GLOBAL CHANGE

Soil microbiomes and climate change

Janet K. Jansson * and *Kirsten S. Hofmockel* *

Abstract | The soil microbiome governs biogeochemical cycling of macronutrients, micronutrients and other elements vital for the growth of plants and animal life. Understanding and predicting the impact of climate change on soil microbiomes and the ecosystem services they provide present a grand challenge and major opportunity as we direct our research efforts towards one of the most pressing problems facing our planet. In this Review, we explore the current state of knowledge about the impacts of climate change on soil microorganisms in different climate-sensitive soil ecosystems, as well as potential ways that soil microorganisms can be harnessed to help mitigate the negative consequences of climate change.

Permafrost
Soil that has been frozen for at least 2 consecutive years.

Carbon use efficiency
The difference between the amount of carbon respired as CO_2 and that incorporated into the cellular biomass.

Earth and Biological Sciences Directorate, Pacific Northwest National Laboratory, Richland, WA, USA.

e-mail: janet.jansson@pnnl.gov; kirsten.hofmockel@pnnl.gov

https://doi.org/10.1038/s41579-019-0265-7

Over the past century, CO_2 levels have steadily increased and global temperatures have risen accordingly. As outlined in the recent US national climate assessment[1], the climate is predicted to continue to change with weather patterns becoming more erratic and extreme. As soil microorganisms are largely responsible for cycling of soil organic carbon (SOC) and other nutrients, they have a key role in climate feedback, including production or consumption of greenhouse gases such as CO_2, CH_4 and N_2O. However, whether soil will become a source or sink of greenhouse gases under future climate scenarios has been difficult to predict[2,3] due to unknown changes in soil carbon and nitrogen pools, and differences in microbial responses between soil locations. Thus, although the importance of soil microbial ecology for prediction of future climate impacts has been recognized, it remains a challenge to integrate with landscape-scale climate models[4].

In this Review, we provide an overview of research describing responses of soil microorganisms to the following anticipated changes in climate[1]: elevated levels of atmospheric carbon dioxide (eCO_2); elevated temperature; increased drought; increased precipitation and/or flooding; and increased fire frequency. Although discussed independently, we also emphasize where compounding disturbances occur due to a combination of climate change impacts[5]; for example, heat waves can include both eCO_2 and increases in temperature[6], and there can be combined effects of drought and warming[7]. This knowledge should elevate our understanding of how microbial communities and the ecosystem services they provide are influenced by the combined pressures of changing climate and compounding disturbances, which in turn will be useful for protecting, managing and mitigating ecosystem resilience.

One major concern with climate change is that soil microorganisms will mineralize more SOC and contribute substantially to greenhouse gas (CO_2 and CH_4)

emissions, thus exacerbating warming trends. This is a concern because the total amount of soil carbon, including within permafrost, is estimated to be ~3,300 petagrams (Pg) — approximately five times larger than the current atmospheric pool of CO_2 (REFS[8,9]). However, there is considerable uncertainty in climate models on whether this pool of soil carbon will increase or decrease in the future. The majority of empirical data from climate change studies in the field have relied on measurement of changes in soil respiration. In order to improve models of soil carbon–climate feedback, there is also a need to determine how bulk soil carbon stocks change with changes in climate[10].

Soil microorganisms carry out the dichotomous roles of mineralization of SOC and stabilization of carbon inputs into organic forms. The balance between these two processes governs the net flux of CO_2 and CH_4 to the atmosphere. The proportion of carbon substrate that is retained in the microbial biomass compared with that respired as CO_2 is referred to as the microbial carbon use efficiency. Heterotrophic respiration of SOC has globally increased as a result of climate change, thus contributing to increased atmospheric inputs of CO_2 (REF.[11]). However, losses of soil carbon to the atmosphere could be countered by increased soil carbon inputs due to increased plant growth[12] and autotrophic fixation by soil microorganisms. Also, the temperature sensitivity of decomposition of SOC varies with the quantity and chemistry of plant litter and pre-existing SOC[13]. Thus, even within specific biomes, the local biogeochemical environment strongly influences microbial metabolic responses to climate (BOX 1). Developing a mathematical understanding of the microbial ecology that drives ecosystem carbon use efficiency and the feedback with climate forcing is therefore a pressing need for improving climate change models.

Nitrogen cycling also has a strong influence on climate change, because nitrogen availability is closely

correlated to the production of CO_2, N_2O and CH_4 (REF.[14]). In particular, management of N_2O emissions remains a pressing issue because N_2O is a potent greenhouse gas, with 298 times the warming potential of CO_2, and emissions from soil represent 56–70% of all global N_2O sources[15]. Managing N_2O emissions within soil ecosystems has been a formidable challenge due to the complexity of the microbial communities involved[16] and the spatial and temporal variation of the soil environment[17,18]. Recently, microorganisms were discovered that can completely oxidize ammonia to nitrate (comammox)[19] without generating N_2O as a by-product, and these are abundant in soil[20]. This finding illustrates the importance of gaining a better understanding of soil microbial physiology and metabolism and how those processes are impacted by climate change.

Current status and knowledge gaps

Soil represents one of the most highly diverse ecosystems on our planet with an interacting community of bacteria, archaea, viruses, fungi and protozoa: collectively referred to as the 'soil microbiome'. The soil abiotic environment is also highly heterogeneous, with disconnected air-filled and/or water-filled pores, and patchy resources that can serve as hotspots for microbial growth[21]. When combined with the influence of plants and soil fauna (for example, insects and earthworms) as well as changes in soil moisture, temperature and fluctuating redox states, the soil environment is highly dynamic. However, climate change is introducing more extended and higher extremes of change with unknown consequences on the stability and resilience of the soil microbiome[22]. Therefore, better understanding of microbial traits that

---

Box 1 | Climate-sensitive soil ecosystems

The Arctic

The Arctic is one of the most climate-sensitive regions on Earth, with average temperatures increasing at nearly twice the global rate[138], resulting in drastic changes in the landscape including permafrost thaw, changes in precipitation patterns and changes in vegetation. With permafrost thaw, microorganisms become more active and start to decompose the enormous reservoir of stored carbon (~1,300–1,580 Pg of carbon)[139], which is approximately half of the total soil carbon stock. Recent estimates suggest that ~5–15% of the carbon currently contained in permafrost is susceptible to microbial decomposition, resulting in a substantial source of CO_2 emissions over the next few decades[139]. Although this is less CO_2 than that emitted from current fossil-fuel emissions, adding CH_4 to the equation greatly accelerates the warming impact because CH_4 has 34 times the climate-forcing influence than CO_2 (REF.[140]). As the huge reservoir of carbon in high latitude soils is released, positive feedback to climate change is expected at the planetary scale.

Forests

Forests, ranging from boreal to temperate to tropical, together cover ~30% of the total land surface and have important roles as soil carbon sinks with large amounts of stable organic matter[141]. It is possible that predicted losses of soil carbon to the atmosphere due to increased microbial decomposition of soil organic carbon under warming will be partly countered by increased carbon inputs due to increased plant growth[142]. However, with increasing temperature, drought severity and fire frequency, forest ecosystems have the potential to transform from net sinks to net sources of CO_2 in the future[142]. Both fungal and bacterial communities in forest soils have been shown to respond to changes in climate, but the types of microorganisms and their specific responses differ among forest ecosystems. This is partly because of the differences in the litter type and quality depending on the plant communities (for example, coniferous versus deciduous forests) and differences in soil pH[142].

Grasslands

Grasslands comprise ~26% of the global land area and store an estimated 20% of the total soil carbon stock[143]. The grassland soil carbon pool is large, approximately one or two orders of magnitude larger than the above-ground plant biomass pool, due to the deep and abundant rhizosphere that deposits carbon in the soil[144]. As a result, the projected vulnerability of grasslands to changing climate is intimately related to plant–microorganism interactions occurring in the rhizosphere, and to bulk soil processes that cycle carbon and other nutrients. With climate change, most grassland ecosystems are experiencing increased periods of drought and fire, mixed with more periodic and extreme precipitation events. The resulting changes in soil moisture influence both the above-ground plant growth and the microbial community compositions and functions in soil. Owing to differences between soil types and plant cover across grassland ecosystems, it has proven difficult to generalize what the long-term impacts will be on microbial community functions and climate feedback.

Wetlands

Wetlands interface terrestrial and aquatic systems, resulting in various ecosystems amenable to microbial greenhouse gas production. Wetland CH_4 emissions are the largest natural source of CH_4 and contribute approximately one-third of total emissions[145]. Presently, conventional greenhouse gas mitigation policies do not include feedback associated with wetland CH_4 emissions[146] and could be improved with more accurate representation of microbial responses. Water availability is generally a strong predictor of CH_4 emissions: reduced precipitation enhances O_2 availability, promotes organic matter decomposition, increases CO_2 release and reduces CH_4 emissions, whereas increased precipitation and more anaerobic conditions favour CH_4 production.

Drylands

Deserts and other dryland soils are characterized by water deficiency that restricts plant and microbial activity. Owing to the expanse of global arid regions (approximately one-third of the planet's surface), they collectively store ~27% of the total terrestrial organic carbon stocks[147]. Climate change is resulting in an expanse of soil desertification and dryland areas are projected to increase by 11–23% by the end of this century[76]. These changes in water availability can have profound and lasting impacts on soil microbiomes. However, because arid soil ecosystems are globally distributed, it is difficult to generalize microbial responses to increasing drought across soils and regions.
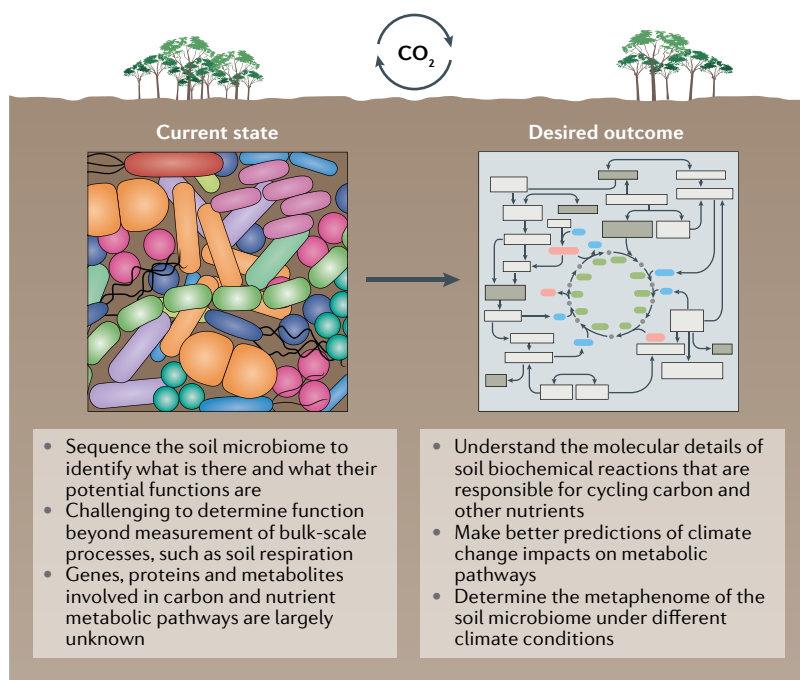
Fig. 1 | **Current state and desired outcome of soil microbiome science.** Owing to advances in sequencing technologies, it is currently possible to determine the taxonomic composition of soil microbial communities and to determine how climate change influences the community membership. Understanding the details of biochemical pathways, such as those involved in soil respiration, that are carried out by interacting members of soil communities and how key functions are impacted by changes in climate are crucial science frontiers that can be addressed with multi-omics approaches and other emerging technologies. Colours in the left panel represent different microbial cells and in the right panel represent different steps in biochemical pathways.

r-Strategists
Species that typically have high growth rates and are able to respond quickly to resources as they become available.

K-Strategists
Species that typically are slow growing and adapted to utilize minimal resources.

Metaphenome
A community phenotype that is the product of genomic potential encoded in metagenomes and the environmental conditions that govern which genes are expressed.

microbiome, such as the abundance of fast-growing, opportunistic 'r-strategists' compared with slow-growing 'K-strategists', as well as environmental properties can help to predict how the soil microbiome will respond to different climate change scenarios[26].

High-throughput sequencing has been instrumental in revealing the microbial diversity and composition in various soil ecosystems[27], providing a valuable baseline for comparison as the climate changes. It is now recognized, however, that compositional information does not always inform function (FIG. 1). Not all members of a community, or even cells within a specific population, are active at any given time. Activity is governed by a complex interaction of gene regulation that governs which genes are expressed and access to resources. Variability in moisture, temperature and local atmospheric chemistry within the soil impacts the phenotypic response of the soil microbiome with feedback to climate change. The diverse genetic potential within the soil microbiome interacts with environmental shifts to induce microbial gene expression. This collective phenotypic output of the microbiome, the metaphenome, generates ecosystem-scale elemental cycling[28]. Understanding the parameters connecting local microbial phenotypes to larger-scale ecosystem responses is thus an important frontier for improving climate models and for managing soil microbiomes in response to climate change (FIG. 1).

Currently, little is known about the fundamental microbial-scale mechanisms that control ecosystem-scale responses to climate change. Soil microorganisms do not respond to mean environmental conditions, but rather to instantaneous conditions at the microscale that trigger biochemical reactions, microbial responses and metabolic interactions. Biogeochemical responses to abrupt environmental change often include temporal lags as the soil microorganisms adapt. By contrast, a gradual change, such as an increase in temperature, allows more time for evolution by selection for species or genes that enable resistance to heat and associated stress conditions. The historical context also has a role in the community response. One study found that the historical exposure of grassland and adjacent forest soils to changes in soil water content influenced the ability of the soil microbiome to respond to new changes in soil moisture[29]. These findings imply that different soil ecosystems are sensitive to climate change to different degrees.

Influence of the soil environment on microbial responses to climate change. As soils vary tremendously with respect to their biotic and abiotic properties, it is difficult to generalize the impact of climate change on soil microbiomes across different soil ecosystems (BOX 1). Within a specific soil class, there are differences in biogeochemistry that govern the types of microorganisms that are present, including pH[30] and salinity[27]. In addition, the soil structure and the soil moisture content influence the creation of microbial habitats and niches[31] with cascading effects on carbon and nutrient transformations. Therefore, understanding the fine-scale distribution and connectivity of soil microbial communities is required to better understand how climate change influences species interactions and metabolism[32]. For example, this

confer ecosystem resilience to climate change is needed for predicting and managing ecosystem responses to climate change.

Influence of the soil microbiome on emergent ecosystem properties. As soil habitats are dynamic systems, most soil microorganisms have evolved strategies to cope with changing environmental conditions. Generally, as environmental conditions shift, the resident microorganisms either adapt, become dormant or die. Soil microorganisms respond to environmental stress in different ways, depending on their genetic and physiological states[23]. Acclimation and adaption to change is dependent on the degree of perturbation and the time necessary to regulate gene transcription and translation and/or accumulate mutations or new genes through horizontal gene transfer. However, at present, quantifying microbial physiological responses (for example, drought resistance, dormancy or reactivation) remains a major gap in modelling ecosystem responses to change[24].

Changes in microbial community structure may influence the stability and resilience of the community to future disturbances. Climate change will impact interactions between microbial populations in communities which in turn impact the ability of single species to adjust[25]. There can be mismatches between the responses of different species to rising temperature, for example, that can lead to changes in their dispersal patterns. Focusing on specific functional traits in the soil

knowledge is important for carbon cycling because the way that microbial species allocate carbon will ultimately determine whether carbon persists in soil[31] and how changes in environmental conditions influence these processes. Although it is well established that consortia of microorganisms within various soil niches interact and respire CO_2, N_2O and CH_4, the energetics and thermodynamics of the organic carbon electron acceptors that drive microbial metabolism are not well characterized in the context of the soil habitat. Our present frontier is to describe the physiological response surface (that is, the metaphenome) of soil microbial communities among the soils of our planet.

Impacts of climate change

In this section, we consider different types of community and physiological responses that soil microorganisms use to cope with changing environmental conditions caused by climate change. Although it is not possible to generalize across different terrestrial ecosystems, due to different predicted climate change variables across geographical regions (BOX 1), we provide some examples for context.

Elevated CO₂. Several eCO₂ field experiments have provided valuable data about microbial responses to this anticipated change in climate. The free-air CO_2 enrichment experiments were set up across a range of ecosystem types to compare long-term exposure to elevated and ambient CO_2 levels. Several studies have demonstrated shifts in the microbiome with eCO₂. A 10-year cross-biome study found ecosystem-specific responses as well as common responses of soil bacteria, such as increases in Acidobacteria with eCO₂ (REF.[33]). In Australian grasslands, eCO₂ resulted in shifts in archaea and fungi, and specific groups of bacteria[34]. Efforts are being made to understand how phylogenetic shifts represent ecological traits of microbial populations[35]. A trait-based approach provides a framework for integration of microbial physiology into ecosystem ecology.

Changes have also been found in potential functions carried out by the soil microbiome under eCO₂ through screening gene abundances in metagenomes. For example, the BioCON grassland experiment revealed eCO₂-stimulated increases in gene families associated with decomposition, nitrogen fixation and dissimilatory nitrate reduction, and lower abundances of gene families involved in glutamine synthesis and anaerobic ammonium oxidation[36]. In arid grasslands exposed to eCO₂, microbial genes involved in decomposition, nitrogen fixation, carbon fixation, CH_4 metabolism, nitrogen mineralization and denitrification were all increased[37]. Knowledge of shifts in gene functions involved in soil organic matter (SOM) cycling enables a deeper understanding of how microorganisms are affected by eCO₂. However, because eCO₂ field experiments have not been performed globally, with replica data sets, it remains challenging to inform global terrestrial ecosystem models[22].

Plant–microorganism interactions are an important scientific frontier for quantifying carbon exchange between the atmosphere and the soil. eCO₂ can enhance plant biomass, allocation of carbon to roots and soil microbial activities[38–40]. Different plant species respond differently to eCO₂, influencing the amount and types of carbon inputs to the rhizosphere. For example, C4 plants are more efficient at photosynthesis than C3 plants[41] and may allocate more carbon below ground to rhizosphere-associated microorganisms, resulting in shifts in community composition[34]. The increased rhizodeposition in response to eCO₂ can 'prime' microbial decomposition of existing SOC[42]. Priming is the stimulation of decomposition of old SOC through the addition of new microbial substrates that could include root exudates and/or increased litter inputs, both of which may be enhanced by eCO₂. A study combining meta-analysis and modelling revealed that eCO₂ initially stimulates photosynthesis and carbon inputs to soil. However, over decadal timescales, eCO₂ increased the microbial decomposition of SOM[43,44]. Predicting the balance between carbon accrual through mineral association and soil aggregation[45] and accelerated decomposition through priming[46] remains an additional challenge. This is because changes in soil carbon stocks are difficult to detect[47] and the fundamental biology regulating SOM decomposition has not been discovered. A recent comparison of priming effects in temperate and tropical forest soils found that the amount of soil carbon released by priming was not proportional to the rates of soil respiration, due to differences in SOC turnover rates in the different soil biomes[39]. These results suggest that priming is influenced both by the amount of organic matter deposition and the rate of SOC turnover.

It is difficult to uncouple the compounding effects of elevated eCO₂ from warming, as can also be seen in our discussion of temperature impacts below. For example, with an increase in soil moisture due to eCO₂, there can also be an increase in warming, which dries the soil[34]. In the Australian grassland study[34], although total fungal abundance increased under eCO₂, when eCO₂ was in combination with warming there was a decrease. The long-term effects of eCO₂ on soil carbon stocks also depend on water and nutrient availability, which influence photosynthesis, microbial decomposition and the net accrual of soil carbon. Understanding how changes in CO_2 interact with other important environmental variables including temperature, precipitation and nutrients (such as phosphorus) is therefore crucial for predicting microbiome responses among soil ecosystems. This highlights the need for continued and future long-term field studies that apply the suite of major climate-associated changes that are likely to occur in a given region.

Increased temperature. Temperature determines the growth rates and yields of pure cultures of microorganisms. Some physiological responses of microorganisms to higher temperatures include changes in lipid compositions of cell membranes to reduce membrane fluidity and the expression of heat shock proteins. It has been more difficult to assess the temperature response of soil microorganisms in situ, although advances in sequencing and functional gene arrays have revealed community and functional gene shifts in response to increased temperatures in the field[48–50]. The community and physiological responses of the soil microbiome to

higher temperatures also depend on the biome under study (for example, forest compared with grassland). For instance, warming has been shown to have contrasting impacts on soil fungi in different boreal forest ecosystems, resulting in either stimulation[51] or suppression[52] of fungal biomass and activity; these differences are presumably due to differences in soil moisture and/or vegetation at different sites[52].

To determine the impacts of extended soil warming on the temperate forest soil microbiome, the Harvard Forest Ecological Research Station Long Term Ecological Research site carried out a long-term soil warming experiment where the soil was warmed by 5 °C above ambient temperature for up to 26 years[48]. One of the major findings of this long-term study was the acclimation of microbial respiration and associated microbial mechanisms in four phases: rapid carbon loss through respiration; microbial community reorganization; a shift towards a more diverse, oligotrophic microbial community with higher soil respiration in heated plots than in controls; and a reduction in more recalcitrant carbon pools with an anticipated further change in microbial community structure[48]. Over the short term, the apparent acclimation of soil respiration was attributed to reduced microbial biomass and thermal adaptation of soil respiration[10]. Yet the physiological adjustments of individual populations remain to be quantified in the field context. New isotopic methods provide opportunities to bridge this knowledge gap and quantify microbial population dynamics under field conditions[53].

The Harvard Forest warming experiment resulted in an initial loss of soil labile carbon, followed by increased degradation of more recalcitrant carbon compounds[48]. The authors estimated a loss of ~710 g of carbon per square metre of soil and, by extrapolation, a loss of 190 Pg of carbon by the end of the century with continued warming trends, which is comparable with the amount produced over the past two decades from fossil-fuel emissions[48]. Therefore, sustained warming for 26 years resulted in depletion of SOC with corresponding reductions in microbial biomass, suggesting deleterious consequences of long-term warming for soil sustainability[48]. The reduced carbon availability corresponded with decreased abundance of fungi and Actinobacteria, and an increased abundance of oligotrophic bacteria[54], reinforcing the idea that microbial traits may be associated with ecosystem shifts in respiration. These studies provide further evidence that understanding the physiology of microbial populations and communities can enhance our predictive understanding of ecosystem responses to climate change.

In contrast to the Harvard Forest study, experimental warming of different grassland soils for 2 years[7] or 3 years[55] resulted in an increase in microbial biomass. However, both forest and grassland studies found shifts in microbial community compositions, including decreases in fungal-to-bacterial ratios[48,55–57] and increases in Gram-positive bacteria[34,48,58]. The decrease in fungi with warming could reflect the fact that bacteria have traits that provide a competitive advantage at higher temperatures, including faster growth rates and better nutrient competition. One study summarized three main responses to 12 years of warming in grassland soil experimental plots as follows: changes in microbial community structure, largely driven by changes in the plant community structure (there was a shift to favour growth of C4 plants over C3 plants); differential impacts on bacteria, but not fungi; and enhanced nutrient cycling that can feedback to promote plant growth[59].

The resilience of microbial communities to higher temperatures is ultimately dependent on the compounding impacts of drought, warming and plant type. The Prairie Heating and CO_2 Enrichment (PHACE) experiment, on Wyoming grasslands, studied the impacts of 12 years of eCO_2 in combination with warming[37]. Genes involved in carbon and nitrogen cycling were enriched under eCO_2 alone and in combination with warming. However, nitrogen cycling was suppressed under warming alone. The positive plant community response that resulted in increased biomass compounded the effect of shifts in precipitation[7,55]. Therefore, although warming stimulated both the carbon input into soils and soil respiration, carbon loss through respiration was mainly offset by the increased plant biomass. Together, these responses would act to weaken the positive feedback to climate warming and reduce soil carbon loss. In summary, although most climate models predict positive feedback as a result of warming due to increased soil respiration and a decrease in soil storage[2,60], there are confounding experimental results that are largely ecosystem dependent.

Permafrost thaw. A serious consequence of global warming is the thaw of permafrost soils in the Arctic. As permafrost soils store a huge reservoir of carbon (BOX 1), the potential feedback to the climate upon permafrost thaw is also huge[61]. Climate change is resulting in increases in the depth of the seasonally thawed active layer at the expense of the underlying permafrost. As the permafrost thaws, liquid water becomes more available and microbial activity increases. This can result in an increased decomposition of SOC and an increase in production of the greenhouse gases CO_2 and CH_4 (REF.[62]).

A general feature of permafrost thaw is a change in soil moisture that largely governs microbial activity. For example, the ability to produce CH_4 is a distinguishing feature of certain thawed permafrost environments[63–65], depending on the landscape hydrology[64], soil depth and redox conditions[66]. Experimental warming in the field resulted in a lower redox potential at the permafrost boundary and an increase in methanogens as a result[66]. By contrast, the redox conditions in mineral permafrost layers can favour iron reduction. A recent landscape transect of discontinuous permafrost in Alaska suggested the importance of Fe(II) content as a direct driver of microbial community composition[67]. This hypothesis is supported by the finding of abundant proteins corresponding to iron-reducing bacteria in Alaskan permafrost[63].

Several recent studies have used molecular approaches to unravel microbial community responses to permafrost thaw[63–65,68]. Metagenome sequencing revealed that the microbial community membership and functional potential in permafrost are dissimilar from those in the active layer[63,64,68] and that the permafrost microbiome

changes rapidly upon thaw[68]. In addition, permafrost microbiomes are not the same everywhere and different species compositions have been found across sampling locations in the Arctic[64,69]. Most studies find an increase in Actinobacteria with depth into the permafrost, but the species can differ depending on location[64,69]. To understand how permafrost microorganisms are genetically equipped to survive in permafrost and respond to thaw, metagenome-assembled genomes (MAGs) have been assembled from permafrost metagenomes, including from previously uncharacterized taxa[64,65]. MAGs from seasonally thawed active layer soils revealed traits that are needed for survival of discontinuous freezing and thawing cycles, including the capacity for production of cold and heat shock proteins, cryoprotectants and DNA repair mechanisms[64]. Examination of the MAGs also provided clues as to how specific members of the permafrost soil microbiome respond to changing resource availability with permafrost thaw. For example, MAGs obtained from a permafrost thaw gradient had genes required for degradation of plant polysaccharides, including cellulases and xylanases[65], suggesting that they were poised to degrade these plant-derived substrates as they became available. In another study, MAGs containing genes for carbohydrate metabolism increased after 4.5 years of 1 °C of warming in the field[66]. Several MAGs correspond to methanogens, in particular, in wetter locations where methanogenesis occurs[64–66]. However, a diverse capacity for CH_4 oxidation has also been revealed in MAGs, suggesting genetic mechanisms for consumption of CH_4 from thawing permafrost before it reaches the atmosphere[70].

These molecular studies are helping to piece together genomic-level details of inter-kingdom responses to changing conditions in the Arctic. Interestingly, thousands of viral sequences were found in Arctic metagenomes and some of them included auxiliary metabolic genes for metabolism of plant polymers and numerous host linkages to diverse carbon cycling microorganisms[71]. Viral sequences were shown to differ across a permafrost thaw gradient, with a shift from 'soil-like' viruses in the drier soils to 'aquatic-like' viruses in the wetter soils[72]. Several of the viruses could be linked to potential bacterial hosts, many of which are key players in SOM decomposition[72]. Together, these findings suggest that both bacteria and viruses may have a role in carbon turnover in thawing permafrost. Although less is reported about fungi in permafrost, there have been reports of an increase in some taxa in sequence data, including mycorrhizal fungi following thaw[73]. One study found differences in the fungal community compositions in the rooting zone of permafrost compared with an adjacent water-saturated bog, with an increase in putative saprotrophic and pathogenic fungi following thaw[74]. Functionally, these shifts in fungal sequences were mainly correlated with associated shifts in plant types due to warming[74].

Drought. Drought is expected to be the major consequence of future climate change in mesic grassland ecosystems[75] (BOX 1). In addition, increased desertification is predicted for most semi-arid or arid regions in the coming decades[76]. Increasing drought is predicted to result in declines in microbial functions that are important for ecosystem sustainability[77]. As soil becomes drier, there is less water in soil pores, resulting in disconnected resource islands; subsequently, less SOC is decomposed and respired to CO_2 (REF.[78]). Together, these factors interact to generate responses that range from decreased productivity under drier conditions[79] to reduced carbon loss through suppressed respiration[60].

As arid soil ecosystems are widely distributed, ranging from hot and cold deserts with limited annual rainfall to Mediterranean grasslands with dry summers and wet winters, it is difficult to generalize microbial responses to increasing drought with climate change. For example, life in desert soils is often constrained due to carbon and moisture limitation, and is therefore dominated by surface-dwelling photoautotrophs[80]. This results in the formation of biological soil crusts (biocrusts); for example, >40% of drylands have biocrusts[81]. Biocrust populations (for instance, cyanobacteria and lichens) carry out fixation of carbon and nitrogen, and are often the major primary producers where these elements form. The concern is whether biocrusts will be able to adapt to more intermittent rainfall and harsher and more extreme conditions in the future[82,83]. There are also major repercussions for soil degradation because biocrusts bind and stabilize the surface soil.

In grassland ecosystems, drought can have long-lasting impacts on the soil microbiome because of shifts in vegetation to more drought-tolerant plant species and their subsequent selection for different root-associated microorganisms[26,85]. Network analyses in mesocosms[84] and multi-year field experiments[85] revealed that bacteria are more sensitive to drought than fungi in grasslands. Fungi thus potentially contribute to the maintenance of carbon and nitrogen cycling when water is scarce[86]. Also, as soils become drier and microbial dispersion becomes more constrained within physically protected soil pores[87,88], fungal hyphae may help to bridge spatially discrete resources[89], which may help the bulk microbiome as well. Thus, it is important to better understand how inter-kingdom interactions generate community responses to drought stress.

Soil microorganisms have evolved various physiological strategies to cope with drought stress, such as osmoregulation, dormancy or reactivation and extracellular enzyme synthesis[90]. In order to survive under lower water matric potentials, microorganisms accumulate solutes (osmolytes) to retain cell turgor[78]. However, osmolyte accumulation might be too energetically expensive under intense drying conditions[91,92]. Soil microorganisms might simply persist in a dehydrated state and recover and regrow when moisture becomes available[93]. Another physiological strategy is the production of extracellular polymeric substances to retain water at low matric potentials[29]. Also, members of some bacterial taxa, such as Actinobacteria and Bacilli, can persist in drought-impacted soils[94,95] because of their ability to conserve activity and become dormant under dry conditions.

Another physiological hurdle for arid soil microorganisms is how to cope when the soils are re-wet[78]. As microbial activity diminishes, extracellular enzyme

Metagenome-assembled genomes
(MAGs). Genomes that are derived from assembled metagenome data; often using a process called 'binning'.

Auxiliary metabolic genes
Genes on viral sequences (genomes or contigs) that represent non-viral metabolic genes, such as genes involved in carbon metabolism.

Matric potentials
The potential energy of water that is due to adhesion of water molecules to soil particles.
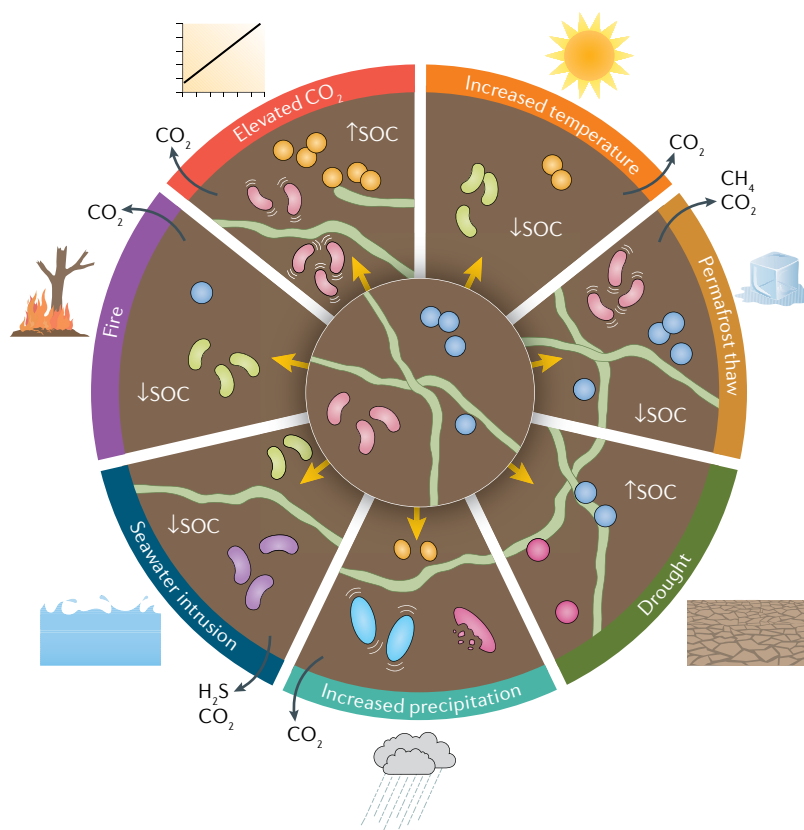
activity may persist, causing bioavailable substrates to accumulate, facilitating reactivation when moisture returns[90,96]. Re-wetting a dry soil results in a pulse of microbial activity — the so-called Birch effect[97]. High mortality has been observed for bacteria and fungi upon

Fig. 2 | **Soil microbial responses to climate change.** A soil microbial community of bacteria, archaea (red and blue) and fungal hyphae (green) in the absence of climate change pressures is depicted in the centre. Examples of climate responses are shown at the periphery (note that changes in cell colour to orange, green or purple indicate a community shift). Increases or decreases in soil organic carbon (SOC) are indicated by up and down white arrows, respectively. Elevated CO_2 can result in an increase in carbon below ground due to increases in plant growth, with corresponding increases in soil microbial biomass and shifts in community composition; note that, in the long term, SOC may decompose at a faster rate than it is formed. White lines indicate increased microbial activity. Increased temperature can result in loss of SOC, shifts in bacterial and/or archaeal compositions and decreases in fungal abundance. Permafrost thaw results in a deepening of the seasonally thawed active layer and an increase in microbial degradation of SOC. Viruses (not shown) have been detected in thawed permafrost and have been implicated in carbon cycling. Depending on landscape hydrology, methanogens in wetter and more anaerobic areas can generate CH_4. Drought can result in less decomposition of SOC, lower microbial biomass and less CO_2 production. Surviving bacteria may produce molecules to retain cell turgor (osmolytes) and/or enter a dormant physiological state (as represented by a change in shape of the red cell). Under drought, fungal hyphae can be better suited to bridge disconnected soil pores and serve as a fungal highway for other microbial cells. Increased precipitation can increase water saturation and anaerobic soil zones. This panel illustrates a case for wetting dry soil when there is a sudden increase in water and nutrient availability, which may cause some cells to burst (as shown by the burst red cell) and serve as a substrate for other cells to become more active (white lines by blue cells indicate increased activity), respire and produce CO_2 (Birch effect); there can also be some community shifts. Seawater intrusion can also increase soil saturation and anaerobic zones. Furthermore, saltwater can introduce alternate electron acceptors (for example, sulfate) that can result in community shifts (purple cells represent sulfate-reducing bacteria). Fire results in a turnover of soil carbon and nitrogen stocks, reduction in microbial biomass, depletion of fungi and some community shifts.

wetting, suggesting that a sizeable portion of the wet-up response could be driven by degradation of dead microbial cells[98] and hinting at a role for viral predation of bacteria in this response. One study compared modelling simulations and empirical data to determine that soil microbial diversity was higher under dry conditions[99], presumably because there were more disconnected soil niches in the dry soil (FIG. 2). Following wetting, there was enhanced connectivity, more dispersal, more anaerobic niches and a sudden increase in nutrients, resulting in an increase in anaerobic taxa and a decrease in diversity. The community was, however, resilient and returned to its previous state following re-drying[99]. By contrast, in a California grassland, the microbial biomass increased during the dry season, and then declined during the wet season[100]. A comparison of different arid ecosystems, including deserts, suggested that increases in aridity may result in a decrease in stability and genetic potential of the soil microbiome[101]. Therefore, the question is how resilient the soil microbiome will be to increasing periods of drought and less predictable weather patterns in the future.

Increased precipitation and flooding. Some areas are experiencing increases in soil moisture due to flooding and/or severe and erratic precipitation events. For example, increased heavy precipitation events are predicted to occur in wet tropical regions[102]. Climate change is also predicted to shift precipitation in northern regions to more rain at the expense of snow, resulting in reduced snow pack and increasing freeze–thaw cycles[103]. As soil moisture increases, soil pores become water-filled and anaerobic, thus providing ripe conditions for methanogenesis and denitrification, and the potential for release of CH_4 and N_2O. Differences in moisture and vegetation due to changing precipitation patterns can give rise to contrasting results with respect to microbial community responses. Therefore, predictive metabolic models are needed for more accurate simulations under future climate scenarios[104].

Wetlands represent the interface between terrestrial and aquatic environments, and are hotspots that are sensitive to changes in climate. The major determinants of CH_4 concentrations in wetlands include soil temperature, water-table depth and composition of SOC[105]. Wetland areas, such as peatlands, may transition from carbon sinks to carbon sources in the future, thus aggravating current warming trends. However, when peatlands are flooded, oxidative decomposition of SOC in peat may be inhibited, resulting in a net uptake of carbon.

A special case is the increase in saltwater-impacted soils associated with sea-level rise. Many coastal areas are experiencing saltwater intrusion because of the increasing global sea level, at a rate of 3.2 ± 0.4 mm per year[106]. The intrusion of saltwater into vulnerable coastal soil ecosystems introduces salt and sulfate: the latter acts as a terminal electron acceptor and changes the redox cycling dynamics of the system with resultant increases in soil microbial biomass[107] and increases in mineralization of SOC, resulting in increased levels of CO_2 production (FIG. 2). Therefore, the implications are a future net increase in greenhouse gas production through

increased CO_2 emission as seawater levels rise. However, different coastal soils respond differently to increased salinity[108]. With extended periods of flooding, microbial activity was shown to decrease due to resource depletion; representing a 'boom and bust' situation[109]. The ultimate climate impact of rising seawater levels will therefore depend on the soil microbial community dynamics and the availability of SOC and electron acceptors that govern the balance between carbon and nutrient storage and release of greenhouse gases.

Increased fire frequency or intensity. Fires are globally increasing in frequency and/or intensity as a result of extended, drier fire seasons combined with unsustainable land management practices. There are several compounding disturbances associated with fire impacts on soil microorganisms[110]. Fire can directly feedback to climate through release of large amounts of CO_2 to the atmosphere[111]. Fire intensity and duration impact the characteristics of SOC, with higher fire intensities and longer residence times resulting in greater heat transfer to the underlying soil. When the organic layer of soil combusts, it can generate further heat. In soils with higher moisture content, soil heating can be delayed but may kill more microorganisms through pasteurization[112]. Extremely intense fires can also destroy soil aggregate structure and reduce soil aeration. Post-fire consequences include land degradation and erosion as soil washes into waterways, thus compounding effects on soil ecosystems. Fire also results in a substantial reduction in soil carbon and nitrogen stocks[113,114]. As a result, the microbial biomass has been shown to decrease following a fire event due to a depletion of resources to support microbial growth[112] (FIG. 2).

Several factors are important in determining the impact of fire on SOC reserves and the soil microbiome, including landscape topography (for example, mountains compared with flatter, low-lying areas) and plant inputs. In boreal mountain regions, a serious concern with fire is the potential depletion of soil carbon from thawing permafrost following fire events. One study found that following an intensive fire event in the Nome Creek area of Alaska, the soil carbon was largely drained along with soil water from the mountain slope, and the underlying permafrost soil layer thawed[115]. This effect was accompanied by a decrease in abundance of most members of the soil microbiome, although some bacteria were enriched post-fire (for example, members of the AD3 candidate phylum). By contrast, in a study of temperate pine-dominated forests, fire resulted in new inputs into the system, such as charcoal and plant litter[112].

Direct effects of fire on soil microorganisms include cell death due to protein denaturation and cell lysis and/or combustion, resulting in a reduction in microbial biomass[112]. However, a short-term increase in available nutrients immediately after fire can lead to a short-term increase in microbial activity. One study found increased microbial biomass and activity immediately following fire treatment, with an increase in relative abundances of archaea, and hypothesized that this was because archaeal cell walls are more heat resistant[116]. Another study found

that the proportion of fungi decreased and Actinobacteria increased following fire[114]. However, because different groups of bacteria, archaea and fungi are more or less heat sensitive, it is difficult to make generalizations across different ecosystems and the long-term functional consequences of these shifts are unknown.

Indirect effects of fire can also impact the soil microbiome. For example, fire-induced changes in plant cover have a large impact on the soil microbiome due to their association with plant roots. Additional indirect effects include increased solar penetration, changes in albedo due to soil blackening, chemical changes in the soil and deposition of alkaline ash and charcoal[112]. Fire-derived charcoal is chemically and biologically stable and in one study was shown to maintain activity of nitrifying bacteria in boreal forests following fire[117]. Another compounding effect of fire is an increase in soil pH — a major driver of soil microbial diversity and richness[30]. Fungal diversity in boreal forests was found to initially increase after fire, presumably due to the increase in pH, but then declined over time[111]. When fire is compounded with other climate extremes, such as drought, the soil microbiome may be negatively impacted and less resilient to future disturbances[114]. However, sweeping generalizations of fire impacts on soil microorganisms are complicated because some ecosystems, such as biological soil crusts in fire-adapted grasslands, are naturally resilient to low-intensity fires[118].
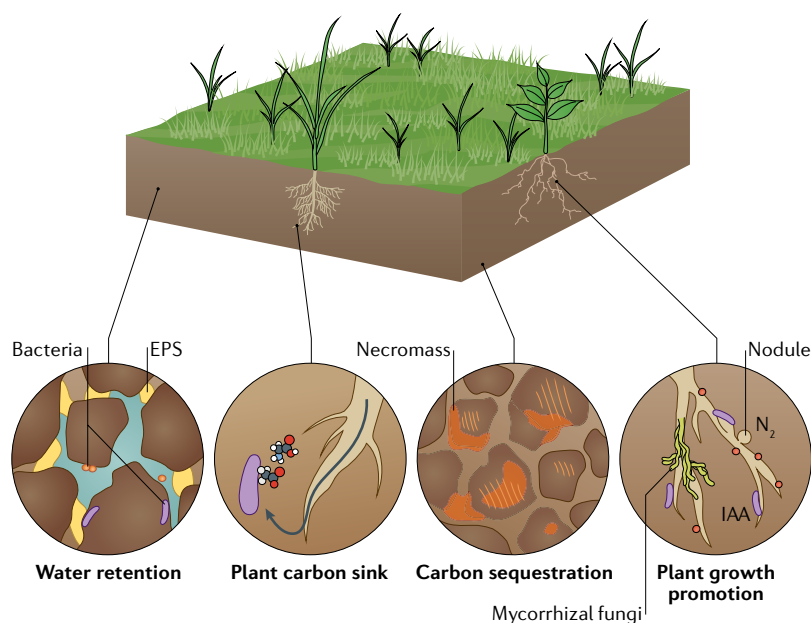
Soil microbiome manipulation efforts

Our increasing awareness of the impacts of climate change on the soil microbiome is resulting in an emerging urgency to harness soil microbial capabilities to mitigate the negative consequences of change. These interests vary from direct manipulation of soil microbial communities to indirect manipulation of their functions through changes in land management practices or use of inoculants as environmental probiotics (FIG. 3).

Carbon sequestration. Atmospheric carbon stocks may be reduced by sequestration into stable, non-gaseous forms through biotic and/or abiotic processes. Carbon enters the soil through assimilation of atmospheric CO_2, mainly by plants but also by autotrophic soil microorganisms. The fraction of photosynthate released to the rhizosphere by plants, either through root exudation, sloughed root cap cells or mycorrhizal fungi, is substantial (up to 20%)[119]. Carbon inputs stimulate symbiotic and free-living organisms, which spread the carbon through the soil matrix. Microbial biochemical transformations of carbon, and subsequent exchange among communities, cause bioavailable forms of carbon to cycle and persist in non-bioavailable forms. The capacity of soils to sequester carbon is greater in soils with higher biodiversity[45]. This sequestration includes the concerted activities of soil bacteria and fungi to produce carbon polymers that facilitate the formation of soil aggregates and to occlude soil carbon in the process.

Avenues being explored for carbon storage include mining the untapped biochemical capacity of the soil microbiome for novel reactions that increase the deposition of carbon into soil. Single microorganisms or

Fig. 3 | Manipulating the soil microbiome to mitigate the negative consequences of climate change. Examples of methods to harness the soil microbiome to mitigate the negative consequences of climate change are shown. Microorganisms can improve water retention in soil as a drought mitigation strategy; for example, through production of extracellular polymeric substances (EPS) to plug soil pores as a strategy for retaining soil water under dry conditions. Soil microorganisms can serve as a plant carbon sink through microbial uptake of carbon exported from plant roots that is subsequently stored as cellular biomass or transformed to stable metabolites. Carbon can be sequestered in soil as dead microbial biomass (necromass). Plant growth-promoting microorganisms can be used to enhance plant production in soils that are negatively impacted by climate change. Examples include increasing the provision of nutrients such as N_2 through symbiotic or associative nitrogen-fixing bacteria, enhancing nutrient uptake through mycorrhizal fungi and the production of microbial plant growth-promoting hormones, such as indole-3-acetic acid (IAA).

Necromass
Residue mixtures of molecules derived from microorganisms, including biomass, intracellular and extracellular biomolecules/aggregations.

Biochar
Fire-derived (pyrolysed) carbon (also known as black carbon) that has been proposed as a soil carbon-storage amendment.

---

photosynthate to optimize the plant–microorganism–soil system for both optimal plant yield and soil carbon deposition[41]. To avoid field application of genetically modified plants, this will require collaboration between plant breeders and soil microbiologists to design the best pairing of specific beneficial microorganisms with specific plant genotypes[125].

Microorganisms as beneficial plant inoculants. Beneficial plant growth-promoting (PGP) bacteria and fungi that inhabit the rhizosphere may help counteract the negative consequences of drought by optimizing growth of plants in increasingly stressful conditions[126] (FIG. 3). PGP microorganisms can be applied as seed coatings, or as liquid or granular supplements to plants growing in the field. The classical example of a PGP strain is that of *Rhizobium* spp. inoculants that are applied for biological nitrogen fixation in association with legumes (FIG. 3). Currently, there is growing interest in going beyond traditional application of inoculants as biofertilizers and biopesticides, to also harness other beneficial properties of PGP microorganisms to mitigate the deleterious consequences of climate change[127].

Several avenues are being explored to use PGP microorganisms to alleviate drought stress in plants[125]. For example, some soil bacteria produce extracellular polymeric substances, resulting in hydrophobic biofilms that can protect plants from desiccation[126]. Beneficial soil microorganisms could also be exploited to increase tolerance of crops to drought stress through their production of phytohormones that stimulate plant growth, accumulation of osmolytes or other protective compounds, or detoxification of reactive oxygen species[125,128] (FIG. 3). For example, some bacteria synthesize indole-3-acetic acid in the rhizosphere, resulting in increased root production[129] that can help alleviate water stress[125]. Rhizosphere microorganisms have also been shown to secrete metabolites that can accumulate in plant cells to alleviate osmotic stress[130,131]. Resistance to drought stress and nutrient acquisition can also be enhanced by associations with beneficial arbuscular mycorrhizal fungi, for example, by regulating the plant production of specific molecules known as aquaporins that reduce water stress[122,132]. Arbuscular mycorrhizal fungi can also directly access water by extension of their mycelia into water-filled soil pores that are not otherwise accessible to plant roots.

Synchronizing plant demand with microbial nitrogen supply also holds great promise for mitigating microbial N_2O production. For example, arbuscular mycorrhizal fungi can be used to acquire ammonium and mitigate N_2O production. Other biological strategies to mitigate N_2O emissions include inoculation with N_2O-consuming communities[133] or blocking nitrification using biological inhibitors of the ammonia oxidation pathway[134]. Together, these examples illustrate how beneficial properties carried out by soil microorganisms can be leveraged to help maintain ecosystem services in a changing climate.

Agriculture results in additional compounding factors that are not discussed in this Review. It is noteworthy that the US National Academy of Science

interacting members of consortia that catalyse these reactions can drive the carbon decomposition pathways towards more recalcitrant and stable end products[120]. Alternatively, soil microbiomes can be manipulated in situ, through addition of amendments that enhance their activity to take up and store carbon in soil. For example, persistent carbon produced from microbial residues could be stored in deeper soil layers[121]. Microbial residues can include macromolecules from extracellular polymeric substances or dead biomass (necromass) (FIG. 3) that have been shown to persist in soil[122]. Another avenue being considered is to use pyrolysed carbon (biochar) as an amendment to sequester soil carbon in a relatively stable state[123]; stability depends on whether components in the biochar are respired by soil microorganisms.

Interactions between plants and soil rhizosphere microbiomes can also be manipulated to facilitate soil carbon storage[41,124]. For example, root exudate deposition can be enhanced by increasing the plant sink of carbon to the rhizosphere where it is transformed into stable metabolites and/or stored in microbial biomass[41]. In this scenario, the plant can also be genetically modified to select for beneficial root-colonizing microorganisms that trap specific carbon exudates produced by the plant (FIG. 3). Future strategies could lead to an ability to genetically control the allocation of

recently published the scientific breakthroughs needed for food and agriculture by 2030 (REF.[135]), which include a strategy for manipulating the soil microbiome to increase crop productivity in the face of climate change. Additional research priorities include a need to understand the biogeochemical pathways underpinning SOC decomposition and production of greenhouse gases in order to derive better practices to prevent carbon loss from soil. For example, although the redox chemistry of electron donor molecules is understood, the energetics and thermodynamics of organic carbon electron acceptors that drive microbial metabolism are not well characterized in the context of the soil habitat. Our present frontier is to describe the physiological response, or metaphenome, of the soil microbiome. This knowledge will facilitate predictions of the impacts of climate change on soil functions and better enable harnessing beneficial properties of the soil microbiome to help mitigate negative consequences of climate change.

Conclusions

While writing this Review, we came to have an even greater appreciation of the value of our living soil and a heightened concern about the future as these fragile resources are being imperilled by the negative consequences of climate change. Soil, which many 'take for granted' and often overlook, is a non-renewable resource and is currently being depleted at a faster rate than it is being formed[136]. Although not within the scope of this Review, when combined with unsustainable soil management practices, we are on course to lose much of our fertile soils. The ecosystem services carried out by soil microbiomes are vital for retaining soil carbon and for the provision of nutrients to plants, and the importance of soil microbiomes in preserving a healthy soil for future generations cannot be overstated. There is an urgent need to gain a better understanding of the repercussions of climate change on key biogeochemical processes carried out by soil microorganisms, to use this information to make better predictions of climate impacts and to, ultimately, design microbial strategies to combat further climate warming and soil degradation. Although we review several methods to harness soil microorganisms to help mitigate climate change, we do not by any means propose that this will be sufficient to counterbalance the loss of soil and the generation of greenhouse gases that is already occurring. Instead, an integrated approach is urgently needed that would employ best practices for sustainable soil management to support plant production, store and supply clean water, maintain biodiversity, sequester carbon and increase resilience in a changing climate. To achieve this goal, we must connect the fine-scale detail arising from microbiome studies to the landscape-scale resolution of ecosystem services and many Earth system climate models. Most importantly, we need the political will and a global dedicated effort to curb the emissions of greenhouse gases that are the root of climate change. We note that these concerns are in line with the recent 'warning to humanity' that serves as a wake-up call to the importance of microorganisms in establishing ecosystem stability in the future as climate changes[137].

Published online 4 October 2019

1. U.S. Global Change Research Program. Impacts, risks, and adaptation in the United States: Fourth National Climate Assessment Vol. II (USGCRP, 2018).
2. Friedlingstein, P. et al. Climate–carbon cycle feedback analysis: results from the C⁴MIP model intercomparison. J. Clim. 19, 3337–3353 (2006).
3. Wang, K. et al. Modeling global soil carbon and soil microbial carbon by integrating microbial processes into the ecosystem process model TRIPLEX-GHG. J. Adv. Modeling Earth Syst. 9, 2368–2384 (2017).
4. Wieder, W. R., Bonan, G. B. & Allison, S. D. Global soil carbon projections are improved by modelling microbial processes. Nat. Clim. Change 3, 909–912 (2013).
5. Wahl T. et al. When environmental forces collide. Eos.org https://eos.org/features/when-environmental-forces-collide (2018).
6. Berard, A., Pierre, R. & Kaisermann, A. Soil microbial community responses to heat wave components: drought and high temperature. Clim. Res. 3, 243–264 (2014).
7. Sheik, C. et al. Effect of warming and drought on grassland microbial communities. ISME J. 5, 1692–1700 (2011).
8. Tarnocai, C. et al. Soil organic carbon pools in the northern circumpolar permafrost region. Glob. Biogeochem. Cycles 23, GB2023 (2009).
9. Bruhwiler, L. et al. in Second State of the Carbon Cycle Report (SOCCR2): a sustained assessment report (eds Cavallaro, N. et al.) 42–70 (U.S. Global Change Research Program, 2018).
10. Bradford, M. A. et al. Thermal adaptation of soil microbial respiration to elevated temperature. Ecol. Lett. 11, 1316–1327 (2008).
11. Bond-Lamberty, B., Bailey, V., Chen, M., Gough, C. & Vargas, R. Globally rising soil heterotrophic respiration over recent decades. Nature 560, 80–83 (2018).
    Based on existing data, this study determines trends towards increased soil microbial mineralization of SOC, leading to increased CO₂ emissions as a result of climate change.
12. Rustad, L. et al. A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. Oecologia 126, 543–562 (2001).
13. Nottingham, A. T. et al. Climate warming and soil carbon in tropical forests: insights from an elevation gradient in the Peruvian Andes. Bioscience 65, 906–921 (2015).
14. Vitousek, P. M. et al. Human alteration of the global nitrogen cycle: sources and consequences. Ecol. Appl. 7, 737–750 (1997).
15. Syakila, A. & Kroeze, C. The global nitrous oxide budget revisited. Greenh. Gas Meas. Manag. 1, 17–26 (2011).
16. Regan, K. et al. Spatial and temporal dynamics of nitrogen fixing, nitrifying and denitrifying microbes in an unfertilized grassland soil. Soil Biol. Biochem. 109, 214–226 (2017).
17. Groffman, P. M. et al. Methods for measuring denitrification: diverse approaches to a difficult problem. Ecol. Appl. 16, 2091–2122 (2006).
18. Butterbach-Bahl, K., Baggs Elizabeth, M., Dannenmann, M., Kiese, R. & Zechmeister-Boltenstern, S. Nitrous oxide emissions from soils: how well do we understand the processes and their controls? Phil. Trans. R. Soc. B 368, 20130122 (2013).
19. van Kessel, M. A. H. J. et al. Complete nitrification by a single microorganism. Nature 528, 555–559 (2015).
20. Xia, F. et al. Ubiquity and diversity of complete ammonia oxidizers (comammox). Appl. Environ. Microb. 84, e01390-18 (2018).
21. Kuzyakov, Y. & Blagodatskaya, E. Microbial hotspots and hot moments in soil: concept & review. Soil Biol. Biochem. 83, 184–199 (2015).
22. Norby, R. J. et al. Model–data synthesis for the next generation of forest free-air CO₂ enrichment (FACE) experiments. New Phytol. 209, 17–28 (2016).
23. Schimel, J., Balser, T. C. & Wallenstein, M. Microbial stress-response physiology and its implications for ecosystem function. Ecology 88, 1386–1394 (2007).
24. Evans, S. E. & Wallenstein, M. D. Climate change alters ecological strategies of soil bacteria. Ecol. Lett. 17, 155–164 (2014).
    This study assesses the phylogenetic conservation of ecological strategies in response to drying–re-wetting in incubation studies on soils from the Rainfall Manipulation Plot Study (RaMPS) in the US tallgrass prairie.
25. Berg, M. P. et al. Adapt or disperse: understanding species persistence in a changing world. Glob. Chang. Biol. 16, 587–598 (2010).
26. de Vries, F. T. & Shade, A. Controls on soil microbial community stability under climate change. Front. Microbiol. 4, 265 (2013).
27. Thompson, L. R. et al. A communal catalogue reveals Earth's multiscale microbial diversity. Nature 551, 457–463 (2017).
28. Jansson, J. K. & Hofmockel, K. S. The soil microbiome—from metagenomics to metaphenomics. Curr. Opin. Microbiol. 43, 162–168 (2018).
29. Waldrop, M. P. & Firestone, M. K. Response of microbial community composition and function to soil climate change. Microb. Ecol. 52, 716–724 (2006).
30. Fierer, N. & Jackson, R. B. The diversity and biogeography of soil bacterial communities. Proc. Natl Acad. Sci. USA 103, 626–631 (2006).
31. Schimel, J. & Schaeffer, S. Microbial control over carbon cycling in soil. Front. Microbiol. 3, 348 (2012).
32. Cordero, O. X. & Datta, M. S. Microbial interactions and community assembly at microscales. Curr. Opin. Microbiol. 31, 227–234 (2016).
33. Dunbar, J. et al. Common bacterial responses in six ecosystems exposed to 10 years of elevated atmospheric carbon dioxide. Environ. Microbiol. 14, 1145–1158 (2012).
34. Hayden, H. L. et al. Changes in the microbial community structure of bacteria, archaea and fungi in response to elevated CO₂ and warming in an Australian native grassland soil. Environ. Microbiol. 14, 3081–3096 (2012).

35. Allison, S. D. A trait-based approach for modelling microbial litter decomposition. *Ecol. Lett.* **15**, 1058–1070 (2012).
 This article describes a trait-based modelling approach that links phylogenetic and functional information to predict ecosystem processes carried out by microbial communities.

36. Tu, Q. et al. Metagenomic reconstruction of nitrogen cycling pathways in a CO_2-enriched grassland ecosystem. *Soil Biol. Biochem.* **106**, 99–108 (2017).

37. Yu, H. et al. Elevated CO_2 and warming altered grassland microbial communities in soil top-layers. *Front. Microbiol.* **9**, 1790 (2018).
 This study uses a gene array to measure the functional gene composition, structure and metabolic potential of soil microbial communities under warming, eCO_2 and eCO_2 with warming conditions in a semi-arid grassland.

38. Adair, C. E., Reich, P. B., Trost, J. J. & Hobbie, S. E. Elevated CO_2 stimulates grassland soil respiration by increasing carbon inputs rather than by enhancing soil moisture. *Glob. Chang. Biol.* **17**, 3546–3563 (2011).

39. Brêchet, L. M. et al. Distinct responses of soil respiration to experimental litter manipulation in temperate woodland and tropical forest. *Ecol. Evol.* **8**, 3787–3796 (2018).

40. Bengtson, P., Barker, J. & Grayston, S. J. Evidence of a strong coupling between root exudation, C and N availability, and stimulated SOM decomposition caused by rhizosphere priming effects. *Ecol. Evol.* **2**, 1843–1852 (2012).

41. Jansson, C., Vogel, J., Hazen, S., Brutnell, T. & Mockler, T. Climate-smart crops with enhanced photosynthesis. *J. Exp. Bot.* **69**, 3801–3809 (2018).

42. Qiao, N. et al. Labile carbon retention compensates for CO_2 released by priming in forest soils. *Glob. Chang. Biol.* **20**, 1943–1954 (2014).

43. van Groenigen, K. J., Qi, X., Osenberg, C. W., Luo, Y. Q. & Hungate, B. A. Faster decomposition under increased atmospheric CO_2 limits soil carbon storage. *Science* **344**, 508–509 (2014).

44. Drake, J. E. et al. Increases in the flux of carbon belowground stimulate nitrogen uptake and sustain the long-term enhancement of forest productivity under elevated CO_2. *Ecol. Lett.* **14**, 349–357 (2011).

45. Lal, R. Soil carbon sequestration impacts on global climate change and food security. *Science* **304**, 1623–1627 (2004).
 This paper discusses different land management strategies to optimize soil carbon sequestration through soil microbial activities.

46. Kuzyakov, Y. Priming effects: interactions between living and dead organic matter. *Soil Biol. Biochem.* **42**, 1363–1371 (2010).

47. Scharlemann, J. P. W., Tanner, E. V. J., Hiederer, R. & Kapos, V. Global soil carbon: understanding and managing the largest terrestrial carbon pool. *Carbon Manag.* **5**, 81–91 (2014).

48. Melillo, J. M. et al. Long-term pattern and magnitude of soil carbon feedback to the climate system in a warming world. *Science* **358**, 101–104 (2017).
 This article describes the results of long-term warming field studies at the Harvard Forest field station on soil carbon flux and how the soil microorganisms acclimate to the warmer soil conditions.

49. Romero-Olivares, A. L., Allison, S. D. & Treseder, K. K. Soil microbes and their response to experimental warming over time: a meta-analysis of field studies. *Soil Biol. Biochem.* **107**, 32–40 (2017).

50. Schindlbacher, A. et al. Experimental warming effects on the microbial community of a temperate mountain forest soil. *Soil Biol. Biochem.* **43**, 1417–1425 (2011).

51. Clemmensen, K. E. et al. Roots and associated fungi drive long-term carbon sequestration in boreal forest. *Science* **339**, 1615–1618 (2013).

52. Allison, S. D. & Treseder, K. K. Warming and drying suppress microbial activity and carbon cycling in boreal forest soils. *Glob. Chang. Biol.* **14**, 2898–2909 (2008).

53. Morrissey, E. M. et al. Evolutionary history constrains microbial traits across environmental variation. *Nat. Ecol. Evol.* **3**, 1064–1069 (2019).

54. DeAngelis, K. M. et al. Long-term forest soil warming alters microbial communities in temperate forest soils. *Front. Microbiol.* **6**, 104 (2015).

55. Zhang, B. et al. Responses of soil microbial communities to experimental warming in alpine grasslands on the Qinghai–Tibet Plateau. *PLOS ONE* **8**, E103859 (2014).

56. Deslippe, J. R., Hartmann, M., Simard, S. W. & Mohn, W. W. Long-term warming alters the composition of Arctic soil microbial communities. *FEMS Microbiol. Ecol.* **82**, 303–315 (2012).

57. Guo, X. et al. Climate warming leads to divergent succession of grassland microbial communities. *Nat. Clim. Change* **8**, 813–818 (2018).

58. Frey, S. D., Drijber, R., Smith, H. & Melillo, J. Microbial biomass, functional capacity, and community structure after 12 years of soil warming. *Soil Biol. Biochem.* **40**, 2904–2907 (2008).

59. Zhou, J. et al. Microbial mediation of carbon-cycle feedbacks to climate warming. *Nat. Clim. Change* **2**, 106–110 (2011).

60. Heimann, M. & Reichstein, M. Terrestrial ecosystem carbon dynamics and climate feedbacks. *Nature* **451**, 289–292 (2008).
 This article provides evidence and discusses uncertainties about terrestrial ecosystem feedback with climate change.

61. Turetsky, M. R. et al. Permafrost collapse is accelerating carbon release. *Nature* **569**, 32–34 (2019).

62. Mackelprang, R., Saleska, S. R., Jacobsen, C. S., Jansson, J. K. & Taş, N. Permafrost meta-omics and climate change. *Annu. Rev. Earth Planet. Sci.* **44**, 439–462 (2016).

63. Hultman, J. et al. Multi-omics of permafrost, active layer and thermokarst bog soil microbiomes. *Nature* **521**, 208–212 (2015).

64. Tas, N. et al. Landscape topography structures the soil microbiome in Arctic polygonal tundra. *Nat. Commun.* **9**, 777 (2018).

65. Woodcroft, B. J. et al. Genome-centric view of carbon processing in thawing permafrost. *Nature* **560**, 49–54 (2018).
 This study assembles thousands of genomes from soil metagenomes, corresponding to primarily uncultivated and uncharacterized microorganisms, along a permafrost thaw gradient in Sweden.

66. Johnston, E. R. et al. Responses of tundra soil microbial communities to half a decade of experimental warming at two critical depths. *Proc. Natl Acad. Sci. USA* **116**, 15096–15105 (2019).

67. Bottos, E. M. et al. Dispersal limitation and thermodynamic constraints govern spatial structure of permafrost microbial communities. *FEMS Microbiol. Ecol.* **94**, 1–14 (2018).

68. Mackelprang, R. et al. Metagenomic analysis of a permafrost microbial community reveals a rapid response to thaw. *Nature* **480**, 368–371 (2011).

69. Müller, O. et al. Disentangling the complexity of permafrost soil by using high resolution profiling of microbial community composition, key functions and respiration rates. *Environ. Microbiol.* **20**, 4328–4342 (2018).

70. Singleton, C. M. et al. Methanotrophy across a natural permafrost thaw environment. *ISME J.* **12**, 2544–2558 (2018).

71. Emerson, J. B. et al. Host-linked soil viral ecology along a permafrost thaw gradient. *Nat. Microbiol.* **3**, 870–880 (2018).

72. Trubl, G. et al. Soil viruses are underexplored players in ecosystem carbon processing. *mSystems* **3**, e00076-18 (2018).
 This study characterizes viruses in thawing permafrost peatlands and suggests that viruses can impact the biogeochemistry of their hosts and carbon metabolism.

73. Penton, C. R. et al. Fungal diversity in permafrost and tallgrass prairie soils under experimental warming conditions. *Appl. Environ. Microb.* **79**, 7063–7072 (2013).

74. Schütte, U. M. E. et al. Effect of permafrost thaw on plant and soil fungal community in a boreal forest: does fungal community change mediate plant productivity response? *J. Ecol.* **107**, 1737–1752 (2019).

75. Cook, B. I., Ault, T. R. & Smerdon, J. E. Unprecedented 21st century drought risk in the American Southwest and Central Plains. *Science Adv.* **1**, e1400082 (2015).

76. Huang, J. P., Yu, H. P., Guan, X. D., Wang, G. Y. & Guo, R. X. Accelerated dryland expansion under climate change. *Nat. Clim. Change* **6**, 166–171 (2016).

77. McHugh, T. A. et al. Climate controls prokaryotic community composition in desert soils of the southwestern United States. *FEMS Microbiol. Ecol.* **93**, fix116 (2017).

78. Schimel, J. P. Life in dry soils: effects of drought on soil microbial communities and processes. *Ann. Rev. Ecol. Evol. Syst.* **49**, 409–432 (2018).
 This article reviews current knowledge of microbial community dynamics and physiological responses to drought.

79. Hyvonen, R. et al. The likely impact of elevated [CO_2], nitrogen deposition, increased temperature and management on carbon sequestration in temperate and boreal forest ecosystems: a literature review. *New Phytol.* **173**, 463–480 (2007).

80. Pointing, S. B. & Belnap, J. Microbial colonization and controls in dryland systems. *Nat. Rev. Microbiol.* **10**, 551–562 (2012).

81. Garcia-Pichel, F., Johnson, S. L., Youngkin, D. & Belnap, J. Small-scale vertical distribution of bacterial biomass and diversity in biological soil crusts from arid lands in the Colorado Plateau. *Microb. Ecol.* **46**, 312–321 (2003).

82. Steven, B., Kuske, C. R., Gallegos-Graves, L. V., Reed, S. C. & Belnap, J. Climate change and physical disturbance manipulations result in distinct biological soil crust communities. *Appl. Environ. Microb.* **81**, 7448–7459 (2015).

83. Reed, S. C. et al. in *Biological Soil Crusts: An Organizing Princincipal in Drylands* (eds Weber, B., Büdel, B. & Belnap, J.) 451–476 (Springer, 2016).

84. Upton, R. N., Bach, E. M. & Hofmockel, K. S. Belowground response of prairie restoration and resiliency to drought. *Agric. Ecosyst. Environ.* **266**, 122–132 (2018).

85. de Vries, F. T. et al. Soil bacterial networks are less stable under drought than fungal networks. *Nat. Commun.* **9**, 3033 (2018).
 This study uses network analyses to show that bacterial networks are less resilient to drought than fungal networks, suggesting that bacteria are less stable to environmental change than fungi.

86. Treseder, K. K., Berlemont, R., Allison, S. D. & Martiny, A. C. Drought increases the frequencies of fungal functional genes related to carbon and nitrogen acquisition. *PLOS ONE* **13**, e0206441 (2018).

87. Carson, J. K. et al. Low pore connectivity increases bacterial diversity in soil. *Appl. Environ. Microb.* **76**, 3936–3942 (2010).

88. Dechesne, A., Wang, G., Gülez, G., Or, D. & Smets, B. F. Hydration-controlled bacterial motility and dispersal on surfaces. *Proc. Natl Acad. Sci. USA* **107**, 14369–14372 (2010).

89. Guhr, A., Borken, W., Spohn, M. & Matzner, E. Redistribution of soil water by a saprotrophic fungus enhances carbon mineralization. *Proc. Natl Acad. Sci. USA* **112**, 14647–14651 (2015).

90. Barnard, R. L., Osborne, C. A. & Firestone, M. K. Responses of soil bacterial and fungal communities to extreme desiccation and rewetting. *ISME J.* **7**, 2229–2241 (2013).
 This study finds different responses of potentially active bacterial and fungal communities to desiccation and re-wetting across three grassland sites in California, United States.

91. Boot, C. M., Schaeffer, S. M. & Schimel, J. P. Static osmolyte concentrations in microbial biomass during seasonal drought in a California grassland. *Soil Biol. Biochem.* **57**, 356–361 (2013).

92. Kakumanu, M. L., Cantrell, C. L. & Williams, M. A. Microbial community response to varying magnitudes of desiccation in soil: a test of the osmolyte accumulation hypothesis. *Soil Biol. Biochem.* **57**, 644–653 (2013).

93. Meisner, A., Leizeaga, A., Rousk, J. & Bååth, E. Partial drying accelerates bacterial growth recovery to rewetting. *Soil Biol. Biochem.* **112**, 269–276 (2017).
 Based on experiments and other recent results, this article proposes a framework for microbial response patterns after drying–re-wetting, in which the harshness of drying determines the response pattern of bacteria upon re-wetting dried soils.

94. Bouskill, N. J. et al. Belowground response to drought in a tropical forest soil. II. Change in microbial function impacts carbon composition. *Front. Microbiol.* **7**, 323 (2016).

95. Naylor, D., DeGraaf, S., Purdom, E. & Coleman-Derr, D. Drought and host selection influence bacterial community dynamics in the grass root microbiome. *ISME J.* **11**, 2691–2704 (2017).

96. Unger, S., Maguas, C., Pereira, J., David, T. & Werner, C. The influence of precipitation pulses on soil respiration—assessing the "Birch effect" by stable carbon isotopes. *Soil Biol. Biochem.* **42**, 1800–1810 (2010).

97. Birch, H. F. The effect of soil drying on humus decomposition and nitrogen availability. *Plant Soil* **10**, 9–31 (1958).

98. Blazewicz, S. J., Schwartz, E. & Firestone, M. K. Growth and death of bacteria and fungi underlie rainfall-induced carbon dioxide pulses from seasonally dried soil. *Ecology* **95**, 1162–1172 (2014).
    This study uses stable isotope probing with H$_2$^{18}O combined with quantitative PCR to determine the dynamics of growing and dying bacterial and fungal populations following soil desiccation and re-wetting.
99. Stovicek, A., Kim, M., Or, D. & Gillor, O. Microbial community response to hydration–desiccation cycles in desert soil. *Sci. Rep.* **7**, 45735 (2017).
100. Schaeffer, S. M., Homyak, P. M., Boot, C. M., Roux-Michollet, D. & Schimel, J. P. Soil carbon and nitrogen dynamics throughout the summer drought in a California annual grassland. *Soil Biol. Biochem.* **115**, 54–62 (2017).
     Using a long-term field experiment in annual dry grasslands, this study demonstrates a positive relationship between drought length, microbial biomass carbon and nitrogen, extractable carbon and nitrogen, and microbial activity upon re-wetting.
101. Neilson, J. W. et al. Significant impacts of increasing aridity on the arid soil microbiome. *mSystems* **2**, e00195-16 (2017).
102. Intergovernmental Panel on Climate Change. Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (eds Pachauri, R. & Meyer, L.) (IPCC, 2014).
103. Sorensen, P. O., Templer, P. H. & Finzi, A. C. Contrasting effects of winter snowpack and soil frost on growing season microbial biomass and enzyme activity in two mixed-hardwood forests. *Biogeochemistry* **128**, 141–154 (2016).
104. Roy Chowdhury, T. et al. Metaphenomic responses of a native prairie soil microbiome to moisture perturbations. *mSystems* **4**, e00061-19 (2019).
105. Gedney, N., Cox, P. M. & Huntingford, C. Climate feedback from wetland methane emissions. *Geophys. Res. Lett.* **31**, L20503 (2004).
106. Moomaw, W. R. et al. Wetlands in a changing climate: science, policy and management. *Wetlands* **38**, 183–205 (2018).
107. Chambers, L. G., Osborne, T. Z. & Reddy, K. R. Effect of salinity-altering pulsing events on soil organic carbon loss along an intertidal wetland gradient: a laboratory experiment. *Biogeochemistry* **115**, 363–383 (2013).
108. Steinmuller, H. E. & Chambers, L. G. Can saltwater intrusion accelerate nutrient export from freshwater wetland soils? An experimental approach. *Soil Sci. Soc. Am. J.* **82**, 283–29 (2018).
109. Sjogaard, K. S., Valdemarsen, T. B. & Treusch, A. H. Responses of an agricultural soil microbiome to flooding with seawater after managed coastal realignment. *Microorganisms* **6**, 1–18 (2018).
110. Knelman, E. J., Schmidt, K. S., Garayburu-Caruso, V., Kumar, S. & Graham, B. E. Multiple, compounding disturbances in a forest ecosystem: fire increases susceptibility of soil edaphic properties, bacterial community structure, and function to change with extreme precipitation event. *Soil Syst.* **3**, 1–16 (2019).
111. Sun, H. et al. Fungal community shifts in structure and function across a boreal forest fire chronosequence. *Appl. Environ. Microb.* **81**, 7869–7880 (2015).
112. Hart, S. C., DeLuca, T., Newman, G., MacKenzie, D. & Boyle, S. Post-fire vegetative dynamics as drivers of microbial community structure and function in forest soils. *For. Ecol. Manag.* **220**, 166–184 (2005).
113. Nave, L. E., Vance, E. D., Swanston, C. W. & Curtis, P. S. Fire effects on temperate forest soil C and N storage. *Ecol. Appl.* **21**, 1189–1201 (2011).
114. Hinojosa, M. B., Parra, A., Laudicina, V. A. & Moreno, J. M. Post-fire soil functionality and microbial community structure in a mediterranean shrubland subjected to experimental drought. *Sci. Total Environ.* **573**, 1178–1189 (2016).
115. Tas, N. et al. Impact of fire on active layer and permafrost microbial communities and metagenomes in an upland Alaskan boreal forest. *ISME J.* **8**, 1904–1919 (2014).
116. Goberna, M., García, C., Insam, H., Hernández, M. T. & Verdú, M. Burning fire-prone mediterranean shrublands: immediate changes in soil microbial community structure and ecosystem functions. *Microb. Ecol.* **64**, 242–255 (2012).
117. DeLuca, T. H. & Sala, A. Frequent fire alters nitrogen transformations in ponderosa pine stands of the inland northwest. *Ecology* **87**, 2511–2522 (2006).
118. Bowker, M. A., Belnap, J., Rosentreter, R. & Graham, B. Wildfire-resistant biological soil crusts and fire-induced loss of soil stability in Palouse prairies, USA. *Appl. Soil Ecol.* **26**, 41–52 (2004).
119. Averill, C., Turner, B. L. & Finzi, A. C. Mycorrhiza-mediated competition between plants and decomposers drives soil carbon storage. *Nature* **505**, 543–545 (2014).
120. Hicks, N. et al. Using prokaryotes for carbon capture storage. *Trends Biotechnol.* **35**, 22–32 (2017).
121. Schmidt, M. W. I. et al. Persistence of soil organic matter as an ecosystem property. *Nature* **478**, 49–56 (2011).
     This article describes a paradigm shift in understanding the composition of persistent SOCs, including determination of microbial cell macromolecules that persist in soil.
122. Kapilan, R., Vaziri, M. & Zwiazek, J. J. Regulation of aquaporins in plants under stress. *Biol. Res.* **51**, 4 (2018).
123. Jansson, C., Tuskan, G. A., Wullschleger, S. D. & Kalluri, U. C. Phytosequestration: carbon biosequestration by plants and the prospects of genetic engineering. *Bioscience* **60**, 685–696 (2010).
124. Wallenstein, M. D. Managing and manipulating the rhizosphere microbiome for plant health: a systems approach. *Rhizosphere* **3**, 230–232 (2017).
     This article discusses several strategies to harness soil microorganisms in the plant rhizosphere to store soil carbon and help mitigate negative consequences of rising atmospheric CO$_2$ levels.
125. Lakshmanan, V., Ray, P. & Craven, K. D. Toward a resilient, functional microbiome: drought tolerance-alleviating microbes for sustainable agriculture. *Methods Mol. Biol.* **1631**, 69–84 (2017).
126. Naylor, D. & Coleman-Derr, D. Drought stress and root-associated bacterial communities. *Front. Plant Sci.* **8**, 2223 (2018).
127. Compant, S., van der Heijden, M. G. A. & Sessitsch, A. Climate change effects on beneficial plant–microorganism interactions. *FEMS Microbiol. Ecol.* **73**, 197–214 (2010).
128. Vurukonda, S. S. K. P., Vardharajula, S., Shrivastava, M. & SkZ, A. Enhancement of drought stress tolerance in crops by plant growth promoting rhizobacteria. *Microbiol. Res.* **184**, 13–24 (2016).
129. Armada, E., Azcon, R., Lopez-Castillo, O. M., Calvo-Polanco, M. & Ruiz-Lozano, J. M. Autochthonous arbuscular mycorrhizal fungi and *Bacillus thuringiensis* from a degraded Mediterranean area can be used to improve physiological traits and performance of a plant of agronomic interest under drought conditions. *Plant Physiol. Biochem.* **90**, 64–74 (2015).
130. Pereyra, M. A., García, P., Colabelli, M. N., Barassi, C. A. & Creus, C. M. A better water status in wheat seedlings induced by *Azospirillum* under osmotic stress is related to morphological changes in xylem vessels of the coleoptile. *Appl. Soil Ecol.* **53**, 94–97 (2012).
131. Casanovas, E. M., Barassi, C. & Sueldo, R. J. *Azospirillum* inoculation mitigates water stress effects in maize seedlings. *JSTOR* **30**, 343–350 (2002).
132. Quiroga, G., Erice, G., Aroca, R., Chaumont, F. & Ruiz-Lozano, J. M. Enhanced drought stress tolerance by the arbuscular mycorrhizal symbiosis in a drought-sensitive maize cultivar is related to a broader and differential regulation of host plant aquaporins than in a drought-tolerant cultivar. *Front. Plant Sci.* **8**, 1056 (2017).
133. Itakura, M. et al. Mitigation of nitrous oxide emissions from soils by *Bradyrhizobium japonicum* inoculation. *Nat. Clim. Change* **3**, 208–212 (2012).
134. Subbarao, G. V. et al. Evidence for biological nitrification inhibition in Brachiaria pastures. *Proc. Natl Acad. Sci. USA* **106**, 17302–17307 (2009).
135. National Academies of Sciences, Engineering and Medicine. *Science Breakthroughs to Advance Food and Agricultural Research by 2030* (National Academies, 2019).
136. Lal, R. Soil erosion and the global carbon budget. *Environ. Int.* **29**, 437–450 (2003).
137. Cavicchioli, R. et al. Scientists' warning to humanity: microorganisms and climate change. *Nat. Rev. Microbiol.* **17**, 569–586 (2019).
     This work presents a petition for a call to action to better understand and predict how climate change will impact crucial processes currently carried out by Earth's microorganisms across a range of ecosystems.
138. Intergovernmental Panel on Climate Change. Climate Change 2007: Synthesis Report. Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change (eds Core Writing Team, Pachauri, R. K. & Reisinger, A.) (IPCC, 2007).
139. Schuur, E. A. G. et al. Climate change and the permafrost carbon feedback. *Nature* **520**, 171–179 (2015).
     This article discusses evidence for gradual and sustained greenhouse gas emissions from permafrost as the climate warms. The authors also discuss the need for more integration of data with models to improve climate change predictions.
140. Stocker, T. F. et al. Climate Change 2013. The Physical Science Basis. Working Group I Contribution to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. (Cambridge Univ. Press, 2014).
141. Llado, S., Lopez-Mondejar, R. & Baldrian, P. Forest soil bacteria: diversity, involvement in ecosystem processes, and response to global change. *Microbiol. Mol. Biol. Rev.* **81**, e00063 (2017).
142. Kirschbaum, M. U. F. Will changes in soil organic carbon act as a positive or negative feedback on global warming? *Biogeochemistry* **48**, 21–51 (2000).
143. Ramankutty, N., Evan, A. T., Monfreda, C. & Foley, J. A. Farming the planet: 1. Geographic distribution of global agricultural lands in the year 2000. *Glob. Biogeochem. Cycles* **22**, GB1003 (2008).
144. Jones, D. L., Nguyen, C. & Finlay, R. D. Carbon flow in the rhizosphere: carbon trading at the soil–root interface. *Plant Soil* **321**, 5–33 (2009).
145. Tian, H. et al. The terrestrial biosphere as a net source of greenhouse gases to the atmosphere. *Nature* **531**, 225–228 (2016).
146. Zhang, Z. et al. Emerging role of wetland methane emissions in driving 21st century climate change. *Proc. Natl Acad. Sci. USA* **36**, 9647–9652 (2017).
     This study determines the potential sensitivities of terrestrial wetlands to rising temperatures, and emphasizes the importance of including CH$_4$ feedback from wetlands in climate models.
147. Makhalanyane, T. P. et al. Microbial ecology of hot desert edaphic systems. *FEMS Microbiol. Rev.* **39**, 203–221 (2015).
     This article reviews the microbial communities of hot desert terrestrial biotopes, the processes that govern their assembly, the possible effects of global climate change on hot desert microbial communities and the resulting feedback and directions for future research.