Plant-Microbe Eco-Evolutionary Dynamics in a Changing World

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Summary

Both plants and their associated microbiomes can respond strongly to anthropogenic environmental changes. These responses can be both ecological (e.g., a global change affecting plant demography or microbial community composition) and evolutionary (e.g., a global change altering natural selection on plant or microbial populations). As a result, global changes can catalyze eco-evolutionary feedbacks. Here we take a plant-focused perspective to discuss how microbes mediate plant ecological responses to global change and how these ecological effects can influence plant evolutionary response to global change. We argue that the strong and functionally important relationships between plants and their associated microbes are particularly likely to result in eco-evolutionary feedbacks when perturbed by global changes and discuss how improved understanding of plant-microbe eco-evolutionary dynamics could inform conservation or even agriculture.

Key Words: holobiome, microbe-mediated adaptation, rapid adaptation, species interactions, symbiosis, eco-evolutionary dynamics

Introduction

Global changes, ranging from climate change to biological invasions, nutrient deposition, pollution, and salinification, can intensify both abiotic and biotic stresses for plants and their associated microorganisms. In many cases, microorganisms can harm plants, yet beneficial microbiomes can sometimes significantly expand both the stress tolerance and the adaptive potential of plants (Kivlin *et al.*, 2013; Hawkes *et al.*, 2020; Porter *et al.*, 2020; Petipas *et al.*, 2021). When such beneficial microbes reduce the effects of global change on plant fitness, they also may reduce the strength of selection favouring the evolution of plant stress tolerance traits or increase the strength of selection favouring plant traits that attract or promote the growth of the stress-mitigating microbes. Any plant evolutionary responses might then alter plant and/or microbial ecological processes, at the population, community, or ecosystem level, potentially initiating eco-evolutionary dynamics. Such eco-evolutionary dynamics occur when ecological processes affect evolution and evolution affects ecological processes (Hendry 2020), for example, when an evolutionary change in either the plant or microbe alters an ecological process that further changes natural selection and evolution.

Few studies have quantified the full eco-evolutionary plant-microbiome feedback resulting from a global change, but here we argue that they are likely because: 1) global changes cause strong environmental perturbations that can affect both plants and microbes (reviewed in Allison & Martiny, 2008; Blankinship *et al.*, 2011; Franklin *et al.*, 2016) and can cause strong selection on plant (e.g., Lau *et al.*, 2014; Kleynhans *et al.*, 2016) or microbial traits (Weese *et al.*, 2015), and 2) many plant-associated microbes have large population sizes, the capacity for lateral gene transfer, short generation times, and provide key ecosystem functions. We first identify the mechanisms through which microbiomes may help plants mitigate global change responses. We then outline examples by which microbiomes alter plant evolutionary responses to global change and how plant evolution might result in eco-evolutionary feedbacks between plants and their associated microbiota. We take a broad view of global changes, including both long-term, persistent changes like nutrient addition and more variable stressors like the increased frequency of drought plants in many areas will experience in the face of climate change. Both sudden and more persistent global changes, like any disturbance or shift in environmental conditions, may be particularly likely to instigate eco-evolutionary feedbacks that are mediated by microbes for the two reasons detailed above. Such plant-microbe eco-evolutionary feedbacks may also be important to population, community, and ecosystem process given the pace of many global changes (and capacity for microbes to respond quickly), the potential for strong selection on both plants and microbes in global change contexts, and the wide range of functions driven by microbial and plant processes.

1. How do microbes affect plant ecological responses to global change?

Recent studies have illustrated the myriad ways diverse microorganisms mitigate global change effects on plants. Beneficial microbes associated with plants can stimulate plant growth and enhance plant resistance to abiotic stresses (e.g., salinity, drought, flooding) and biotic stresses (diseases) (Porter *et al.*, 2020). Beneficial microorganisms can be classic mutualists such as many plant growth-promoting rhizobacteria (PGPR), arbuscular mycorrhizal fungi (AMF), and nitrogen-fixing bacteria, however, increasing evidence also suggests that diverse soil microbial communities associated with roots, leaves, and soil can also promote plant fitness under stress (Lau & Lennon, 2012; Giauque

et al., 2019; Hawkes *et al.*, 2020). Such microbes can influence plant responses to global changes through at least four mechanisms (Table 1).

First, the microorganism can physically alter the abiotic (often the soil) environment. Bacteria, fungi, and protists have diminutive dimensions but they still can affect soil structure from small to large scales (Chenu & Cosentino, 2011; Erktan *et al.*, 2020). This structural change occurs through a variety of mechanisms. For instance, bacteria can form supracellular structures called biofilms. Biofilms are bacterial communities in which cells are embedded in a matrix of extracellular polymeric substances or exopolysaccharides (EPS). EPS can improve microbial root colonization and also can enhance aggregation of soil particles and benefit plant growth and yield by maintaining soil moisture (Naseem & Bano, 2014; Costa *et al.*, 2018). As a result biofilms may increase plant fitness responses to the increased drought facing many regions as a result of climate change. For instance, the EPS-producing *Pantoea* sp. had a positive effect on rhizosphere soil aggregation and microporosity and an overall positive effect on plant growth under drought (Amellal *et al.*, 1998), and a high EPS-producing *Pseudomonas fluorescens* strain stimulated seed germination and enhanced soil moisture and seedling growth under drought compared to other strains with lower production of EPS (Niu *et al.*, 2018). Similarly, AMF can produce glomalin and glomalin-related soil proteins. These compounds act as a substrate for microbes and a gluing agent for aggregates, promoting soil water holding capacity in a similar way to biofilms, potentially reducing plant drought stress (Rillig, 2004; Singh, 2012). They also can, promote the chelation of heavy metals and toxic pollutants, potentially increasing plant survival and fecundity in increasingly contaminated environments (Singh, 2012).

Second, microorganisms can secrete chemicals that mimic plant hormones (e.g., auxins, cytokinins, abscisic acid, and gibberellins) (Friesen *et al*. 2011). These chemicals can cause physiological changes in nearby plants that can stimulate plant growth under various stress conditions such as the increased temperature or drought plants are likely to experience under climate change (Forchetti *et al.*, 2010; Cohen *et al.*, 2015). For example, *Azospirillum sp.* produced absicic acid (ABA) and/or increased plant produced ABA, promoting plant drought tolerance (Cohen *et al*. 2015). The ability of microbes to synthesize phytohormones under extreme stress where plant synthesis may be reduced can provide plants with an extra pool of these compounds, potentially helping to maintain or regain function. For example, high temperatures reduced plant production of auxin in developing anthers causing male sterility, but the exogenous application of auxin

completely reversed this effect (Sakata *et al.*, 2010). In this case, the auxin was not microbially-produced, but illustrates the potential for microbially-produced phytohormones to maintain function. Microbes also can facilitate plant growth by decreasing hormones associated with stress like ethylene by producing enzymes that are capable of cleaving precursors in the plant ethylene pathway. Plant growth promoting bacterial endophytes produced one such enzyme, 1-aminocyclopropane-1-carboxylate deaminase (ACC), which reduced the build-up of salt in plants and increased plant growth and investment in reproductive structures in the face of salinity stress compared to a mutant that did not produce the enzyme (Ali *et al.*, 2014).

Third, microorganisms can alter plant gene expression, triggering physiological changes that in some cases increase tolerance to stressors imposed by the global change (e.g., Nautiyal *et al.*, 2013). For example, environmental stress can increase plant production of reactive oxygen species (ROS). Microbes can change the expression of genes involved in ROS scavenging and ethylene biosynthesis, increasing plant growth and photosynthetic performance to better tolerate global change stressors like salinity, drought and heavy metals (Gururani *et al.*, 2013; Harman & Uphoff, 2019). In other examples, volatile organic compounds emitted by some PGPR can trigger induced systemic resistance, which can prime the whole plant for enhanced defence against a broad range of pathogens and insect herbivores (Farag *et al.*, 2013; Pieterse *et al.*, 2014). Soil bacteria also can alter plant gene expression to improve plant responses to salt stress (Zhang *et al.*, 2008).

Finally, microorganisms can also mitigate the negative effects of global changes by facilitating access to limiting resources. Microbes can affect plant nutrition directly, by increasing nutrient availability (e.g., AMF or ectomycorrhizal fungi (EMF) scavenging and solubilizing phosphates, or rhizobia fixing nitrogen) or indirectly by affecting plant metabolism and growth in ways that promote plant uptake of minerals (Richardson *et al.*, 2009). Microbial promotion of nutrient access may be a major benefit to plants experiencing global changes that reduce access to nutrients (e.g., drought stress reducing access to nitrogen) or that promote increased growth that then increases nitrogen limitation (e.g., elevated CO_2 concentrations). In such cases, any negative effects of global change might be minimized (or positive effects increased in the case of elevated CO_2) by microorganisms. For example, legumes that strongly associate with nitrogen-fixing rhizobia and plant species that associate with EMF are among those species that benefit most under elevated CO_2 (Terrer *et al.*, 2016). Ultimately, however, these benefits

may require that the associated microbes are also adapted to the new environmental conditions. For instance, only salt-tolerant rhizobium strains increased *Vicia faba* biomass and nitrogen content under increasing salinity; two other tested strains did not (Benidire *et al*., 2017).

All the mechanisms described above detail how microorganisms can benefit plants and minimize the negative consequences of global change on plant growth and fitness. However, other global changes can destabilize the plant-microbe symbiosis itself (Kiers *et al.*, 2010) and inhibit beneficial microbial functions. For example, nitrogen addition can shift plant-microbe resource mutualisms towards parasitism (Johnson *et al.*, 1997), potentially hastening the decline or exclusion of plant taxa that benefit most from such mutualisms (e.g., legumes, Suding *et al.*, 2005). These effects are reviewed elsewhere both in the context of global changes (e.g., Kiers *et al*. 2010) and in terms of the context dependence of species interactions (e.g., Chamberlain *et al.*, 2014).

Table 1. Microbes can promote plant tolerance to climate change by: 1) modifying the physical environment, 2) secreting plant hormones and defence-related proteins, 3) modifying plant gene expression, and 4) promoting plant access to nutrients. Effectors (enzymes or compounds underlying the mechanism) are in italics and the details about the plant benefit provided are in bold.

Mechanism	Examples of plant stress amelioration
Physical modification of the environment	-*Glomalin, EPS, and biofilm* from fungi and bacteria **improved soil aggregation stability and increased moisture in the rhizosphere**, increasing plant survival and biomass under drought[1,2] and germination under salt stress[3]. -Bacterial *biofilms* **decreased uptake and accumulation of arsenic in plant tissues and improved plant growth**[4].
Secretion of phytohormones	-Rhizobial *auxins* **promoted rubisco and low molecular-weight osmolyte production**, increasing drought tolerance[5] and **promoted adventitious root growth** to counteract flooding[6]. -Bacterial *cytokinins* **increased relative water content, leaf water potential and production of root exudates** under drought[7]. -Endophytic fungal *gibberellins* **regulated plant hormones resulting in higher nutrient assimilation** under salt and drought stress[8]. -Bacterial *abscisic acid* **enhanced proline levels and photosynthetic and photoprotective pigments**, reducing plant water lost under drought[9]. -*ACC-deaminase* genes in bacteria **increased root elongation and pathogen resistance**[10].
Modification of plant gene expression	-Bacterial *volatile organic compounds* **triggered induced systemic resistance** against a pathogen[11]. -Bacteria enhanced mRNA expression of various **ROS-scavenging enzymes, improved PSII photochemistry and plant tolerance** to water deficit, salinity, and heavy-metal toxicity[12].

Plant nutrient acquisition	-*Nitrogenases* from *Rhizobia* **increased plant biomass and nitrogen content** under salinity[13]. -AMF and bacterial *phosphatases* **increased plant biomass and total phosphorus (P) content** under P deficiency in acid soils[14] and salt stress[15]. -Three distinct bacterial *ferripyoverdines* **improved iron deficiency chlorosis**[16].

[1]Wu *et al.*, 2008; [2] Sandhya *et al.*, 2009; [3]Qurashi & Sabri, 2012; [4]Mallick *et al.*, 2018; [5]Defez *et al.*, 2017 ; [6]Kim *et al.*, 2017; [7]Liu *et al.*, 2013 ; [8]Waqas *et al.*, 2012 ; [9]Cohen *et al.*, 2015 ; [10]Wang *et al.*, 2000 ; [11]Lee *et al.*, 2012; [12]Gururani *et al.*, 2013; [13]Benidire *et al.*, 2017; [14]Rubio *et al.*, 2002; [15]Tchakounté *et al.*, 2020; [16]Lurthy *et al.*, 2020.

2. How do microbes affect plant evolutionary responses to global change?

Microbes affect plant ecological responses to global change (i.e., individual plant fitness) (section 1) but also can affect plant adaptive responses to global change (i.e., the strength or direction of selection acting on plant traits). Specifically, because microbes can reduce the negative consequences of global change for plant fitness, they may reduce the strength of selection favouring plant stress tolerance traits and/or increase the strength of selection favouring plant traits that attract beneficial microorganisms. Beneficial microbial communities could also strengthen selection on traits that allow plants to detect or respond more effectively to microbial signals. For example, microbes that modify the physical environment in ways that protect plants or promote nutrient acquisition (see ecological mechanisms 1 and 4 in Table 1) might both reduce selection on plant stress tolerance traits and increase selection on traits that help attract or cultivate beneficial microorganisms. Beneficial microbial communities that protect plants from global changes by secreting plant phytohormones or modifying plant gene expression similarly could increase selection on microbial attraction traits, but also could increase selection on traits that make plants more receptive to these microbial signals, or even might allow for resource re-allocation away from hormone production to other plant functions. In all cases, relying on microbiomes to protect plants from global changes poses further evolutionary challenges. For example, theory suggests that such beneficial microbes will alter the evolution of immune function as plants struggle to differentiate between friend and foe, potentially making plants more susceptible to novel pathogens (Metcalf & Koskella, 2019). And theory identifying when plants should evolve to rely on microbes for stress tolerance is still limited (e.g., Hawkes *et al.*, 2020). In this section, we discuss each of the possible ways microbes might mediate plant evolutionary responses to global change. However, we note here that the ultimate evolutionary effects of global changes

will also be affected by the direct selective effects of the global change on the plant and trade-offs between plant traits mediating interactions with microbes vs. plant traits directly affected by the global change. As a result, the microbiome can accelerate plant evolutionary responses to global change when the microbe-mediated selective effects act in the same direction as the direct selective effects of the global change on plant traits, but can also slow plant evolutionary responses when microbe-mediate effects oppose the direct selective effects of global change.

2.1 Microbes reduce the strength of selection on plant stress tolerance traits

As described above, microbes can protect plants from the negative consequences of global changes in a number of different ways (Table 1). As a result, the direct selective effects of that global change on plant traits may be reduced. For example, if microbes increase soil water holding capacity under drought stress, there may be limited drought impacts on plant fitness and little selection favouring plant drought tolerance traits like increased investment in roots. Variation in microbial diversity or community composition certainly can alter natural selection on plant traits (Lau & Lennon, 2011; Chaney & Baucom, 2020), but few studies have assessed whether they commonly do so by reducing the negative effects of global change.

2.2 Increase the strength of selection favouring plant traits that attract beneficial microorganisms.

The presence of beneficial microbial communities that mitigate the effects of global change could strengthen selection favouring traits that promote interactions with these beneficial microorganisms, such as root exudation or root architecture traits (Friesen *et al.*, 2011; Verbon & Liberman, 2016). Although it can be challenging to identify the specific traits that promote specific microbial communities, evidence from a variety of systems suggest that different genotypes recruit different microbial communities (e.g., Walters *et al.*, 2018; Kavamura *et al.*, 2020). Other studies have identified specific traits likely to contribute these interactions with microbes (e.g., Pérez-Jaramillo *et al.*, 2017). In stressful conditions, for example in flooding, plant genotypes with higher ability to form aerenchyma may promote heterotrophic, sulfur-oxidizing, methane-oxidizing, and nitrifying bacteria growth (Laanbroek, 1990; Stubner *et al.*, 1998). These bacteria in turn protect the plant from high amounts of phytotoxic compounds (e.g. reduced sulfur or

excess of ammonia), which are more abundant in flooded conditions (Lamers *et al.*, 2013; Neori & Agami, 2017). Therefore, one might hypothesize that genotypes with higher aerenchyma would be highly adapted to flooding, not only because of the direct benefits of aerenchyma to plants in such anoxic waterlogged conditions (Evans 2004), but also because aerenchyma promote the growth of certain bacterial communities. In this case, microbes may strengthen selection on this plant stress tolerance trait as the direct fitness benefits of aerenchyma combine with the benefits resulting from increased colonization from beneficial microbes.

Exudate production may be another trait under strong selection in the face of global change. For example, in the rhizophagy cycle, it is hypothesized that microbes acquire soil nutrients (especially micronutrients) in the free-living phase and enter plant roots via meristematic cells. Nutrients are then extracted oxidatively inside the plant roots. After the nutrients are exhausted, the microbes exit the plant and return to the soil through root hairs (White *et al.*, 2018). In this case, selection may favour increased exudate production to attract microbes, cell wall traits that control microbial entrance, and the production of reactive oxygen to extract nutrients from microbes (Paungfoo-Lonhienne *et al.*, 2010; White *et al.*, 2012). In contrast to rhizobial symbiosis that is limited to some plant families, the rhizophagy process may be widespread among plants. However, few studies of natural selection measure belowground traits (but see Colom & Baucom, 2020) or plant developmental traits, and as a result, we may be both misidentifying the traits commonly underlying adaptation and underestimating the role microorganisms play in plant adaptation.

2.3 Strengthen selection favouring strong plant responses to microbial signals

In cases, where microbes promote plant tolerance to global change via microbial synthesis of plant phytohormones or microbial modification of plant gene expression, selection might favour plant traits promoting interactions with these microbes, but also could favour increased plant receptiveness to microbial signals. Theory suggests plants might evolve to rely on microbial signals for phenological responses, for example, because microbes might provide the most accurate environmental signal or because microbes are able to detect cues that their hosts cannot (Metcalf *et al.*, 2019). In these circumstances, plants best able to respond to those microbial signals might be favoured by selection. In other cases, microbial synthesis of plant hormones or alteration of plant gene expression might elicit stronger shifts in adaptive plant traits than simple genetic

changes in the plant itself. In such scenarios, plants are predicted to evolve increased reliance on even diffuse microbiomes for stress tolerance (Hawkes *et al.*, 2020).

3. Plant-microbe eco-evolutionary feedbacks under global changes

Eco-evolutionary feedbacks describe the reciprocal effects between two pathways: how ecological change affects evolution, and how evolutionary change affects ecological processes (Hendry, 2020). The interaction between plants and microbes provides an excellent framework to study eco-evolutionary feedbacks because 1) plant-microbe interactions can strongly affect ecosystem functions that are likely to feedback to affect selection on plant and microbial traits (terHorst & Zee, 2016), and 2) microbes' short generation times, high population densities, and diverse communities make rapid ecological and evolutionary responses likely over short time-scales (Lau & Lennon, 2012; Chase *et al.*, 2021). However, even for plant-microbe interactions, often only one pathway of the eco-evolutionary feedback is empirically investigated. Here, we illustrate how plant-microbe interactions could promote eco-evolutionary feedbacks and discuss the potential prevalence of eco-evolutionary feedbacks in plant-microbe interactions under global change scenarios (Figure 1).

Global changes can frequently cause rapid responses of soil microbial communities and their associated ecosystem functions (Allison & Martiny, 2008; Rillig *et al.*, 2019) and can cause rapid evolution of soil microbes (Weese *et al.*, 2015) (Arrow a, Figure 1). In most cases, it is hard to distinguish the ecological changes, i.e. shifts in microbial community composition, from rapid evolution of microbial populations. But regardless of whether the microbial shift is ecological or evolutionary in nature it might influence plant fitness responses to global change (Arrow b, Figure 1) (see section 1) and ultimately selection on plant traits (see section 2). As described above, this ecological effect caused by the shift in microbial community composition might weaken selection favouring plant stress tolerance traits (Arrow c). However, if plant genotypes vary in their ability to condition the soil in ways that attract the most beneficial microbes, for example by producing certain types of exudates, then one might expect to see stronger selection favouring increased exudate production in plants (Arrow d). While a number of studies have now demonstrated that microbial communities shift in ways that affect plant fitness responses to global change (Lau & Lennon, 2012; Giauque *et al.*, 2019), few studies have

taken the next step to show how the shifts in microbial communities affect selection on plant traits. That said, a handful of studies have demonstrated how changes in microbial diversity can influence selection on plant traits, suggesting that this latter pathway is possible (Lau & Lennon, 2011; Chaney & Baucom, 2020). Any evolutionary increase in exudate production or other traits that condition for beneficial microbes will cause further increases in the densities of those protective microbes (Arrow e), amplifying the eco-evolutionary feedback. In some cases, these feedbacks can promote stronger co-evolutionary plant-microbe interactions: a recent bacterial experimental evolution study focusing on the *Arabidopsis thaliana* rhizosphere showed that host plants can steer the evolution of an associated *Pseudomonas* strain to mutualism (Li *et al.*, 2021). Despite suggestions that eco-evolutionary feedbacks mediated by plant-microbe interactions may be common and strong (terHorst & Zee, 2016), few studies demonstrate the entire feedback cycle from ecology to evolution and back to ecology. While there is potential for long-term eco-evolutionary dynamics in plant-microbe systems (Box 1), many questions remain to be answered:

(1) *Are eco-evolutionary feedbacks more common or stronger in tight pairwise symbioses than more diffuse interactions between plants and diverse microbial communities like those that inhabit soils or leaves*? Plant-microbe interactions can be diffuse, where plant hosts interact with the hyper-diverse microbial communities inhabiting soil or leaves, or can be tight, pairwise, coevolved symbioses, like the interactions between legumes and rhizobia. While some of the same mechanisms that stabilize and promote reliance on microbes for stress tolerance in tightly coevolved systems can apply to more diffuse interactions that are continuously reassembled from generation to generation, the evolution of plant reliance on microbes for stress tolerance may occur under a more restricted set of conditions in these diffuse systems (Hawkes *et al.*, 2020). One might predict that more tightly interacting plant-microbe partners have higher likelihood for eco-evolutionary feedbacks to occur, while more diffuse associations, like those between plants and the soil microbial community, have weaker but more stable interactions that would dampen eco-evolutionary feedbacks.

(2) *How does the type, rate, or intensity of environmental change influence the likelihood or magnitude of eco-evolutionary feedback?* Across all systems most studies documenting eco-evolutionary feedbacks occur in systems perturbed by human-caused environmental change (either natural or experimental). For example, one of the classic cases of eco-evolutionary feedbacks investigated alewives in landlocked lakes. In such

lakes alewives' intensive selective grazing depleted large-body zooplankton resulting in strong selection causing a shift in alewives' foraging traits to increase predation on small-body size zooplankton (Smith *et al.*, 2020). Similarly, some of the strongest effects of microbial community responses on plant fitness arise from variables associated with climate and climate change (e.g., drought stress or aridity gradients Lau & Lennon, 2012; Giauque *et al.*, 2019), and a recent example illustrates how microbial evolution in response to nitrogen-addition affects plant communities in experimental mesocosms (Lau *et al.*, unpublished manuscript). Does the prevalence of human-caused environmental change in many classic examples of eco-evolutionary feedback result from bias in choosing systems to investigate eco-evolutionary feedback or are global changes more likely to perturb systems in ways that elicit eco-evolutionary feedbacks? One might predict that large, rapid environmental changes (e.g., exceptionally warm years, extreme drought, or higher rates of nitrogen deposition) will produce strong ecological responses that alter natural selection and cause strong, persistent evolutionary responses that may feedback to affect ecological process. On the other hand, more gradual changes might be more likely to produce stronger evolutionary responses because larger population densities can be maintained to promote adaption before extinction (Gonzalez *et al.*, 2013).

(3) How does the context dependency of plant-microbe interactions catalyze or inhibit eco-evolutionary feedbacks? Both mutualistic and antagonistic plant-microbe interactions are heavily influenced by abiotic factors ranging from resource availability to elevated temperatures, and biotic factors like the presence and diversity of other microbes, herbivores, or plant competitors (Chamberlain *et al.*, 2014). These are the same factors likely to be directly or indirectly affected by many global changes. In some cases, this context dependency could catalyze eco-evo feedbacks. For example, nitrogen addition causes shifts in the legume-rhizobium mutualism, reducing the benefits rhizobia provide to plant hosts and typically reducing plant investment in rhizobia (Streeter & Wong, 1988). Through a variety of potential mechanisms, including the reduced investment in rhizobia causing rhizobia to spend more time in non-symbiotic free-living life stages, nitrogen addition selects for less cooperative rhizobia (Weese *et al.*, 2015). Hypothetically, this evolution of reduced cooperation could then impose an additional cost on plants, accelerating legume declines in high nitrogen environments, further increasing the time rhizobia spend in free-living life stages and accelerating the evolution of reduced cooperation.

In other cases, this context dependence could dampen or inhibit eco-evolutionary feedbacks. For example, many studies, particularly those investigating evolutionary pathways in the eco-evo feedback cycle, employ single strain inoculations or otherwise simplistic growing environments (e.g., a single species host plant community, Lau & Lennon, 2012), but plant-microbe interactions are inherently diffuse, potentially involving dozens of plant species and 100s or 1000s of microbial taxa. These taxa can combine to produce novel functions. For example, when two bacterial strains interacted they produced a novel microbial volatile, not produced by any of the strains separately, with antimicrobial and quorum sensing disruption properties (Kai *et al.*, 2018). As a result if microbial community composition shifts rapidly across space or time, selection may be so variable that strong, directional evolutionary responses are inhibited.

4) Many global changes are occurring simultaneously--will multiple simultaneous global changes inhibit or promote plant-microbe eco-evolutionary feedbacks? Adaptation to multiple simultaneous novel selective agents is challenging. However, the diverse traits and functions of diffuse microbial communities could facilitate plant adaptation in such a scenario. If different microbial taxa fulfill different functions or protect plants from different global changes, then multiple global changes may increase plant reliance on microbes for adaptive responses even more, potentially strengthening selection on plant traits that attract or promote the growth of diverse microbial communities. In such a scenario, then one might expect plant-microbe eco-evolutionary feedbacks to become even more likely and also more important to plant responses to global change. Alternatively, given that multiple global changes combine to reduce microbial diversity (Rillig *et al.* 2019), the capacity for microbe-mediated adaptation may be reduced, as functional diversity is reduced and stress tolerant clades dominate.

4. Eco-evolutionary changes resulting from global changes disrupting plant-microbe symbioses

In the previous sections we considered eco-evolutionary feedbacks that result from beneficial microbes mitigating the effects of global change for their plant hosts. However, eco-evolutionary feedbacks can also result from global changes causing the breakdown of plant-microbe symbioses. For example, Evans and coauthors (2016) found that the invasive species, *Alliaria petiolata*, destroyed AMF networks that benefited native species, producing strong eco-evolutionary feedbacks. Specifically, in high

interspecific competition, natural selection favoured increased production of the antimycorrhizal allelochemical sinigrin by *A. petiolata*. High sinigrin concentration inhibited the growth of competing native species that relied on AMF, facilitating *A. petiolata's* success while also shifting competition from interspecific to primarily intraspecific competition. Because high sinigrin concentrations are costly and of little benefit to intraspecific competition, selection favours reduced sinigrin production when *A. petiolata* densities become high enough. In this case, microbes mediate the effects of global change and played a large role in an eco-evolutionary feedback, not because they protect their host plants, but because they themselves are inhibited by the global change (invasion by *A. petiolata*).

Such effects may even occur in human dominated systems, although in many such cases selection on the plants is artificial rather than natural. Breeding for increased production in high resource environments has resulted in more recent agronomic cultivars benefiting less from high quality microbial partners or having less ability to impose sanctions on less-effective partners (Perez-Jaramillo *et al.*, 2016). For example, soybeans have lost defence mechanisms against poor-quality rhizobium partners in comparison with ancestral cultivars (Kiers *et al.* 2007). While loss of such sanctioning ability may not be costly in high nutrient environments, it may limit soybean production in more marginal lands and increase reliance on synthetic fertilizers or other management techniques. Selection on microbes in agricultural systems also may be strong, inadvertently further favouring the development of cultivars that are less reliant on microbial symbionts. For example, conventional agriculture, tillage, and annual monocropping can reduce the diversity of potential microbial partners (Hartmann *et al.*, 2015; Bowles *et al.*, 2016; Vukicevich *et al.*, 2016) and damage AMF that help the plants take up phosphorus and nitrogen (Bowles *et al.*, 2016), perhaps even causing the evolution of less cooperative AMF or rhizobia (Kiers *et al.*, 2002). Both the selection of cultivars that have lesser interaction with the soil microbes and the reduction of potential microbial partners might restrain potentially beneficial eco-evolutionary feedbacks in these agronomic systems.

Conclusions

Capitalizing on a long history of research illustrating how microbes can promote plant stress tolerance, researchers are now applying these ideas to global change contexts and linking them to both plant evolution and eco-evolutionary feedbacks. Plant-microbe

interactions have the potential to play important roles in plant adaptation (Petipas *et al.*, 2021), yet more empirical and theoretical work is needed to predict when microbes are likely to be most important to plant evolution and to catalyze eco-evolutionary feedbacks. Once we have a better understanding of when and how microbes promote plant adaptation to the stresses caused by rapid anthropogenic environmental changes, we can begin to identify which plants and microbes may be most affected by global change, understand how to manage for beneficial microbial communities, and manipulate the composition of microbial communities or the conditions that select for beneficial microbial communities, for applications ranging from ecological restoration to agriculture.

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Figure Legends

Figure 1: Global changes can cause shifts in microbial community composition or alter microbial evolution (a) and also can influence plant fitness (b). These shifts in microbial

community composition or microbial evolution can sometimes reduce the negative effects of the global change on plant fitness. As a result, these global change induced shifts in microbial communities or populations have the potential to reduce selection on plant stress tolerance traits (c) or increase selection on plant traits that promote interactions with beneficial microbes (d). Because many of these plant traits are likely to promote the growth of some microbes over others, evolutionary shifts in plant traits may result in further changes to microbial communities, initiating eco-evolutionary feedbacks (e).

Box 1: The potential for eco-evolutionary dynamics in plant-microbe systems.

Global changes have the potential to kick start eco-evolutionary feedbacks that alter plant-microbe interactions in similar ways to classic examples of eco-evolutionary feedbacks mediated by predator-prey interaction traits (e.g., Yoshida et al. 2003). Theory and empirical studies suggest that many potential outcomes from eco-evolutionary multispecies interactions are possible, including the cycles previously observed in the Yoshida et al. (2003) predator-prey system, damped oscillations (e.g., Frickel et al. 20116), or a complete breakdown of coexistence (Kremer & Klausmeier 2013). In one potential scenario depicted here, some microbes benefit plants under global change. For example, perhaps certain microbes promote plant resilience to drought. Because of the increased benefit provided by these microbes in the face of global change, plants experience strong selection on traits that promote the growth or attraction of these beneficial microbes (e.g., the production of particular exudates) (panel A). Increases in the plant traits that attract or benefit those beneficial microbes (resulting from positive selection on those traits) will increase the abundance of those beneficial microbes. As the beneficial microbes increase in abundance in the soil microbial community, selection favouring plants that produce copious exudates weakens as there is little need to promote the growth of or attract more beneficial microbes (panel B) until selection may even favour reduced investment in these microbial interaction traits as there is little need to recruit more of these microbes to the rhizosphere and the costs of producing the trait outweigh any benefit (panel C). As a result, the frequency of plants in the population producing many exudates is reduced and beneficial microbes decline in abundance, which then begins the cycle again by causing selection to once again favour plant phenotypes with high exudate production (panel D).

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