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Soil Microbiomes Under Climate Change and Implications for Carbon Cycling

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Abstract

Communities of soil microorganisms (soil microbiomes) play a major role in biogeochemical cycles and support of plant growth. Here we focus primarily on the roles that the soil microbiome plays in cycling soil organic carbon and the impact of climate change on the soil carbon cycle. We first discuss current challenges in understanding the roles carried out by highly diverse and heterogeneous soil microbiomes and review existing knowledge gaps in understanding how climate change will impact soil carbon cycling by the soil microbiome. Because soil microbiome stability is a key metric to understand as the climate changes, we discuss different aspects of stability, including resistance, resilience, and functional redundancy.

We then review recent research pertaining to the impact of major climate perturbations on the soil microbiome and the functions that they carry out. Finally, we review new experimental methodologies and modeling approaches under development that should facilitate our understanding of the complex nature of the soil microbiome to better predict its future responses to climate change.

Contents

1. INTRODUCTION

The soil microbiome contributes to ecosystem health in a variety of ways, including biogeochemical cycling, bioremediation, plant growth, and primary productivity (1, 2). Its role in greenhouse gas emissions and mediating soil organic carbon (SOC) is of particular interest in light of future climate predictions. Climate change and shifts in land management practices can adversely affect soil fertility and SOC (3, 4), which in turn impacts the soil microbiome and its net influence on soil carbon sequestration. Here, we review the state of knowledge of the soil microbiome and how its transformation of SOC is influenced by climate change factors. In particular, we address challenges and metrics associated with studying the soil microbiome; we review effects of climate change disturbances on taxonomic and functional profiles, as well as biochemical pathways; we discuss the importance of interkingdom interactions in multiple soil systems; and we describe recent advances in technical and modeling approaches.

2. CURRENT CHALLENGES

Soil ecosystems are highly complex and subject to different landscape-scale perturbations that govern whether soil carbon is retained or released to the atmosphere (5). The ultimate fate of SOC is a function of the combined activities of plants and belowground organisms, including soil microbes. Although soil microorganisms are known to support a plethora of biogeochemical functions related to carbon cycling (6), the vast majority of the soil microbiome remains uncultivated and has largely cryptic functions (7). Only a mere fraction of soil microbial life has been catalogued to date, although new soil microbes (7) and viruses are increasingly being discovered (8). This lack of knowledge results in uncertainty of the contribution of soil microorganisms to SOC cycling and hinders construction of accurate predictive models for global carbon flux under climate change (9). Therefore, we are constantly refining our understanding of the biochemical potential of the soil microbiome and the metabolic fate of SOC.

The lack of information concerning the soil microbiome metabolic potential makes it particularly challenging to accurately account for the shifts in microbial activities that occur in response to environmental change. For example, plant-derived carbon inputs can prime microbial activity to decompose existing SOC at rates higher than model expectations, resulting in error within predictive models of carbon fluxes (10). To account for this, a conceptual model known as the microbial carbon pump has been developed to define how soil microorganisms transform and stabilize soil organic matter (11). In this model, microbial metabolic activities for carbon turnover are segregated into two categories: ex vivo modification, referring to transformation of plant-derived carbon by extracellular enzymes, and in vivo turnover, for intracellular carbon used in microbial biomass turnover or deposited as dead microbial biomass, referred to as necromass. The contrasting impacts of catabolic activities that release SOC as carbon dioxide (CO_2), versus anabolic pathways that produce stable carbon compounds, control net carbon retention rates. In particular, microbial carbon sequestration represents an underrepresented aspect of soil carbon flux that the microbial carbon pump model attempts to address (11). A related area of uncertainty is how the type of plant-derived carbon enhances microbial SOC storage or alternatively accelerates SOC decomposition (12). For example, leaf litter and needle litter serve as sources of carbon for microbial growth in forest soils, but litter chemistry and pH varies by vegetation type [e.g., between root and foliar litter (13) or between deciduous and coniferous forest litter (14)]. In turn, these biochemical differences influence SOC levels through changing decomposition dynamics (14). Also, increased diversity of plant communities increases rates of rhizodeposition, stimulating microbial activity and SOC storage (15), although soils eventually reach a saturation point beyond which they cannot store additional carbon (16). Taking local environmental and biogeochemical variables into account will help address our lack of understanding about net carbon flux in soils.

Quiescence also impacts microbial metabolic rates. Many soil microorganisms are transiently active, alternating between dormant and active states (17). Even during dormancy, some soil microorganisms are capable of utilizing their energy reserves to metabolize SOC and contribute to soil biomass turnover, albeit at slower rates (17, 18). Nevertheless, active members of the soil community contribute the most to biogeochemical transformations, and a new paradigm is to shift analyses away from taxonomic profiles and toward microbiome functional pathways and phenotypes (19). However, current sequencing technologies for community composition also measure dormant microorganisms and even exogenous DNA (20, 21) and are thus biased against active functioning members of the community. Refining approaches to focus on function is therefore anticipated to aid model construction through more accurate assessment of real-world processes.

Another challenge is accounting for the chemistry and physical structure of soils themselves, both of which influence SOC decomposition. Traditionally, slow rates of carbon turnover were

thought to be attributable to physical protection of carbon molecules in microaggregates or mineral associations (22), or to their chemical recalcitrance to biodegradation (23). The current paradigm expands on how mineral associations occur, namely through soil particles' sorption of biopolymers from microbial and plant necromass (24, 25)—indeed, deep soil organic matter is mainly comprised of microbe-derived products (26). Additionally, the spatiotemporal structure of soils is heterogeneous and dynamic, with "hot spots" or "hot moments" of microbial activity (27). For instance, water availability is typically uneven, so carbon cycling is limited to areas with sufficient water, or to microbes capable of dealing with desiccation stress [e.g., through production of extracellular polymeric substances to maintain a hydrated microenvironment (28)]. In addition, other factors influencing SOC mineralization include presence of anaerobic versus aerobic microsites (anaerobic respiration of carbon being less energetically favorable than aerobic), availability of electron acceptors, and redox status of the soil (29). Carbon profiles also matter: For example, carbon compounds recalcitrant to anaerobic degradation (e.g., lipids) are preferentially retained in anaerobic aggregates (29). Therefore, comprehensive comparisons of SOC decomposition profiles across different soil types and structures are necessary to better understand soil microbial metabolism and carbon flux.

Mineralization: conversion of an element (e.g., carbon or nitrogen) from an organic to an inorganic form, for example when organic carbon is converted to carbon dioxide and inorganic nutrients through microbial metabolism

Resistance: the capacity of a microbiome to retain a consistent community and functional composition in the face of an external perturbation

Resilience: the capacity of a microbiome to recover to an initial stable state after cessation of an external perturbation

3. STABILITY METRICS OF THE SOIL MICROBIOME

A major concern of climate change is its impact on soil microbiome stability and function and by extension ecosystem sustainability (30–32). Meta-analyses have demonstrated that in approximately 80% of published studies, soil disturbances evoked measurable effects on microbiome stability (30, 33). Community stability is typically qualified with respect to one or more of three main metrics: resistance (remaining unchanged during disturbance), resilience (recovery to a stable state), and functional redundancy (functional profiles are maintained despite taxonomic shifts) (32). Ideally, all of these metrics would be incorporated into microbiome disturbance studies, but limitations in sampling time and effort often preclude this possibility. In particular, the degree of resistance is often measurable during and immediately after a disturbance, but resilience trends may only be visible years later (34). As climate disturbances increase in severity or frequency, understanding microbiome reaction patterns will improve prediction of future responses. Therefore, these metrics represent an important consideration to take into account when designing disturbance experiments, and each is reviewed in detail below.

3.1. Resistance

The majority of disturbance studies have focused on resistance rather than resilience due to its comparative ease of quantification. Resistance is commonly measured as shifts in community or functional profiles under stress. For example, soil water limitation adversely affects members of the Proteobacteria phylum and increases relative abundances of members of Actinobacteria and/or Firmicutes phyla (35). Through their effects on phylogenetic profiles, disturbances will in turn affect ecosystem functioning. For example, soil drying altered the abundance of guilds for microorganisms involved in methane oxidation (36), whereas soil warming or elevated carbon dioxide (eCO_2) affected ammonia-oxidizing microbes (37). Anthropogenic nitrogen deposition (through excessive fertilizer addition) can enrich for nitrogen-cycling processes, including urea decomposition and tricarboxylate transport (38, 39). Some environmental stresses may hinder carbon cycling through decreasing metabolic diversity of a community (40) or by limiting microbial uptake of carbon through decreased diffusion rates (41). For example, enzymatic activity rates, including that of carbon cycling enzymes (beta-glucosidase, aminopeptidase) or other nutrient cycling enzymes

(acid phosphatase, arylsulfatase), have been shown to be suppressed under drought and following soil burning (42, 43). As a consequence, predictions of how stress affects biogeochemical processes for carbon and nitrogen mineralization need to account for microbial responses.

Microbial life strategies are closely tied to resistance, namely ratios of *K*- to *r*-selected organisms. (*K*-selected microbes maximize survival by being slow growing and resource efficient, whereas *r*-selected organisms are energy and resource inefficient but maximize survival through rapid rates of growth and reproduction.) In one study, communities with higher ratios of Gram-positive (normally *K*-selected) to Gram-negative (normally *r*-selected) bacteria were more resistant to eCO_2 (44). *K*-selected organisms are associated with slower growth, higher enzyme substrate affinities, and usage of more recalcitrant forms of carbon (45), traits tied to stress resistance. By contrast, *r*-selected organisms are normally more dependent on labile carbon compounds for growth, such as those released into the rhizosphere through plant root exudates. Because some endemic plant species decrease rhizodeposition into soil under drought stress to maintain a carbon supply for their own survival, there is a depletion of labile SOC stocks into the surrounding soil. As the principal remaining carbon sources are recalcitrant carbon molecules, *K*-strategists are favored over *r*-strategists (35).

Rhizosphere: the region of soil surrounding and directly influenced by plant roots, including their related secretions and exudates, harboring microbes, and microbial processes essential for plant health

Physiological adaptation is a resource-intensive but effective means of conferring stress resistance. Some soil microbes have adopted thicker cell walls to tolerate desiccation stress (35), and/or membrane adaptations to tolerate exposure to toxic metals (34). Previous exposure to a stress condition (34) can prime a community to resist future stresses with a similar mode of action, for example, through upregulation of and/or increased dispersion of resistance genes (32, 46). However, investment into a novel resistance mechanism often has the trade-off of losing a previous one, and microbes may become susceptible to a stress that they were previously resistant to (34). These trends have been observed for numerous (nonclimate change–related) ecological disturbances: For example, long-term copper stress hindered the soil microbiome's capacity to respond to fluctuating environmental conditions (47). Similarly, chronically trampled dryland soils were less able to respond to rewetting than non-trampled ones (48). The most resistant communities often display functional plasticity and shift metabolic profiles as a function of environmental conditions, enhancing their survivability if a particular niche is destroyed (33). However, it remains to be seen whether physiological adaptations and/or functional plasticity will be widespread enough under climate change disturbances to ensure the survival of soil ecosystems.

3.2. Resilience

The phenomenon of soil microbiome resilience is arguably underreported, as studies incorporating a long-enough time course to track full recovery are uncommon (32). Even when explicitly measured, pre-disturbance profiles may take years to re-establish (49), and in some cases putatively irreversible changes occur (30, 50); these trends emphasize the importance of long-term studies incorporating decadal timescales to track microbial responses to disturbance (51–53). In a meta-analysis of short- and long-term disturbances, recovery was generally observed in less than half of the studies (33). As disturbances increase in frequency and duration, such as during climate change, it is imperative to understand how, if at all, microbiomes are able to recover.

Similar to resistance, microbiome resilience may be assessed based on taxonomic and/or functional profiles. One approach for measuring resilience is through clustering taxa based on recovery patterns—for example, taxa that increase under stress before subsequently decreasing during recovery would form one cluster, whereas taxa that show the opposite trend would form another (54). Resilience can also vary by rate of recovery. For example, members of the Planctomycetes, Crenarchaea, and Acidobacteria phyla recovered faster after a soil warming treatment than did

Actinobacteria or Verrucomicrobia (55). However, not all members of a given phylum respond universally in the same manner. For example, specific classes within the Acidobacteria and Proteobacteria phyla were shown to differ in their resiliencies to drought stress (35). Distinct resilience trends by phyla have implications for the carbon cycling processes they mediate, as individual taxa have characteristic growth and carbon assimilation patterns (56). For example, Actinobacteria abundance was negatively associated with carbon mineralization, whereas Bacteroidetes and Proteobacteria were positively associated (57). Therefore, rates of soil carbon cycling will largely depend on how fast members from these phyla recover to a given stress. Similarly, for functional profiles, resilience depends on the function in question and the phylogenetic resolution that is being examined. For example, nitrification is less resilient than denitrification (32, 58), likely because it is mediated by a narrower guild of microbes. Therefore, functions based on broadly distributed enzymes generally have more resistance but lower resilience, whereas those with narrowly distributed enzymes, such as complex polysaccharide degradation, have less resistance but higher resilience (59). Another discrepancy between resistance and resilience is the influence of prior stress—previous exposure to a stress often decreases rates of resilience to a new one, whereas resistance is generally strengthened (43).

Several factors contribute to microbial resilience. One is prevalence: Highly abundant and/or widely dispersed organisms are less likely to be obliterated by a stress. Another strategy for resilient microbes is to enter dormancy, forming what is known as the microbial seed bank (60). In both scenarios, surviving microbes are better poised to reseed the soil microbiome upon stress amelioration (33). Rapid ribosome synthesis and shorter generation times are advantageous traits, as they increase the speed of recovery; however, fast-growing taxa (e.g., *r*-strategists) are often highly resource dependent and therefore more susceptible to stress (45). Overall community resilience is also aided by stress resistance mechanisms, as they may be passed from tolerant to susceptible individuals via gene flow to aid recovery (61). Alternatively, tolerant but less altruistic organisms may keep resistance mechanisms to themselves, growing rapidly under a given stress condition while susceptible organisms die off (60). In extreme cases, opportunistic individuals have been shown to adapt their metabolic pathways to incorporate an otherwise stressful toxic compound as a carbon/nitrogen source (62). Even outright antagonism against other recovering groups may aid resilience, which was posited as the reason behind increased survivability for bacteria relative to fungi after soil heating (63).

3.3. Functional Redundancy

Functional profiles may be resistant or resilient under stress even if taxonomic profiles change. Desiccation-rewetting cycles have been shown to alter community composition, but often functions (extracellular enzyme activity, methane oxidation, carbon cycling) remain resilient (36, 42, 48). In such cases, the relative abundances of members of a functional guild might shift depending on their inherent stress susceptibilities, where the more resistant members predominate after stress is lifted (60). Functional redundancy can also be tied to ubiquity. For example, common processes such as respiration are conserved in all but the most extreme disturbances, whereas more specific processes such as nitrification may not be (30).

The disconnect between function and phylogeny is exacerbated by limitations of current methods (20). To track members of a functional guild, a typical approach is to perform amplicon sequencing of a gene involved in the function. However, if gene variants or functional orthologs with dissimilar sequences exist, a significant proportion of the functional guild will remain uncaptured through this approach (32). Resolving this discrepancy will reconcile how a function remains constant in the face of taxonomic shifts (e.g., confirming that a guild member increases in abundance to

compensate for loss of another). The greater functional redundancy a soil community displays, the more resilient it will be following disturbance (59), highlighting the importance of understanding functional redundancy in the context of other microbiome stability metrics. Accordingly, certain aspects of stability metrics are now being incorporated into new trait-based microbial models in soils (64).

4. CLIMATE CHANGE IMPACTS ON THE SOIL MICROBIOME

Climate change–associated disturbances can significantly alter soil microbial community and functional profiles (5). If soil carbon and/or nitrogen cycling are affected, this can in turn affect climate change either through positive feedbacks to the atmosphere (e.g., greenhouse gas emissions) or negative feedbacks (e.g., carbon immobilization into microbial or plant biomass) (12). Better understanding of how soil microorganisms respond to climate change will therefore ultimately improve climate models. However, climate change can invoke several distinct perturbations or even compounding disturbances, which can exert contrasting effects on the soil microbiome (5). Given the uncertainty as to the interplay between different climate change factors, recent studies have begun to incorporate multiple factors in combination (37, 65–67). Here, we specifically review soil microbiome responses to soil warming and eCO_2, and how these factors interact with one another directly and indirectly to effect change in soil community and functional profiles.

4.1. Soil Warming

Current climate models predict a global temperature rise of roughly 3.7°C by 2100 (68). Considering that soil microbial communities are demonstrably affected by warming (5), this represents an unavoidable impact of climate change on the soil microbiome. Soil warming is thought to impact resident microbial communities in a stepwise fashion. First, organic carbon decomposition rates are enhanced over the short term, increasing microbial biomass. One study found that the soil microbial population size increased by 40–150% under soil warming (55). Next, microbial respiration has been shown to decline over time as labile carbon is depleted (69). After years of exposure, changes have been observed in microbial physiologies, community composition, and functional profiles, both as microbes adapt to warming, and as their metabolism shifts to utilize the remaining recalcitrant carbon sources (70). The nuances behind these steps are outlined below.

Warming has been observed to increase microbiome community diversity and richness (55, 71, 72), as well as to enrich for members of the Acidobacteria and Actinobacteria phyla and class Alphaproteobacteria (55, 69, 73). These taxonomic shifts overlap with functional profiles: Oligotrophic taxa (i.e., slow-growing microbes capable of surviving in nutrient-poor conditions, e.g., Actinobacteria) are promoted over copiotrophic taxa (i.e., fast-growing microbes optimized for nutrient-rich environments, e.g., Bacteroidetes), possibly as a response to changing soil carbon composition (74). For example, warming treatments lasting 5 to 8 years were shown to favor more recalcitrant carbon-degrading taxa from the Actinobacteria or Acidobacteria, despite few overall measurable responses in community composition (52). Measurable differences in functional guilds responsible for ammonia oxidation (37) or diazotrophy (72) have also been observed following soil warming.

Microbial function can be impacted by warming both directly (e.g., through acceleration of enzymatic rates) or indirectly (stimulating plant growth and rhizodeposition and altering soil properties). For example, cycling of phosphorus and sulfur has been shown to be stimulated under warming (70, 75), but making inferences for carbon and nitrogen cycling is more difficult. Warming has been demonstrated to raise rates of nitrogen cycling processes, including denitrification,

nitrogen fixation, nitrification, and nitrogen mineralization (75), although its exact effects depend on the gene/process under study (70). For example, in some cases warming suppressed certain nitrogen cycling functions (65, 72). One explanation is negative feedback: Warming increases soil inorganic nitrogen and plant nitrogen pool sizes (66), ultimately depressing rates of microbial decomposition and nitrogen cycling (76, 77). Therefore, it is possible that nitrogen cycling can shift over time as a function of the duration/magnitude of warming and nitrogen availability.

Copiotrophs: fast-growing microorganisms that are prevalent in nutrient-rich environments with labile sources of carbon

Oligotrophs: slow-growing microorganisms that are prevalent in low-nutrient environments

By contrast, carbon cycling has been shown to be initially accelerated by warming (73, 74) if carbon bioavailability is sufficient. The temperature optima of extracellular enzymes for carbon degradation are such that warming can act as a stimulus (69). Over long periods of warming, studies have observed decreased numbers of genes involved in labile carbon degradation, with increases in those for recalcitrant carbon metabolism (65, 70, 74) and a higher diversity of the responsible functional guild (73). These findings may be at least partly attributable to water loss from evaporation during heating. When soil moisture is controlled, labile carbon degradation can remain stimulated while degradation of recalcitrant carbon is unchanged (75). Carbon cycling shifts also vary by soil layer, where organic and mineral horizons have different responses in carbohydrate-degradation potential after decadal timescales of warming (52). Analyzing soil warming as a single factor thus represents a suboptimal approach, as warming is likely to be coupled with other climate change factors that also influence carbon cycling, not only depletion of soil moisture but also eCO_2.

4.2. Elevated Carbon Dioxide

As with warming, eCO_2 has both direct and indirect effects on the soil microbiome (**Figure 1**). In the short term, eCO_2 increases respiration rates, microbial biomass, and genetic signals for carbon cycling processes (78). It also stimulates plant production and rhizodeposition, in turn priming copiotrophs in the rhizosphere to break down labile and (later) recalcitrant carbon (65, 79, 80). Nevertheless, taxonomic trends for soil microbiomes under eCO_2 are by no means consistent. One study analyzing trends of eCO_2 across soil ecosystems found that the only common response was depletion of Acidobacteria Groups 1 and 2 (81). Similar to warming, however, over a long timescale eCO_2 is predicted to enrich for oligotrophs. After 14 years of eCO_2 in a California grassland, decreases in copiotrophic (*r*-selected) Bacteroidetes were observed, along with increases in microbes with lower rRNA copy numbers, a common trait of oligotrophs (*K*-selected) (82). Under warming, enrichment of oligotrophic microorganisms is expected, due to decreased soil moisture and depletion of labile carbon. By contrast, eCO_2 is predicted to stimulate plant and microbial growth, which depletes soil nitrogen. As a result, soil carbon cycling is predicted to decline. Indeed, over longer timescales of eCO_2 treatment, there was a reported marked decrease in soil carbon cycling, with little to no change in carbon degradation (82). Such conditions will thus favor slower-growing, resource-efficient oligotrophic microorganisms.

Under eCO_2, enzymatic activities for phosphorus cycling tend to increase (65, 78, 82, 83), but nitrogen cycling is more variable. Increases in plant net primary production, microbial immobilization of soil nitrogen, and microbial denitrification rates will all deplete soil mineral nitrogen (66, 82, 84). As a consequence, maintaining soil nitrogen availability (and by extension plant/microbial growth rates) necessitates an increase in relative rates of nitrogen cycling and mineralization. Enhanced nitrogen cycling under eCO_2 has been observed (37, 53, 78, 79, 85, 86), although actual enzymatic rates are often unchanged or decline (82). This discrepancy may be attributable to higher abundances of nitrogen fixers (e.g., Rhizobiales) or ammonia oxidizers (37, 85), although this is not a universal trend (44, 77). Differing results for nitrogen cycling are occasionally observed across eCO_2 studies and may be influenced by variability in confounding factors such as soil moisture availability, proximity to root exudates, soil depth, and degree of nitrogen

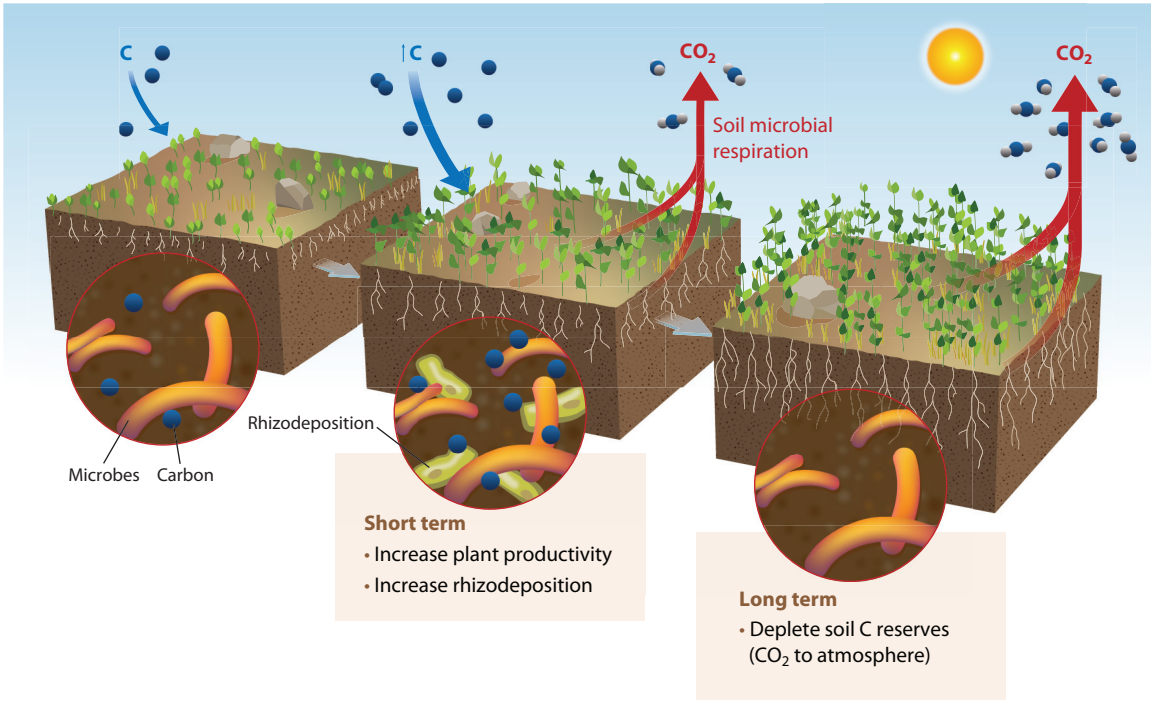


Figure 1

Predicted effects of elevated carbon dioxide (eCO_2) on soil carbon reserves. In the short term, plant growth is stimulated by eCO_2, resulting in increased rhizodeposition, priming microbes to mineralize soil organic carbon (SOC) and adding CO_2 to the atmosphere through respiration. But the net impact on greenhouse gas emissions will be reduced by the increased uptake of CO_2 from the atmosphere by increased plant growth. However, over the long term, soil reserves of easily decomposed carbon will be depleted by the increase in microbial activity, resulting in increased catabolism of SOC reservoirs, thus increasing atmospheric CO_2 concentrations beyond what is taken up by plants. This is predicted to be a particular problem in thawing permafrost that contains large reserves of SOC that are becoming increasingly susceptible to microbial degradation as the permafrost thaws (195, 196).

limitation (44, 79). In addition, the ecosystem in question, e.g., agroecosystems, may have different results from uncultivated forests (81).

4.3. Combinatorial and Indirect Effects

Considering any climate change factor in isolation fails to address the interplay between them that is likely to impact soils in real-world scenarios. To account for this knowledge gap, many recent studies have incorporated multifactorial designs, whether with eCO_2 and warming (37, 65–67), eCO_2 and elevated ozone (79, 85, 87), eCO_2 and nitrogen addition (44), or other combinations. Often, differing results are found for combinations compared to single-factor treatments, highlighting the importance of this approach. For instance, in one experiment modeling the effects of warming and/or eCO_2 on field soils in a cotton agroecosystem, the combination of warming with eCO_2 provoked shifts in ammonia-oxidizing microbial communities and increases in soil nitrification rates, whereas few significant effects were seen for warming alone (37). Often, a combination of perturbations results in one factor attenuating the effects of the other. With respect to eCO_2 and warming, often eCO_2 counteracts warming-induced decreases in soil moisture or promotes plant

rhizodeposition to maintain carbon cycling and heterotrophic respiration as carbon is depleted under warming (65). It is likely that the relative importance of the two factors varies by environment. For example, different trends might be seen in grasslands compared to forests, or agroecosystems compared to arctic biomes (5). For instance, in a dryland community study, warming prevailed over eCO_2 (67), while in a grassland study the opposite trend was observed (65). In the latter study, the combination of eCO_2 and warming had similar effects to eCO_2 alone—warming decreased signals for carbon cycling, ammonia oxidation, and production, whereas eCO_2 and the combination had the opposite trend. Notably, a subset of eCO_2-stimulated genes for nitrogen cycling and carbon degradation were no longer enriched under the combination, including genes for recalcitrant carbon degradation (65), which may be a result of increased rhizodeposition of labile carbon precluding the necessity of such genes.

A complicating factor for studying disturbance responses in the soil microbiome is disentangling direct from indirect effects. As discussed above, eCO_2 indirectly impacts soil communities through increased plant rhizodeposition, soil nitrogen limitation, and higher soil moisture content (eCO_2 induces plant water conservation through reduced stomatal conductance) (65, 83, 88), as well as through root exudate profiles, soil structure, or leaf litter chemistry (85). Conversely, warming stimulates plant growth but lowers soil moisture through evaporation, and such shifts in water availability may have a greater impact on the soil microbiome than warming alone (55, 89). Specifically, enrichment for oligotrophs under warming may be at least in part due to their higher enzyme substrate affinities representing an advantage as diffusion decreases under water limitation (74). Other complicating factors include treatment duration (73, 79), seasonality (83), and soil depth or horizon (52, 81, 90). Such discrepancies highlight the importance of accounting for confounding parameters during soil perturbation studies.

4.4. Microbial Biochemical Pathways and Climate Change

Although the response of the soil microbiome is often studied at a high level, such as community-wide taxonomic shifts, another important aspect of climate change response is how specific biochemical pathways are affected. A recent study on warmed soils from Arctic and Antarctic environments found numerous common metabolic responses (84). For example, methane production and metabolism of acetate and di- and mono-methylamine increased as temperatures were raised from 1°C to 30°C, whereas decreases were seen in propionate and acetate oxidation as well as metabolism of H_2 and formate (91). Furthermore, as temperatures were raised above 7°C, the rate-limiting step for methane production shifted from propionate oxidation to polysaccharide hydrolysis. Similarly, the drying of Puerto Rican soils increased signals for carbon metabolism enzymes including beta-glucosidase, cellobiohydrolase, *N*-acetylglucosaminidase, and xylanase (92). However, this effect was reduced through pretreatment of soils with simulated drought, suggesting long-term changes to soil functioning in response to a disturbance may ameliorate effects of future stresses.

Microbial biochemical pathways are also indirectly affected through climate change impacts on plant-microbe interactions. A recent study found that microbes take up less plant-derived carbon under both heat and drought stress (93). Additionally, if environmental stresses cause exotic or invasive species to thrive, root exudate profiles (representing a major source of bioavailable carbon for microbes) will shift. A study contrasting native with exotic plants found that soil microbiomes in the presence of the latter shifted to osmotic stress conditions, but had an increased supply of labile carbon inputs (94). Furthermore, climate change may alter plant cover (88) or plant community profiles, e.g., through plant migration to colder climes (77) or increased ratios of C_4:C_3 plant types (75). Responses in rhizodeposition under stress can also vary by plant species or cultivar

(85). For example, wild-type plants were shown to have higher rates of root exudation under eCO_2 than cultivated varieties (88), as did C_4 grasses relative to C_3 plants (70, 75). As a consequence of changing type and quantity of plant-derived carbon inputs to the soil, different microbial pathways for carbon uptake and metabolism will be stimulated.

5. INTERKINGDOM INTERACTIONS AND SOIL CARBON

Biotic and abiotic factors, including climate change disturbances, can affect carbon cycling through altering interspecies and interkingdom interactions. The functional relationships between organisms capable of fixing atmospheric CO_2 (e.g., plants and autotrophic microorganisms) and heterotrophic organisms who obtain carbon byproducts through mutualistic, commensalistic, or parasitic interactions continue to be explored. Active areas of investigation include elucidating keystone species or symbiotic interaction trends of soil communities, and how these interactions inform carbon cycling shifts under disturbances. However, trends may be particular to a given environment, so here we review interkingdom interactions across multiple soil ecosystems, including rhizospheres and biological soil crusts.

5.1. Interkingdom Interactions in the Rhizosphere

Plant-microbe interactions are among the most prominent interkingdom interactions in soil. For example, plants can stimulate microbial growth and activity in the rhizosphere through root exudate secretion. A higher aboveground plant diversity has been shown to be beneficial for soil microbial community diversity and nutrient cycling (15). Higher plant species richness can increase microbial biomass and necromass and accelerate microbial growth and turnover, although microbial carbon-use efficiency and respiration were not shown to be affected (95). In mesocosm experiments, soil warming selected for larger and more productive plant species, but a less diverse plant community (96). However, bacterial and protist abundances increased, leading to greater soil multifunctionality (96). Together these findings demonstrate the importance of plant-microbe interactions for regulating ecosystem responses to environmental change and the potential for managing plant-microbe interactions to mitigate environmental impacts.

Soil interkingdom interactions are also influential in carbon flow. In a recent study tracking plant-derived carbon in soil through stable-isotope probing, rhizodeposits from *Zea mays* moved through bacteria, unicellular fungi, and protists, likely using arbuscular mycorrhizal fungi (AMF) as a shunt for fresh root exudate supply to microbes (97). The researchers also observed trophic webs involving different flagellates, amoeba, and ciliates in the rhizosphere and surrounding soil, although isotopic labeling of filamentous saprotrophic fungi was not apparent (97). AMF were also observed to act as a carbon shunt from plants to soils in a study tracking ^{13}C passage (98), with subsequent direct carbon transfer from AMF to bacteria and fungi, and indirect transfer to protozoa and nematodes. The authors hypothesized that eCO_2 levels changed the nature of these interkingdom interactions, not only by increasing rhizodeposition but also by provoking emergence of distinct AMF and soil microbial communities, which in turn altered soil carbon cycling profiles (98). This study signifies the importance of studying carbon flow in the context of climate change factors, thereby discovering which additional factors affect carbon flow and what their specific effects might be.

5.2. Interkingdom Interactions in Biological Soil Crusts

Another soil ecosystem that has been extensively studied with respect to interkingdom interactions is biological soil crusts, or biocrusts. Biocrusts are stratified communities of photoautotrophs

(cyanobacteria, algae, lichens) and heterotrophs (fungi, bacteria, archaea). They cover ~12% of Earth's landmass and contribute to carbon and nitrogen cycling, soil stability, and water retention in arid environments (99–101). Biocrust successional development can occur over years to decades and is hypersensitive to environmental and physical disturbances (101). Over the course of succession, photoautotrophic organisms facilitate assembly of specific microbial communities, establishing a network of interactions (99). For example, a putative mutualism exists between keystone cyanobacteria *Microcoleus vaginatus* and copiotrophic diazotrophs, where both carbon- and nitrogen-fixation activities are covered through the interaction. This consortium has been posited as the "true" pioneer community enabling biocrust colonization of nitrogen-poor soils (102). Other interactions are not so beneficial: Later in succession, production of the alkaloid sunscreen pigment scytonemin by heat-tolerant cyanobacteria *M. steenstrupii* results in biocrust surface warming by up to 10°C, allowing them to replace the susceptible *M. vaginatus* (103).

Climate stresses are predicted to alter the nature of interactions in biocrusts. Rewetting cycles are common disturbances in these systems and have significant impacts on the interactions therein. One recent study found hydration pulses result in large blooms of members of the bacterial order, Bacillales, accompanied by collapse of pioneer cyanobacteria within the Oscillatoriales order (101). Mortality of cyanobacteria in the above manner may have important implications for carbon balance in semiarid ecosystems. For example, if hydration pulses cannot sufficiently stimulate autotrophs (i.e., cyanobacteria) to the extent where photosynthesis compensates for respiration (104), biocrusts will experience autotroph mortality and net carbon loss (101).

5.3. Fungal Loops Link Rhizospheres and Biocrusts

In arid ecosystems lacking large reserves of soil organic matter, biotic retention of nutrients is critical to primary production. Spatiotemporal resource partitioning and a variety of species interactions can aid ecosystem stability in the face of an increasingly arid environment (as is predicted to occur with climate change) by retaining resources within a biotic loop. For example, although autotrophic bacteria within biocrusts are directly responsible for carbon inputs, the fungal loop hypothesis proposes that fungal hyphae function as reservoirs of carbon and as conduits to translocate resources between soils and host plants (105, 106). At lower water potentials, fungi can take up nutrients produced by biocrusts, reserving them in the biotic pool until larger water pulses allow plants to take them up. In return, plants can contribute excess photosynthate to their fungal symbionts. This example illustrates how fungal association can connect the spatially and temporally distinct activities of biocrusts and plants (106).

5.4. Interactions Across Microbial Trophic Levels

In soils, filamentous fungi cope with heterogeneous environments and resource distributions via growth of extensive hyphae that penetrate air-water interfaces and traverse air-filled pores. Such "fungal highways" may mobilize bacteria, connect microbial microhabitats, and disperse nutrients (107). Bacteria are impacted by presence of mycelia in several ways: For example, mycelia promote horizontal gene transfer between bacteria (108). In another study, mycelia enabled contact between the bacterial predator *Bdellovibrio bacteriovorus* 109J and its prey *Pseudomonas fluorescens* LP6a, allowing for foraging and shaping of prey populations in a manner not seen in the absence of mycelia (107). Low soil pH was shown to limit survival and dispersal of *Paraburkholderia terrae* BS001; however, this effect was attenuated by a fungal hyphae-mediated increase in soil pH, suggesting fungi exert protective effects on bacterial cells (109). Together, these studies demonstrate fungi occupy a myriad of roles that can influence bacterial survival.

Apart from plants and fungi, soil bacteria and archaea also display significant associations with protists and viruses. Some protists have been shown to promote plant-beneficial functions, accelerate nutrient cycling, and regulate population growth of specific bacterial species within the soil microbiome (110). They can occupy central hubs in soil microbial networks, thus linking diverse bacterial and fungal populations (110). An increased fungal:bacterial ratio was also shown to be negatively correlated with phagotrophic protists (111). This may be attributable to phagotrophic activity, as protists graze on bacteria of certain morphologies, thereby regulating which bacterial morphotypes persist in a soil community (112).

Viruses can also directly influence their microbial hosts and play a key role in controlling host abundances. Recently, viruses have been proposed to participate in regulation of the structure of local soil microbial communities through transfer of resistance or metabolic genes (113). In peatland soils under a permafrost thaw gradient, as well as in mangrove soils, viruses have been implicated in contributing to carbon metabolism by carrying auxiliary metabolic genes, such as glycoside hydrolase genes (e.g., endomannanase), that can complement activities carried by their bacterial hosts (114, 115). As a result, viruses can potentially affect local and global biogeochemical cycles through supplementing the soil microbiome with genes involved in different metabolic pathways. Although viruses have been extensively studied in aquatic systems, the ecological role of viruses is a pressing frontier in terrestrial ecosystem science. New methods are emerging to address this knowledge gap, including analyzing viral sequences within bulk-soil metagenomes or optimizing viral recovery from soil through new viral resuspension protocols (113). Current research frontiers include determining the rates of viral turnover in soil, infectivity rates of phages toward soil bacterial and fungal hosts, and potential functional roles of soil viruses (116).

6. MINERAL WEATHERING AND SOIL CARBON

Soil microorganisms also interact during weathering of soil mineral interfaces, which in turn affects the global carbon cycle through sequestration of atmospheric carbon in weathered products. Mineral weathering is enhanced by plants and microbes—for example, lichens and microbial biofilms play a role in chemical weathering of rocks (117). Plant-associated arbuscular mycorrhizal and ectomycorrhizal fungi have been shown to accelerate weathering of carbonate rocks, where the rates of weathering depend on the precise nature of the plant-fungi symbiosis (118). In turn, soil weathering accelerates development of soils and drawdown of large amounts of CO_2 from the atmosphere. Under climate change, weathering is projected to be subject to negative feedback, where weathering rates initially go up with higher concentrations of atmospheric CO_2, thereby increasing CO_2 drawdown and reducing weathering (119, 120).

Mineral weathering also yields highly reactive secondary clay minerals that alter soil biogeochemical properties. As community composition is a function of the soil mineral profile, and carbon breakdown and mineralization are in turn a function of community composition (121), weathering therefore has an influence over microbial carbon cycling. Quantifying microbial soil carbon turnover in the presence of clay minerals is therefore essential in the context of shifts in the soil matrix, such as those that may occur under climate change disturbances. One relevant influence that clay minerals have is for carbon persistence, where carbon molecules' interactions with minerals physically protects them from degradation (122). Soil organo-mineral interactions thus create microenvironments of distinct carbon and mineral profiles, primed for microbial growth and development. Characteristics of these microenvironments (mineral content, soil texture, aggregate size) influence the stability of soil organic matter, microbial growth, and community composition (123, 124). Depending on how community profiles shift, there may be further implications for carbon mineralization and storage. For example, a higher fungal:bacterial ratio favors soil carbon

storage, as fungi are primary contributors to soil carbon decomposition, whereas bacteria typically assimilate carbon substrates into biomass or respire them back into the atmosphere (125).

Although the importance of soil and associated secondary minerals in stabilizing carbon is recognized, the links between processes governing land-atmosphere carbon exchange are not well understood. Recent studies have demonstrated that over time mineral weathering first increases then decreases nutrient availability and soil carbon stabilization, due to reductions in nutrient- and carbon-stabilizing capacity, and less carbon inputs from plants (126). Additionally, drastic changes such as land conversion and erosion can lead to removal of weathered and reactive soil materials. These changes affect both the soil matrix and carbon storage capacity (127). They also negatively impact both soil nutrient quality and can result in declining forest ecosystem sustainability. Under these conditions, rhizosphere bacteria and fungi can promote carbon and nutrient cycling to maintain nutrient supplies to associated plants (128). Ultimately, the influence of geochemical factors needs to be better integrated into soil microbial ecology as they represent a complex, integral part of global carbon cycling.

Metatranscriptomics: comprehensive analysis of gene expression at the transcriptional level within a complex community/environmental sample

Metaproteomics: comprehensive analysis of proteins produced within a complex community/environmental sample, as a means to quantify gene expression at the translation level, following post-transcriptional modifications

7. ADVANCES IN APPROACHES TO STUDY SOIL MICROBIOMES

As the soil microbiome is very heterogeneous and complex, the direct application of omics techniques to discern microbial community function, not to mention synthesis of multiple omics types into coherent ecological information, is very difficult. Even the comparatively simple analysis of amplicon sequencing for community composition can yield different results as a consequence of variations in sequencing depth, primer bias, choice of processing pipeline, or DNA extraction protocol (129, 130). When moving to metagenomics analysis, computational demand becomes an issue, due to the processing power required to assemble metagenomes containing tens of thousands of species (131). Although metatranscriptomics has the benefit over amplicon sequencing or metagenomics approaches, in that one can determine which species are active and which genes are expressed, it is not without its drawbacks (132). Extraneous ribosomal RNA represents the predominant fraction of extracted RNA, requiring an additional rRNA depletion step and/or necessitating greater sequencing depth to make this analysis feasible (133). Ultimately, metaproteomics provides valuable information about gene expression and subsequent translation patterns (134), although proteomics methods are currently too low-throughput for widespread adoption. Similarly, soil metabolomics are useful for informing biogeochemical cycling through obtaining high-resolution snapshots of soil nutrient profiles and metabolite flux patterns, although these techniques may be limited by underannotated reference databases and discerning metabolite origins (e.g., between microbes, plants, or other sources) (135). As each omics technique becomes more inexpensive and high-throughput, a desirable avenue will be incorporating multiple omics datasets into a combined data stream.

Rapid advances in technology development are helping to overcome current limitations and enabling multi-omics data streams that are well-suited for determining taxonomy, phenotypic features, and metabolic functions of soil communities. For example, a combination of metagenomics, metatranscriptomics, and metaproteomics was used to determine the response of permafrost soil microbial communities to thaw (136). This study revealed that functional inferences from multi-omics approaches corresponded better with process rates in thawed soils than those for frozen soils, while also discovering novel strategies for microbes to maintain activity and survive under frozen conditions (136). The application of multi-omics (amplicon sequencing, metatranscriptomics, and metabolomics) to determine how soil microbial communities responded to soil wetting or soil desiccation demonstrated consistent metabolic responses to wet-dry cycles, including production of sugars and osmolytes as a drying response (137). Ultimately, the combination of

multiple data streams will benefit soil analyses by providing a more complete, multilevel picture of soil processes than would be achievable through any technique in isolation.

Another approach to overcome the complexity of the soil habitat is to obtain model, simplified soil communities and study them in highly controlled soil-emulating environments. A variety of simulated soil environments are under development that range from microscale- (e.g., microfluidic devices) to mesoscale-simulated soil ecosystems. Two recent studies characterized reduced-complexity microbial consortia from parent soil that were cultured either in liquid media (138, 139) and/or sterilized soil (139). In the former study, it was concluded that community-level function and high-level taxonomy were predictable, governed by nutrients, and ultimately a generalizable feature of community assembly. In the latter, vastly different consortia resulted from soil versus liquid microcosms, indicating a physical selective pressure exists for community assembly. One benefit in using a simplified microbial community is its utility for determining key mechanisms governing soil microbial community ecology (139), specifically by enriching for the subcommunity implicated in a process of interest. In doing so, experimentally tractable subsets can be obtained that maintain native interactions while allowing for the opportunity to study these subcomponents of the parent microbiome at high resolution.

7.1. Stable Isotope Probing

The evaluation and tracking of stable isotopes represent a powerful approach for determining the fate of organic carbon in soils. The use of stable isotopes (most commonly ^{13}C or $H_2{}^{18}O$) can disentangle carbon cycling processes by determining the turnover rate(s) of specific carbon compounds or pools, and by parsing active from dormant microbial populations. For example, the methods by which carbon enters the soil may also be distinguished by tracking different distribution profiles of naturally occurring isotopes—for example, photosynthate from C_3 plants has a ^{13}C:^{12}C ratio of ~27%, whereas that of C_4 plants is closer to 12% (140). As a result, measuring these ratios can specify the metabolic pathways by which carbon is cycled through plants and microbes, and subsequently whether it is entombed as microbial necromass or respired as CO_2 (**Figure 2**).

Stable isotope tracers have been used to characterize the mechanisms driving soil carbon turnover in soils, as well as informing their representations in predictive models. In one technique, pulse-chase labeling, communities are successively supplied with a heavy isotope-labeled compound, then an unlabeled version of the same compound, allowing real-time tracking of the label over time. For instance, ^{13}C isotopic tracers have demonstrated microbial biomass contributions to stabilized organic matter (141), as well as revealed bacterial versus fungal contributions to soil organic matter formation (142). Relative bioavailability (turnover rate, carbon use efficiency) of different carbon molecules will impact tracer rates. Residual microbial necromass is of particular interest, given its role in belowground carbon storage. To investigate this area, stable isotope probing has been used to track how carbon assimilated as microbial biomass is subsequently mineralized and recycled into other organisms after cell death (143, 144). Stable isotope probing can also be used to conduct real-time analyses of how soil carbon flux is affected by perturbations (145), in particular with respect to climate disturbances.

A new methodology, termed quantitative stable isotope probing (qSIP), can quantify taxon-specific microbial contributions to biogeochemical processes (146, 147). One benefit of qSIP is that it enables detection of phylogenetic traits that can be used in predictive frameworks of microbial ecology in complex systems. For example, by tracking the response of multiple populations concurrently, qSIP can measure relative growth rates or carbon assimilation rates across all members of a community (148). This push beyond targeting isotopes in fatty acids that are

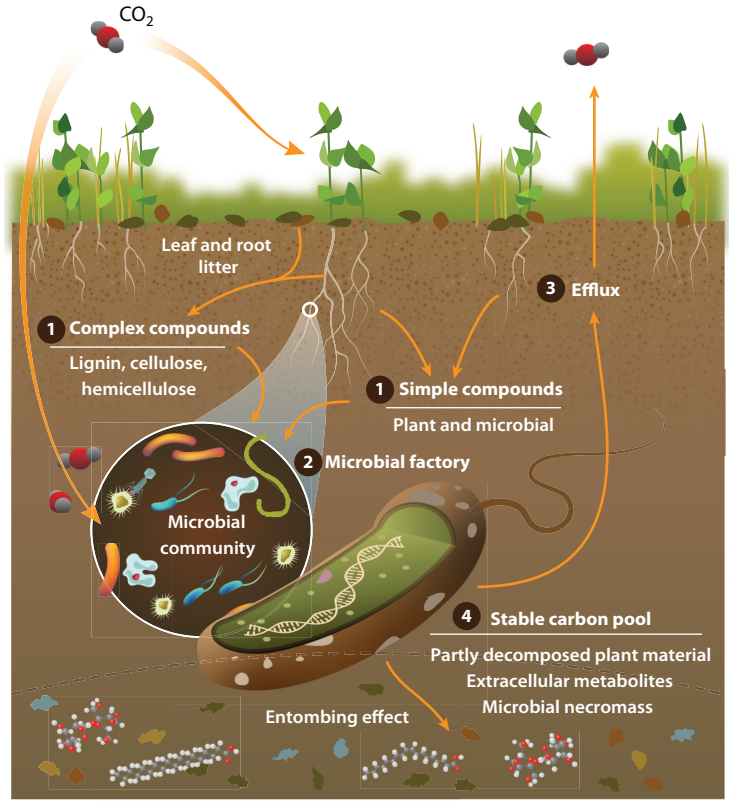


Figure 2

Soil carbon (C) cycle through the microbial loop. Carbon dioxide (CO_2) in the atmosphere is fixed by plants (or autotrophic microorganisms) and added to soil through processes such as ❶ root exudation of low-molecular weight simple carbon compounds, or deposition of leaf and root litter leading to accumulation of complex plant polysaccharides. ❷ Through these processes, carbon is made bioavailable to the microbial metabolic "factory" and subsequently is either ❸ respired to the atmosphere or ❹ enters the stable carbon pool as microbial necromass. The exact balance of carbon efflux versus persistence is a function of several factors, including aboveground plant community composition and root exudate profiles, environmental variables, and collective microbial phenotypes [i.e., the metaphenome (19)]. Figure inspired by 197.

coarse biomarkers or using nucleic acid probes (Chip-SIP) provides an unprecedented opportunity for comprehending how specific microbial clades impact ecosystem-level biogeochemistry. As an example, one recent study used ^{13}C SIP to predict that rhizosphere-associated *Saccharibacteria* ferment root exudates and microbial necromass (149), providing a new conceptual model of above- and belowground carbon cycle linkages.

From an ecosystem perspective, molecularly resolved stable isotopes help to explain environmental responses to perturbation. Pulse-chase isotope experiments have been used to demonstrate that wet-dry cycles impact soil organic matter stabilization through rhizosphere processes modulated by plant growth (150), that root-associated communities implicated in drought survival have roles in regulating rhizodeposition and carbon accumulation in deep soils (151), and that photosynthate transfer from plants to soil microbes is inhibited under drought (152). Such studies will serve to upscale these microbial stress-response mechanisms into predictive ecosystem models.

Finally, advances in isotopically informed metabolomics have shed light on the function of specific microbial/biochemical pathways for soil carbon fates. For example, natural abundance ^{13}C nuclear magnetic resonance (NMR) spectroscopy has identified the solutes accumulated by bacteria under osmotic stress (153). The nondestructive nature of NMR spectroscopy is a clear advantage for biological studies and may be used to identify organic solutes in intact cells or cell extracts. Additionally, metabolites that are labeled at specific positions can be used to track active processes in soil microbial communities. Through tracking production of isotopically labeled carbon after addition of differentially labeled glucose and pyruvate, a study calculated carbon flux rates through specific metabolic pathways (154). Carbon flux patterns can then be used to calculate carbon-use efficiency, energy production and usage, substrate metabolism, nitrogen demand, and oxygen consumption (155).

Advances in detecting isotopic signatures across molecular data types have advanced mechanistic understanding of belowground carbon storage in highly dynamic systems. From an experimental perspective, stable isotopes have the potential to link all aspects of environmental systems. For example, ^{13}C-labeled photosynthate might be tracked through roots, mycorrhizal associations, bacteria, nematodes, plant roots, leaves, litter, and eventually saprotrophs. In total, these approaches have the potential to not only disentangle belowground processes, but also increase model accuracy.

8. MODELING CLIMATE CHANGE IMPACTS ON SOIL CARBON

An International Soil Carbon Network was recently established to identify gaps in SOC modeling (156). One of the biggest challenges identified was detection of changes in SOC, due to both its spatiotemporal variation across soil ecosystems and an incomplete understanding of the processes governing whether SOC is stabilized or decomposed. Ideally, models would be derived from mechanistic understandings of SOC dynamics, but most are instead based on simulations, due to challenges in obtaining empirical data and measuring SOC (156). Examples of current research priorities include understanding of SOC dynamics in soil (micro)aggregate microenvironments and how priming influences soil carbon turnover (156). Eventually, integration of mechanistic insights from molecular data into climate models will better predict the fate of soil carbon under climate change.

Another area that needs to be addressed is inclusion of climate-relevant microbial processes. Most climate models assume that soil organic matter decomposition is a first-order decay process between conceptual pools. In 2009 there were 33 SOC models represented within the Global Change and Terrestrial Ecosystems Soil Organic Matter Network database, and 30 of those were multicompartment, process-based models (157), in which decay rates are typically expressed as a function of carbon concentration and a rate constant. Although global models incorporate information about soil and climate properties (4), microbial processes may not be included in first-order assumptions (157). Upon their inclusion, however, the predictive ability for SOC fate under climate is demonstrably improved (158). This has resulted in continued development of improved Earth System Models (ESMs) that integrate microbial influences on SOC flux (4, 157), and new models for linking decomposition to the size and activity of the soil microbiome (159). These developments highlight the importance of second-order processes (microbial activities for SOC transformation) for predicting SOC flux either as microbial biomass or as respiratory loss to the atmosphere as CO_2.

Models aim to predict how climate warming will impact soil-sourced greenhouse gas emission in the future, which necessitates empirical determinations of the extent of soil carbon feedbacks. However, climate predictions may be based on outdated soil models that do not reflect the current

scientific consensus on soil carbon formation and stabilization (160). For example, although SOC is the result of net outputs (respiration) and inputs (carbon fixation) of plant-derived carbon, the majority of empirical data have focused on outputs alone, failing to account for possible compensatory effects such as heightened soil carbon formation (160). A balance of carbon outputs and inputs is captured by ESMs (158), but is not yet widely included in global predictions (161).

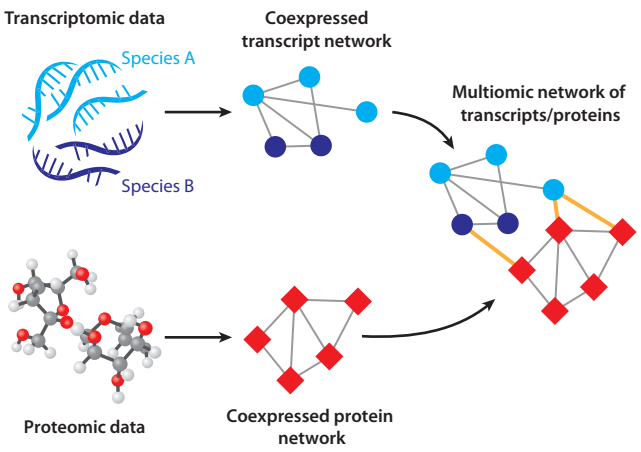
By contrast, models on SOC flux have begun to include aspects of the plant-soil ecosystem, including plant types and mineral interactions, which may have variable effects on SOC flux depending on specific circumstances. The CORPSE (Carbon, Organisms, Rhizosphere and Protection in the Soil Environment) model includes aspects of priming and soil protection, which promote soil decomposition and carbon storage, respectively (12). However, upon obtaining empirical data, they found contrasting results from the two soil warming experiments: At one site (Oak Ridge, Tennessee), carbon stabilization in the soil exceeded SOC loss from priming under warming, whereas at a separate site (FACE at Duke Forest, North Carolina) the opposite trend was found, resulting in net SOC loss (12). These simulations demonstrated increased CO_2 levels stimulated priming to a greater extent than carbon storage, which will yield a net global carbon loss under climate change. Other models have incorporated information on plant functional types (e.g., C_3 versus C_4 grasses, broadleaf versus needleleaf) that in turn distinguish between plant soil inputs (157). Recently a new model (MEMS v1.0) was proposed, linking soil organic matter chemistry with both microbial processing and interactions with soil minerals, to improve climate model predictions (162).

On a related note, a modeling approach has recently been proposed that takes into account microbial life strategies (64). Although soil microbial life strategies have typically been assigned to two categories—fast-growing *r*-strategists and slower-growing, energy-conserving *K*-strategists—the new model splits life strategies into three categories: Y for growth yield, A for resource acquisition, and S for stress tolerance. Each of these three categories would represent an advantage under a different set of environmental conditions and availabilities, such that it would be unlikely for a microbe to belong to more than one (64). Furthermore, as each category has a distinct profile for carbon use, validating this framework will help to predict overall microbial carbon cycling rates and active processes.

Further needs for improving SOC models include obtaining empirical data from across scales, for example laboratory and field experiments (**Figure 3**). Currently, interpolation between systems of widely varying spatial resolution is challenging, as information gleaned at one scale is often erroneous when applied to others (163). For example, soil carbon fluxes cannot be measured at scales larger than 1 m^2 (164), which is a hurdle when attempting to extrapolate to landscape-scale processes.

8.1. Metabolic and Network Modeling of Soil Microbes and the Carbon Cycle

Although the above SOC models focus solely on the biogeochemical turnover of bulk/coarse-grained carbon pools, it is also possible to model the influence of microbe-microbe interactions on carbon cycle metabolic processes and their response to climate change. Current experiments can collect tens to hundreds of omics datasets to infer feature coexpression networks (137). Although specific methods vary, all networks are based on linking pairs of features (e.g., species, transcripts, proteins, metabolites) across variable environmental conditions, where linkages are based on similarities in expression or abundance. Such networks can reveal characteristics of the system in question, including how features are related to each other by expression or abundance, which functional processes are coordinated, which features occupy central positions in the growth and bioactivity of the system, which transcripts/proteins act in regulatory pathways, what



Outcomes of networks	Examples
Identification of critical transcripts/proteins	Red squares or blue circles with multiple edges (gray or orange lines)
Viewing how processes/pathways are related	Identifying functional groups of proteins/transcripts that are linked
Where are the links between species?	Edges connecting transcripts from different species (varying blue circles)
How does all of this respond as a function of climate change?	Inference of multiple networks reflecting control and climate change data, comparison of networks to identify differences

Figure 3

Feature coexpression networks can be based on multiple types of omics data. Coexpression networks from different data types (metatranscriptomics, metaproteomics, etc.) allow for a more refined understanding of how functions respond across expression levels. Questions that may be answered through this approach (as described in the *box* on the right) include which features (proteins, transcripts, metabolites, etc.) are coexpressed, the identity of keystone features central for system functioning, and relatedness among species or metabolic pathways. Furthermore, by gathering omics data from a system under different sets of conditions (e.g., climate change perturbations), one can visualize which aspects of the network shift and therefore how overall functioning will be impacted as a consequence of disturbance.

putative functions of uncharacterized genes may be, and more. Co-occurrence networks for microbial species abundance have been inferred for many different systems, including soil microbiomes under climate stresses (165–167), often finding that factors such as similarities in pH, aridity, and nutrient preferences lead to interspecies interactions. Thus, co-occurrence analyses can identify groups able to withstand climate change by linking the species with known stress resistance profiles (84).

Co-occurrence networks may also be used to identify keystone members central to soil function. In this analysis, microbial species are represented as nodes within a network, and centrality measures are determined for each, where centrality is usually estimated by degree (number of edges a node shares with other nodes) or betweenness (how important a node is for connecting two other nodes) (168). Nodes of high centrality measures may be thought of as keystone nodes, as their removal would have deleterious effects on network structure and by extension soil functioning. This analysis has been successfully applied to soil microbiome networks to identify keystone taxa and factors influencing community structure (169, 170). New, emerging methods take advantage of multiple omics data types to link microbes and metabolites, or to link genes between microbial species to identify coordination of metabolism across species (171). Others apply a network approach to transcripts and proteins, determining which processes and pathways might be coexpressed under disturbances (168) (**Figure 3**). Such network approaches will inform how interkingdom interactions, and by extension microbiome stability, are impacted by climate change–related disturbances.

8.2. Importance of Cross-Scale Experimentation and Data-Model Integration

Chemical transformations that occur in soil are greatly influenced or even controlled by processes occurring at the micrometer to nanometer scale (microscale hereafter). In a physical context,

transformations in soil aggregate pore spaces, down to the very mineral interfaces composing said aggregates, strongly govern larger soil processes (172). Beyond this, evidence has shown how the microscale size and position of aggregates influence their resident microbial community composition (173, 174). The role of geography on soil microbial diversity has been confirmed, whether across countries (175, 176), a continent (177), or the globe (178, 179)—all while revealing the role that local microscale constraints have on microbial processes.

The biogeochemical reactions occurring at the microscale are orders of magnitude smaller than their corresponding ecosystem-scale effect size. This fact is more striking when we consider that soil biogeochemistry is largely regulated by microbial metabolism that is, in turn, fueled by exchange of electrons. Microbial metabolic interactions reflect how the hyperdiverse soil microbiome responds to its physical and chemical landscape: Historical conditions influence microbial responses to novel conditions created by compounding disturbances [e.g., hydrological moments of wetting and aqueous phase connectedness (180)]. A central challenge in soil microbiology is understanding the emergent, nonadditive effects of microscale microbial metabolism at the ecosystem scale or larger. Complicating matters further, these processes not only have a physical space dependence but a temporal one as well. Seasonal and subseasonal variability in soil microbial properties continues to be resolved (181), as well as multiyear trends (182). Combined, the spatiotemporal result of microscale reactions has a cumulative outcome disproportionate to its effective size, as evidenced by the microbial influence on Earth's atmosphere (183). However, it remains a significant challenge to incorporate microscale processes into models that are relevant at larger scales (**Figure 4**).

In the field context, measuring microscale biochemical reactions in the soil remains unattainable. As a result, our understanding of soil ecology is based on research conducted along a continuum of scales, from in vitro studies of pure microbial cultures (184) to ecosystem experiments replicated around the globe (185). One approach undertaken by multiple groups is development of mesocosms or microfabricated devices that both emulate the soil microenvironment as well as directly visualize microbial processes (186–189). The use of rhizobox-like and universal mesocosms (190), in conjunction with transparent material mimicking soil structure and gas exchange properties (189, 191), will help bridge this continuum of scales. Ultimately, the frontier of soil microbial ecology is to connect the knowledge and understanding across these scales (**Figure 4**), for example corroborating lab-based and field-based studies. Furthermore, it will be beneficial to incorporate novel analytical methods such as SIP, reduced-complexity consortia, and other new omics tools (192, 193) to elucidate the mathematical relationships governing microbial population dynamics.

Beyond conducting studies at a variety of scales and resolution, coupling empirical with computational efforts will ultimately improve confidence in predictive models relating the soil microbiome with ecosystem function (5, 19). Recently, to understand the influence of soil moisture at the cellular scale, a tandem empirical-computational strategy was used to demonstrate how the distribution of water in unsaturated soil systems impacts the range and frequency of microbial interactions (189). This concept has been further supported by microscale imaging that demonstrates fungal hyphae prefer to grow in air-filled soil pores rather than saturated habitats (188). Such controlled model-experimental studies can be linked to similar soil incubation and field studies. For example, individual-based models for microbial community activity in soil aggregates demonstrate the importance of hydration dynamics in regulating carbon use and greenhouse gas emissions under field conditions (194). This approach elegantly scales the microbial habitat (soil pores) to soil structure (aggregates) to simulate and validate soil biogeochemical processes (ecosystem scale). Together, these studies demonstrate the power of designing experiments where empirical data are generated to test and parameterize computational models.

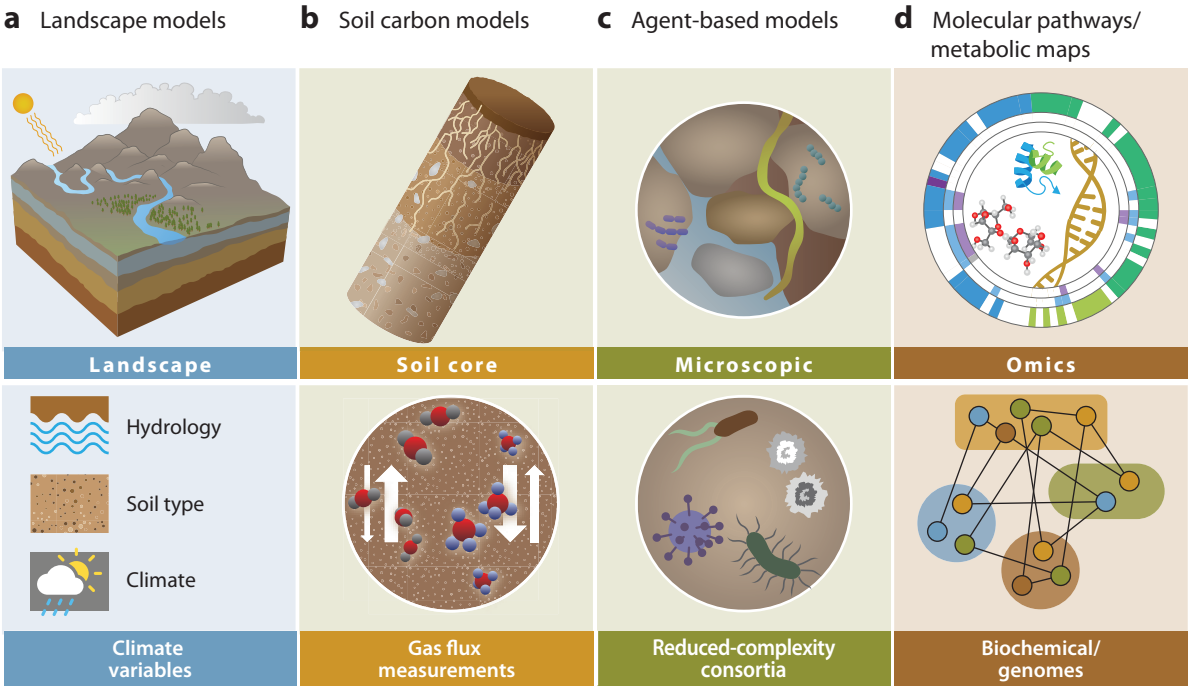


Figure 4

A central challenge in predicting climate change effects is integrating predictions derived from models across different scales of resolution. (*a*) Landscape-scale models couple hydrologic, climatic, and soil-ecosystem models (198). (*b*) Soil carbon models (e.g., 158) integrate simulations of overall microbial activity and greenhouse gas flux from aboveground, surface, and subsurface soil horizons. (*c*) Agent-based models, which detail processes occurring at the microbial population scale, allow for both elucidation of what properties of a system are attributable to individual groups of microbes and what are emergent (169, 199, 200). (*d*) Molecular pathways/metabolic maps (e.g., metagenomics, metatranscriptomics, metaproteomics, metabolomics) can be used to model soil microbial phylogenetic and phenotypic responses to change, including elucidating which metabolic pathways are represented in a soil system and the rates at which they occur.

9. CONCLUSIONS

A recent call to action emphasized the importance of understanding environmental microorganisms in the face of climate change (2). Abundant evidence reveals that soil microbes are affected by climate change–associated disturbances with important feedbacks to ecosystem health and climate forcing. Under these disturbances, shifts in microbial community composition and function will in turn have repercussions for interkingdom interactions, biogeochemical cycling, and carbon flow, in ways that may exacerbate or attenuate climate change. As we begin to fully understand key roles carried out by microorganisms inhabiting soil ecosystems, this knowledge may be used to predict how critical metabolic processes are impacted by environmental change, and furthermore may be leveraged for mitigation of negative aspects of climate change (5).

SUMMARY POINTS

1. Soil microbiome stability in the face of external perturbations is a combination of resistance, resilience, and functional redundancy. Incorporating all three metrics into studies will provide more comprehensive analyses of microbiome disturbances.

2. Historical conditions influence microbial responses to novel conditions created by compounding disturbances.
3. Interkingdom interactions influence population dynamics and metabolic exchanges with repercussions for soil carbon and nitrogen cycling and persistence.
4. Chemical weathering of rocks alters soil mineral profiles, and the resultant microbial community shifts will have impacts on soil carbon mineralization and storage.
5. Studying soil responses to disturbance will benefit from integrating disparate data streams through multi-omics approaches.
6. Stable isotope probing yields quantitative insights into biogeochemical transformations and population dynamics within the soil microbiome.
7. Acquiring sufficient empirical data on carbon cycling–relevant soil microbial processes and networks, across a range of scales, is necessary to improve predictive climate models.

FUTURE ISSUES

1. What are the factors that influence the balance between soil carbon storage and respiration?
2. How does the combination of various climate change–related factors (eCO2, soil warming, drought, etc.) interact to affect soil microbiomes, both directly and indirectly?
3. In what way are interkingdom interactions and their associated carbon flow impacted by climate change factors?
4. To what extent does functional redundancy play a role in resistance and resilience to climate change?
5. To what extent are organo-mineral interactions and the associated mineral carbon stabilization impacted by the shifting microbial communities under climate change?
6. How can we integrate the multiple data streams from different omics approaches together, in a cost-effective and computationally efficient manner, for higher-resolution study of microbiomes?
7. How will we be able to identify the correct parameters, build appropriate databases, and integrate omics data to improve climate models?

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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