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# Climate Disruption of Plant-Microbe Interactions

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## Abstract

Interactions between plants and microbes have important influences on evolutionary processes, population dynamics, community structure, and ecosystem function. We review the literature to document how climate change may disrupt these ecological interactions and develop a conceptual framework to integrate the pathways of plant-microbe responses to climate over different scales in space and time. We then create a blueprint to aid generalization that categorizes climate effects into changes in the context dependency of plant-microbe pairs, temporal mismatches and altered feedbacks over time, or spatial mismatches that accompany species range shifts. We pair a new graphical model of how plant-microbe interactions influence resistance to climate change with a statistical approach to predict the consequences of increasing variability in climate. Finally, we suggest pathways through which plant-microbe interactions can affect resilience during recovery from climate disruption. Throughout, we take a forward-looking perspective, highlighting knowledge gaps and directions for future research.

## 1. INTRODUCTION

Climate change has the potential to disrupt plant-microbe interactions at local to global scales, and improved understanding of these effects could alter future predictions and management of ecological and evolutionary responses to global environmental change. This potential for disruption sparked a recent "warning to humanity" about the importance of microbial responses to climate change (Cavicchioli et al. 2019). Plant-microbe interactions can affect the resistance (ability to remain unchanged) of plants or microbes to climate disruption and mediate ecological resilience to change (ability to recover from disturbance). Furthermore, plant-microbe interactions create feedbacks to climate in two important ways. First, as mutualists or pathogens, microbes alter primary production, thereby influencing the magnitude of the plant-based carbon (C) sink (Sulman et al. 2019). Second, microbes associated with plants influence decomposition and soil C, affecting respiration and the release of C back to the atmosphere (Classen et al. 2015, Song et al. 2019).

In this review, we first describe the diverse associations between plants and microbes and their ecological functions (Section 1.1), highlighting ways to improve the characterization of their natural history and biodiversity (Section 1.2). Second, we introduce an organizing framework to understand the effects of climate change on plant-microbe interactions across different spatiotemporal scales (Section 2). At the scale of individual organisms, disruptions to pairs of partners can occur through changes in context dependency, in which the outcome for fitness depends on the climate context. At the population scale, mismatches between plant-microbe partners can occur temporally through altered phenologies or repeated interactions (feedbacks) that affect population abundance. At the community scale, spatial mismatches can result from the loss of historical interactions or gain of novel interactions, as species migrate in response to climate change. Looking forward, we suggest how future research can help address key challenges in applying this spatiotemporal framework to plant-microbe interactions (Section 3). We then develop a new graphical and statistical approach to understanding how plant-microbe interactions influence resistance to climate disruptions (Section 4). Finally, we consider how plant-microbe interactions alter resilience following climate disruptions (Section 5). Throughout, we identify gaps in knowledge and suggest directions for future research.

### 1.1. Diverse Plant Microbiomes

Plants interact with microbes that are diverse in composition, function, and location within plant tissues. We briefly summarize this microbial diversity to set the stage for our review, describing microbial roles in plant resistance or resilience to climate stress and diversity in the degree of host-specificity and interaction outcomes.

**1.1.1. Aboveground interactions.** Plant leaves and stems are colonized by fungal and bacterial pathogens as well as endophytes, which are nonpathogenic for at least part of their life cycle (Rodriguez et al. 2009). Leaves are colonized by generalist, heterotrophic bacteria (e.g., Proteobacteria, Bacteroidetes) that disperse via wind, water, or insects (Frank et al. 2017). The majority of these ubiquitous fungal endophytes, mostly in the Ascomycota and Basidiomycota, spread horizontally among plant leaves and stems. Some function as decomposers in decaying litter and soil (Osono 2006); others may be latent pathogens, such as rusts or smuts. A minority of plants, including some legumes, morning glories, and grasses, host vertically transmitted fungi that grow into seeds and are obligately plant associated (Panaccione et al. 2014).

**1.1.2. Belowground interactions.** Roots support diverse endophytic and rhizospheric microbes that are horizontally transmitted through soil, air, water, or animal dispersers. These microbes include well-studied mutualists (e.g., mycorrhizal fungi, rhizobia) and ecologically important rhizosphere inhabitants that do not grow on or inside roots (Kariman et al. 2018). Most plant species (>80%) associate with arbuscular mycorrhizal (AM) fungi in the Glomeromycotina. Although a smaller fraction of species host ectomycorrhizal fungi (Ascomycota or Basidiomycota), these ectomycorrhizal plants have large geographic distributions (Smith & Read 2008, Soudzilovskaia et al. 2019, Steidinger et al. 2019). Other mycorrhizal types form in specialized plant lineages. Ericaceous plants support ericoid fungi in the Ascomycota, and orchids host orchidaceous mycorrhizal fungi, mostly Basidiomycota (Smith & Read 2008). Many, if not all, roots also have other nonpathogenic fungi, in addition to root pathogens. For example, in desert and alpine biomes, dark septate fungal endophytes (Ascomycota) commonly dominate roots (Porras-Alfaro & Bayman 2011). Hyaline and melanized ascomycetes are abundant in roots, even in ecosystems such as prairies, where AM fungi have been the primary focus of research (Jumpponen et al. 2017). Plant roots and rhizospheres also host bacteria from multiple phyla, including Actinobacteria and Proteobacteria (Hardoim et al. 2015). Some plant lineages (e.g., Fabaceae) create specialized nodules for nitrogen (N)-fixing bacteria (e.g., *Rhizobium*, *Frankia*), which convert atmospheric N into plant-available forms (Menge et al. 2019).

**1.1.3. Resistance and resilience to climate stressors.** Pairwise plant-microbe interactions can modulate species' responses to climate and related stressors in several ways. Leaf endophytes can improve plant tolerance of drought, heat, or salinity, increase tissue nutrient concentrations, and deter herbivores or pathogens (reviewed by Kivlin et al. 2013, Hardoim et al. 2015, Busby et al. 2016). Mycorrhizal fungi acquire up to 80% of plant N and 75% of phosphorus (P) (van der Heijden et al. 2008) and increase water uptake from soil (Smith & Read 2008). Root ascomycetes can acquire soil N and protect plants under drought or heat stress (Porras-Alfaro & Bayman 2011, Kivlin et al. 2013). Some fungi and plant growth-promoting bacteria produce analogs of plant hormones that stimulate germination or growth (Rana et al. 2019). Rhizosphere bacteria, such as *Streptomyces*, can increase plant fitness under drought or disease (Hardoim et al. 2015, Fitzpatrick et al. 2018). N-fixing bacteria boost N in leaves, roots, rhizospheres, and seeds (Hardoim et al. 2015, Frank et al. 2017). All these benefits can help plants resist and recover from climate-related stress. However, despite many potential benefits, a neutral stage is common in many microbial life cycles. For example, some endophytes that are neutral in living leaves degrade litter as primary decomposers, gaining first-priority access to senesced tissue (Osono 2006). Alternatively, non-neutral effects may be triggered only by specific stressors, producing a continuum of fitness outcomes even for the same pair of plant-microbe species.

**1.1.4. Continua in interaction outcomes and specialization.** Even with strong evidence for modulation of climate stressors, pairwise plant-microbe interactions typically span a continuum of outcomes, from beneficial to parasitic, as well as a range of specializations, from obligate to facultative. The outcomes depend on the benefits (resources or services) provided and their costs. The key plant resource exchanged is C from photosynthesis, but C exchange varies widely among interactions. At one extreme, AM fungi depend obligately on plant C. At the other, achlorophyllous plants and orchid seedlings receive all C from their mycorrhizal partner through another host plant (e.g., Merckx et al. 2009). In pathogenic interactions, some bacteria and fungi directly degrade plant cell walls for C (necrotrophy), whereas others parasitize only living tissues (biotrophy) (Berger et al. 2007). To categorize interactions along the continuum, a global database has binned >13,000 fungi by similarity of resource use, including endophyte, pathogen, and mycorrhizal guilds, and identified approximately 16% as beneficial symbionts and approximately 50% as pathogens (Nguyen et al. 2016). No such database yet exists for plant-associated bacteria. In addition, the utility of such designations depends on the degree to which interaction outcomes are stable (see Section 2.2), and many taxa should likely receive multiple guild designations (e.g., pathogen and endophyte).

### 1.2. Future Directions in Characterizing Plant-Microbe Associations

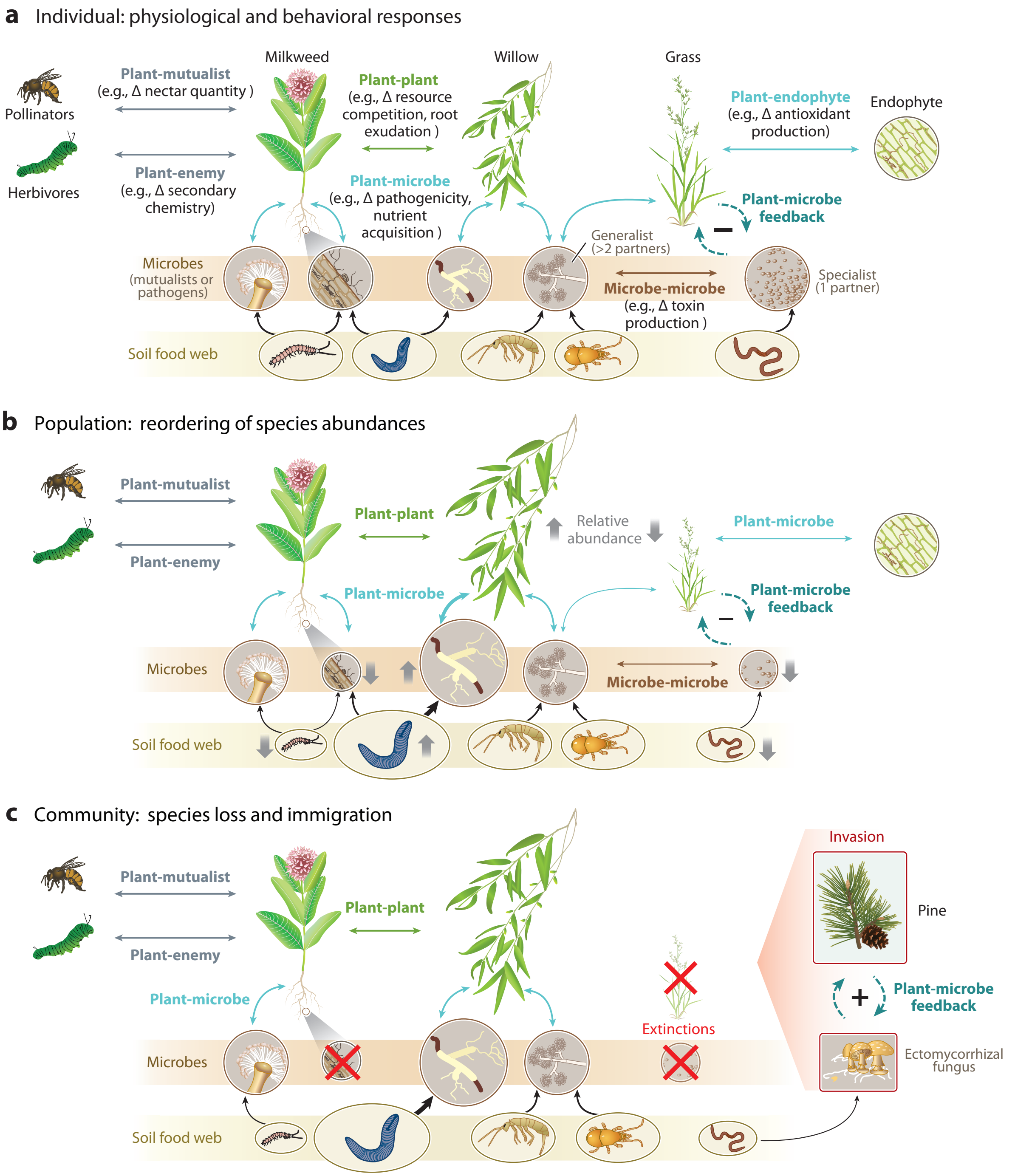
Much is left to discover about the diversity and function of plant-associated microbes. Future progress may be enhanced by mining DNA repositories of plant samples for microbial sequences (Datlof et al. 2017) or using herbarium specimens to characterize microbial associations over wide frames of time or space (Daru et al. 2019). Identifying microbes in seeds and pollen can advance understanding of microbial community assembly during plant ontogeny and succession (Shade et al. 2017). For example, recent work detected priority effects in microbial community assembly through seedling-litter interactions (Christian et al. 2017). Studies that characterize the full plant microbiome—in roots, leaves, stems, and seeds—may uncover novel microbial biodiversity and inform on microbial overlap among plant tissue compartments. Certain biomes remain understudied, such as boreal forests, tropical grasslands, and alpine habitats (Harrison & Griffin 2020).

The discovery of microbial biodiversity has greatly outpaced understanding of function in plant-microbe interactions. Culture collections can enable new experiments, well-curated omics data can circumscribe potential functions, and tools such as quantitative stable isotope probing can separate active from dormant microbes in field environments (Morrissey et al. 2019). Growing evidence indicates that interactions among microbes will be crucial to understanding net outcomes of the full microbiome for plants. For example, the ecological functions of endophytes and pathogens can depend on endohyphal bacteria or viruses (Márquez et al. 2007, Arora & Riyaz-Ul-Hassan 2019), and bacterial inoculations can mediate benefits from mycorrhizal fungi (Hoeksema et al. 2010). Therefore, linking climate-altered networks of microbe-microbe interactions to altered functions is an important research goal.

## 2. BUILDING A HIERARCHICAL RESPONSE FRAMEWORK FOR PLANT-MICROBE INTERACTIONS: HOW HAS CLIMATE CHANGE DISRUPTED PLANT-MICROBE INTERACTIONS ACROSS SPATIOTEMPORAL SCALES?

Climate disruptions can affect plants and microbes through a hierarchical series of events. Thus, we have expanded the hierarchical response framework (HRF) to encompass the plant microbiome as well as plant-plant, plant-mutualist, and plant-enemy interactions both above and below ground (**Figure 1**). The HRF was originally proposed for ecosystem dynamics (Smith et al. 2009) and later adapted to soil food webs (Bardgett et al. 2013). This framework organizes responses to climate disruption into three spatiotemporal scales: individual, population, or community.

First, at the smallest scale, individual organisms respond to climate through physiological, behavioral, or phenological changes that reflect their sensitivity to climate variables (**Figure 1*a***; Section 2.2). For example, foliar fungal endophytes can upregulate antioxidants that protect plants



**a** Individual: physiological and behavioral responses

**b** Population: reordering of species abundances

**c** Community: species loss and immigration

*(Caption appears on following page)*

**Figure 1** (*Figure appears on preceding page*)

Hierarchical response framework conceptual diagram showing pathways of climate disruption on plant-microbe interactions. (*a*) Individual: physiological and behavioral responses. In the first stage, climate affects the physiological and behavioral processes of individual organisms, including activities and phenology, but does not alter the relative abundances of species. Here, climate disruption is indicated by Δ. Three plant species interact with five microbes, which vary from specialist (only one partner) to generalist (more than one partner) and may be mutualists or pathogens. Plants also interact with nonmicrobial enemies (e.g., herbivores) and mutualists (e.g., pollinators) that can indirectly alter their interactions with microbes. Microbes feed other organisms within the food web (*gray arrows*). Plant-microbe feedback requires repeated interactions over time (*dashed teal arrows*) that affect the physiology or activities of interacting species, here as a net negative (−) change. (*b*) Population: reordering of species abundances. In the second stage, the effects of climate disruption on physiological processes and activities become strong enough to alter population growth rates, which reorder the relative abundances (represented by relative image size) of species in the community but do not affect the presence or absence of species. For example, the willow plant and its specialized ectomycorrhizal fungus become relatively more abundant, as represented by a larger image size and thickened blue arrows, whereas the grass and its specialized bacterium decline, as represented by their smaller image size. In addition, climate change creates a temporal mismatch between the milkweed plant and its root fungus, which reduces both fungal abundance (reduced image size) and the abundance of its millipede consumer in the soil food web (reduced image size) but does not cause extinction from the local community. (*c*) Community: species loss and immigration. In the third stage, the effects of climate disruption on demographic processes become strong enough to cause local species extinctions, indicated by species with a red X: the grass, its specialist bacterium, and the root fungus of the milkweed plant are lost from the community. Climate change can also create new opportunities for immigration. A pine and its ectomycorrhizal fungus (*red boxes*) invade. Dashed teal arrows represent positive (+) plant-microbe feedback for the new immigrants, in which the pine promotes microbes that increase its relative abundance in the community through repeated interactions over time. The pace of the transition from panel *b* to panel *c* will depend on the magnitude of population declines and species' dispersal rates. Figure inspired by Smith et al. (2009) and Bardgett et al. (2013).

against reactive oxygen species produced under drought stress (Woodward et al. 2012) (see the plant-endophyte interactions in leaves in **Figure 1*a***). Climate change can create context dependency (e.g., flip a pathogen species to a mutualist) by altering the magnitude or direction of these individual-scale responses as the underlying environmental conditions change beneath a particular plant-microbe pair (**Figure 2*a***).

Second, over time, these individual responses to climate create fitness differences among species that reorder their relative abundances in the community by altering rates of population growth (see Section 2.3). In our example, a woody shrub and its ectomycorrhizal fungus increase in abundance under climate change, while a grass and its specialist bacterium decline (**Figure 1*b***). Such changes in population abundances can cause temporal mismatches (**Figure 2*b***) between pairs of plants and microbes at the population scale of the hierarchy. Here, the same species are retained in the community, but their interactions are offset temporally in ways that disrupt plant-microbe interactions. For example, in **Figure 1*b***, the milkweed plant no longer temporally overlaps with and promotes the root fungal endophyte. Temporal mismatches can be caused by shifting phenologies at the individual response scale (**Figure 1*a***) that prevent species interactions, even when both species remain in the community. In addition, temporal shifts in community composition can occur through well-studied plant-microbe feedbacks, in which repeated interactions between plants and microbes alter their population abundances over time (**Figure 1*b***). Here, a net negative feedback occurs (see the dual dashed blue arrows in **Figure 1*b***), in which the pairwise plant-microbe interaction reduces plant population abundance over time relative to interactions with microbes from other plant species. We develop this concept further in Section 2.3.2.

Third, at the largest spatiotemporal scale of the community, climate effects on species abundances eventually cause species losses or enable successful immigration, altering community succession (see Section 2.4). Potential community-level changes are illustrated in **Figure 1*c***, which shows grass and microbe extinctions as well as pine and ectomycorrhizal fungus invasions. Applied to plant-microbe interactions, this community response scale comprises interactions that are lost or gained in space when species distributions shift with climate (**Figure 2*c***). For instance, a recent study predicted that climate change during the next 50 years may cause up to 26% declines in the

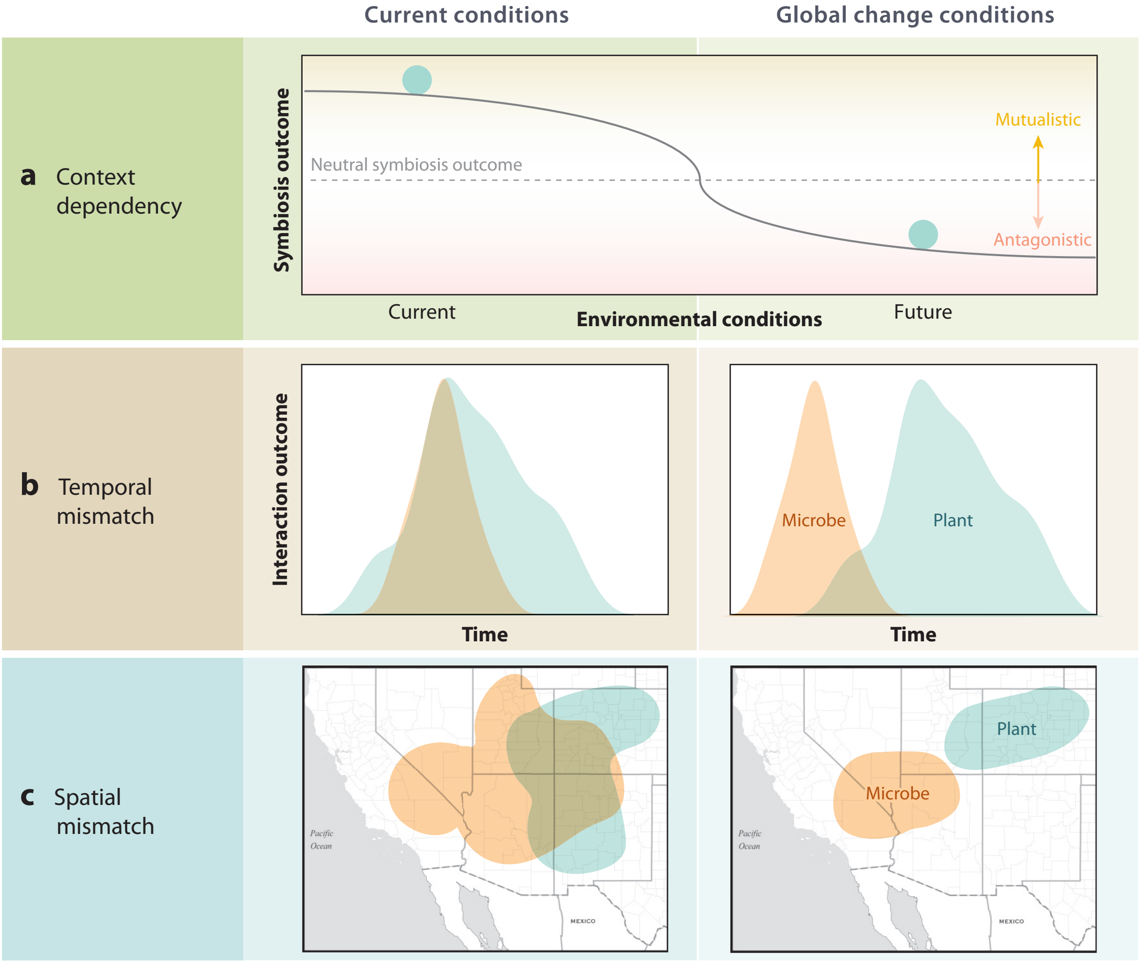


**Figure 2**

Plant-microbe interactions can be altered by climate change in multiple ways. (*a*) Context dependency: Climate change can switch a currently functional plant-microbe mutualism to an antagonism; thus, the fitness outcome (*blue circle*) for a plant species involved in the interaction depends on the climate context. (*b*) Temporal mismatch: Climate change can shift plant and microbe relative abundance or activity over time. Plant-microbe interactions become decoupled temporally under a new climate condition, even when both species remain in the community. (*c*) Spatial mismatch: Over long time periods, climate change can alter the species ranges of plants and microorganisms, causing mismatches in plant-microbe pairings due to losses or gains of species at the community scale.

number of ectomycorrhizal fungal species in pine forests over 3.5 million km$^2$ of North America (Steidinger et al. 2020).

To expand the HRF to plant-microbe interactions, we first describe the types of climate disruptions most relevant to plants and their microbes (Section 2.1), then we provide examples of disruptions at each spatiotemporal scale (Sections 2.2–2.4). Looking forward, we address three challenges in applying the HRF to the study of plant-microbe interactions (Section 3.). Our goal is to inspire integration across scales: linking responses of individual organisms to changes in population growth and ultimately to altered community succession and ecosystem dynamics.

## 2.1. Types of Climate Disruptions Across the Hierarchical Response Framework

The elements of climate change most relevant to plants and microbes include chronic presses (e.g., warming, drying, elevated $CO_2$), extreme events (e.g., drought, deluge, freeze, climate-driven fire), altered timing of events (e.g., seasonal rain pulses, spring warm-up), and increased climate variance or stochasticity at both intra- and interannual timescales. The outcomes of chronic changes or single extreme events are easier to predict from current experiments than are responses to changes in timing or variance, which require more difficult experimental designs (see Section 4.3) and may cause nondirectional selection or favor generalist interactions (Keitt et al. 2016). In addition, historical climate may constrain contemporary plant or microbe responses to future climate change by leaving a legacy in the composition or function of the community (e.g., Hawkes et al. 2017).

The majority of climate experiments focus on single variables; however, multiple aspects of global change are likely to interact (Smith et al. 2009). Although prior work suggests that many treatment effects are additive (Wu et al. 2011, Song et al. 2019), most studies test only 2–3 factors, typically precipitation, warming, and $CO_2$. A recent laboratory study manipulated ten global change factors, including temperature, resources, and pollutants (Rillig et al. 2019), revealing unpredictable nonadditive effects that emerged when >8 factors were combined. As the number of factors increased, taxonomic richness of soil microbes declined, and composition diverged more strongly among replicates, suggesting that nonadditive effects magnified stochasticity. Looking forward, methodological advances that can enhance the precision of estimated responses include nonlinear gradient designs that extend beyond observed extremes, coordinated distributed experiments spanning multiple sites, controlled Ecotrons finely tuned to regional climate projections (Rineau et al. 2019), and space-for-time observation networks that capture complex covariation in meteorological variables.

## 2.2. Individual Scale: Context Dependency in Pairwise Interactions

Climate disruptions can alter the outcome of a given plant-microbe interaction, such that the association between the same partner species shifts along the mutualism-parasitism continuum depending on the climate context (**Figure 2*a***). For example, plants infected with barley yellow dwarf virus, typically a pathogen, recovered from severe drought better than noninfected plants, maintained higher leaf water potential under drought, and made more seeds (Davis et al. 2015).

In mutualisms, climate-driven disruptions via context dependency may be caused by changes to the costs of producing rewards, the benefits of receiving rewards, or both. If rewards become more costly, or even impossible, under climatic stress, partners will reduce investment in trade such that the association becomes parasitic, degrades, or is lost. These effects can be caused by responses in organismal physiology that limit the quality, quantity, or type of resource exchanged (see climate disruption in **Figure 1*a***). For example, in a split-root experiment with peas, drought reduced local N-fixation by bacteria and altered cell redox potential and microbial enzyme activity (Marino et al. 2007).

Even if rewards remain identical in quality and quantity under a new climate, their value to receiving species (the exchange rate) may not remain stable. For instance, plants reduce C to microbes when the microbial resource (e.g., P) becomes abundantly available from the environment (e.g., fertilization) (reviewed by Johnson et al. 2013). When microbial benefits are the amelioration of climate stress (reviewed by Kivlin et al. 2013, Classen et al. 2015), climate disruption may alternatively increase the value of rewards to plants, in addition to altering reward quality or quantity.

Finally, when climate causes species loss or immigration (**Figure 1*c***), opportunities for novel interactions arise. If new partners provide better rewards or are better competitors than original partners, this new community context could disrupt interactions, even if original partners could, hypothetically, continue to interact. For example, comparative work documented lineages of seed plants that switched partners from AM fungi to other symbionts over evolutionary time and suggested this switch was sparked by environmental change (Werner et al. 2018). While many studies demonstrate the phenomenon of context dependency in plant-microbe interactions, an integrated understanding will come from research that measures the resources exchanged; shows that resource exchanges decline (or increase) in quantity, quality, or value under climate stress; and identifies the mechanisms causing the change in resources.

## 2.3. Population Scale: Temporal Mismatches

Climate disruptions can create temporal mismatches between plants and microbes that extend or reduce the time period of an interaction. The timing of biological activity often depends on environmental cues, many of which shift with climate change. If plants and microbes differ in the types of cues they respond to, their sensitivity to those cues, or the magnitude of their phenological responsiveness to climate cues, these responses could alter the number of individuals that interact at a given point in time at the population scale of the HRF (**Figure 1*b***), even when both species remain present in a local community. For example, plant bud burst and flowering phenology cue on spring temperature in temperate biomes, and their timing has advanced 2.5 days per decade since 1971 (Körner & Basler 2010). At the other end of the seasonal spectrum, onset of fall fruiting in macrofungi was increasingly delayed under warmer, drier weather (Diez et al. 2013).

### 2.3.1. Temporal mismatches via phenological change.

Climate effects at the individual response scale of phenology have strong potential to disrupt populations of interacting plants and microbes. For example, in a northern hardwood forest, tree canopy leaf-out has responded more slowly to spring warming than soil biological activity has, creating longer periods of mismatch between root nutrient uptake and microbial mineralization of organic matter, which cause early spring nutrient flushes into the watershed (Groffman et al. 2012). Root activity often initiates later than shoots and extends beyond the termination of leaf activity (Radville et al. 2016). Some variables, such as day length, may affect plants and leaf endophytes but not belowground microbes, which could be more buffered against climate change.

Compared with the temporal dynamics of plants, individual responses of microbial phenologies are much less resolved. Some evidence correlates climate variables with observed microbial phenology or succession. For example, ectomycorrhizal root phenology was most strongly associated with temperature in a dry subtropical forest (Kou et al. 2019), and bacterial microbiomes of wild mustards changed yearly with temperature and soil moisture along an elevation gradient (Wagner et al. 2016). Reviews on crops highlight that warming increases pathogen overwintering survival, and humidity can accelerate pathogen development (e.g., Velasquez et al. 2018). When plant-associated microbes are considered holistically, subsets of taxa likely respond divergently in phenological sensitivity to climate. Studies that compare microbial phenology for leaves and roots in the same ecosystem could evaluate whether the potential for phenological mismatch generally differs above versus below ground. Future work to identify the environmental cues and sensitivities of specific microbial taxa or guilds can guide predictions on how often changing climate will cause temporal mismatches.

### 2.3.2. Temporal mismatches via plant-microbe feedbacks.

Climate disruptions can alter the repeated interactions between individual plants and populations of microbes that generate plant-microbe feedbacks over time (Pugnaire et al. 2019, Beals et al. 2020). Plants accumulate species-specific microbiomes, and feedback occurs when a plant alters microbes in ways that affect the plant's fitness relative to the fitness of its plant competitors (Bever et al. 1997). Plants often develop negative plant-microbe feedbacks, in which the microbes that accumulate in and around plant tissues, such as plant species-specific pathogens, affect individuals of that plant species more negatively than those microbes affect other plant species in the community (**Figure 1*a*,*b***). Negative feedback can generate the negative conspecific frequency dependence that promotes species coexistence, by limiting a plant species most strongly when it becomes relatively more frequent in a community (reviewed by Crawford et al. 2019). Microbial mutualists can also generate negative feedback if they are shared among plant species, and the best plant hosts do not gain the largest benefits (Bever et al. 1997). Alternatively, mutualism drives positive feedback, which destabilizes species coexistence and promotes invasion (**Figure 1*c***), particularly when mutualists are not shared among plant species. Climate disruptions to plant-microbe feedback may be a common mechanism that reorders species' relative abundances in communities (**Figure 1*b***), and the effects of feedbacks on community-level dynamics make them useful tools for extending plant-microbe interactions beyond the population scale.

Few experiments have explicitly tested for climate effects on plant-microbe feedbacks. Among climate variables, drought may cause the largest amplification of negative feedback, but it is also the most studied and had weaker effects than manipulations of plant competition (reviewed by Beals et al. 2020). The timing of climate disruption during the feedback process is likely important. For example, in grassland mesocosms, historical drought made subsequent feedbacks more negative than in nondroughted soils, potentially enhancing plant coexistence (Kaisermann et al. 2017). In contrast, two greenhouse studies applied drought while feedback developed, and this contemporary drought neutralized both positive and negative feedbacks between pairs of grassland forbs (Fry et al. 2018, Snyder & Harmon-Threatt 2019). While the mechanisms causing climate-altered feedback remain largely unknown, microbial reordering and altered plant physiology at the individual response scale (e.g., climate disruption of root exudates in **Figure 1*a***) are likely (reviewed by Pugnaire et al. 2019).

Generalizations about the magnitude and direction of climate impacts on feedback await experiments that address emergent plant or microbe community properties. First, considering microbial functional groups or guilds may aid generalization. In one of the largest feedback studies to date (550 populations from 55 tree species), most trees with ectomycorrhizal fungi had positive feedback, whereas those with AM fungi had negative feedback (Bennett et al. 2017). Leaf guilds can generate feedbacks through the phyllosphere (Whitaker et al. 2017) and could be even more sensitive to climate than microbes in soils (Vacher et al. 2016), but they are far less studied for feedback potential. Second, a general hypothesis to test as more data accumulate is that shifts in feedbacks under climate change are predictable from the relative impacts of climate variables on mutualists versus pathogens. Under climate stress, mutualists that ameliorate that stress will most often weaken negative feedback, whereas specialist pathogens that drive negative feedback will become more effective. For example, seven years of snow addition to arctic tundra increased a specialist pathogen of the dominant shrub, killing its shoots, reducing C storage (Olofsson et al. 2011), and likely amplifying negative feedback. Third, dissimilarity in microbial composition may predict the direction of feedback. For instance, pairs of plant species with more dissimilar communities of endophytic root bacteria had more positive feedback than pairs with similar microbes (Fitzpatrick et al. 2018). This hypothesis could be used to predict feedback outcomes a priori from existing data sets on microbial communities from climate experiments. A next generation of feedback experiments could use microbial inocula from field-based climate treatments to compare feedbacks among communities that have been reordered by climate manipulations (e.g., Kaisermann et al. 2017).

**2.3.3. Temporal mismatches on evolutionary timescales.** An important layer to the HRF is the role of evolution. Evolution is likely to be slower for plants than microbes due to their longer generation times (Frantzeskakis et al. 2020). Long-lived plants may not respond to climate through evolutionary change within the timeframe of microbial species loss and immigration (**Figure 1*c***), whereas microbial evolution could occur even at the timescale of an individual plant's responses (**Figure 1*a***), as in notable examples of rapid evolution of agricultural pathogens (Frantzeskakis et al. 2020). Trait evolution could also slow or speed transitions between stages of the hierarchy (**Figure 1**). Evolutionary sheltering, which occurs when adaptations to climate change in one partner buffer the fitness consequences of change for the other partner, may prevent species from adapting to change (Branco 2019). Alternatively, evolutionary rescue could be microbially mediated, whereby changes in a plant's microbiome improve host fitness and avert extinction (Mueller et al. 2020). For example, a multigeneration drought experiment caused no evolutionary change in drought resistance of the focal plant but quickly reordered soil microbial composition, which promoted subsequent drought resistance (Lau & Lennon 2012). Temporal mismatches may generate conflicting selection pressures on plants versus microbes. Models show that whether coevolutionary dynamics magnify or dampen evolutionary responses to climate change depends on whether a species benefits or suffers from selection on a trait of its partner (Northfield & Ives 2013). Exploring how species interactions modulate evolutionary responses to climate change is a rich area for future investigation (Lau & terHorst 2020).

## 2.4. Community Scale: Spatial Mismatches

Climate disruptions can create spatial mismatches between plants and microbes that involve lost or novel associations at the largest spatiotemporal scale of the HRF (**Figures 1*c*** and **2*c***). Spatial mismatches caused by climate change may arise in several ways. First, species may diverge in their sensitivity to the same climate variables or microbial interactions; one species may survive a new habitat, but another may not. For example, pines colonizing above the tree line differed in their ability to partner with resident mycorrhizal fungi, allowing one species to leapfrog another during upslope migration (Shemesh et al. 2019). When species' migrations are driven by climate change (e.g., Parmesan 2006), climate disruptions cause spatial mismatches in plant-microbe interactions. For example, work on Douglas fir suggested that fungal mismatches with plants could slow migration. When seed origins were spatially mismatched with soil origins across an altitudinal climate gradient, seedlings grew worse than when matched with their home soils, and soil fungi were likely responsible for that mismatch, because fungicide weakened this effect (Pickles et al. 2015). Second, plants and microbes may respond to different climate variables, which then spatially offset their ability to interact as climate changes. Plants may track warming air temperatures, while root microbes follow soil moisture. Third, species can respond to the same climate variables but diverge in their dispersal ability, affecting migration distance. For example, some basidiomycetes disperse more poorly than others or even lack structures for aerial dispersal (Hayward et al. 2015a). This variation could shift interactions from slow- to fast-dispersing partner species as species migrate in response to climate change. Among microbial guilds, dispersal kernels of pathogens were larger than those of some mutualists (Kivlin et al. 2014), suggesting that spatial decoupling of plants and preferred mutualists may occur under climate change, potentially strengthening negative plant-microbe feedback over time.

**2.4.1. Species invasions as case studies for climate-induced spatial mismatches.** Species invasions provide unique opportunities to understand the potential for spatial mismatches caused by climate change. Plants that colonize a new area, whether through human-mediated dispersal or due to climate change, have four main strategies (Dickie et al. 2017). In the first strategy, invading plants do not form associations with new microbes. For example, many introduced plant species have been successful because they can persist without mycorrhizae. This facultative strategy was identified as the most successful for plant invasions (Moyano et al. 2020) and may be important in climate-induced migrations. Many invasive species reach high densities in the absence of enemies in their new range (the enemy release hypothesis) (Keane & Crawley 2002), although few cases are explicitly linked to climate change. For example, a range-expanding forb had neutral to positive interactions with soil biota from its newly expanded poleward range but net negative interactions with soils from its original range (van Grunsven et al. 2010). However, the explicit role of climate variables in this spatial mismatch is unresolved.

In the second strategy, plants associate with ubiquitous microbes that occur in both their native and nonnative ranges. For example, generalist AM fungi have broad geographic ranges (Soudzilovskaia et al. 2019), and plants may profit from this guild even when arriving on a new continent.

Plants that form novel associations with new local species represent the third strategy. Some hosts of N-fixing bacteria pair with new species in their nonnative range (Birnbaum et al. 2016). However, a lack of microbial associations may be a more common barrier for climate migrants than is currently recognized.

In the fourth strategy, plants move with their current symbionts (i.e., coinvasion) (Núñez & Dickie 2014). For example, many pines invade only if they arrive with specialized ectomycorrhizal fungi (Núñez et al. 2017). *Pinus contorta* can establish in new habitats in Patagonia with only one species of ectomycorrhizal fungus (Hayward et al. 2015b), while in its native range, it hosts hundreds of fungal species. When species coinvade, context dependency may become important. For example, in *Brachypodium* grass, a foliar fungus that was beneficial in the native range became detrimental in the nonnative range because herbivore protection was less valuable (Vandegrift et al. 2015).

The same four strategies apply to microbes that colonize new areas or are left behind when their partners migrate, but few examples exist outside of agricultural ecosystems. Drier climate was predicted to slow the spread of the widely invasive pathogen *Phytophthora cinnamomi* because greater densities of inoculum were required to initiate pathogenicity in drier soils (Homet et al. 2019). For specialized microbes with obligate host associations, range shifts to track climate may hinge on the availability of suitable plant hosts.

**2.4.2. Mapping the global picture.** Understanding spatial mismatches between plants and microbes requires data on geographic distributions, climate niches, and dispersal capabilities, especially for microbes other than agricultural pathogens. For example, recent efforts to map mycorrhizal fungi and N-fixing bacteria using global forest inventories forecasted a 10% decline in trees hosting ectomycorrhizal fungi by 2070 under climate warming (Steidinger et al. 2019). Such a decline could have large impacts on forestry and on biogeochemical cycles, causing negative feedbacks to climate change, because ectomycorrhizal hosts dominate slow-to-decompose environments while simultaneously increasing the photosynthesis C sink under elevated $CO_2$ (Terrer et al. 2016, Steidinger et al. 2019). Another global study linked these projections with microbial N-uptake, which expanded future estimates of global C storage through reduced N-limitation of photosynthesis (Sulman et al. 2019). While these studies take big steps forward in global scaling of plant-microbe interactions and their biogeochemical consequences, they make the simplifying assumption that partnerships remain stable and functionally similar in future climates, despite evidence for context dependency (see Section 2.2). In addition, advances in range estimates for specific plant-associated microbes can improve these distribution models. For example, niche models for a native grass revealed a 20% increase of niche breadth into drier habitats when the models included symbiosis with a fungal endophyte (Afkhami et al. 2014). Knowledge of codistributions and their climate predictors can begin to estimate the potential for spatial mismatches under future climates, improving the management of species migrations and refining biogeochemical projections.

## 3. EXTENDING THE HIERARCHICAL RESPONSE FRAMEWORK TO PLANT-MICROBE INTERACTIONS: FUTURE CHALLENGES

### 3.1. Challenge One: Decoupling Plant Responses from Their Complex Microbiomes

Complex microbiomes complicate the ability to decouple direct effects of climate on plants from the effects mediated by their resident microbes. Many climate experiments report plant responses at each stage of the HRF (Smith et al. 2009). These include changes in individual plant physiology or phenology (**Figure 1*a***), reordering of plant species abundances (**Figure 1*b***), and reduced primary production at the ecosystem scale (e.g., Smith et al. 2009, Wu et al. 2011, Wilcox et al. 2017a, Ploughe et al. 2019, Song et al. 2019). Resurvey studies have also documented shifts in species ranges (**Figure 1*c***) over altitudinal and latitudinal gradients that coincide with changing climate (Parmesan 2006). However, it remains largely unknown how much the plant responses reported to date were buffered (or exacerbated) by microbes. This requires experiments that alter climate in combination with manipulations of microbial communities.

Those experiments are demanding outside controlled environments and complex at scales beyond individual plants. For example, to replicate climate-induced migrations, helicopters moved turfs containing plant communities both upslope and downslope among alpine meadows (Alexander et al. 2015). Novel plant communities from low elevations more successfully outcompeted alpine plants than their current alpine competitors, especially at warm, low elevation. However, even this massive effort did not factorially manipulate microbes to separate their effects from plant competition and likely missed important priority effects during plant (and microbe) early establishment. In another study, a vertically transmitted fungal leaf endophyte was jointly manipulated with rainout shelters and rain additions in a primary succession dune. The host grass grew larger with the endophyte than without but responded minimally to precipitation. Treatment effects were additive, suggesting the endophyte did not modulate host plant response to rainfall (Emery et al. 2015). However, the endophyte reduced plant community diversity as new species colonized, and that effect weakened nonadditively under both augmented and reduced rainfall (Rudgers et al. 2015). The leaf endophyte also decreased the diversity of AM fungi in roots, altered how rhizosphere bacteria tracked soil moisture, and slowed litter decomposition (Bell-Dereske et al. 2017a,b). Thus, complex microbiomes can complicate the ability to decouple direct effects of climate on plants from the indirect effects mediated by plant-associated microbes. We suggest a two-pronged approach to this decoupling challenge. First, experiments that add microbes to sterile plants can test for synergies from the bottom up (e.g., Connor et al. 2017). Second, experiments that suppress particular guilds (e.g., selective antibiotics; see Pickles et al. 2015) can take a knockout approach to microbial interactions.

### 3.2. Challenge Two: Linking Responses of Microbes Across Stages of the Hierarchical Response Framework

Compared to what is known about plants, less is known about how climate disruption directly affects plant-associated microbes across the hierarchy of responses (**Figure 1**). For example, studies on plant responses to climate change connect individual-scale responses or traits, such as leaf turgor loss point, to changes in plant species reordering at the population scale, then to species loss at the local community scale, and even to ecosystem-scale primary productivity (e.g., Griffin-Nolan et al. 2019). While measurements at each scale do exist for plant-associated microbes, integration across scales is missing for any single system. For example, at the individual scale (**Figure 1*a***), phenology of fruiting basidiomycetes has received some attention (Diez et al. 2013), but do these changes cascade to species reordering or the loss or gain of species in communities? In climate experiments, disruptions clearly alter microbial activity (**Figure 1*a***) and biomass of whole microbial communities (**Figure 1*b***). However, connecting individual responses of microbe species to changes in community structure remains technically challenging because of the inability to visualize and track individual microbes in plant tissues or in soils in the field. In addition, little is known about microbial phenology (**Figure 1*a***) or succession (**Figure 1*c***) because most microbial studies take single snapshots in time using environmental sequencing or other approaches (Harrison & Griffin 2020). However, some time series data do exist for soil microbes in response to climate variables. For example, six years of experimental warming reduced the importance of stochastic processes in microbial succession, driving stronger directional change in soil fungal than soil bacterial assemblages (Guo et al. 2018). Filling knowledge gaps on the climate tolerances of individual plant-associated microbial species (e.g., via laboratory experiments on environmental response surfaces or environmental niche modeling) will be crucial (see Section 4). Toward this end, it is challenging, but possible, to separate out the direct effects of climate on plant-associated microbes from plant responses to climate [e.g., using hyphal isolation (Barrett et al. 2014)].

### 3.3. Challenge Three: Integrating Indirect Pathways of Climate Disruption

Climate disruptions may influence plant-microbe interactions indirectly by altering other types of surrounding biotic interactions. Like the direct effects of climate, these indirect disruptions represent a rich area for research progress across the spatiotemporal hierarchy, from short-term physiological and metabolic changes to species reordering to wholesale species losses or gains (**Figure 1**). Under stressful climates, plant-plant interactions may shift between competitive and facilitative (Ploughe et al. 2019) and then influence microbes. For example, intraspecific plant competition exacerbated negative plant-soil feedback in a large meta-analysis of pairwise comparisons (Crawford et al. 2019). Conversely, microbes can alter plant-plant interactions under climate change. Soil microbes intensified intraspecific plant-plant competition under increasing drought (Hawkins & Crawford 2018). Climates that reorder plant species abundances can affect microbial dynamics indirectly through changes in host-specific microbes. For example, increased plant diversity reduced disease caused by specific plant pathogens (Schnitzer et al. 2011). Microbe-microbe interactions could respond to climate disruptions, then alter microbial interactions with plants. For instance, coinoculations of foliar fungi nonadditively benefited switchgrass plants under drought (Connor et al. 2017), suggesting microbe-microbe synergisms. Climate changes to plant-enemy and plant-mutualist interactions (**Figure 1*a***) may also cascade to plant-microbe interactions. For instance, drought increased insect herbivory, which altered foliar pathogen transmission (Davis et al. 2015), and changes in pollination could influence nectar microbiomes (Gómez & Ashman 2019).

## 4. HOW DO PLANT-MICROBE INTERACTIONS INFLUENCE RESISTANCE TO CLIMATE DISRUPTIONS?

### 4.1. Climate Sensitivity Functions

Species interactions affect resistance to climate disruption by modifying inherent plant (or microbe) sensitivity to climate variables, beginning with the individual response scale (**Figure 1*a***).

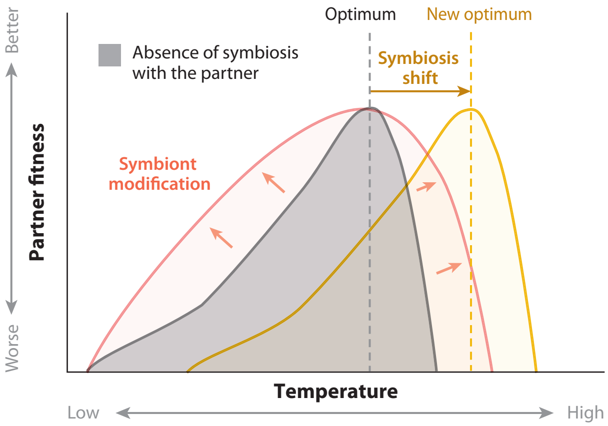


**Figure 3**

Hypothesized climate sensitivity functions for thermal response curves illustrating partner (microbe or plant) fitness as a function of temperature. Gray is the curve in the absence of symbiosis with the partner. The yellow curve is a case in which symbiosis shifts the thermal optimum (peak) to a warmer temperature but does not change the shape of the response curve. The red curve depicts a symbiont modification that increases the range of temperatures at which the partner maintains high fitness but does not alter the thermal optimum. The asymmetrical shape of the curve reflects the pattern for plants and animals in which heat tolerance is more sharply constrained than cold tolerance (Araújo et al. 2013).

Our graphical model illustrates how plant-microbe interactions can alter the shape of a climate sensitivity function (**Figure 3**), which plots fitness (or population growth) against a climate variable (Rudgers et al. 2018a). In the first mechanism, interactions shift the fitness peak (optimum) to a new value (see the yellow curve in **Figure 3**). For example, three-way symbiosis among the fungus *Curvularia*, its virus, and a grass from geothermal hot springs increased the plant's thermal optimum by boosting survival at 65°C (Márquez et al. 2007). In the second mechanism, interactions buffer fitness of one partner by expanding the range of climate conditions under which fitness is high (see the red curve in **Figure 3**) without shifting the fitness optimum. A single plant-microbe interaction could also affect the optimum and the range simultaneously. If these effects on resistance to climate change are common, symbiogenics—harnessing microbes to resist plant declines in extreme climates—could be an important management tool to mitigate the ecological consequences of climate change (Woodward et al. 2012).

Several approaches can help fill gaps on understanding species' climate sensitivities. First, experiments that manipulate climate using regression-based designs will improve quantitative inference on the relative importance of the two mechanisms of resistance (**Figure 3**). For instance, thermal tolerance curves have been determined for some plant pathogens (reviewed by Branco 2019). In a mutualism example, Afkhami et al. (2014) tested a grass in the presence and absence of a leaf endophyte across 10 levels of greenhouse watering. Plants grew best with the most water, regardless of symbiosis (no shift in optimum), but the fungus increased plant survival under the worst drought (buffering; see the red curve in **Figure 3**). Second, for practical reasons, most studies focus on a single microbial taxon, guild, or functional group, yet most plants support consortia of diverse microbes. Studies filling gaps on common guilds that have received less attention, such as root ascomycetes (reviewed by Kivlin et al. 2013), could improve understanding of the net effects of plant microbiomes. Third, studies on microbial networks, particularly the active taxa, can advance knowledge by linking microbiome structure to function. For instance, warming reduced interactions among soil fungi in alpine meadows (Che et al. 2019), and drought disrupted soil bacteria networks more than fungi in temperate grasslands, where bacteria became increasingly more connected as communities recovered from drought (de Vries et al. 2018). These interaction network studies can be extended beyond soil microbes to include the microbiomes of plants. Finally, while microbial mediation of plant resistance has been a primary focus, plants may also help microbes resist climate change at the individual response scale, thereby slowing the pace of reordering, species loss, or migration relative to free-living microbial assemblages (**Figure 1**).

## 4.2. Microbial Traits as Climate Resistance Mechanisms

At the individual stage of the HRF, improved understanding of microbial traits may enable generalizations about when and how much plant-microbe interactions affect resistance to climate disruption. In addition, knowledge of variation among taxa in traits, such as maximum growth rate or thermal tolerance, can link membership at the community response scale to ecological function through community aggregated traits, for which expression at the community scale is predictable from community composition (Hall et al. 2018). Efforts to build trait databases for microbes, such as the Fun$^{\mathrm{Fun}}$ database for fungi (Zanne et al. 2020) or phylogenetically based predictions for bacteria (Martiny et al. 2015), could predict their sensitivities to climate by aggregating trait, life history, and trophic information. For example, a prior synthesis hypothesized slower response times for species at higher trophic positions (Bardgett et al. 2013).

Considering not only species-level trait averages but also complete trait distributions across environmental gradients has high potential to link scales of population and community change to functional roles, addressing Challenge Two to applying the HRF to plant-microbe interactions. For example, the shapes of thermal response curves for animals and plants are well described and asymmetrical, with much sharper declines in fitness under heat stress than cold stress (Araújo et al. 2013) (**Figure 3**). Whether plant-associated microbes are similarly constrained is unresolved. For fungi, we have the least data for physiological traits among all the trait information in current databases (Zanne et al. 2020). While lab-based microbial trait measurements would not capture the abiotic buffering of residing in or near plants, such direct measures of microbial responses to climate variables (including RNA sequencing for functional changes) would address Challenge One of decoupling plant and microbial direct responses to climate. Such information would also help interpret results from field-based climate experiments involving complex communities. Finally, transcriptomic approaches can provide insight by simultaneously characterizing changes in the expression of many functional genes for microbes and their host plants (e.g., Varoquaux et al. 2019) and will be particularly valuable in field-based climate change experiments.

## 4.3. Resistance to Climate Variance

In considering the types of climate disruption most relevant to plant-microbe interactions, the current focus has been on long-term trends in climate means or single extreme events. Yet climate models also forecast increasing climate variance, including a greater frequency of extreme climate events (IPCC 2013). Predicting the consequences of changes in intra- or interannual variance in climate requires separating the effects of variance from changes in the mean (Vazquez et al. 2017). Plant and microbe species could respond concordantly or divergently to climate variability, a possible direction for future research. For instance, in a desert plant community, mesquite shrubs benefitted from experimentally amplified rainfall variability, but grasses declined (Gherardi & Sala 2015). In addition, a hidden benefit of microbes may be to buffer plants against the negative effects of environmental stochasticity, but detection of such benefits requires long-term data over highly variable climates.

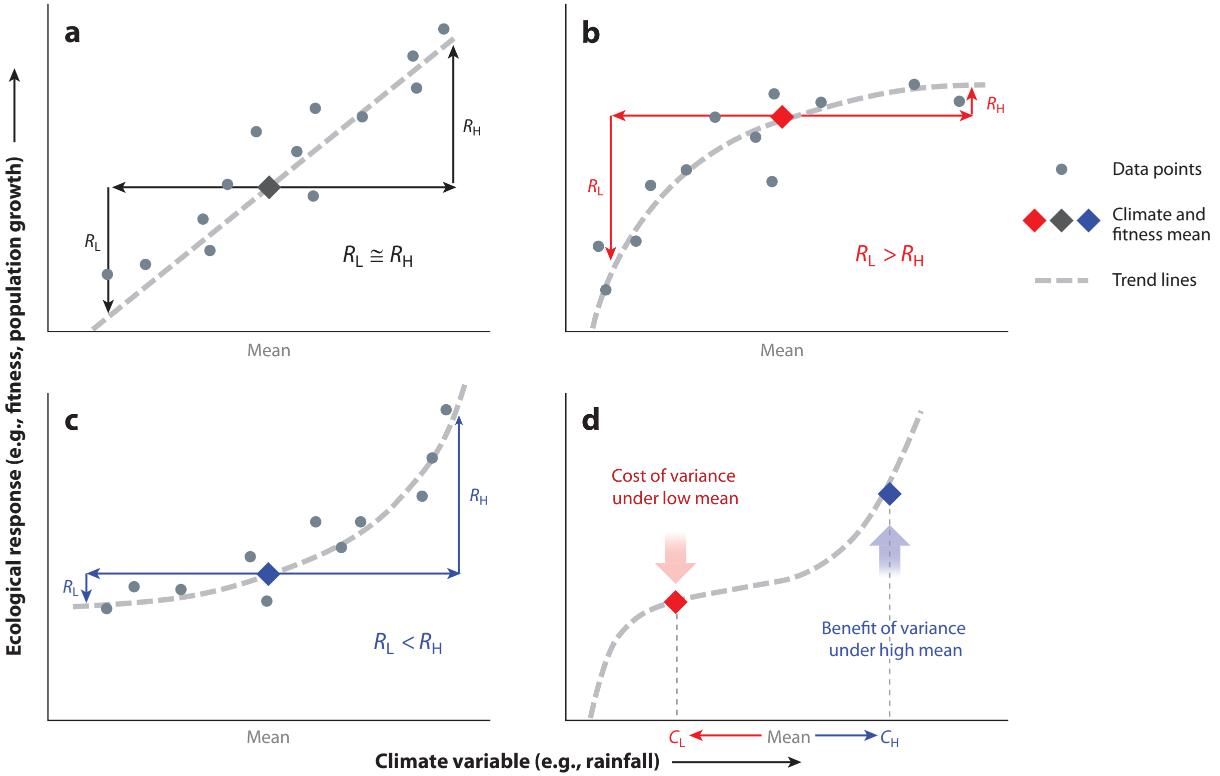


**Figure 4**

Climate sensitivity functions in which ecological responses (e.g., fitness, population growth) to a climate variable (e.g., rainfall) depend on the shape of the nonlinear relationship. Diamonds indicate the climate and fitness mean. (*a*) Linear relationships predict no sensitivity to increased variance in climate because as climate becomes equally more extreme at both ends of the climate axis, increases in the ecological response under extreme highs ($R_H$) are equivalent to decreases in the ecological response under extreme lows ($R_L$). (*b*) Concave down sensitivity to climate predicts a cost of increased climate variance because declines in the ecological response under extreme lows are larger than increases in the ecological response under extreme highs. (*c*) Convex up relationships signal benefits of increased climate variance because declines in the ecological response under extreme lows are smaller than increases in the ecological response under extreme highs. (*d*) The effects of variance can also depend on the mean climate. Here, increased variance in climate is predicted to be costly under a low mean climate ($C_L$) but beneficial under a high mean climate ($C_H$). Such mean-variance interactions may occur when variance in climate increases in concert with chronic warming, which changes the climate mean.

While experiments that force variance in climate are rare, observations collected over naturally variable climates can help predict when variability should be beneficial, costly, or neutral. The nonlinear shapes of climate sensitivity functions generate these predictions (**Figures 3** and **4**), and we have developed a statistical approach to estimate these shapes (Rudgers et al. 2018a). While the mathematical theory underlying variance effects is more than a century old (Jensen's inequality), it has gained recent traction in ecological climate change studies (reviewed by Vazquez et al. 2017). When a sensitivity function is linear, increased climate variance alone should not change the ecological outcome (**Figure 4*a***). However, when a sensitivity function is nonlinear over the range of observed climate, increased climate variance should alter the long-term ecological outcome, even if average climate does not change. A concave function (**Figure 4*b***) results in net costs of increasing variance because small values of the climate variable (e.g., drought) cause large declines in fitness that are not offset by the small increases in fitness under large values of the climate variable (e.g., deluge). Concave functions might occur if nutrients became the most limiting factor to fitness under wet extremes. In contrast, a convex function (**Figure 4*c***) yields net benefits of increasing variance because small values of the climate variable (e.g., drought) cause only small declines in fitness, whereas large values (e.g., deluge) cause large increases. If the function changes shape over the observed range of climate (**Figure 4*d***), then increased variance in climate could have positive or negative effects depending on the climate mean, because the mean and variance interact.

Sensitivity to climate variability may differ between plants and plant-associated microbes. For example, in a review of grassland experiments, aboveground primary production had a saturating, concave relationship with altered precipitation (Wilcox et al. 2017a), suggesting costs of increased climate variance (**Figure 3*b***). In contrast, belowground plant production was both less responsive to precipitation and linear (Wilcox et al. 2017a), consistent with neutral effects of variance. In a microbial synthesis, the direction of nonlinearity flipped with the magnitude of rainfall manipulation. Under extreme disruptions, microbial biomass was more sensitive to drought than to extreme wetting (Zhou et al. 2018), suggesting costs of increasing climate variance (concave function) and the potential for interactions between the climate mean and the variance in climate (**Figure 4**). Divergent responses of plants and microbes to climate variance at all stages of the HRF could decouple their interactions through temporal or spatial mismatches.

Plant-microbe interactions provide useful systems for testing theory on the consequences of climate variability due to the rapid turnover rates of microbes. Observations collected over spatiotemporally variable climates would enable climate sensitivity functions to be evaluated for plant-microbe symbioses. In addition, tracking microbial responses along with plants in ongoing manipulations of climate variability (e.g., Gherardi & Sala 2015) could advance understanding of the ecological importance of the variance aspect of climate change.

## 5. HOW DO PLANT-MICROBE INTERACTIONS ALTER RESILIENCE FOLLOWING CLIMATE DISRUPTIONS?

Plant-microbe interactions may alter the pace of ecological recovery following climate disruption. For instance, long-term experiments that inoculated native AM fungi and N-fixing bacteria into a desertified Mediterranean ecosystem greatly enhanced plant establishment and soil fertility (Requena et al. 2001). Restoration of European grasslands created different plant successional trajectories by adding soil microbes from different source grasslands (Wubs et al. 2016). These benefits of microbial inoculation to disturbed ecosystems, combined with large shifts in microbial composition at the community scale following climate disturbance (see Section 2.4), suggest that harnessing microbial interactions could improve resilience to climate disruption at the scales of communities and ecosystems.

New studies can enable generalizations about which plant-microbe combinations have the greatest potential to promote resilience. Studies can compare microbial inocula that differ in their climate histories to determine whether the microbial taxa lost during climate disruption are those most critical for recovery (e.g., Waring & Hawkes 2018). Climate histories that include large variability may generate assemblages that promote resilience. For example, soil microbes exposed to long-term drought and high variance in precipitation were more resilient to contemporary perturbations of drought and regained activity levels near optima more quickly after rewetting than soils without such a drought history (de Nijs et al. 2019). However, such lab incubations of field soils, while commonly used, may not recapitulate field dynamics because close linkages between microbes and plants are broken, and plant subsidies, such as root exudates, are absent. Therefore, there is untapped potential to inoculate microbes from climate experiments onto plants to explore the consequences of climate legacies.

## 5.1. Evolutionary Change and Resilience

Understanding plant-microbe interactions under field-manipulated or natural changes in climate is complicated because climate can be a strong selective filter on allele frequencies. For example, drought may select for drought-resistant genotypes and reduce genetic diversity (Whitney et al. 2019). Given that plant genotypes also differ in plant-soil feedbacks (reviewed by Rúa et al. 2016), if climate change–resistant genotypes support different interactions than susceptible genotypes, this divergence could alter ecological resilience in complex ways. In what is likely the best example of this scenario to date (Gehring et al. 2017), a period of natural drought selected for drought-resistant genotypes of piñon pine. Drought-resistant genotypes supported distinctive communities of ectomycorrhizal fungi, a trait that was inherited by seedlings. Drought-resistant genotypes also grew 25% bigger than drought-susceptible genotypes, but only when their genotype-specific fungi were present. Following severe drought, genotype-specific interactions could slow recovery to predrought conditions. Thus, a complete understanding of the roles of plant-microbe interactions in recovery from climate disruption must account for contemporary evolutionary change in both plant and microbe populations.

## 5.2. Pathways to Promote Recovery from Climate Disruption

The types of pathways through which plant-microbe interactions could promote recovery from climate disruption have important implications for both the rate and magnitude of recovery. First, interaction networks can be a source of ecosystem stability that retain resources within a biotic loop and slow resource losses caused by physical processes (e.g., erosion, leaching). Such coupling occurs in marine food webs (the microbial loop), where microbial interactions retain nutrients that would otherwise drop to the ocean floor. In terrestrial ecosystems, resource retention in a biotic loop of plant-microbe interactions may boost primary production (Rudgers et al. 2018b). Microbial guilds that differ in subnetwork structure likely have different contributions to resilience, making it useful to compare network structures among guilds during and following climate stress. For instance, drought increased connectedness in networks of grassland soil bacteria (but reduced soil fungal connectedness), and following drought, resilience in bacterial composition correlated positively with plant resilience (de Vries et al. 2018). Second, the degree to which plant-microbe interactions couple C-N-P dynamics may be important to resilience. Drought reduces nutrient concentrations in plant tissues as well as microbial biomass (reviewed by Pugnaire et al. 2019). Plant nutrient concentrations, such as C:N:P ratios, can alter plant competitive dynamics, and soil C:N:P ratios can influence plant water use efficiency and the recruitment of symbionts that ameliorate drought (Smith & Read 2008, Johnson et al. 2013, Sardans et al. 2017). Thus, plant-microbe interactions that restore the stoichiometry of C:N:P to predisruption levels may speed ecosystem recovery. High species diversity and diverse interaction outcomes (mutualism and parasitism) likely enhance resilience and resistance to climate change, as suggested by theory and studies of metacommunities (e.g., Mougi & Kondoh 2012). Finally, asynchronies among species in their timing of activity in response to climate, captured in climate sensitivity functions (**Figures 3** and **4**), may also promote resilience to change (Wilcox et al. 2017b).

# 6. CONCLUSION

In conclusion, we advocate for a deeper understanding of climate-driven plant-microbe interactions over space, from individuals to landscapes, and time, from within-generation phenologies to long-term evolution. Thus, we propose an expansion of the HRF to include plant-microbe interactions. There is a general need for integrated studies that connect individual-scale responses and their molecular mechanisms (**Figure 1*a***) to changes in population abundance (**Figure 1*b***) that ultimately alter community structure and succession (**Figure 1*c***). Looking forward, there are several directions that may fuel research advances on climate disruption of plant-microbe interactions. We have organized these directions into levels representing the individual (1–3), population (4–6), and community (7 and 8) response scales of the HRF.

## FUTURE ISSUES

1. There are many gaps to fill to characterize climate sensitivity functions for individual plant-associated microbes, particularly thermal and desiccation tolerance; improved trait databases and phylogenies will facilitate generalization beyond individual case studies.
2. Understanding variation in how genotypes of plants and microbes jointly respond to climate may be critical to predicting and managing the trajectory of recovery following climate disturbance.
3. Community aggregated traits can improve predictive scaling from individual microbial taxa to community-scale function, and technologies such as RNA sequencing will help identify coordinated molecular responses to climate change across the plant-microbe symbiotic boundary.
4. Experiments that manipulate the community composition of microbial guilds can determine how much microbes weaken or amplify the resistance and resilience of plant populations to climate change, including through feedbacks over time.
5. Studies that consider plant-microbe interactions across spatiotemporal gradients of climate can detect nonlinear climate sensitivity functions to predict the effects of increasing climate variability on species abundance.
6. Identifying community characteristics that promote resistance or resilience to climate disruption (e.g., interaction diversity, interaction network structure, asynchronies in species abundances, plant-microbe coupling of C:N:P dynamics, community aggregated traits) will promote much-needed generalization across ecosystems.
7. Niche models built from herbarium specimens, DNA repositories, and geographically broad field collections can link microbe and plant distributions and use future climate scenarios to predict the probability of spatial mismatches.
8. Increasing knowledge of microbial contributions to community and ecosystem resistance and resilience to climate disruption will be useful to land managers, farmers, and restoration practitioners in developing climate-ready ecosystems.

## 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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