Review

Up Against The Wall: The Effects of Climate Warming on Soil Microbial Diversity and The Potential for Feedbacks to The Carbon Cycle

Grace Pold And Kristen M. DeAngelis *

Microbiology Department, University of Massachusetts Amherst, Amherst, MA 01003, USA;
E-Mail: apold@microbio.umass.edu

*   Author to whom correspondence should be addressed; E-Mail: deangelis@microbio.umass.edu;
    Tel.: +1-413-577-4669; Fax: +1-413-545-1578.

Abstract: Earth's climate is warming, and there is evidence that increased temperature alters soil C cycling, which may result in a self-reinforcing (positive), microbial mediated feedback to the climate system. Though soil microbes are major drivers of soil C cycling, we lack an understanding of how temperature affects SOM decomposition. Numerous studies have explored, to differing degrees, the extent to which climate change may affect biodiversity. While there is ample evidence that community diversity begets ecosystem stability and resilience, we know of keystone species that perform functions whose effects far outweigh their relative abundance. In this paper, we first review the meaning of microbial diversity and how it relates to ecosystem function, then conduct a literature review of field-based climate warming studies that have made some measure of microbial diversity. Finally, we explore how measures of diversity may yield a larger, more complete picture of climate warming effects on microbial communities, and how this may translate to altered carbon cycling and greenhouse gas emissions. While warming effects seem to be ecosystem-specific, the lack of observable consistency between measures is due in some part to the diversity in measures of microbial diversity.

1. Introduction

Soil is one of the most diverse habitats on Earth, but also one of the least characterized in terms of the identification and ecological roles of the microbiota. Soils also contain the largest repository of organic carbon (C) in the terrestrial biosphere, and the activities of heterotrophic soil organisms are responsible for large portions of the annual CO_2 flux to the atmosphere. A substantial fraction of soil C occurs in relatively complex organic compounds, which tend to be resistant to decomposition under current environmental conditions. It is likely that soil organic matter (SOM) decay will change under future climate, and of the approximately 3100 Pg of carbon stored in soils, an estimated 5% will be lost in the next decade due to warming [1,2]. These estimates illustrate the vulnerability of this stored C, though the mechanisms of how the C will be lost are not well understood.

Microorganisms catalyze key processes related to greenhouse gas fluxes between soils and the atmosphere [3,4], but the role that microbes will play in the evolution of Earth's climate over decades to centuries is undefined. A more complete understanding of how global warming will affect carbon-cycle feedbacks to the climate system is central to model projections of future climate [5]. Preliminary data from the longest-running soil warming study at Harvard Forest suggests that over 20 years of warming results in a loss of labile, microbial available C that puts the soil microbes "up against the wall" metaphorically, forcing adaptation that will affect global C cycling [6–8]. Advances in molecular biological methods, including high-throughput sequencing [9,10] combined with manipulative field experiments such as *in situ* soil warming [11,12] make it possible to identify and model relationships between microbial communities and climate system feedbacks. This paper focuses on understanding how climate warming affects soil microbial community diversity, and its impacts on ecosystem function.

Two non-mutually exclusive diversity hypotheses developed for macroecology [13] can be applied to describe observed changes in carbon cycling with climate warming. The first community diversity hypothesis suggests that an overall increase in diversity has resulted in communities more resistant to higher and more extreme temperatures. This hypothesis is based on evidence that in general, more diverse communities are more resistant to stress and more efficient [13–15], possibly because taxonomic and functional richness often go side by side [16,17]. The alternative hypothesis is somewhat complementary: the keystone species hypothesis suggests that the increase in populations specifically associated with a function, such as the ability to degrade more recalcitrant or previously physically protected soil carbon, is responsible for observed changes in carbon cycling. The increased relative (or absolute) abundance of these functional populations may be independent of changes in overall diversity. In the next sections, we explore the support for each hypothesis, and then evaluate the literature for evidence of diversity or keystone functions in previously published climate warming studies.

2. Functional Implications of Diversity

The community diversity hypothesis predicts that diversity-taxonomic diversity, but especially species count (richness)—has a value in and of itself. More diverse communities are not only more productive [18], but they tend to be better able to maintain ecological functions under stress (resistance) and more able to recover function when the stressor is relieved (resilience) [19,20]. These patterns are often explained using niche theory; each organism has a niche defined by the range of environmental conditions it requires to survive, but only realizes a fraction of this potential because of

competition with other organisms which share some portion of this niche [21]. Organisms may only survive under a narrow set of conditions (specialists), or have a broad niche (generalists). In general, more diverse communities are better at taking advantage of the resource space (*i.e.*, range of conditions present in an environment), and therefore are able to more completely and efficiently convert resources into biomass [13,18].

Environment dictates total resource space, and therefore carrying capacity of the ecosystem, but also the range of niches available to organisms. Furthermore, because organisms differ in their susceptibility to stressors, such as drought and temperature [22–24], changes in the environment affect the relative abundance of organisms in an environment. If lower species richness is indicative of reduced niche overlap, then species loss should have a disproportionately high impact on ecosystem function in species-poor (depauperate) communities. In other words, species-rich assemblages may have another phylotype ready to expand its realized niche into the newly-vacated portion of its fundamental niche, but species-poor ones may not [25]. Functional stability is also expected to be favored by a high proportion of generalists, or in a community with diverse metabolisms represented [15,26]. Furthermore, if diverse communities are more resistant to changes in function, then they may prevent changes in the ecosystem itself, allowing for less resistant organisms to recolonize once the disturbance passes [19]. For example, due to variation in environmental tolerances, an initially diverse arbuscular mycorrhizal fungal community may be necessary to survive an extended drought and maintain a soil structure resistant to erosion [27,28].

Although the community diversity hypothesis is rooted in much theory, it originated in macroecology, which considers communities with apparently lower richness and functional redundancy than soil microbial communities. Therefore, it is unclear how well this hypothesis can predict soil microbial responses to warming. For example, while Hol *et al.* found that reducing microbial species richness through dilution increased plant biomass and nutritional quality [29], Wertz *et al.* found no reduction in nitrification or denitrification activity when they diluted soils, and richness did not increase resistance to or recovery from a short period of high temperatures [30]. However, Wertz and colleagues did confirm that functional groups differed in their sensitivity to warming; this knowledge can help us identify steps in the carbon cycle, for example, where ecosystem function is most likely to break down. This is particularly important in the context of the cross-feeding which characterizes many detritivorous pathways [31]. If these syntrophic interactions are highly-specific or dependent on a specific organism, we expect loss of diversity to reduce productivity or some other measure of ecosystem function.

As a counter point to the community diversity hypothesis, the keystone species hypothesis predicts that some taxa have a disproportionate effect on ecosystem function. For example, *Leptospirillum* group III only accounted for 10% of the cells in an acid mine drainage biofilm, but since this organism was the only one with a complete nitrogen fixation pathway, it likely supplied all the nitrogen used by the community [32]. Single phylotypes can be important for ecosystem function in much richer communities too [33]; while members of the *Desulfosporosinus* only accounted for 0.006% of the microbial population in a peatland soil, they were responsible for the majority of soil sulfate reduction, competing effectively with methanogens for resources and producing the less potent greenhouse gas carbon dioxide instead [34]. These results are consistent with a meta-analysis of studies that manipulated soil microbial diversity, in which Nielsen *et al.* [31] found that increasing species diversity only improves ecosystem function in species poor (<10 species), but not species rich, soils.

The authors concluded that changes in community composition and loss of keystone species are likely to have a stronger effect on ecosystem function than loss of richness, *per se.*

Together, these findings imply that sequential loss of taxa in initially rich habitats such as soil should not lead to a significant loss of ecosystem function until one of these keystone species is lost. These patterns open the door to the possibility that a reduction in diversity may lead to a loss of functional stability. Thus, while many soil microbes may appear to be functionally redundant, they differ in their environmental tolerance [35–39], and substrate preferences [40,41], and in some instances may be the sole mediators of an ecological process.

3. Warming Effects on Diversity

Climate warming is an abiotic stressor, with the potential to alter the diversity of the soil microbial community, and therefore the range of processes they complete [15]. Of particular interest is the effect of elevated temperatures on soil organic matter decomposition, which a growing number of studies are addressing. A small subset of these incorporate some measure of microbial community diversity, using a biochemical approach such as phospholipid fatty acid (PLFA) analysis, or a molecular approach such as community fingerprinting or sequencing, with some metric of microbial activity or biomass (Table 1). These two approaches can provide different—though complementary—views of microbial communities.

Table 1. Geographic and climatic data for sites compared in this paper.

Biome	Site	Coordinates	MAT	MAP	References
Tall-grass prairie	Kessler Farm Field Laboratory, Washington OK	34.98°N, 97.52°W	16.3 °C	967mm	[42–44]
Old field grassland	National Ecological Research Park, Oak Ridge TN	35.90°N, 84.33°W	14.9 °C	1360 mm	[45,46]
Mixed hardwood forest	Harvard Forest LTER, Petersham MA	42.5°N, 72.18°W	7.6°C	1100mm	[6]
Temperate mountain forest	North Tyrolean Limestone Alps, Austria	47.58°N, 11.64°E	5.7 °C	1480mm	[47]
Taiga boreal forest	Delta Junction, AK	63.92°N, 145.73°W	−2.6 °C	1290mm	[48–50]
Sub-Arctic blanket bog	Abisko, Sweden	68.21°N, 18.49°E	−0.6 °C	352mm	[51,52]
Sub-Arctic heath	Abisko, Sweden	68.19°N, 18.51°E	−0.6 °C	352mm	[53]
Sub-Antarctic	Signy Island	60.72°S, 45.38°W	−2 °C	400mm	[54–56]
Sub-Antarctic	Falkland Islands	51°S, 59.05°W	7.9 °C,	575mm	[54–56]
Antarctic	Anchorage Island	67.57°S, 68.13°W	−2 °C	500mm	[54–56]

The net effect of warming on soil microbes tends to be increased microbial activity over the short term, which translates to increased soil respiration [12,57,58]. An early lab incubation study of temperate forest soils demonstrated that this increase in activity can be accompanied by shifts in microbial biomass and community composition [59]. However, of the field studies conducted that ran for three years or more [57,58], few that observed increases in microbial activity also examined changes in microbial community composition (Table 2). Despite this, some general patterns are beginning to emerge. For example, there is evidence that not all soil microbial communities respond similarly to warming, with warming more likely to have a negative effect on microbial abundance (density) in cool, dry locations [60]. Furthermore, response to warming is rapid, and perhaps more rapid than shifts in community structure. Therefore it is likely that some of the warming effect is attributable to changes in the active fraction of the biomass, rather than the community's constituents [59,61,62]. Here, we will discuss how warming has affected microbial community diversity, biomass, and activity in a series of long-term warming experiments in different biomes, before turning to potential drivers of these changes and the consequences for the carbon cycle.

Long-term experiments at the Kessler Farm Field Laboratory (KFFL) in the plains of central Oklahoma found increased diversity under warming and drought, suggesting that warming may have somehow "primed" the community to be more resilient and resistant to further disturbance. These tall-grass prairie plots have been continuously warmed 2 °C above ambient since 1999, with half of each plot also being clipped annually [42]. In the second and third full years of treatment, Zhang *et al.* found that warming treatment increased fungal and decreased bacterial biomass as measured using PLFA analysis, but only in unclipped plots, demonstrating the importance of plant effects in driving the response. Furthermore, the authors found that while there was no effect of warming on total microbial biomass, net N mineralization decreased and there was a significant shift in the substrate utilization profiles, indicating a change in the metabolic capacity of the community. In years five to seven of the KFFL soil warming study, Sheik *et al.* found the effect of warming on microbial community structure and activity was strongly dependent on whether or not the site was facing drought [43]. In regular precipitation years, warming increased population size, but that the community was less rich and diverse. Under drought, however, warming decreased population size and increased its diversity, richness, and evenness without any change in community composition. The authors suggested that shifts in relative abundance of extant species rather than recruitment of novel ones drives ecosystem function under altered climate.

As a follow up to this study, Zhou *et al.* used high-throughput technologies to determine the functional significance of these shifts in diversity and potential feedback response of microbial communities to eight years of warming [44]. Pyrosequencing of the 16S ribosomal RNA gene showed a large shift in the community composition, and despite data collection in a non-drought year, higher microbial abundance using GeoChip and PLFA analysis [44]. However, not all populations involved in SOM decay were equally stimulated by warming; while those involved in the degradation of labile compounds such as starch, hemicellulose, cellulose, and chitin were stimulated, those involved in lignin degradation were not, and activity of the ligninase peroxidase even decreased. Soil respiration increased at this site, but its temperature sensitivity decreased, suggesting a weakened positive feedback to the climate system. Since there was a shift in the taxa detected without a change in

diversity at this site, this implies immigration or recruitment of microbes from the rare biosphere may be responsible for the shift towards labile substrate use.

Table 2. *In situ* field studies examining the effect of warming on soil microbial community[a].

Biome	Location	Heating[b]	Duration	Key Findings[c]	Ref.
Tall-grass prairie	Kessler Farm Field Lab, Washington OK	+1.8–2.7 °C (2 °C), IR, continuous	2−3 years	MC: Strong overall shift in absence of clipping MB: No overall change in biomass; increased fungi[d] MA: No change in C mineralization	[42]
			4−6 years	MC: Increased diversity but no shift under drought; strong overall shift if above-normal precipitation MB: Decreased population size in drought years; increased if above-normal precipitation. MA: n.d.	[43]
			8 years	MC: Strong overall shift MB: Increased microbial PLFA's; non-significant increase in bacterial and fungal biomass, no change in F:B ratio MA: Increased C mineralization; increased labile C-degrading genes, unchanged recalcitrant C-degrading genes	[44]
Old field grassland	National Ecological Research Park, Oak Ridge TN	+3 °C, OTC, continuous	2−3 years	MC: Strong overall shift MB: Increased Firmicutes, decreased Gram-negative bacteria, arbuscular mycorrhizal fungi and saprophytic fungi MA: n.d.	[45]
			4 years	MC: Strong overall shift MB: Increased fungal abundance; decreased bacteria (QPCR) MA: n.d.	[46]
Mixed hardwood forest	Harvard Forest LTER, Petersham MA	+5 °C, HC, continuous	12 years	MC: Strong overall shift MB: Decreased microbial biomass, decreased fungi, increased Gram-positives and Actinomycetes MA: Decreased biomass-specific respiration	[6]
Temperate mountain forest	North Tyrolean Limestone Alps, Austria	+4 °C, HC, snow-free seasons only	4−6 years	MC: No overall changes MB: No overall change in biomass; decreased Actinomycetes and Gram-negatives. MA: Increased biomass-specific respiration, stress biomarkers	[47]

Table 2. *Cont.*

Biome	Location	Heating[b]	Duration	Key Findings[c]	Ref.
Taiga boreal forest	Delta Junction, AK	+0.5 °C, CTC, continuous	0–3 years	MC: Change in active (BrdU) fungi MB: >50% decrease in fungi and bacteria MA: Lower chitinase, lower respiration rate in late growing season.	[48]
Taiga boreal forest	Delta Junction, AK	+1.2 °C, CTC growing season only	0-3 years	MC: No overall changes in fungal community MB: n.d. M.A.: Increased β-glucosidase and N-acetyl-glucosaminidase activity; no change in respiration	[49]
Sub-Arctic	Blanket bog, Abisko, Sweden	+0.3−2.8 °C (1°C), OTC, seasonal	9 years	MC: No overall changes MB: Decreased microbial biomass under summer warming MA: No change in soil peptidase activity; increased N-flux	[52]
Sub-Arctic	Sub-Arctic heath, Abisco, Sweden	+1.2−2 °C, OTC, snow-free seasons only	15 years	MC: No overall changes MB: decreased microbial biomass C; increased fungal:bacterial ratio[e]; no change in G+: G-MA: n.d.	[53]
Antarctic and sub-Antarctic	Falkland, Signy, & Anchorage Islands	+0.5−2 °C, OTC, continuous	3 years	MC: No overall changes MB: Increased fungi, bacteria, and ratio of Alphaproteobacteria to Acidobacteria MA: Increased N-cycling	[56]

[a] Studies were included in this table if they looked at microbial community composition and at least one of microbial biomass, and microbial community were examined. They must also have at least three full growing seasons of data, unless there is subsequent data from the same site to corroborate the early warming effects. [b] Heating methods include "OTC," passive open-top chambers; "HC," resistance heating cables; "CTC," closed-top chambers; and "IR," infrared radiators suspended 1.5m off the ground. In cases where there is no feedback regulation of warming treatment, temperature is provided as a range followed by the mean treatment in brackets. [c] Key findings are for "MC," microbial community profiles; "MB," microbial biomass; and "MA," microbial activity, where "n.d." indicates no data for this category. [d] This trend observed only in treatments without clipping. [e] top 5cm only.

The effects of warming on microbial processes are expected to be greatest at higher latitudes [1,63], though studies indicate that effects are mixed, and some ecosystems may in fact be more resistant to warming than originally thought. For example, in a blanket bog in northern Sweden, Weedon *et al.* [52] found that 9 years of seasonal 0.2–2.2 °C warming increased soil respiration, particularly from older, deeper carbon [51], and increased nitrogen cycling, but did not lead to any significant changes in vegetation [52]. However, warming did not change the DGGE profile of the microbial community or peptidase activity, but decreased the microbial abundance detected using qPCR. The relative resistance of the microbial community to elevated temperatures may reveal a tight association to plants in this

system. This is consistent with the finding of Rinnan *et al.*, where it took more than 15 years for 1.2–2 °C of experimental warming to affect microbial community composition in a subarctic heath at the same site [53] although addition of nitrogen at a rate designed to mimic warming-induced mineralization led to an effect sooner [64]. The authors hypothesized that nitrogen addition increased plant productivity, but there was a time delay between the increased plant productivity and support of greater microbial biomass. In a final example, after three years of continuous 0.5–2 °C warming at three sites in the Antarctic and sub-Antarctic, Yergeau *et al.* found no effect of warming on the rRNA profile of the community, but higher microbial abundance and Alphaproteobacteria:Acidobacteria ratio. Sequences for a number of processes were reduced under warming, including cellulose, chitin, and lignin degradation, although those for nitrogenase were higher under warming [56]. Together these results imply that the ecological functions were relatively redundant in the initial community and distributed across the phylogenetic tree, indicating both functional and phylogenetic diversity aided with the survival of the community through time. However, Allison and Treseder found that the fungal community in a taiga boreal forest of Alaska was highly-sensitive to just 0.5 °C of seasonal warming; microbial biomass, soil respiration and chitinase activity were reduced by about half late in the growing season [48]. Using the nucleotide analog BrdU, they also observed a shift of the active fungal community away from a *Thelephorid* fungus and towards Ascomycetes and Zygomycetes. The relatively large change in community composition for a small increase in temperature implies a keystone species may have been lost, changing the functionality of the community and allowing an otherwise apparently small pressure to cascade.

Long-term field warming experiments in two temperate forested sites provide contrasting consequences of warming on microbial community composition. Following four years of 4 °C seasonal warming in the North Tyrolean Limestone Alps of Austria, Schindlbacher *et al.* found an increase in respiration and a non-significant increase in the rRNA:DNA ratio, another measure of activity [47]. There was no change in microbial biomass C or the PLFA profile of the community as a whole, but there was a slight reduction in one PLFA associated with Actinomycetes and Gram-negative bacteria. These large increases in activity without much change in community identity suggest that warming improved conditions for the extant microbes without necessarily favoring one group over another, creating a more productive community. Alternatively, twenty years of warming at in a mixed deciduous stand at the Harvard Forest in Massachusetts led to an initial increase in respiration, followed by a subsequent decrease to control levels, and then an increase to above ambient again (Jerry Melillo, personal communication) [65]. This secondary increase in respiration may be explained under the community diversity hypothesis, which suggests that an overall increase in diversity has resulted in communities more resistant to higher and more extreme temperatures, or by the keystone species hypothesis, which suggests an increase in populations capable of degradation of more recalcitrant or previously physically protected soil carbon.

In a PLFA survey of the soil microbial community at this site just before soil respiration increased again, Frey *et al.* found evidence to support the keystone species hypothesis; while fungal and bacterial biomass decreased overall, there was a relative increase in Gram-positives and Actinomycetes, and a strong shift in PLFA profile despite no change in its diversity[6]. However, PLFA markers don't align well with phylogeny, and metabolic capacities vary non-randomly with phylogeny [17], so the data do not have enough resolution to decisively say whether whole community diversity or keystone species

or functions are more important. Approaches that resolve finer changes in the microbial community, such as the metagenomic study we are completing at the Harvard Forest, are necessary if we are to better understand how microbial community composition affects soil carbon cycling, and how this will change under future climate.

4. Mechanisms and Consequences of Warming Effects on Microbial Diversity

A number of patterns emerge from the warming experiments above, the first of which is the lack of congruence between phylogenetic and functional diversity in the studies that measured both. The second pattern which emerges is that warming only sometimes affects the efficiency with which microbes convert carbon to biomass (carbon use efficiency), leading to shifts to a community characteristic of higher carbon use efficiency in some instances [6], with no predictable change [45] or a reduction in others [47,56]. The third pattern is that changes in microbial biomass are inconsistent, increasing at some sites [43,44,56] and decreasing at others [6,7,45,48,52] while at some sites there was no change [47] or a delayed response [42,64]. These inconsistencies may be methodological, site-specific, or due to plant communities, which are well known links to below ground communities [66].

The lack of apparent congruence between phylogeny and function may be due to a "priming" effect not observed in all studies, where of one stress (for example, drought or fire) favors growth of species or functions that aid in providing resistance to a secondary stress (experimental warming). The primed species could derive from an initially diverse community (community diversity hypothesis), or a handful of organisms whose keystone role is their ability to weather the change in the environment. The increased diversity under drought and warming at the Great Plains site implies the former [43], while Yergeau's Antarctic and sub-Antarctic study indicates the latter. In this instance, warming reduced functional gene richness with no effect on microbial abundance or activity [56]. This may indicate that functional redundancy of the community was reduced by warming, and so the community may be more sensitive to further disturbances.

Carbon use efficiency is a key determinant of the long-term stability of carbon in soil, because microbial biomass, rather than recalcitrant plant matter, is most resistant to decay [67–69], and because microbial activity contributes significantly to terrestrial CO_2 emissions [11,12]. Fierer *et al.* loosely classified bacteria into two groups based on the kinds of carbon they prefer and the efficiency with which they grow: copiotrophs, which grow rapidly but with low efficiency in high resource environments, and oligotrophs, which grow slowly but efficiently, thriving in low resource environments [70]. While Proteobacteria and Bacteroidetes tended towards copiotrophy, Acidobacteria, Verrucomicrobia, and the Gram-positive phyla Actinobacteria and Firmicutes leaned towards oligotrophy [70]. This implies that in environments where Bacteroidetes or β-Proteobacteria increase in relative abundance, carbon use efficiency has declined, favoring respiration, soil carbon loss, and positive feedbacks to climate. However, studies have provided mixed support for this so far (Table 2), with one study finding increased oligotrophs and lower biomass-specific respiration [6], while a second found no obvious change [45], and two more found increased copiotrophs [56] and biomass-specific respiration [47], an indication of low carbon use efficiency. Unfortunately, explicit conclusions regarding the effects of experimental warming on carbon use efficiency are few and far between, and inconsistencies in the methods used [8,71] precludes a more direct generalization of this microbial response. Furthermore, we have found that when we extract data from long-term warming

studies and calculate proxies for carbon use efficiency, the magnitude and direction of the change depends on the metric used.

Changes in community structure may mask effects of warming on carbon use efficiency. All microbes inherently use labile substrates at a higher efficiency than complex ones [8,72], copiotrophs and oligotrophs differ in their substrates of choice [70], warming changes substrate quality [6,44], and carbon use efficiency decreases with temperature [72]. At the Harvard Forest, warming induced a significant shift in the microbial community [6], which was paralleled by a reduction in soil respiration and thermal adaptation of microbial carbon use efficiency on phenol [8]. It is unclear whether changes in carbon use efficiency are directly driven by changes in soil carbon chemistry or indirectly through warming- or substrate-mediated shifts in community structure. Unfortunately, in many cases the lack of taxonomic resolution in community data following disturbance prevents determination of whether shifts towards or away from oligotrophy was driven by changes in few keystone or many taxa.

It is likely edaphic factors such as secondary soil drying with warming, and changes in soil carbon availability, also play a role in microbial response to warming. In studies which test both warming and precipitation, it is often observed that precipitation treatment has an as strong if not stronger effect on soil microbial communities than warming [45,73,74]. However, this trend is muddied by inconsistencies in methods and associated errors in estimation. For example, PLFA profile can differ depending on the soil type and lipid extraction method used [75–77], "universal" primers for qPCR are never universal [41], and chloroform fumigation extraction efficiency is known to be pH sensitive [78]. However, microbes differ in their sensitivity to moisture stress [23,79], so moisture likely directly affect community composition and function, though the relative contributions of warming to drying are not well understood.

Inconsistencies in biomass may also be due to difference in plant effects across studies, many of which conclude that the strength and direction of the effect depends on how plants respond [47,56,74,80]. Soil warming induces nitrogen mineralization, which increases plant productivity [12,44], and plant community composition often also changes with warming [81–84]. Since plants stressed by warming may increase production of structural carbohydrates and secondary compounds that reduce decomposability of senesced litter [85], species shifts may stimulate soil microbes and result in increased N mineralization as a side effect. In fact, while warming at the Great Plains site led to an increase in labile (and microbially available) carbon [44], it led to a reduced capacity to use labile substrates at the Harvard Forest [6], where fine root production [86] and soil carbon quality declined [7]. These differences in microbial activity are unlikely to be purely due to direct effects of increased nitrogen availability; rate of nitrogen cycling [11,44] and soil N availability [42,44,87] have been affected similarly in both sites. While aboveground biomass removal has demonstrated that moderate warming is unlikely to have direct effects on the microbial community [42], direct determination of the relative role of changes in carbon and nitrogen availability on microbial community and activity is complicated by the fact that clipping reduces both C and N availability [88]. Nonetheless, the increase in diversity of genes involved in labile carbon utilization at the grassland site shows that many taxa were involved in the warming response, supporting the community diversity hypothesis.

The patterns outlined above have important implications for the carbon cycle and feedbacks to climate. Warming initially increases respiration, which, if heterotrophic soil microbes respond to

warming on a time scale much faster than the dominant vegetation, would lead to depletion of the soil carbon pool. While this was true for one temperate forest [6,7], it was not the case for another [47,71], or in a subarctic heath, despite the apparently slow vegetation response there [53]. Microbes adapt to changes in carbon quality and temperature, through plasticity in their metabolisms or through shifts in community. If conditions favor more efficient microbes, more of the carbon assimilated will be directed to microbial biomass, a relatively stable carbon pool, but more biomass also means greater respiration and greater carbon loss. As soil carbon chemistry becomes more complex [85], or as temperatures increase, carbon use efficiency decreases independent of any change in the community [72]. Understanding which of these processes has dominated—as well as how diversity may affect the resistance of the soil microbial community to further change—is important for understanding how feedbacks to climate are mediated in the soil.

5. Future Directions

The lack of consistency in microbial community taxonomic response to warming among current field studies is likely due to many confounding factors, not limited to edaphic and methodological variables. To meet the goal of an improved understanding of processes driving the microbial response to warming, we need improved understanding of microbes, from the level of the gene and the physiology of individual microbes all the way to microbial community composition and interactions. Long term warming studies, especially at LTER sites such as the Harvard Forest, and the cross-latitudinal NEON sites, are especially suited for this because of the immense amount of biogeochemical and other site data.

To understand the role of microbes in ecosystem functioning, there are a wide range of choices to make in terms of measuring diversity, and in the end, relatively few direct measures of the contributions of microbes to ecosystem function. Microbes function on a scale which by definition we cannot see, yet drive the majority of energy and nutrient transformations which shape ecosystem function. New technologies such as NanoSIMS which, when coupled with FISH staining, enable us to visualize how microbes interact with each other and their environment, are changing this. Simpler techniques such as co-culture of novel isolates may also help improve our understanding for less money, in addition to "ground-truthing" some of the functions assigned to phylotypes in the masses of metagenomic data we are now able to collect.

Understanding the ecological function of microbial communities in their natural environment is essential, but microbial processes are often placed in a "black box" because the microbes present could not be determined or quantified. Rapid advances in genomic sequencing technology are transforming microbiology and in particular ecological research, and yet there is still value in making more traditional measures of microbial biomass and diversity in order to understand the portion of carbon or biomass that populations occupy, which is also a measure of functional potential. Though this is not always the case, genomic, genetic or informatics approach should be undertaken along with functional or absolute measures of diversity. Overall, we have much to learn about microbial diversity and its importance in the context of carbon cycling, and we have better tools than ever to do so.

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