Soil Microbiomes and Climate Change

Janet K. Jansson and Kirsten Hofmockel

Earth and Biological Sciences Directorate, Pacific Northwest National Laboratory,
Richland, Washington

janet.jansson@pnnl.gov
kirsten.hofmockel@pnnl.gov

Abstract
The soil microbiome governs biogeochemical cycling of carbon, nitrogen and other elements and is vital for growth of plants and animal life. Understanding and predicting the impact of climate change on soil microbiomes and the ecosystem services they carry out presents a grand challenge and major opportunity as we direct our research efforts towards one of the most pressing problems facing our planet. Here we review 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 microbes can be harnessed to help mitigate the negative consequences of climate change.

Introduction

The summer of 2018 was a record hot summer for much of the northern hemisphere, with news headlines heralding several climate disasters, including thawing of permafrost in the arctic, severe drought in Europe and extensive wildfires across the western United States. These events are all symptomatic of changing weather patterns due to higher temperatures. As outlined in the recent U.S. national climate assessment[1], the climate is predicted to continue to change with weather patterns becoming more erratic and extreme. The response of soil microbiomes to the changing climate has feedbacks to the atmosphere, both directly through greenhouse gas production, and indirectly through effects on ecosystem processes such as plant growth, soil organic matter formation, and nutrient cycling. Therefore, it is critical to understand and predict large and small-scale implications of climate change on the soil microbiome.

Soils and soil microbiomes are not the same everywhere. Because soils vary tremendously with respect to their biotic and abiotic properties (**Figure 1**), it is difficult to generalize the impact of climate change on soil microbiomes across different soil ecosystems Even within a specific soil class, there can be local differences in hydrology and biogeochemical properties that largely govern the types of microorganisms that are present. For example, soil pH has a large impact on the diversity and richness of soil bacterial communities[2] as does salinity[3]. The types of minerals, nutrients, redox conditions, organic carbon composition, also all select for specific soil microbes that can grow under those conditions and with the resources that are available. Thus, the different soil ecosystems on Earth represent distinct microbial habitats.

In the following sections, we review the impact of climate change on soil microbiomes and the functions they carry out across different climate-sensitive soil ecosystems (**Figure 2).**

Climate sensitive soil ecosystems

The Arctic

The Arctic is one of the most climate-sensitive regions on Earth, because average temperatures are increasing at nearly twice the global rate[4], resulting in dramatic changes in the landscape, including permafrost thaw and change in vegetation. As the climate warms, the permafrost thaws and microorganisms in the permafrost become more active and start to decompose the enormous reservoir of terrestrial C (~1300-1580 Pg C, including surface C and deep C (>1m) in Yedoma and river deltas [5]); levels equivalent to the current total amount of atmospheric C (~750 Pg) plus the amount of C contained in plant biomass (~560 Pg). Recent estimates suggest that approximately 5-15% of the C currently contained in permafrost is susceptible to microbial decomposition, resulting in a substantial source of CO_2 emissions over the next few decades [5]. Although this is less CO_2 than 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 [6]. As the huge reservoir of C in high latitude soils is released, compounding effects are expected at the planetary scale.

Several recent studies have used molecular approaches to unravel microbial community responses to permafrost thaw [7,8,9,10]. Metagenome sequencing has revealed that the microbial community membership and functional potential in permafrost are dissimilar from those in the seasonally thawed active layer[7,11,12] and that the permafrost microbiome changes rapidly upon thaw[7]. The ability to produce CH_4 is a distinguishing feature of certain thawed permafrost environments[8,9,10], depending on the landscape hydrology[9]. To understand how permafrost microbes 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 [9, 10] (**Figure 3**). MAGs from seasonally-thawed active layer soils revealed the capacity for production of cold and heat shock proteins, cryoprotectants and DNA repair mechanisms that are needed for survival of discontinuous freezing/thawing cycles. [9] Furthermore, MAGs obtained from a permafrost thaw gradient had genes required for degradation of plant polysaccharides, including cellulases and xylanases[10]. Interestingly, several viral sequences were found in arctic metagenomes and some of them included auxillary metabolic genes (AMGs) for metabolism of plant polymers [13]. These recent findings suggest that viruses may play a role in C turnover in permafrost and other terrestrial ecosystems that have yet to be explored. In another study, a diverse capacity for methane oxidation was revealed in MAGs, suggesting genetic mechanisms for consumption of CH_4 from thawing permafrost before it reaches the atmosphere[14]. These studies are helping to piece together details of how soil microbes will respond to changing conditions in the arctic.

Forests

Forests cover ~30% of the total land surface and play important roles as C sinks with large amounts of stable organic matter stored in the surface soils[15]. The total C stock in forests is estimated to be 860 Pg, ~44% of which is stored in the soil[15]. 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 due to decline in plant productivity[15]. Both fungal and bacterial communities in forest soils have been shown to respond to changes in climate, but the types of microbes and their specific responses differ among forest ecosystems, as explored below. This is partly because of the differences in the litter type and quality depending on the plant communities (e.g. coniferous versus deciduous forests) and differences in the soil pH[15].

Boreal forest ecosystems contain ~1/3 of the terrestrial C stock and are considered a net sink for atmospheric CO_2 due to plant uptake[4]. With temperature increases, these forests have an extended growing season, promoting both C uptake and faster soil C decomposition rates. Recent estimates suggest that with climate change boreal ecosystems may become a net carbon source[16]. Thus, it is important to understand how shifts in plant cover and concomitant changes in precipitation and nutrient inputs influence microbial metabolic pathways that lead to greenhouse gas emissions in forest ecosystems. Warming has been shown to have contrasting impacts on soil fungi in different boreal forest ecosystems, resulting in either stimulation[17] or suppression[18] of fungal biomass and activity; these differences are presumably due to differences in soil moisture and/or vegetation at different sites[18]. In addition, as fires increase in frequency in boreal forests, they are releasing larger amounts of atmospheric CO_2[19]. Tas *et al*.[20] found that following an intensive fire event in the Nome Creek area of Alaska, the soil C was largely drained along with soil water from the slope, and the deeper permafrost soil layer thawed. This was accompanied by a decrease in abundance of most members of the soil microbiome, although some bacteria were able to survive. Fire can increase soil pH - a major driver of soil microbial diversity and richness[2]. Sun *et al*.[19] found that fungal diversity in boreal forests initially increased after fire, presumably due to the increase in pH, but then declined over time. The long-term functional consequences of these shifts in soil microbial community structure remain largely unknown.

Temperate forests are characterized by temperatures between -30 and 30 °C, whereas boreal forests have lower temperatures and longer winters. Tree deposition of litter on the soil surface can serve as a source of carbon to soil microbial communities. In one study of a coniferous forest, litter deposition "primed" soil microbial metabolism of soil organic C resulting in an increased CO_2 flux to the atmosphere[21]. To determine the impacts of soil warming on the temperate forest soil microbiome, the Harvard Forest Ecological Research Station Long Term Ecological Research (LTER) 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. At earlier sampling periods (5 and 8 years), there was no significant change in the soil microbiome. However, after 20 years, there was a shift with some members of the microbiome responding positively or negatively to warming[22]. Extended years of elevated temperature also resulted in an initial loss of soil labile C, followed by increased degradation of more recalcitrant C compounds[23]. The authors estimated a loss of ~710 g of C per square meter of soil in the Harvard Forest experiment, and by extrapolation a loss of 190 Pg C by the end of the century with continued warming trends, which is comparable to the amount produced over the last two decades from fossil fuel emissions[23]. Fire also results in a significant reduction in soil C and N stocks in temperate forests[24]. As a result, the microbial biomass is predicted to decrease following a fire event due to a depletion of resources to support microbial growth.

Tropical forests contain about one third of the total terrestrial soil C stock and they are responsible for a majority of the C flux to and from the atmosphere[25]. Climate change is predicted to result in an increase in temperature in the tropics by 1.8 to 5 °C over the next century. The warmer temperatures are predicted to result in an increased microbial mineralization of stable soil organic matter (SOM) and a corresponding increased flux of CO_2 [26]. In tropical regions it is unclear how climate change will affect ecosystem resilience, biodiversity and ecosystem services[27]. It is possible that predicted losses of soil C to the atmosphere due to increased microbial decomposition of SOM under warming will be countered by increased C inputs due to increased plant growth [28]. The temperature sensitivity of decomposition of SOM varies with the quantity and chemistry of plant litter and preexisting SOM[25]. Thus, even within specific biomes, the local biogeochemical environment strongly influences microbial metabolic responses to climate change.

Grasslands

Grasslands are productive ecosystems that have long been used by humans for intensive agriculture and grazing. On a global scale, grasslands comprise approximately 26% of the land area (70% of the agricultural area) and store an estimated 20% of the total soil C stock[29]. The grassland soil C pool is large, ~1-2 orders of magnitude larger than the plant biomass pool, due to the deep and abundant rhizosphere that deposits C to the soil[30]. As a result, the projected vulnerability of grasslands to changing climate is intimately related to plant-microbe interactions occurring in the rhizosphere and to bulk soil processes that cycle carbon and other nutrients. At a global level, drought is expected to be the major consequence of future climate change in grassland regions over the next several decades[31]. With a negative water balance, the net land-atmosphere exchange of C (biomass production - respiration) will reflect the drought tolerance of plants and soil microbes, rooting responses (depth) and water-holding capacity of soil. Together these factors interact to generate a response space that may range from suppressed C uptake through N limitation[32] and decreased productivity under drier conditions, to reduced C loss via suppressed respiration[33]. Drought can also have long-lasting impacts on the soil microbiome because of changes in vegetation to more drought tolerant plant species and their subsequent selection for associated soil microbes in the rhizosphere[34,35]. Understanding what drives these ecosystem responses requires an understanding of the plant-microbe-soil interactions occurring within grassland ecosystems.

Wetlands

Wetlands interface terrestrial and aquatic systems, resulting in a variety of microenvironments amenable to microbial production of greenhouse gases. As a result, global wetlands are important emitters of CH_4, N_2O and CO_2. Shifts in moisture and temperature with changing climate will thus influence global greenhouse gas emissions from wetlands. Wetland methane emissions are the largest natural source of CH_4 and contribute approximately 1/3 of total emissions[36]. Presently conventional greenhouse gas mitigation policies do not include feedbacks associated with wetland CH_4 emissions[37]; climate change predictions and mitigation could be improved with more accurate quantification of microbial responses from wetland environments. Water availability is generally a strong predictor of methane emissions, where reduced precipitation enhances O_2 availability, promotes organic matter decomposition, increases CO_2 release, and reduces CH_4 emissions. The opposite is true for increased precipitation, which favors microorganisms that produce methane, or methanogens. These organisms are most prevalent in anaerobic conditions that prevail in wetlands.

Wetlands are diverse ecosystems with variable microbial responses. In northern latitude wetlands, (including Boreal forest ecosystems and peatlands), increasing temperatures are linked to permafrost thaw, increased microbial activity and greater CH_4 production[38]. In tropical wetlands (including peatlands, swamps and floodplains) precipitation shifts alter soil moisture, groundwater depth and wetland area, which can affect CH_4 production[39]. Recent evidence suggests that CH_4 emissions may be greatest in young wetlands dominated by methanogens, while N_2O emissions are prevalent in riparian zones, particularly in agricultural landscapes[40]. Even under saturated conditions, wetlands harbor many geochemical niches due to aeration in the root zone of wetland plants as well as fluctuating water tables at the wetland surface. As a result, wetland microbiomes can be involved in a variety of biogeochemical processes, such as C decomposition and greenhouse gas production.

Wetlands are expanding in many coastal areas because of the increasing global sea level, at a rate of 3.2 +/- 0.4 mm/year, and that rate is expected to accelerate over coming decades[41]. Rising seawater levels and more extreme storm events are resulting in increased flooding of low-lying coastal areas and introduction of seawater to soil ecosystems that are not normally flooded. Saltwater intrusion has been shown to stimulate microbial activity, resulting in increased greenhouse gas production and loss of nutrients from coastal soils[42]. Leaching of dissolved nutrients from soils into coastal waters can also lead to increased eutrophication[42]. 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 soil system. The introduction of sulfate increases soil microbial activity and biomass[43] and increases the rate of mineralization of organic C, resulting in increased levels of CO_2 production. Therefore, the implications are for a net increase in greenhouse gas production through increased CO_2 emission as seawater levels rise. However, different coastal soils respond differently to increased salinity[42]. With extended periods of flooding, microbial activity was shown to decrease due to resource depletion; representing a “boom and bust” situation[44]. Soil microbial community compositions also shifted significantly after flooding and were correlated with increases in heterotrophic activity, high ammonium production, and eventual depletion of labile soil organic matter from the system. Therefore, the ultimate climate impact of rising seawater levels on coastal ecosystems will depend upon the soil microbial community composition and dynamics, the soil C content and the availability of electron acceptors; these in turn will govern the balance between C and nutrient storage and release of greenhouse gases.

Peatlands are a class of wetlands (e.g. bogs, fens, mires, swamps) that are consistently inundated with water to such an extent that dead plants accumulate to form peat. Peatlands occupy just 3% of the land surface yet contains an estimated 25% of the world’s C[45]. Peat mosses of the genus *Sphagnum* are the dominant primary producers in many peatlands and contribute substantially to slow ecosystem decomposition rates and acidification of the surrounding environment[46]. *Sphagnum* insulates underlying permafrost, dampening the influence of raising temperatures. N fixers associated with *Sphagnum* can also influence C cycling through methane oxidation[47]. Symbiotic methanotrophic diazotrophs can oxidize CH_4 and produce CO_2, supporting *Sphagnum* photosynthesis[48], while simultaneously reducing atmospheric CH_4 concentrations. As the climate is changing, vegetation shifts, replacing *Sphagnum* with shrubs and trees, which in turn alters plant-microbe interactions, carbon chemistry within the ecosystem and temperate effects on microbial metabolism. Therefore, peatlands and the vast amounts of C they store, are vulnerable to direct and indirect effects of elevated temperatures[49].

Drylands

Desert soils, classified as aridisols (Fig. 1), are characterized by water deficiency and low organic matter content. Owing to the expanse of global arid regions (~⅓ of the planet's surface), they collectively store approximately 27% of the total terrestrial organic C stocks[50]. 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[51]. Water availability in dryland ecosystems is determined by the balance between precipitation and evaporation as well as the level of salts. Salts become concentrated as the soil desiccates, leading to osmotic stress to the resident microbes.

A comparison of different arid ecosystems, including extremely arid deserts, suggested that increases in aridity may result in a decrease in stability and genetic potential of the soil microbiome [52]. Also changing precipitation patterns have been shown to cause major shifts in the compositions of desert microbiomes[53]. Stovicek *et al*.[54] compared modeling simulations and empirical data to determine how dryland soil microbial diversity and composition was impacted by a rain event. The diversity was higher under dry conditions, presumably because there were more disconnected soil niches in the dry soil. Following wetting there was enhanced connectivity, more dispersal, more anaerobic niches and a sudden increase in nutrients; together this resulted 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[54]. The question is how resilient the desert soil microbiome will be to increasing temperatures and less predictable weather patterns in the future.

Microbial life in desert environments is often constrained due to C and moisture limitation and therefore dominated by surface-dwelling photoautotrophs[55]. This results in the formation of biological soil crusts (biocrusts) in many desert environments; e.g. >40% of the drylands in have biocrusts[56]. Biocrust populations (e.g. cyanobacteria and lichens) carry out fixation of C and N and are the primary producers in the desert ecosystems where they form. The biocrusts are exposed to intermittent rainfall events that have major repercussions on the microbial composition[57]. The concern is as precipitation patterns change and heat increases whether the biocrusts will be able to adapt to these harsher and more extreme conditions[58].

Cross-biome studies have shown that the bulk soil compositions of desert soil microbial communities can be distinguished from microbiomes in other soil ecosystems[59]. Most aridisols have an alkaline pH and pH is known to be a major driver of microbial community composition[2]. A recent study[60], found that the soil microbiomes of arid environments formed a distinct cluster when compared to other biomes with high pH. A survey of 10 unique genomes that were only present in the arid soils showed that they contained more genes encoding functions for tolerance to alkaline and/or saline conditions compared to genomes from other locations. These genomes may provide systems for bioprospecting of novel functions that confer resilience to drought. The annual heat moisture index (that combines precipitation and temperature variables) was found to correlate to microbial diversity and richness, resulting in a prediction that in a hotter and drier climate the community richness of desert soils in the US southwest will decline[61]. These authors also suggested that extremes in climate conditions (temperature and moisture) will be more impactful on desert microbiomes that are dominated by a narrow range of taxa compared to more diverse environments and that climate change could result in a decline in ecosystem stability and functions that are important for element cycling and plant community dynamics in arid environments.

Dryland ecosystems include Mediterranean ecosystems that are characterized as semi-arid regions with mild to hot, dry summers and cool, wet winters. In addition to the Mediterranean Basin region, other areas include much of the western coastal regions of the continental US, and South America, and coastal temperate regions of Asia, South America, Africa and Australia. Most climate models predict that these regions will be dryer in the future. By contrast, some models predict more precipitation in some regions (e.g. California) with climate change that would result in more rain, but with less snow due to warmer temperatures[62]. These changes in water availability can have profound and lasting impacts on soil microbiomes. Waldrop and Firestone[63] found that the historical exposure of soil microbiomes to changes in soil water content represented by soils from grasslands and adjacent oak forests, influenced the ability of the microbial communities to respond to new changes. These findings imply that different soil ecosystems are sensitive to climate change to different degrees. Over the long term, drought is predicted to result in a decrease in plant growth in Mediterranean ecosystems and a decline in microbial biomass and carbon and nitrogen content of the soils[64].

Soil microbiome responses to change

Soil microbial communities are constantly changing as they respond to changing resource availability. Some grow quickly to use resources as they become available, and some are adapted to grow slowly and use more chemically complex substrates. At a general level as environmental conditions shift, the resident microbes either adapt, become dormant, or die. The ability to adapt is dependent on the degree of perturbation and time necessary to accumulate mutations, regulate gene transcription and translation, and/or accumulate genes through horizontal gene transfer. Because soil habitats are dynamic systems, most soil microbes have evolved phenotypic strategies to cope with changing environmental conditions. In general, microbes acclimate to stress caused by climate change by altering allocation of resources from growth to survival strategies[65]. Yet little is still known about the fundamental microbial-scale mechanisms that control ecosystem scale responses to climate change. Deciphering how changes in physicochemical conditions influence the metabolism of extant soil microbial communities is a key area of interest for mitigating atmospheric greenhouse gas concentrations. Here we discuss two general concepts that govern the soil microbiome's response to change: 1) connectivity of the soil habitat and 2) the combined physiological status of the soil microbial community members (i.e. metaphenome); followed by discussions of microbial community and physiological responses to specific changes in climate.

Connectivity

Soil is a unique habitat for microbial life because soil microorganisms are confined to microscopic "hot-spots" that contain water, gases and nutrients to support life and these hot spots are more or less discrete depending on the ability of microorganisms and resources to move through interconnected pores in the soil matrix. For example, as soil becomes drier, there is less water in soil pores resulting in disconnected islands of resources and microbial life is more constrained within physically protected soil pores. Understanding the fine scale distribution and connectivity of soil microbes and resources is required to better understand how changes in climate influence species interactions and metabolism[66]. Currently we have a poor understanding of the influence of soil structure on creation of habitats and niches[67], the cascading effects of connectivity on C and nutrient transformations and the influence of hydrologic perturbations on those transformations. This knowledge is important because the way that microbial species allocate C will ultimately determine whether C persists in soil or not[67] and how changes in environmental conditions influence these processes.

Another aspect of connectivity is the metabolic connectivity between interacting members of microbial communities. Microbial communities have evolved complex networks of interacting populations whose individual members are fine tuned to coordinate efficient use of resources as they become available, or conversely to respond to stress. Network analysis enables visualization of co-occurring taxa and identification of potential keystone taxa that are highly connected in the network and whose removal would potentially be disruptive to microbiome function[68]. Microbial networks may be destabilized by climate change with repercussions for ecosystem function[69]. For example, in grassland mesocosms network analysis was used to visualize that bacterial networks are less stable than fungal networks to drought[69]. Similarly, multi-year field experiments in restored prairies revealed that bacteria are more sensitive to drought and environmental changes across sampling years compared to fungal communities[35].

Metaphenome

The diverse genetic potential within the soil microbiome interacts with environmental shifts to induce microbial gene expression. This collective metaphenome (metagenome x environment) generates ecosystem scale elemental cycling[70]. Understanding variability in moisture, temperature and local atmospheric chemistry within the soil is essential for accurately predicting the metaphenomic response of the soil microbiome to climate change. This is because soil microbiomes do not respond to a mean environmental condition, but rather to instantaneous conditions that trigger biochemical reactions, microbial responses, and metabolic interactions. In turn, biogeochemical responses to extreme events (heatwaves, wildfires, floods, drought) often include temporal lags. For example, a gradual increase in temperature allows more time for evolution by selection for species/genes that enable resistance to heat and associated stress conditions. However, abrupt change, such as resulting from intense fires or flooding, will be more disruptive to native soil microorganisms because they will not have had adequate time to adapt. 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. We also have a limited understanding of the influence of population-level microbial physiology (viability, dormancy, activity, etc.) on emergent properties of the system. In the following section we consider different types of community and physiological responses that soil microbes use to cope with changing environmental conditions caused by climate change.

Changes in soil moisture: Soil microbes have evolved various life strategies to cope with stress caused by drought, such as osmoregulation, dormancy/reactivation, and extracellular enzyme synthesis to accumulate substrates[71]. Understanding microbial traits that confer ecosystem resilience to drought holds promise for predicting and managing ecosystem responses to climate change. Members of some bacterial phyla, like Actinobacteria, are known to accumulate in drought impacted soils[72,73] because of their ability to conserve activity and become dormant under dry conditions. Recent studies have also shown that drought also selects for some fungi, potentially contributing to the maintenance of C and N cycling when water is scarce[74]. Some fungi also can produce hyphae that can bridge resources and distribute water across the soil habitat[75], contributing to fungal resistance to drought. Associating compositional shifts with resiliency traits is thus an important step towards understanding interkingdom interactions that generate consistent community responses to environmental drought stress.

By contrast, with climate change, some areas are expected to be impacted by increased soil moisture caused by flooding or severe and erratic precipitation events. As soil moisture increases, the soil pores become water filled and anaerobic, thus providing ripe conditions for methanogenesis and denitrification, and the potential for release of N_2O and CH_4 greenhouse gases.

Increased Temperature: Several field studies have explored the short-term and/or long-term responses of the soil microbiome to increased temperature[23,76,77]. Higher soil temperatures have been shown to result in an initial increase in soil metabolic activity and decomposition of SOM, resulting in a higher flux of CO_2, but no increase in microbial biomass[23], although warming has been shown to stimulate growth of some soil fungi[78]. At the Harvard forest LTER location, sustained warming for 26 years resulted in depletion of soil organic C with corresponding reductions in microbial biomass, suggesting deleterious consequences of long-term warming for soil sustainability[23].

Increased CO_2 emissions: Rising concentrations of atmospheric CO_2 can stimulate plant growth and belowground biomass, however the long-term effects on soil C stocks depends on water and nutrient availability, which influence photosynthesis, decomposition and the net accrual of soil C. There have been several elevated CO_2 field experiments that have provided valuable data about the plant and soil microbial response to this anticipated change in climate. However, they have not been globally distributed, making it challenging to inform global terrestrial ecosystem models[79]. A combination of meta-analysis and modeling revealed that elevated atmospheric CO_2 stimulated microbial decomposition of soil organic C[80]. Increases in C input was offset by the turnover of soil C, limiting soil C accumulation[80]. Nutrient feedbacks can dampen CO_2 stimulation of plant growth and enhance plant-microbe interactions to liberate nutrients from soil organic matter[81]. Also, different plant species respond differently to elevated CO_2 levels and this can impact the amounts and types of C inputs to the rhizosphere. For example, C_4 plants, a plant functional type to which corn, sorghum, *Miscanthus*, and switchgrass belong, have a more efficient photosynthesis than C_3 plants like rice and wheat[82] and may allocate more C belowground to rhizosphere-associated microbes and mycorrhizal fungi. Understanding how changes in CO_2 interact with other important environmental variables including temperature, precipitation and nutrients (such as P) are critical for predicting microbiome responses among soil ecosystems.

Soil microbiome manipulation efforts

Our increasing awareness of the impacts of climate change on the soil microbiome is resulting in an emerging urgency in developing ways to harness soil microbial capabilities to mitigate negative consequences of environmental perturbations. 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.

Carbon sequestration

A potential means of reducing atmospheric C stocks is via sequestration into stable, non-gaseous forms through biotic and/or abiotic processes. C enters the soil via assimilation of atmospheric CO_2, mainly by plants but also by photoautotrophic and chemoautotrophic soil microbes. The fraction of photosynthate released to the rhizosphere by plants, either as direct root deposition through exudation, sloughed root cap cells, or via mycorrhizal fungi, is significant (up to 20%)[83]. C inputs stimulate symbiotic and free-living organisms, that spread the C through the soil matrix. Microbial biochemical transformations of the C, and subsequent exchange among communities causes bioavailable forms of C to cycle and persist over the years.

There are several avenues being explored to exploit the soil microbiome for C storage. First of all, the soil microbiome has a largely unexplored and untapped biochemical capacity that could be mined for novel reactions that increase the deposition of C into soil. These reactions could be manipulated to drive the C decomposition pathways towards more recalcitrant and stable end products[84]. Alternatively, natural microbial species or consortia could be selected that have the desired metabolic routes and then introduced into soil ecosystems to trap C.

Soil C storage can be increased by judicious land management practices[85]. Soil management practices such as no-till farming[86] and diversified crop rotations[87] reduce the disturbance of soils and the decomposition of soil organic matter, influencing soil C storage. Incorporating hay, forage, or green manures into cropping systems offers multiple benefits to the farmer and to the environment. These legume or manure-based systems also promote greater total and biologically active soil organic matter (SOM) which can enhance soil carbon storage[87].

Alternatively, soil microbiomes can be manipulated *in situ*, through addition of amendments that enhance their activity to take up and store C in soil. One mitigation strategy would be to encourage production of stable C, resulting from microbial products, that can be stored in deeper soil layers[88]. Soil microorganisms can contribute to formation of soil organic matter either by formation of stable metabolites or by their own dead biomass (necromass)[88]. Biochar has also been proposed as a soil amendment to sequester soil C[89]. The soil microbiome is indirectly linked to the promise of biochar because the extent of microbial activity will determine whether the biochar is respired or alternatively retained in soil.

There is increasing interest in optimizing interactions between plants and soil rhizosphere microbiomes to facilitate soil C storage[82,90]. For example, genetic modification of plants has been proposed to produce biomass that is more resistant to microbial degradation; i.e. more lignin, that is retained in soil. Another strategy is to harness plant-microbe interactions to enhance root exudate deposition by increasing rhizospheric sink strength, thereby facilitating soil C storage[82]. Yet another option is to genetically engineer the plant to select for beneficial colonizing microbes. Future strategies could lead to our ability to control the allocation of photosynthate to optimize the plant-microbe-soil system for both optimal plant yield and soil C deposition[82]. This will require collaboration between plant breeders and soil microbiologists to design the best pairing of specific beneficial microbes with specific plant genotypes[91].

Microbes as beneficial plant inoculants

Climate change is predicted to result in increasing drought with negative impacts on plant growth and agricultural productivity[1]. 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[92]. PGP microbes 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* inoculants that are applied for biological N fixation in association with legumes. Currently there is growing interest in going beyond traditional application of inoculants as biofertilizers and biopesticides, to also harness other beneficial properties of PGP microbes to mitigate the deleterious consequences of climate change[93].

Several avenues are being explored to use beneficial plant-associated soil microbes to alleviate drought stress in plants[91]. For example, some soil bacteria produce extracellular polysaccharides (EPS) resulting in hydrophobic biofilms that can protect plants from desiccation[92]. Therefore, there is growing interest in use of soil bacteria to reduce stress to plants during drought through the formation of EPS that retains water in the soil and makes it more accessible to plant roots.

Beneficial soil microbes could also be exploited to increase tolerance of crops to drought stress through their production of phytohormones that stimulate plant growth, through accumulation of osmolytes or other protective compounds or detoxification of reactive oxygen species[91,94]. For example, some species of *Bacillus* were shown to synthesize indole-3-acetic acid (IAA) in rhizosphere soil, resulting in increased root production[95]. Introducing soil bacteria that produce IAA can stimulate plant root initiation and elongation[91] and the added root biomass and root length can help the plant to access water and alleviate water stress, as well as potentially contribute to soil organic matter formation. Rhizosphere microbes have also been associated with accumulating metabolites in plant cells and alleviating osmotic stress due to water imbalance in plant tissues[96]. For example, inoculation with *Azospirillum* helped to protect maize plants subjected to drought stress by accumulation of the osmoprotectant proline[97] and in another study wheat seedling by increasing water flow through the plant[96]. Bacterial inoculants can also directly influence the plant metabolome. Schmidt *et al.*[98], studied the composition of secondary metabolites following inoculation with different bacterial strains onto chamomile plants[98]. Inoculation with strains of *B. subtilis* and *Paenibacillus polymyxa* resulted in increased production of a bioactive metabolite, apigenein-7-O-glucoside[98]. Bacteria that produce 1-aminocyclopropane 1-carboxylate (ACC) deaminase can lower levels of ethylene, a stress hormone[99]. Some endophytic strains of *Azospirillum* were demonstrated to control stomatal closure in maize through signal transduction routes regulated by production of gibberellins[100]. Resistance to drought stress and nutrient acquisition can also be enhanced by fungal associations. Many plants, including most of those with agronomic value, form symbiotic associations with beneficial arbuscular mycorrhizal (AM) fungi. These associations are known to promote plant growth, for example by increasing bioavailability of soil phosphorus to plants. As climate changes, these beneficial relationships might also be exploited to increase the tolerance of plants to different environmental stresses. As one example, AM fungi were reported to improve the ability of maize plants to cope with drought stress by regulating the plant production of specific molecules known as aquaporins[101]. Aquaporins are known to reduce water stress by regulating the amount of water loss by the plant[102]. AM fungi can also directly access water by extension of their mycelia into water-filled soil pores that aren’t otherwise accessed by plant roots. Together these examples illustrate how understanding soil microbiomes creates myriad opportunities to leverage the power of microbes to adapt to our changing climate and enhance ecosystem services.

Concluding remarks

During the writing of 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 imperiled 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[103]. Although, not within the scope of our review, when combined with unsustainable soil management practices, we are on course to lose much of our fertile soils, due to erosion, rising seawater levels, increasingly extreme storm events, desertification, nutrient depletion and degradation. The ecosystem services carried out by soil microbiomes are vital towards retaining soil C and provision of nutrients to plants and the importance of soil microbiomes in preserving a healthy soil for future generations cannot be overstated. Although there is great interest in application of soil microbes to mitigate climate change, or to stimulate plant growth under a changing climate, there remain significant challenges for their widespread application. Better soil microbial inoculation and amendment strategies are needed to optimize the beneficial metabolic routes of natural microbial communities that will lead them towards sequestration of soil C for example. There is an urgent need to gain a better understanding of the repercussions of climate change to key biogeochemical processes carried out by soil microbes, 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 propose several mechanisms by which soil microbes can be harnessed to help to mitigate climate change, we do not by any means propose that this will be sufficient to counterbalance the loss of soil and generation of greenhouse gasses 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[104]. To achieve this goal, we must connect the fine-scale detail arising from microbiome studies to the landscape scale resolution of ecosystem services and most climate models. Therefore, another priority is to incorporate knowledge about soil microbial metabolic pathways and interactions into predictive models of the impacts of climate change on important ecosystem services carried out by the soil microbiome. And 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.

Box 1. Soil organic carbon turnover
Plant and animal detritus are decomposed by soil microorganisms and fauna. Some of the resulting small molecules are assimilated into microbial biomass and used for respiration, enzyme production, metabolites, or reproduction. Collectively these molecules contribute to the active pool of SOC, along with rhizodeposition and other metabolites that fuel microbial populations. As microbes die and turn o ver, some of these molecules stay in the active pool, recycling for months to years, while other components are part of a passive SOC pool that can take thousands of years to turn over[104].The passive pool is comprised of decomposition products that are no longer favorable for microbial metabolism under the current environmental state due to the physical and chemical availability[67]. During SOC decomposition a key environmental factor that determines the flux of greenhouse gases to the atmosphere is the soil hydrology. In wetter, anaerobic soils, organic carbon can be metabolized to CH_4 which is 34 times more potent a greenhouse gas than CO_2.

The residence time of the active SOC pool is dependent on the C use efficiency (CUE) of the soil microorganisms. CUE determines whether the C is respired, producing CO_2 in the process, used to produce enzymes to acquire resources, produce metabolites for chemical signaling and growth regulation, or to build biomass. Abiotic conditions (temperature, substrate availability, redox conditions) influence both cell physiology and CUE. Together, the CUE of populations of species create a community response. At the community scale, greater CUE occurs with efficient biomass production (more biomass production per unit C assimilated). Research suggests that some microbial communities have a higher capacity to store soil C than others. For example, a higher ratio of soil fungi:bacteria can lead to higher amounts of soil C storage, due to retaining of C in fungal biomass compared to C loss by respiration of CO_2; i.e. a higher CUE. This metric is, however, controversial because fungi also have capacity for decomposing complex organic C pools with oxidative enzymes, which may lead to greater decomposition, contributing to the active SOC pool. Predicting how CUE as an organismal trait is expressed at the community scale remains a challenge, because it is difficult to constrain variability in CUE due to interspecies interactions and environmental conditions.

Microbial CUE at the ecosystem scale integrates interspecies interactions and community turnover[105,106], reflecting biomass production and decay relative to soil microbial respiration. Developing a mathematical understanding of what drives ecosystem CUE and the feedbacks with climate forcing is a pressing challenge to advancing C sequestration through microbial activities. Recent predictive models of the impacts of climate change on the soil C flux, i.e. the Community Land Model, have included a module for soil biogeochemistry[107] that accounts for the influence of CUE and the ability of soil microbes to adapt to a changing climate as key parameters. These models still require further cross validation with experimental data, but they could lead to improved predictions of the impacts of climate change on C flux and other biogeochemical processes carried out by soil microbes.

Box 2. Soil nitrogen impacts on climate

Nitrogen cycling has a strong influence on climate change, because N availability is closely linked to the production of all three greenhouse gases[108]. In particular, management of N_2O by soil microbial communities remains a pressing issue because N_2O is a potent greenhouse gas with a warming potential that is 298 times greater than that of CO_2 and is also a predominant stratospheric ozone-depleting compound. N_2O emissions are dependent on the quantity of reactive N in the environment, which has increased 3-5-fold in the past century, due to agricultural intensification, fossil fuel burning, and industrialization. Increases in microbial N cycling in response to increased reactive N has enhanced N_2O production. Agricultural systems contribute 4.3–5.8 Tg N_2O–N yr^{-1} due to N fertilizer use and manure management. Together with natural soils (6–7 Tg N_2O–N yr^{-1}) soil emissions represent 56–70% of all global N_2O sources[109]. Managing the production and consumption of N_2O within soil ecosystems has been a formidable challenge due to the complexity of the microbial ecology[110] and the spatial and temporal variation[111,112].

Development of plant-microbe associations to better synchronize plant demand with microbial N supply holds great promise for mitigating microbial N_2O production. For example, arbuscular mycorrhizal fungi (AMF) form a mutualistic symbiosis with ~80% of land plants and have been shown to assist with plant N acquisition and diminish N_2O production[113]. If AMF are better at acquiring ammonium than slow growing nitrifiers, this provides a clear pathway for enhancing managed soils to mitigate N_2O production. Similarly, decoding the genetic pathways for N_2O consumption within the soil, could further reduce the greenhouse gas contribution of soil microbiomes. Once produced, the only known biological sink for N_2O in the soil is reduction of N_2O by denitrifiers and non-denitrifying N_2O reducers. Inoculation of soil microbiomes with N2O consuming communities may hold potential for mitigating N2O emissions from soil ecosystems[114].

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Suggested references to highlight

Woodcroft et al., 2018 - Assembles hundreds of genomes from soil metagenomes that corresponding to primarily uncultivated and uncharacterized microoganisms along a permafrost thaw gradient in Sweden.

Llado et al., 2017 - Reviews importance of global forests as C sinks through storage of stable organic matter in soils.

Mellilo et al., 2017 - Describe results of long-term warming field studies at the Harvard forest field station on soil carbon flux.

Chapman et al., 2017 - Discuss predicted greenhouse gas emissions from wetland ecosystems.

Steinmuller and Chambers - Found that intrusion of seawater into coastal soils results in an increase in salt and sulfate; the latter can serve as a terminal electron acceptor for sulfate reduction and alter metabolic processes.

Armstrong et al., - Describe major shifts in desert microbiomes with changing precipitation patterns.

Schimmer and Schaeffer, 2012 - Discuss the link between soil structure and connectivity of niches and resources for the soil microbiome.

DeVries et al, 2018 - Used network analyses to show that bacterial networks are less resilient to drought than fungal networks, suggesting that bacteria are less stable to environmental change compared to fungi.

Naylor et al., 2017 - Find that members of some bacterial phyla, such as Actinobacteria, are tend to accumulate in drought impacted soil

Van Groeningen et al., - Used a combination of modeling and empirical data to show a stimulation of soil organic carbon in the presence of elevated levels of atmospheric CO2.

Wallenstein - Discuss strategies for optimization of microorganisms in the plant rhizosphere to store soil carbon.

Lakshmanen - Discuss use of beneficial soil microbes to alleviate drought stress in plants.

Glossary

Permafrost = Defined as soil that has been frozen for at least 2 consecutive years.

Polygons = Type of landscape feature caused by ice wedges during permafrost thaw.

Eutrophication = Type of water pollution due to increase of nutrients that allows for blooms of phytoplankton.

Radiative forcing = Difference between solar energy absorbed by the Earth and energy radiated back to space.

Carbon use efficiency (CUE) = Difference between amount of carbon respired as CO_2 to that incorporated into cellular biomass.

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