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ESA CENTENNIAL PAPER

Direct and indirect effects of climate change on soil microbial and soil microbial-plant interactions: What lies ahead?

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Abstract. Global change is altering species distributions and thus interactions among organisms. Organisms live in concert with thousands of other species, some beneficial, some pathogenic, some which have little to no effect in complex communities. Since natural communities are composed of organisms with very different life history traits and dispersal ability it is unlikely they will all respond to climatic change in a similar way. Disjuncts in plant-pollinator and plant-herbivore interactions under global change have been relatively well described, but plant-soil microorganism and soil microbe-microbe relationships have received less attention. Since soil microorganisms regulate nutrient transformations, provide plants with nutrients, allow co-existence among neighbors, and control plant populations, changes in soil microorganism-plant interactions could have significant ramifications for plant community composition and ecosystem function. In this paper we explore how climatic change affects soil microbes and soil microbe-plant interactions directly and indirectly, discuss what we see as emerging and exciting questions and areas for future research, and discuss what ramifications changes in these interactions may have on the composition and function of ecosystems.

Key words: bacteria; climate change; ecosystem; ESA Centennial Paper; fungi; microbial community; microbiome; plant-microbe interaction; plant-soil feedbacks; rhizosphere; soil; warming.

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INTRODUCTION

Climatic change is altering species distributions and simultaneously impacting interactions

among organisms (Wookey et al. 2009, van der Putten 2012). Natural communities are complex and composed of organisms with very different

life history traits, thermal tolerances, and dispersal ability. Further, interactions among community members can be beneficial, pathogenic, or have little to no functional impact and these interactions may change with environmental stress (Vandenkoornhuyse et al. 2015). Numerous studies show that shifts in species interactions in response to climate change cascade to alter biodiversity and the function of terrestrial ecosystems (Walther et al. 2002, Gottfried et al. 2012, Langley and Hungate 2014), but fewer studies focus on soil communities (Schimel et al. 2007, de Vries et al. 2012). Soil organisms interact with one another as well as with plants in a myriad of ways that shape and maintain ecosystem properties. In fact, soil microbial interactions, with each other as well as with plants, can shape landscape patterns of plant and animal abundance, diversity, and composition (Berg et al. 2010, van der Putten et al. 2013). Plant-microbial interactions are considered negative when the net effects of all soil organisms—including pathogens, symbiotic mutualists, and decomposers—reduce plant performance, while interactions are considered positive when the benefits brought about by the soil community enhance plant performance such as biomass production and survival. Therefore, given their importance in defining ecosystem properties, understanding how soil microbe-microbe and soil microbe-plant interactions respond to climate change is a research priority that will shed light on important ecosystem functions such as soil carbon storage and net primary productivity (Ostle et al. 2009, Berg et al. 2010, Fischer et al. 2014).

The ~120 Gt yearly flux of carbon into and out of terrestrial ecosystems far exceeds the amount of carbon that is being produced by the combustion of fossil fuels (IPCC 2013). Thus, a small change in the amount of carbon an ecosystem exchanges with the atmosphere could have a large impact on future concentrations of atmospheric carbon. Ecosystem models, to date, have considerable uncertainty surrounding carbon feedbacks to the atmosphere from terrestrial ecosystems (Todd-Brown et al. 2012). Much experimental research has, therefore, focused on how to generate more reliable predictions of carbon fluxes with the goal of estimating how much carbon can be stored in terrestrial ecosystems. Soils, in combination with plant biomass,

hold ~2.5× more carbon than the atmosphere (Singh et al. 2010). Soils have the capacity to retain large amounts of carbon and their ability to sequester carbon has helped to mitigate rising atmospheric [CO₂]. Several factors regulate the amount of carbon soils can sequester including climate, the parent material, the age and texture of the soil, the topography, the vegetation type, and the composition of the soil community (Jenny 1941). However, microbial decomposers ultimately regulate the rate limiting steps in the decomposition process and thus the influence of abiotic factors on decomposition. Yet, how microbial activity will influence carbon feedbacks among plants, soil, and the atmosphere is uncertain (Todd-Brown et al. 2012, Treseder et al. 2012, Verheijen et al. 2015). If the activity of the soil community, such as the decomposition rate, increases relative to inputs coming from plants and animals, then the amount of carbon in soil will decrease as carbon enters the atmosphere, which can amplify carbon-climate feedbacks (Zhou et al. 2009, Wieder et al. 2013). In addition to the direct control over the decomposition process, microbial communities can influence important plant properties such as productivity and litter quality (Harris et al. 1985, van der Heijden et al. 1998), properties that regulate fluxes in the carbon cycle. Clearly, microbial activity plays a large role in future terrestrial carbon feedbacks, however our current understanding of climate effects on microbe-microbe or plant-microbe interactions remains uncertain.

Here, we explore how climatic change affects soil microbe-microbe and plant-microbe interactions directly and indirectly as well as some of the ramifications shifts in these interactions may have for the composition and function of ecosystems (Figs. 1 and 2) We also explore some of the key questions that remain unanswered on this topic (Fig. 3). While the direct impacts of climatic change on microbial function have been well reviewed (Blankinship et al. 2011, Henry 2012, Manzoni et al. 2012, A'Bear et al. 2014, Chen et al. 2014), we argue that while the indirect effects via shifts in plant-soil microbe and soil microbe-microbe interactions are less acknowledged they have the potential to mediate important processes such as plant chemistry, plant community composition, and mineraliza-

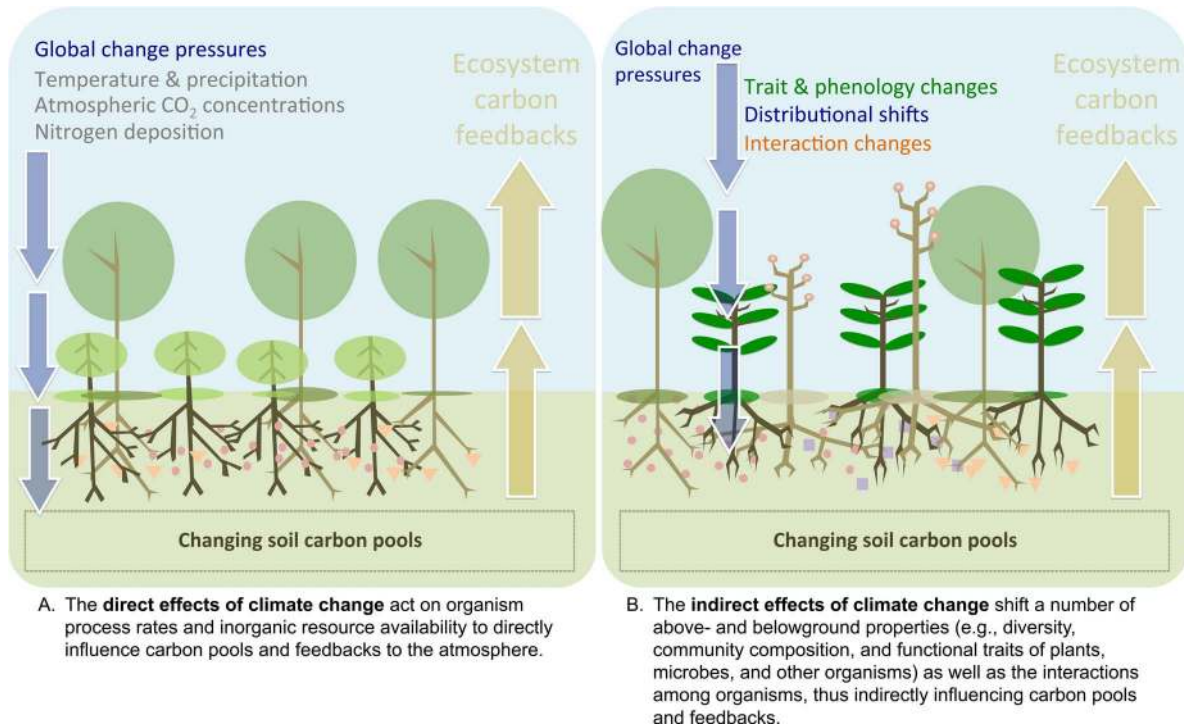


Fig. 1. The direct effects of global change on carbon feedbacks to the atmosphere have received considerable experimental attention (A); however, there has been less of a focus on understanding the magnitude of indirect effects of global change on the composition and function of ecosystems (B). The ecosystem-scale responses to the indirect effects of global change on community interactions (e.g., via changes in species distributions and/or traits) may be as large, or even larger, than the direct effects. Combined, the direct and indirect effects of global change on ecosystems may magnify, counterbalance, or reverse ecosystem carbon feedbacks to the atmosphere.

tion rates much like shifts in other ecological interactions alter important functions (Figs. 1 and 2) (Gilman et al. 2010, Adler et al. 2012, Steinauer et al. 2015).

DIRECT IMPACTS OF CLIMATIC CHANGE ON SOIL COMMUNITIES AND PLANTS

Climatic change alters the relative abundance and function of soil communities because soil community members differ in their physiology, temperature sensitivity, and growth rates (Castro et al. 2010, Gray et al. 2011, Lennon et al. 2012, Briones et al. 2014, Delgado-Baquerizo et al. 2014, Whitaker et al. 2014). The direct effects of climatic change on microbial composition and function have been reviewed extensively (Blankinship et al. 2011, Henry 2012, Manzoni et al. 2012, A’Bear et al. 2014, Chen et al. 2014). Warming by 5°C in a temperate forest, for

example, altered the relative abundances of soil bacteria and increased the bacterial to fungal ratio of the community (DeAngelis et al. 2015). Microbial communities respond to warming and other perturbations through resistance, enabled by microbial trait plasticity, or resilience as the community returns to an initial composition after the stress has passed (Allison and Martiny 2008). Shifts in microbial community composition are likely to lead to changes in ecosystem function when soil organisms differ in their functional traits or control a rate-limiting or fate-controlling step (Schimel and Schaeffer 2012). For instance, specific microbial groups regulate ecosystem functions such as nitrogen fixation, nitrification (Isobe et al. 2011), denitrification (Bakken et al. 2012, Salles et al. 2012), and methanogenesis (Bodelier et al. 2000). Change in the relative abundance of organisms who regulate specific processes can have a direct impact on the rate of

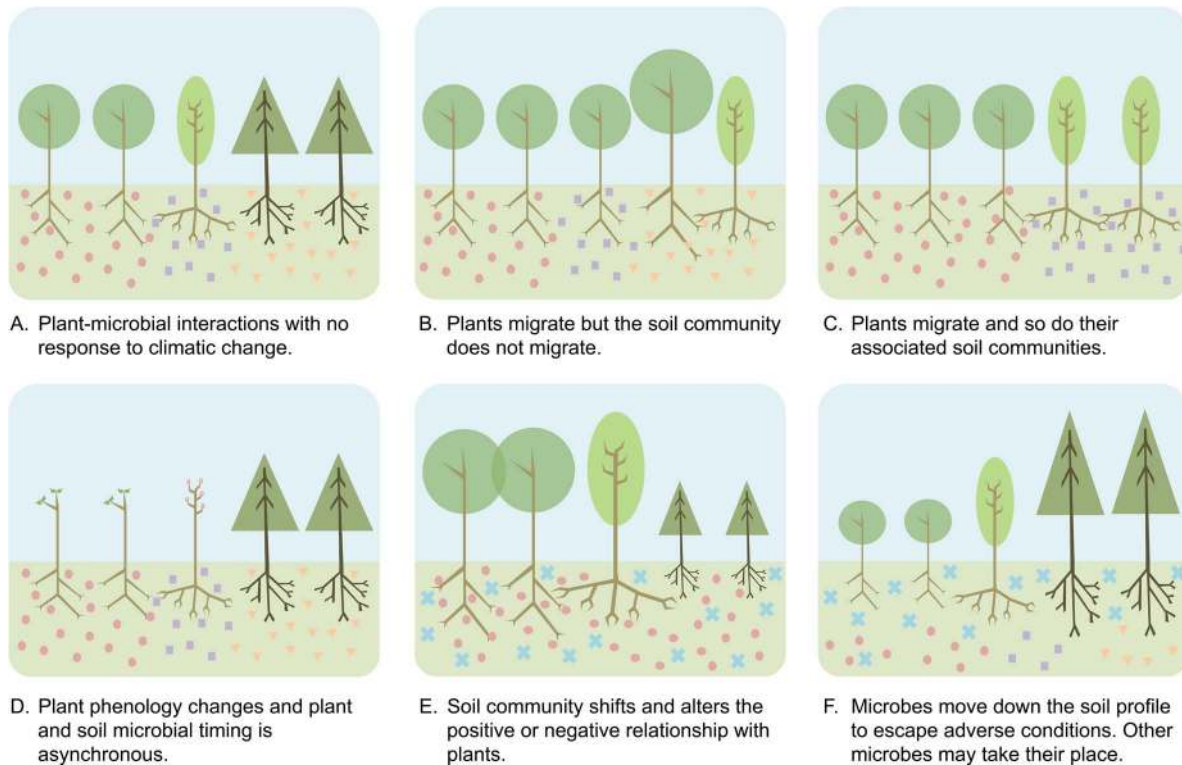


Fig. 2. The potential responses of plant and associated soil communities to climatic change. Plants and microbes may respond by shifting population ranges, symbiotic partners, or timing of phenological events. Each panel illustrates plant and soil community responses to climate change and highlight possible mismatches between interacting plants and microbes. Shapes of plants and microbes signify different species.

that process. However, some processes that occur at a coarser scale, such as nitrogen mineralization, are more tightly correlated with abiotic factors such as temperature and moisture than microbial community composition because a diversity of organisms drives these processes (Hooper et al. 2005).

Global changes such as warming are directly altering microbial soil respiration rates because soil microorganisms, and the processes they mediate, are temperature sensitive. The role of elevated temperature in microbial metabolism has received considerable recent attention (e.g., Bradford 2013, Frey et al. 2013, Hagerty et al. 2014, Karhu et al. 2014). Given no changes in community composition, the intrinsic temperature sensitivity of microbial activity is defined as the factor by which microbial activity increases with a 10°C increase in temperature (Q_{10}). Q_{10} is often used in climate change models to account for microbial temperature sensitivity; however,

using this relationship masks many of the interactions that influence the temperature sensitivity of microbial processes such as decomposition. Therefore, using only Q_{10} to account for temperature sensitivity in models may lead to poor predictions. Further, while decomposition of soil organic matter, soil respiration, and growth of microbial biomass generally increase with temperature, these responses to experimental warming are often short-lived in field studies (Bradford et al. 2008). The transitory effects of warming on soil communities have been hypothesized to occur as labile soil carbon substrates are depleted by increased microbial activity and because of trade-offs as microbial communities either acclimate, shift in composition, or constrain their biomass to respond to altered conditions and substrate availability (Allison and Martiny 2008, Bradford 2013). Experimental warming can initially alter the composition of microbial communities, and shift the abundance

Ten questions:

1. What degree of change in the direct and/or the indirect effects of climate change on microbe-microbe or plant-microbial interactions are relevant for ecosystem functioning?
2. How stable are microbial communities through time? How frequently should they be sampled to capture accurate and meaningful information about their composition and function?
3. At what scale might microbial dispersal limitation begin to matter for ecosystem function and how quickly will microbes adapt to changing climate?
4. Are the indirect effects of climate change on communities as important as the direct effects for ecosystem process rates and carbon feedbacks?
5. Will the asynchronous responses of root, shoot, and microbial phenologies to climate change be important drivers of plant community shifts and ecosystem productivity?
6. At what spatial and temporal scales should we measure microbial processes and interactions in order to understand how climate change will influence microbial diversity, community composition, and function at ecosystem and global scales?
7. Will climate change alter the direction of plant-microbe interactions from positive to negative or vice versa and what will the consequences be for ecosystem function?
8. Are there tradeoffs between plants maintaining symbionts that provide short-term (e.g., nutrient acquisition) vs. long-term (e.g., pathogen protection) benefits? How will climate change affect specialist symbionts?
9. How can we scale up plant-microbial interactions given that plants and microbes function on different spatial and temporal scales? At what scale (e.g., root-soil interface) should we be measuring plant-microbe interactions?
10. How do we standardize methodologies so that microbial communities are comparable across studies and over time?

Fig. 3. Ten questions exploring how climate change affects soil microbe and soil microbe-plant interactions directly and indirectly.

of gram-positive and gram-negative bacteria (Zogg et al. 1997), or warming effects may take many years before a response is evident within the microbial community (Rinnan et al. 2007, 2013). Interestingly, results from field and lab studies often contradict one another (von Lützow and Kögel-Knabner 2009) and both long-term field experiments (Sistla and Schimel 2013) and short-term laboratory tests (Hartley et al. 2008) of thermal compensation by microbial communities can support opposite conclusions. These contrasting results have left the evidence and mechanisms for thermal acclimation debated (Bradford et al. 2008, Hartley et al. 2009, Bradford 2013). Clearly the direct effects of temperature on microbial physiology are complex and likely mediated by microbial adaptations, evolution, and interactions over time.

Temperature changes are often coupled with changes in soil moisture, which may explain some inconsistent results from experiments exploring how microbial communities respond to

climatic change. For example, rates of microbial activity at warmer temperatures can be limited by diffusion and microbial contact with available substrate (Zak et al. 1999). While bacterial communities may respond rapidly to moisture pulses, the slower-growing fungal community may lag in their response (Bell et al. 2008, Cregger et al. 2012, Cregger et al. 2014). Further, drought amplifies the differential temperature sensitivity of fungal and bacterial groups (Briones et al. 2014). Even with small changes in soil moisture availability (<30% reduction in water holding capacity), soil fungal communities may shift from one dominant member to another while bacterial communities remain constant. These patterns indicate greater fungal than bacterial plasticity during non-extreme wet-dry cycles (Kaisermann et al. 2015). Soil communities adapted to low water availability or repeated wet-dry cycles may elicit less of a compositional or functional shift to changing water regimes (Evans et al. 2011). Interactions among microbes

and background temperature and moisture regimes in any given location influence microbial composition and function with changing climate. However, it is still unclear (1) how temperature and moisture, and their interaction, affect specific microbial functional groups, such as methanogens, within a community; (2) what effects microbial community changes have on functions like decomposition of new and old soil organic matter; and (3) which mechanisms drive the net ecosystem response of microbial activities to climate change. We recommend exploring these questions using factorial warming and community manipulations along gradients of temperature (such as elevation) or moisture. Similarly, another useful approach to explore these questions would be to use reciprocal transplants of plants and/or soils along environment gradients. This approach would couple changes in temperature and moisture in order to explore shifts in the microbial community from a functional perspective using PLFA methods (although this is a coarse approach, and more refined analysis would be desirable) and from an evolutionary perspective using phylogenetic dissimilarity methods (e.g., Fierer et al. 2012). If this type of experimental design were performed in ecosystems where ^{13}C had been manipulated for several years (e.g., free-air carbon enrichment sites; see Norby and Zak 2011) then the effects on old (experimentally depleted ^{13}C) and new (higher ^{13}C of recent root and litter inputs) soil carbon dynamics could be teased apart.

Climate change impacts on plant-microbial interactions

With warming, plant species are migrating to higher elevations and latitudes (Grabherr et al. 1994, Walther et al. 2002, Parmesan and Yohe 2003), are leafing out and flowering earlier in the growing season (e.g., Cleland et al. 2007, Wolkovich et al. 2012), and are altering the expression of functional traits (Walker et al. 2006, Hudson et al. 2011, Verheijen et al. 2015). Scaling up to the community level, warming has resulted in shrubification of the arctic as woody shrubs have replaced grasses and forbs in several regions leading to changes in ecosystem properties and carbon feedbacks in these systems (Sturm et al. 2001, Hinzman et al. 2005, Lawrence and Swenson 2011, Pearson et al. 2013). Soil commu-

nities, especially communities that are tightly coupled with plants, may be facilitating or retarding plant community transitions (Figs. 1 and 2). For example, root-associated microbial communities can have a strong influence on plant survival, phenology, and expression of functional traits (Van der Heijden et al. 1998, Friesen et al. 2011, Wagner et al. 2014)—all traits that are responding to changes in climate. The consequences of interactions between plants, their associated microbial community, and climate change on ecosystem functions are still poorly understood (Fig. 1; Fischer et al. 2014, Mohan et al. 2014).

Shifts in the bulk soil microbial community induced by climate change may have long lasting effects on plant performance and/or establishment and soil carbon balance (Fig. 1). In fact, the interactions between plants and soil communities, such as plant-soil feedbacks, are some of the most important, yet least understood, controllers of soil nitrogen and carbon dynamics. If climate change alters soil microbial communities and this change determines plant species establishment and growth, then ecosystem responses will be contingent on the interactions between plants and soil communities. Recent studies suggest that rapid responses of the surrounding soil community can buffer plants to drought stress (Lau and Lennon 2012). Mounting evidence suggests that changes in microbial diversity can alter selection on plant functional traits (e.g., Lau and Lennon 2011). The indirect impacts of climate on plants and their associated soil communities can differ significantly from the direct effects of climate on the bulk soil community (Kardol et al. 2010). For example, Kardol et al. (2010) found that changes in precipitation altered the soil community and its function in a TN (USA) oldfield, but the effect of precipitation on soil community composition and function varied by the plant the soil was collected from. Further, soils that were collected across the site and homogenized to assess the impact of climate change on communities and functions showed a relatively muted response. These results suggest that soil ecosystem responses to climate changes could be offset if plant community composition shifts with climate change. Therefore, these community and functional shifts may be under-represented in most studies because soils are

collected across plant species and homogenized together (Kardol et al. 2010). Given the strong interaction between plants and their associated soil communities the effects of these interactions may build up in the soil system and impact ecosystem function (e.g., carbon cycling) and trajectory (e.g., plant establishment) over time; however, experiments need to be conducted to tease these interactions apart (Figs. 2 and 3).

INDIRECT IMPACTS OF CLIMATIC CHANGE ON SOIL COMMUNITIES AND PLANTS

Climate change alters plant and microbial distribution

While plant species migrations in response to climate change are well described (Grabherr et al. 1994, Walther et al. 2002, Parmesan and Yohe 2003) most studies fail to address the ability of associated soil micro-organisms to shift their range to maintain the positive or negative relationship between the plant and the soil community (van der Putten 2012). Soil biota may be poor dispersers, therefore they may respond to climate change at a different rate than plants (see van der Putten 2012). In fact, we know very little about the dispersal ability of microorganisms at the local community level or if shifts in dispersal ability translate into shifts in coarser-scale functions such as decomposition (Fig. 3). Nonetheless, we do know that differential dispersal abilities among plants and microbes can alter plant establishment and plant productivity as well as the interactions among plants in a community (Bever et al. 1997, Nuñez et al. 2009, Bever et al. 2010), for instance, via shifts in plant litter input quality. Some range expanding plant species are better defended against aboveground herbivores and/or develop less pathogenic activity in their soils compared to their related natives in the new range (Engelkes et al. 2008, Morriën et al. 2011). If plants that successfully establish in new ranges have higher induced levels of plant defense compounds such as polyphenols (Engelkes et al. 2008), then litter input quality will decline and the decomposer community will shift in composition or activity. While it is still relatively unknown how the disconnected geographic migration of plants and microbes will impact the adaptation and establishment of plants in new environments (Fig. 3), the plant

invasion literature indicates that lack of ectomycorrhizal fungi can stop or slow pine invasions (Nuñez et al. 2009). Similarly, geographic disconnects might influence the composition and functioning of the microbial community, but this is also relatively unexplored (van der Putten 2012). Yet, we stress it is still largely unknown if microbial dispersal limitation could scale to impact coarse-scale processes such as decomposition and nutrient mineralization. The rate at which isolated microbial communities are able to adapt to climate change is mostly an unknown. Therefore, simple questions such as at what scale might microbial dispersal limitation begin to matter for ecosystem function and how quickly will microbes adapt to changing climate, still need to be answered (Fig. 3). Experiments using soil and plant reciprocal transplants across transitional areas such as tree lines or ecotonal boundaries might be one way to tackle these sorts of questions.

Relative to aboveground plant structures, soils are buffered to changes in temperature, precipitation, and possibly to extreme events like frost (Durán et al. 2014). Belowground communities are, therefore, structured by different environmental conditions than aboveground communities (Fierer and Jackson 2006) and are constrained by different life history characteristics. For this reason, the direct environmental pressures plants are experiencing under global climate change may be different from what their associated soil community is experiencing. Microbial communities clearly respond to both biotic and abiotic drivers, but the indirect effects of climate change, mediated by plant community shifts, may counteract or be different than the direct effects (Kardol et al. 2010). Soil communities may respond to climate stress by changing their distribution in the soil profile (Fig. 2). For example, they may move down in the soil profile if temperatures at the surface are outside of their thermal optima range. Re-sorting of soil communities, and thus interactions, in the soil profile may further alter plant-microbe-process interactions. However, to what degree a change in the direct and/or the indirect effects of climate change on microbe-microbe or plant-microbe interactions are relevant for ecosystem functioning is still unknown. Decoupling of plant and microbial community responses to the same

environmental drivers using experimental (e.g., reciprocal transplants) and observational (e.g., elevational and environmental gradients) approaches should be a focus of future work (see Marshall et al. 2011, Wardle et al. 2013, and Farrer et al. 2015 for examples of experiments exploring decoupling).

Climate change alters plant phenology, which alters microbial communities

With warming, plant species are leafing out and flowering earlier in the growing season (e.g., Cleland et al. 2007, Wolkovich et al. 2012). However, climate change also impacts root phenology and subsequent plant-rhizosphere interactions, processes less explored in phenology studies (e.g., Iversen et al. 2015). If root growth peaks early in the growing season, aboveground and belowground phenologies can be synchronous (Scagel et al. 2007, Medvigy et al. 2009). However, because root and shoot phenologies are commonly asynchronous (Lahti et al. 2005, Willaume and Pages 2006, Palacio and Montserrat-Marti 2007, Steinaker and Wilson 2008, Abramoff and Finzi 2015), shoot phenology may not always be a reliable predictor of plant response to climate change. Root phenology varies by species and among ecosystems because it is driven by complex interactions between abiotic factors such as temperature and moisture as well as stored plant carbon and nutrients (Abramoff and Finzi 2015). Growing season durations are increasing under climate change (IPCC 2013). Therefore, successive peaks across the growing season in foliar, root, and mycorrhizal biomass may become further asynchronous leading to changes in nutrient and carbon fluxes (Figs. 1 and 2). Variation in root-shoot phenology will impact rhizosphere interactions and may influence the distinct seasonal assemblages of soil microbial groups (Schadt et al. 2003, Waldrop and Firestone 2006, Dumbrell et al. 2010, 2011, Zhang et al. 2014). If the relationship between photoperiod, temperature, and soil moisture becomes asynchronous with climate change, then root, shoot, and microbial phenologies may also become asynchronous (Figs. 1 and 2). These interactions may drive plant community shifts and affect ecosystem productivity under climate change.

Climate change impacts on fine-scale plant-microbe interactions may alter plant traits

Bacteria and fungi often have close associations with plant roots (Bais et al. 2006). These associations can alter the expression of plant traits such as leaf area and nutrient content (Harris et al. 1985, Bishop et al. 2011, Friesen et al. 2011). Root symbionts such as rhizobia bacteria (de Bello et al. 2010) and mycorrhizal fungi (Johnson et al. 1997) affect plant productivity by altering plant nutrient status. The impact of specific strains of rhizobia on other plant traits may be equally important under global change. For example, when a common rhizobia strain was present in nitrogen-fixing mutualisms, plant specific leaf area and carbon assimilation rate increased (Harris et al. 1985). Mycorrhizal fungi associate with nearly all land-plants (Brundrett 2002) and are important players in carbon and nutrient-cycling processes (van der Heijden et al. 1998, Read and Perez-Moreno 2003). Similar to rhizobia, mycorrhizal fungi exchange nutrients for plant carbon, thus influencing plant carbon to nutrient ratios and subsequently plant productivity (Smith and Read 2008). Consequently, mycorrhizal fungi affect decomposition activity within the soil microbial community by altering plant litter quality as well as carbon inputs (Clemmensen et al. 2013, 2015, Moore et al. 2015). Specific mycorrhizal strains can alter plant reproduction (Streitwolf-Engel et al. 2001), tiller production, root biomass production, rooting depth (Ellis et al. 1985), and herbivory rates (Bennett and Bever 2007, Roger et al. 2013). However, the interactions between mycorrhizal strain identity and plant host are not always symbiotic and can change with environmental factors or even plant stress (Johnson et al. 1997, Treseder 2004). Further, mycorrhizal community composition can change with climatic factors such as temperature (Deslippe and Simard 2011). Two current knowledge gaps are: (1) how climate change might alter the direction of plant-root microbe interactions from positive to negative or vice versa (e.g., Soussana and Hartwig 1996); and (2) whether climatic change will alter interactions between plants and their myriad of symbionts in tandem, possibly having additive effects on ecosystem function (e.g., Zanetti and Hartwig 1997, Zanetti et al. 1997).

Climate change influence on microbe-microbe interactions?

Microbes form complex networks of interactions that are continually responding to changes in resources. For example, mycorrhizal fungi foraging can alter free-living bacterial communities in ways that vary nitrogen transfer from the mycorrhizae to the plant (Nuccio et al. 2013) as well as decomposition of organic matter (Clemmensen et al. 2013, Leifheit et al. 2015, Moore et al. 2015). Rising temperatures lead to increased carbon allocation to mycorrhizal hyphae, which may swing the mycorrhizal association from symbiotic to parasitic (Hawkes et al. 2008). Shifts in these mycorrhizal-plant interactions can cascade to alter the soil microbial composition (de Boer et al. 2005, Nazir et al. 2010) and activity (Leifheit et al. 2015; J. A. M. Moore et al., *unpublished manuscript*) in ways that may exacerbate the negative or positive interaction between the plant and its associated community. Other interactions among bacteria and fungi in the free-living community are likely to modify ecosystem functions and carbon feedbacks, but this has been less explored.

ARE WE ASKING QUESTIONS AT THE CORRECT SPATIAL AND TEMPORAL SCALES?

Current challenges in soil ecology involve how to ask and answer questions at the appropriate temporal and spatial scales (Fig. 3). Microbial organisms and communities live and interact in relatively small soil structures, have short life spans, and the majority of individuals can be dormant at any point in time. Further, it is difficult to determine the abundance of active groups in the community and extrapolation of experimental results has been difficult because experiments are often established only at single sites and experimental designs are generally not replicated across ecosystems that vary in vegetation type, soil type, or background climate. In spite of these concerns, scientists have broadly applied plant- and ecosystem-centric measurements to studies of microbial communities and processes in field based systems. This approach may lead us to under-predict how microbe-microbe and microbe-plant interactions will shape ecosystem response to climate change.

Scaling plant-microbe interactions across space

Soil communities are diverse and perform a diversity of functions (Coleman and Whitman 2005, Fierer et al. 2012). Although changes in microbial diversity at a fine scale may not alter certain ecosystem processes, they may at a coarse scale. Soil microbial communities are primarily composed of fungal and bacterial groups and these groups have different functions in the decomposition process. In general, bacterial decomposition pathways quickly decompose labile substrates, while slower fungal-dominated decomposition pathways target more complex organic materials (de Boer et al. 2005). Soil microbes, particularly fungi, play pivotal roles in altering soil structure (e.g., aggregate formation), which can alter carbon processes (Six et al. 2006, Leifheit et al. 2015, Rillig et al. 2015). Changes in the composition (and consequently function) of soil bacteria and fungi are thus expected to affect soil carbon storage (Moore et al. 2015).

Microbial communities operate at very small spatial and time scales, where entire communities may be limited to a single soil particle or soil aggregate and can turn over under an hour (Sessitsch et al. 2001, Gonzalez et al. 2012, Or et al. 2012). However, scientists measure microbial communities across meta-communities (a single soil core), at the individual plant-level (comprising an estimated 10^6 – 10^8 microbes), or the ecosystem level. Thus, scaling microbial interactions and processes from the cell or soil particle to the ecosystem is a significant challenge. The soil matrix is a highly heterogeneous environment and there can be nutrient and moisture oases that promote hotspots of microbial activity and potentially select for microbes that can take advantage of those resources. Soil aggregates, particles bound together by biological residues, can protect microbes from extreme conditions in the external environment and contain water and nutritional resources (Six et al. 2006, Bach and Hofmockel 2014). Further, microbial functions, such as enzyme production and substrate availability, can vary through the soil matrix (Šnajdr et al. 2008). Variation in microbial community composition through the soil profile can affect microbial interactions with plant roots (Hoeksema et al. 2010, Johnson et al. 2015), such as competition for nitrogen (Hodge et al. 2000,

Bardgett et al. 2003). Ecosystem processes emerging from interactions between plants and microbial communities differ when plants interact with different soil communities (van der Heijden et al. 1998, 2008, Kardol et al. 2014). Since soil microbial communities vary across small spatial scales, their processes need to be first scaled up to the level of the plant. This is probably a function of soil resource availability, pH, physical soil properties such as texture and bulk density, and salinity/cation exchange capacity. Observational studies across gradients of these factors that document shifts in microbial communities with and without plants are needed to identify important abiotic factors regulating small-scale microbial beta-diversity. Then the whole plant-microbe interactions need to be scaled up to the level of the ecosystem, which is likely a function of plant diversity and climate. Additionally, because microbial communities influence the expression of plant traits, shifts in plant-associated microbial communities can be scaled to ecosystem properties through the measurement of plant functional traits and the large body of literature linking plant traits to ecosystem function (Chapin et al. 1993, Grime 1998, Díaz and Cabido 2001).

We suggest using elevational gradients of climate or plant diversity gradients to test how plant-microbe interactions vary across space and time. Temperature and the composition of plant communities vary systematically along elevational gradients and, when coupled with experimental warming and species manipulation treatments, they are powerful tools to explore how short- and long-term changes in temperature alter biodiversity, species interactions, and the carbon cycle (Sundqvist et al. 2013). Further, elevational gradients often have a large amount of micro-climatic variation making them excellent test systems (Scherrer and Körner 2010). While the variation across a landscape is vast, it can represent a short snapshot in time. Understanding how plants and microbes will respond to climate over longer time scales that encompass non-overlapping drivers and exploring if there are mismatches where the response of soil communities and plants diverge still remains challenging. Experiments should, therefore, include both a spatial element (e.g., using an elevational gradient) and temporal element

(e.g., sampling over many seasons and years and/or using space for time substitutions).

Scaling plant-microbe interactions through time, from the plant's perspective

Interactions between plant hosts and soil microbial communities shift through time and scaling these interactions to longer time scales remains a challenge from both a plant and a microbe perspective. Plant hosts can live on a landscape from years to centuries while communities living around and in their roots exist anywhere from hours to months (Gonzalez et al. 2012, Or et al. 2012). Thus, the factors shaping the stability of these two communities may differentially shift over time. Most of our understanding on the stability and functioning of plant-rhizosphere interactions comes from rather short-term studies, where 2–3 growing seasons is considered long-term (Bardgett et al. 2005). Yet, from these relatively short studies we learned that plants can select against less beneficial root symbionts (both rhizobia and mycorrhizal fungi) by altering carbon allocation patterns towards beneficial partners, thus promoting the long-term stability of plant interactions with beneficial strains (Kiers et al. 2003, Bever et al. 2009, Kiers et al. 2010). These short-term studies predict specialization of mutualisms over time, in this case the maintenance of only beneficial symbionts. However, natural plant symbiont populations are multi-functional (Smith and Read 2008), and which nutrient acquisition is only a single function occurring with other functions such as protecting the host plant against abiotic (Martínez-García et al. 2015, Zuccarini and Savé 2015) and biotic stressors (Allen et al. 1989, Bennett et al. 2006, Roger et al. 2013). Therefore, overall plant health may increase with a diverse consortium of mycorrhizae or rhizobia strains, even though in the short-term it may be carbon costly to the plant host (van der Heijden et al. 1998, Verbruggen and Kiers 2010).

Changes in host plant ontogeny and shifts in resource need over a plant lifetime may drive long-term dynamics of plant-mycorrhizal interactions. While less explored in plant-soil interactions, this principle is demonstrated in ant-acacia networks where the continuum from positive to negative interactions shifted over the host-plant lifespan (Palmer et al. 2010). Mycorrhizal strains

have a variety of impacts on their plant-host including increased leaf quality (e.g., Smith and Read 2008) or herbivore defense (Bennett et al. 2006, Bennett and Bever 2007, Gehring and Bennett 2009, Roger et al. 2013). If a plant associates with a mycorrhizal partner that increases leaf quality but not herbivore resistance early in their lifespan, then they could be more susceptible to herbivory later in their lifespan. Therefore, tradeoffs may exist in short- versus long-term benefits of microbial association for the host plant and may explain the diverse assemblages of mycorrhizal fungi observed in natural communities (Dumbrell et al. 2010, Davison et al. 2011), although this remains untested (Fig. 3).

Scaling plant-microbe interactions through time, from the microbe's perspective

Microbial populations can evolve on short time scales, thus shifting plant-microbe interactions quickly and altering how we scale ecosystem processes up to longer time periods (Chave 2013). Microbes can be active, potentially active, and dormant at any point in time and these states can shape the responsiveness of the ecosystem to perturbations (Blagodatskaya and Kuzyakov 2013). Even at the scale of a plant's growing season, microbial communities shift in their composition (e.g., Smit et al. 2001, Cregger et al. 2012). In fact, microbial communities can vary more across seasons than in response to long-term (>10 y) climate manipulations (Yuste et al. 2014). Therefore seasonal variation in microbial communities could be more important than inter-annual variation for ecosystem carbon fluxes. In a 6-year precipitation manipulation study, background microbial variation was consistently higher than variation due to altered precipitation (Gutknecht et al. 2012). Microbial adaptation and acclimation are often cited as explanations for why climate manipulations have no effect at long time scales (Bradford et al. 2008). Quick adaptation of microbial communities may allow for survival of plant species to contemporary climate change, as the longer generation times of plant host lag behind the highly dynamic microbial communities (Lau and Lennon 2012). Evolution may swamp long-term effects of climate and background microbial community variation may overwhelm climate treatments on seasonal time-scales. Capturing plant-microbe interactions

through time will require sampling at the appropriate time scale. A good starting point may be matching sampling time points with generation time of the target microbial groups. Moreover, data are often collected using different methods and at different time steps. Facing these challenges, we should be continuously asking whether we are measuring microbial processes at relevant spatial and temporal scales and identifying and counting the relevant members of the community.

EMERGING TECHNOLOGIES ADVANCE OUR UNDERSTANDING OF PLANT-MICROBE RESPONSES TO CLIMATIC CHANGE

Traditionally, studies aimed at understanding microbial dynamics have used methods such as PLFA (phospholipid fatty acid analysis), TRFLP (terminal restriction fragment length polymorphism), DGGE (denaturing gel gradient electrophoresis), or simply measures of biomass to understand complex community dynamics and function. While these methods have exposed patterns of microbial community composition at a coarse level (e.g., Gray et al. 2011), they do not show individual taxa responses and give limited insight into functional shifts. With the advent of new sequencing technologies and in the wake of the -omics revolution, researchers have begun to explore microbial interactions with hosts at a higher resolution and with more functional significance. By using meta-genomics, -transcriptomics, -proteomics, and -metabolomics, scientists are able to define changes in microbial communities that will result in a better understanding of which microbes are present in an ecosystem and what their potential functions are (e.g., Castro et al. 2012, Muller et al. 2013). Further, with technologies such as stable isotope probing, it is possible to target the active microbial community involved in a myriad of functions (e.g., Mau et al. 2015).

As the use of these techniques is increasing, researchers are left with many questions about which techniques yield the most accurate results, and further, what is the most informative and accurate way to analyze these extremely large datasets. Currently, amplicon sequencing of the 16S rRNA gene has become commonplace to characterize bacterial community composition in

ecosystems (Sanschagrín and Yergeau 2014). This yields large amounts of data at a depth that has started saturating species accumulation curves, but gives little to no information on potential functional shifts in communities (Fierer et al. 2012). Because of this, some have started using shotgun metagenomics to understand both microbial community composition and functional potential by assessing the diversity of functional genes within a habitat. Although this method yields data relevant to potential function, it lacks the depth associated with amplicon sequencing, so rare taxa may be overlooked (Shade et al. 2014, Lynch and Neufeld 2015, Zhou et al. 2015). With the rise of numerous new technologies aimed at understanding microbial dynamics in soils, it is important to begin sampling microbial communities at a scale that is relevant to the diversity and or function of these tiny organisms. Due to vast heterogeneity within a soil core, it may be difficult to deduce meaningful diversity patterns about these communities at such a coarse spatial scale (Ranjard et al. 2003). Microorganisms interact at the soil aggregate scale, with considerable variability observed across soil aggregates, or at the scale of the plant root-soil interface (Lombard et al. 2011). To truly begin understanding how microorganism interact with each other and plant hosts, future studies should take the questions they are asking about diversity and or function into account and adequately adjust their sampling scheme.

Beyond issues of what technologies to use to best study microbial communities, is the issue of how to analyze these large datasets (Zhou et al. 2015). An abundance of programs exist today to help with processing and analysis like qiime (Caporaso et al. 2010), mothur (Schloss et al. 2009), or less well known programs like IM-TORNADO (Jeraldo et al. 2014) using a number of diverse taxonomic databases to assign taxa identity. Use of each of these processing pipelines and assigning taxonomy with the different databases may yield different results with any given dataset. Researchers need to begin comparing these methods, and developing a standard protocol, so datasets can be compared across laboratories and research groups. Specifically, researchers need to explore which processing pipeline yields the most relevant results in a timely fashion, which database has the most up-

to-date and accurate taxonomic information for the taxa of interest, and how to standardize analyses across research groups to glean the most information out of a given dataset.

Another area where technological advances are increasing our understanding of the molecular basis for plant-microbial interactions are at the plant root-soil interface, where microorganisms are abundant and interact intimately with plant roots (e.g., Hol et al. 2013). Subsets of these soil microbes infiltrate the plant root and colonize the interior spaces; yet, how these microorganisms invade the plant root is difficult to tease apart. What molecular signaling occurs that allows microbes to evade the innate immune system of the plant and actively infiltrate the plant root? By using new sequencing technologies which allow cost efficient, rapid sequencing of full organismal genomes, we are beginning to piece together the molecular basis for these interactions. In the case of the mutualistic relationship between the ectomycorrhizal fungus *Laccaria* and its plant host, studies have shown that the *Laccaria* genome harbors unexpected features like effector type small-secreted proteins with unknown functions that are only expressed in symbiotic tissues (Martin et al. 2008). Further, one plant host, *Populus*, carries whole gene deletions for the D-mannose lectin-like receptor that significantly reduces *Laccaria* colonization (Labbé et al. 2011). Understanding the molecular basis for these interactions will enable manipulation of the microbial community to enhance plant and ecosystem level functions. It will also allow researchers to begin making predictions about which microbes will be present in the plant root endosphere and start building microbial communities capable of enhancing plant growth, carbon allocation, and carbon storage.

INTERACTIONS THAT INFLUENCE TIPPING POINTS IN SYSTEMS (STABILITY-EXTREME EVENTS)

Major disturbance events, such as heat waves, droughts, frosts, fire, and storms are increasing with global change (Frich et al. 2002). These events can alter large-scale processes such as regional net primary productivity (Ciais et al. 2005, Gu et al. 2008) as well as soil physical and biotic properties (Ajwa et al. 1999, Certini 2005,

Yuste et al. 2014). The stability of an ecosystem after disturbance depends on factors such as previous exposure to disturbance as well as community composition and diversity (Banning and Murphy 2008, Wardle and Jonsson 2014). Similar to aboveground (Maestre et al. 2012), there is growing evidence that belowground diversity is an important component of ecosystem stability and multifunctionality (Lefcheck et al. 2015; X. Jing et al., *unpublished manuscript*). For example, belowground arbuscular mycorrhizal fungal diversity can influence aboveground plant diversity, percent plant cover, soil aggregation, soil moisture, and soil carbon and nitrogen sequestration (Van der Heijden et al. 1998, 2008, Wilson et al. 2009, Yang et al. 2014). Further, when under stress diverse bacterial communities have a more stable biomass because they contain a larger number of organisms that are tolerant to stressors (Awasthi et al. 2014). Similarly, when microbial stress was reduced (e.g., higher soil carbon and nitrogen availability) across 58 studies spanning numerous ecosystems, microbial biomass turnover was slower suggesting a stabilizing effect on ecosystem functions over time (Wardle 1998). With anthropogenic induced changes to precipitation regimes, including increased storm severity and intensity influencing species gains and losses, understanding how belowground community stability may influence aboveground community response to disturbance is key for predicting how ecosystems may respond to global change (van der Heijden et al. 1998, Rillig et al. 2002, Brussaard et al. 2007, Wilson et al. 2009). While extreme events may only happen periodically, they will likely have long-lasting impacts on plant-microbe and microbe-microbe interactions and processes.

CONCLUSION

Interactions among plant and soil communities may be unpredictable when observing their responses to natural fluctuations in climate or at a single time point (Fig. 2). Due to the temperature sensitivity of carbon cycling processes, small changes in temperature could result in a large release of soil carbon back to the atmosphere (Fig. 1). Plant-derived carbon inputs strongly mediate the temperature sensitivity of soil carbon decomposition, but the relative

importance of direct versus indirect effects of climate change on soil carbon dynamics remains unresolved especially in ecosystems that are in transition from one state to another. We posit that the indirect effects of climate change on microbes mediated through plants may be stronger than direct effects of climate on shaping microbial community composition and function. These effects, however, must be measured at appropriate temporal and spatial scales, ideally in microbe-centric studies in order to complement the existing landscape of plant-centric climate change studies. Novel technological approaches will be pivotal in microbe-centric studies as we aim to reveal those taxa most sensitive to climate and those whose responses lead to shifts in microbial community function. Overall, these advances will be critical for making predictions about ecosystem tipping points, effects of extreme events, and the stability of communities under climate change. In sum, if we are to understand whether climate influenced shifts in microbe-microbe and plant-microbe interactions are equal or greater than the direct effects of climate change on the composition and function of ecosystems, we need to determine the best approaches to observe, quantify, and scale these interactions. Combinations of observations along natural gradients, with manipulations and experimental testing as well as modeling of plant and soil microbial communities and their interactions in response to climate change drivers is necessary to predict future ecosystem function.

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