual microbial species and whole microbial communities, as well as their interactions with other soil biota and plants, to single climatic variables (such as increased levels of carbon dioxide (CO_2) and changes in temperature and precipitation) and in multifactorial experimental conditions. This approach should be then tested in contrasting ecosystems differing in climatic, nutritional, chemical and physical properties. Such an integrated approach is essential for gaining a mechanistic understanding of microbial adaptation and feedback responses to individual and interacting global changes. This understanding then can be exploited to predict the feedback response at the ecosystem level using various climate models.

to incorporate microbial data (biomass, community, diversity and activity) into climate models to reduce uncertainty and to improve estimation and prediction. Fifth, we need to better understand the effect of climate change on above-ground and below-ground interactions and nutrient cycling, as well as the role of these interactions in modulating the response of ecosystems to global change. Finally, we need to develop a framework based on the above five points to potentially manage natural microbial systems to enhance carbon sequestration and/or reduce net greenhouse gas emissions.

To answer the above challenges, we need to use an interdisciplinary approach that includes microbial ecology, environmental genomics, soil and plant science, and ecosystem modelling. There have been substantial advancements in the technologies that can be used to examine microbial communities and to relate them to ecosystem functions (BOX 3). These technologies should be applied to study how particular taxa respond to individual and multiple climate variables and how such responses influence ecosystem functions (FIG. 3). There is already some evidence of microbial control of greenhouse gas flux[14,118], and it has been shown that even short-term seasonal change in carbon flux is related to shifts in microbial communities[118]. However, further studies are needed across ecosystem types, and a better mechanistic understanding of fundamental ecosystem processes is required to predict the magnitude of effects using climate models[119,120] and to reduce uncertainties in predictions. This can be achieved using two complementary approaches: a reductionist approach, in which the response of individual taxa or communities is tested separately for each environmental variable (increased temperature, precipitation and CO_2 concentration) to provide important mechanistic information; and a multifactorial approach that also considers trophic interactions to account for the interactive (synergistic or antagonistic) effect of variables. Recently, attempts have been made to incorporate microbial data (biomass, and enzyme and growth kinetics) into climate models[14,118]. However, to further improve predictions, we need to incorporate data on microbial diversity, community structure and physiological capabilities of various taxa. Only after we have such an improved understanding of microbial responses can a framework on management of microbial systems for reduced greenhouse gas emission be developed.

Microorganisms could either greatly help in climate change mitigation, or prove disastrous by exacerbating anthropogenic climate change through positive-feedback mechanisms. No academic article is complete without a call for 'more research', but seldom is there an area — that of microbiology and climate change — that urgently requires so much more research effort and that has so much at stake. Microorganisms may be out of sight, but we cannot afford for them to be out of mind.

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The authors declare no competing financial interests.

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