Received: 30 March 2023 | Accepted: 31 May 2023

DOI: 10.1111/1365-2745.14156

Journal of Ecology BRITISH ECOLOGICAL SOCIETY

MINI REVIEW

Mechanistic approaches to investigate soil microbe-mediated plant competition

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Funding information
Ministry of Science and Technology, Grant/Award Number: 111-2621-B-002-001-MY3; National Science Foundation, Grant/Award Number: DEB-1655522 and DEB-2105482; Taiwan MOE, Grant/Award Number: 111V1010-2

Handling Editor: Chengjin Chu

Abstract

1. Interactions between plants and soil microbes can influence plant population dynamics and diversity in plant communities. Traditional theoretical paradigms view the microbial community as a black box with net effects described by phenomenological models.
2. This approach struggles to quantify the importance of plant–microbe interactions relative to other competition and coexistence mechanisms and to explain context dependence in microbe effects.
3. We argue that a mechanistic framework focused on microbial functional groups will lead to conceptual and empirical advances, as demonstrated by extending resource ratio theory to plant–microbe interactions. We review the diverse pathways by which different microbial functional groups can influence plant resource competition. Finally, we suggest approaches to link theory with observations to measure the key parameters of our framework.
4. *Synthesis*: Our review highlights recent experimental advancements for uncovering microbial mechanisms that alter plant host resource competition and coexistence. We synthesize these mechanisms into a conceptual model that provides a framework for future experiments to investigate the importance of plant–microbe interactions in structuring plant populations and communities.

KEYWORDS
coexistence, competition, plant–microbe interactions, plant–soil feedback, resource ratio theory

1 | SOIL MICROBES MEDIATE PLANT COMPETITION

Plant–soil microbe interactions are ubiquitous, and recognition of their role in mediating plant competition has advanced our understanding of plant coexistence (Bever, 2003; Chung & Rudgers, 2016; Wagg et al., 2011). In the past few decades, negative feedback between plant hosts and their specific soil microbes (negative plant–soil feedback [PSFs]) have become the dominant paradigm for understanding the role of soil microbes in maintaining plant diversity (Crawford et al., 2019; Ke & Miki, 2015). This paradigm holds that plant species cultivate soil legacies via species-specific microbial assemblages that are more detrimental to themselves than co-occurring species; this self-limitation promotes coexistence.

Classic theory for PSFs is an extension of phenomenological models in which coexistence depends on the relative strength of intraspecific and interspecific interactions, without explicit reference to the mechanisms underlying those interactions (Bever et al., 1997; Revilla et al., 2013). This approach is experimentally tractable. The soil community can be treated as a single entity and evaluated based on its net effects on plant hosts. However, this tractability comes at the expense of mechanistic understanding. Recent reviews of PSFs have emphasized their importance (Gundale & Kardol, 2021), but warned of high context-dependence and low predictability (Bennett & Klironomos, 2019; De Long et al., 2019; Smith-Ramesh & Reynolds, 2017). For example, PSF magnitude and direction can change depending on plant age and development stage, resource availability, abiotic environmental gradients and host competitive context (Beals et al., 2020; Chung, 2023). We should not be satisfied with demonstrations that PSFs occur but should strive to quantify their contribution to the maintenance of diversity in nature.

To understand and predict the role of plant–soil microbe interactions in plant competition and coexistence, we must go beyond phenomenological description and consider the underlying plant–soil microbe interactions that drive the feedback. A mechanistic framework that explicitly considers microbial functions will help us predict microbial effects on plant coexistence in changing biotic and abiotic contexts and determine their importance relative to other coexistence mechanisms (Abbott et al., 2021; Semchenko et al., 2022; van der Putten et al., 2016). While microbial functions are hyperdiverse, they interact with plants primarily as mutualists, pathogens or decomposers. Within the context of plant coexistence, PSF research has focused primarily on pathogens due to the emphasis on negative density and frequency dependence. However, strong evidence exists that coexistence-promoting feedback can also be facilitated by mutualists, such as nitrogen-fixing bacteria and mycorrhizal fungi, and decomposers (e.g. Bennett et al., 2017; Bever, 2002; Siefert et al., 2018; Veen et al., 2019; Whitaker et al., 2017). Mechanistic approaches that open up the soil microbial black box may require more measurements than traditional phenomenological approaches (see Section 6) but are essential for predicting the consequences of rapid environmental change without the need to repeat experiments in new environments. We aim to synthesize recent evidence for microbial mechanisms that mediate resource competition between plants and propose a resource-based mechanistic framework for understanding and predicting the role of soil microbes in plant competition and coexistence (Figure 1).

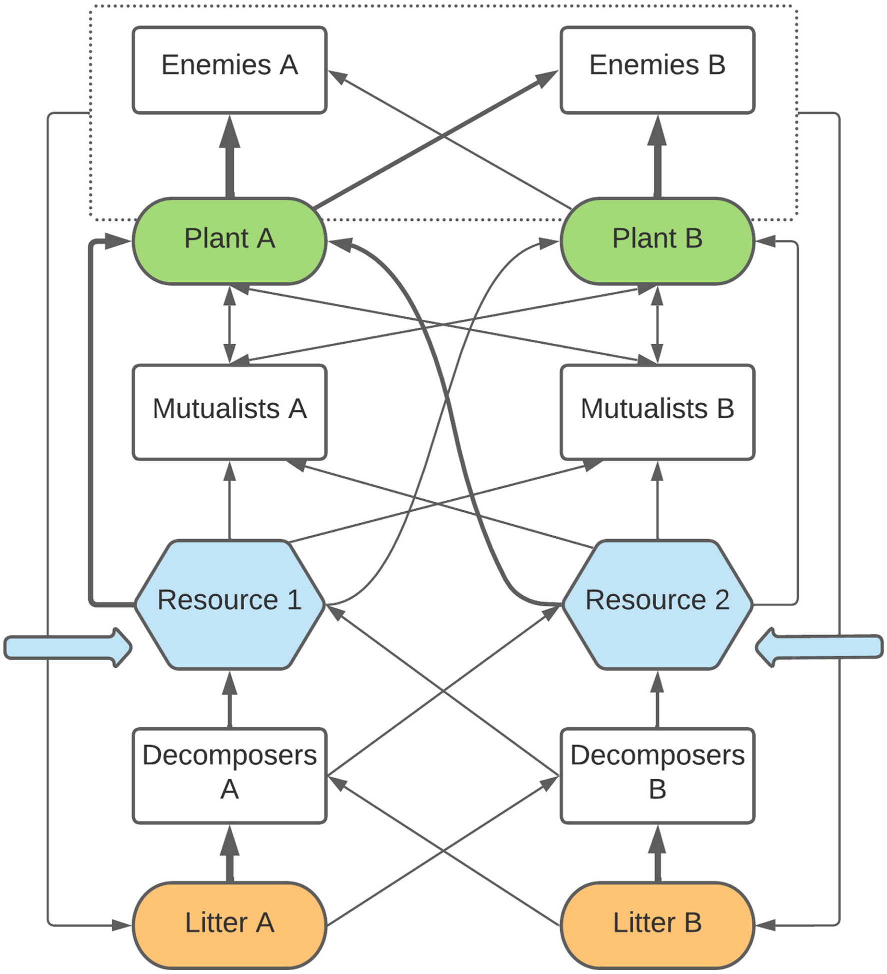

FIGURE 1 This conceptual diagram incorporates different plant–soil microbe interactions into a traditional resource partitioning framework with two plant competitors and two resources. Arrows represent the flow of energy and matter, not effects. The width of arrows indicates the strength of flow, which reflect hypothetical interaction specificity between plants, microbes, and resources (e.g. here each plant is attacked more by its specific enemy, and its specific decomposer processes more host litter). The dashed box represents the plant-enemy system, which contributes to litter via enemy-induced plant mortality. Blue arrows show external supply of resources. When microbes lack host specificity, this figure can be simplified by merging the microbial A and B components for each functional group.

2 | APPLYING RESOURCE RATIO THEORY TO UNDERSTAND MICROBE-MEDIATED PLANT COMPETITION

One of the most important alternative mechanisms for plant coexistence is soil resource partitioning. However, surprisingly few studies have investigated both the effects of resource addition and soil microbes on plant competition, and results have been equivocal due partly to a lack of clear theory (reviewed in Beals et al., 2020). Resource ratio theory (Tilman, 1982) provides a way to directly link plant–soil microbe interactions to the key components of resource competition, namely the system's resource supply, the species' resource consumption and the species' resource requirements (Box 1). These three components are inextricably linked with soil microbes (summarized in Table 1 and reviewed below). Since different microbial functional groups operate simultaneously and are linked by their impacts on resource flow (Figure 1), a clear understanding of microbial function should help us to predict how microbial effects vary with environmental context. Below, we highlight recent evidence for each of these mechanistic pathways and empirical approaches to quantify their effects.

3 | PLANT–SOIL MICROBE INTERACTIONS AND RESOURCE SUPPLY

One key component of the resource ratio theory is the resource supply (black point in Figure 2b in Box 1), defined as the resource availability for plants in the absence of plant consumption. Microbe-mediated decomposition alters resource supply for plants, sometimes in species-specific ways. Changes in resource supply caused by plant–soil microbe interactions could move competitors in and out of regions of coexistence (grey region of Figure 2b in Box 1). Studies in ‘home field advantage’ in litter decomposition show that litter can decompose faster in its ‘home’ location compared with other locations due to local adaptation of decomposers to the prevailing litter chemistry (Veen et al., 2015). This phenomenon can also operate at the scale of different plants within a community, where positive host–decomposer feedback favour competitive exclusion by moving resource supply points out of the coexistence region. For example, two Mediterranean oaks (*Quercus suber* and *Q. canariensis*) differed in their foliar nutrient content and associated saprotroph communities, generating soil conditions that favour the establishment of their own seedlings, which causes local aggregation (Aponte et al., 2013). Among co-occurring European grassland species, grasses with more exploitative sulfur acquisition strategies also increased microbial arylsulphatase activities in their rhizospheres, thus promoting their own growth in a positive feedback loop (Legay et al., 2014).

Microbes can also alter resource availability by mediating nutrient losses. Theoretical models that include decomposition and nutrient recycling have demonstrated that coexistence is promoted when each plant species associates with microbes that accelerate loss of the nutrient that more limits its own growth compared with that of its competitor (Daufresne & Hedin, 2005). On the contrary, host-specific decomposers that accelerate loss of nutrients that more limits its competitor's growth should promote exclusion. In an example that promotes exclusion and leads to monodominance, some pines and poplars thrive in N-poor environments where their litter chemistry and decomposer associations continue to promote N losses. This maintains a favourable environment for these taxa, who are better competitors for N in such systems (Fierer et al., 2001; Northup et al., 1995).

Mutualistic plant growth-promoting bacteria (PGPB) can also increase nutrient availability in the soil via specialized metabolic pathways (Ramakrishna et al., 2019). While the host specificity of these taxa is less well known, plants likely differ in their ability to attract PGPB consortia, which could result in feedback. Finally, interactions between microbial groups could also moderate resource supply. For example, the Gadgil effect suggests that competition between ectomycorrhizal (ECM) fungi and saprotrophs in forest ecosystems can reduce decomposition rates (Fernandez & Kennedy, 2016; Gadgil & Gadgil, 1971). However, whether these effects impact host coexistence may depend on host resource requirements and the N-mining abilities of their respective ECM and saprotroph associates.

4 | PLANT–SOIL MICROBE INTERACTIONS AND RESOURCE CONSUMPTION

The second component determining species coexistence is their resource consumption (consumption vectors in Figure 2b in Box 1), theoretically defined as the relative rates at which plants deplete resources. Differentiation in species' consumption vector stabilizes coexistence via self-limiting negative feedback (Letten et al., 2017). As long as each competitor consumes more of the resource most limiting its growth, then the greater the difference in their consumption vector, the wider the resource supply state-space available for coexistence. A species' consumption vector depends on its resource-specific consumption rates and its stoichiometry, which can be modified by resource mutualisms. For example, mycorrhizal associations increase concentrations of macro- and micronutrients in host tissues, implying increased consumption rates and altered stoichiometry (Lehmann & Rillig, 2015; Smith & Smith, 2011; Verzeaux et al., 2017, but see Nazeri et al., 2014). Rhizobia are known to increase tissue N for legume hosts, and some hosts reap benefits when co-infected with rhizobia and mycorrhizal fungi (Primieri et al., 2022). Pathogens can also indirectly alter host consumption and stoichiometry via effects on host physiology. For example, the bacteria *Candidatus* Liberibacter spp. causes huanglongbing in citrus by disrupting phloem transport and feeder root development. This results in plant hosts with imbalanced photosynthate distribution and decreased micronutrient consumption (Mattos Jr et al., 2020).

Evidence that plant–soil microbe interactions alter the host resource consumption is clear, but there is less consensus about whether such changes increase or decrease opportunities for host coexistence. Among hosts with similar mutualists, the evidence is

BOX 1 Overview of resource ratio theory

The resource ratio theory (Tilman, 1982), and its later generalization as contemporary niche theory (Chase & Leibold, 2003; Koffel et al., 2021), provides a framework to study how different soil microbes affect plant–plant resource competition. We summarize the key components of the framework and the criteria for plant coexistence using a graphical approach.

When two hypothetical plants (green and gold colours in Figure 2a) compete for a single resource (e.g. nitrogen), the amount of resource where per capita growth rate equals zero (i.e. where growth balances mortality and the coloured lines intercept the *x*-axis in Figure 2a) is their resource requirement, R*. In this scenario, the species with the lower R* (gold) will outcompete the other species (green) as it depletes resource to a level where the inferior species experiences negative growth.

When plants are competing for two resources, one needs to consider how the availability of the two resources jointly determines plant population growth and how plants differentially consume different resources. In our example, two hypothetical plants compete for two essential resources that co-limit plant growth according to Liebig's law of minimum, such as nitrogen and phosphorus (Figure 2b; but see Tilman, 1982 for other types of resource pairs). The resource supply point of the environment represents the availability of the two resources in the absence of plant consumption (black point in Figure 2b). Plant species are characterized by the relative rates at which they deplete the two resources (depicted as consumption vectors; dashed arrows in Figure 2b), and their resource requirement, the resource combinations at which growth balances mortality (depicted as zero net growth isoclines, ZNGIs; solid lines in Figure 2b). For purposes of simplicity, we consider essential resources, a plant's ZNGI is a right-angle corner positioned based on its R* values for the two resources, defined as the amount of a resource that causes growth to balance mortality when the other resource is not limiting. A plant is most limited by the resource with a higher R* value. This graphical framework can be extended to substitutable resources.

When the two plants compete for the two essential resources, coexistence is possible when the following three conditions are met. First, their ZNGIs must intersect, indicating a trade-off where each plant is most limited by a different resource. Second, each plant must consume more of the resource it finds more limiting. In Figure 2b, these two conditions are fulfilled as the green plant has a higher R* for nitrogen and consumes more nitrogen relative to phosphorus, and vice versa for the gold plant. A final condition for coexistence is that the supply of the two resources must not disproportionately favour any particular plant; specifically, the supply point must be encompassed by the inverse of the consumption vectors (dotted lines in Figure 2b).

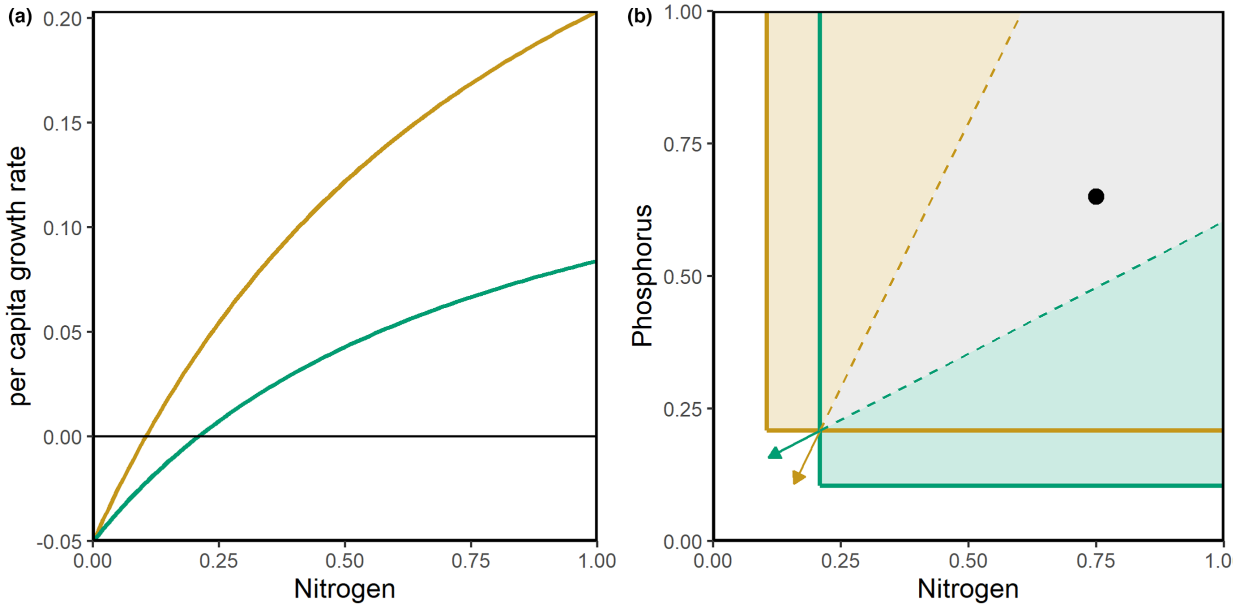

FIGURE 2 (a) State-space diagram of two hypothetical plant species (colored as green and gold) competing for one resource. The colored lines represent a species' per capita growth rate under different resource level. (b) State-space diagram of two hypothetical plant species competing for two essential resources. Here, we depict the coexistence criteria in terms of the elements of niche theory, i.e., the resource requirements (solid lines), the resource consumptions (solid arrows as consumption vectors), and the resource supply (black point). See box text for more details.

TABLE 1 Examples of ways different microbial functional groups can affect coexistence through key components of resource ratio theory. References follow the specific examples discussed in the main text. Empty cells indicate knowledge gaps where the impact of the microbial functional group on the theoretical component requires further research.

	Resource supply	Resource consumption	Resource requirement (R*)
Decomposers	Plant litter stimulates specific decomposer community to alter resource supply rates and ratios. Related to home-field advantage effects (Veen et al., 2019)		
Mutualists	The Gadgil effect suggests that competition between ECM and saprotrophs results in reduced litter decomposition rates in ECM forests (Gadgil & Gadgil, 1971)	Resource mutualists such as mycorrhizal fungi and rhizobia are known to alter host consumption rates and stoichiometry (Primieri et al., 2022, Smith & Smith, 2011)	Resource mutualists can lower R* for hosts by reducing mortality via stress tolerance or protection from antagonists (Kumar & Verma, 2018)
	Some plant growth-promoting bacteria can solubilize phosphorus, calcium, iron and increase their plant availability (Olanrewaju et al., 2017)		Other changes to R* are also possible via changes to host stoichiometry (Jeffery et al., 2018)
Pathogens	Indirectly contribute to litter availability for decomposers via the increased production of senesced host tissues	Pathogens can indirectly alter the host's consumption vector by changing its stoichiometry (Verzeaux et al., 2017)	Pathogens directly increase host R* by increasing mortality.

mixed. For example, several studies have failed to find support for arbuscular mycorrhizal fungi (AMF)-mediated partitioning of plant access to diverse phosphorus forms (Ceulemans et al., 2017; Reynolds et al., 2006; Vogelsang et al., 2006). However, hosts that associate with different mutualists (e.g. AMF, ECM fungi or rhizobia) may have access to different subsets of resources, thus altering their consumption vectors in a way that promotes coexistence (Steidinger & Bever, 2014; Tedersoo et al., 2020). Furthermore, different resource mutualists respond in predictable ways to changing abiotic conditions. For example, plants benefit most from AMF association when phosphorus is limited (high tissue N:P) (Hoeksema et al., 2010). Thus, we can experimentally test the prediction that an increase in P supply will also decrease AMF effects on host resource consumption vectors (see Section 6).

5 | PLANT–SOIL MICROBE INTERACTIONS AND RESOURCE REQUIREMENT

The final determinant of species coexistence in resource ratio theory is the species' resource requirement, reflected by the species' R* for resources. A species' R* is the minimum amount of a resource required to maintain zero population growth (i.e. where growth balances mortality at the population level). Thus, any effects of soil microbes on a host's mortality rate will alter the host's R* values, as long as the effects of the microbes are independent of resource-supply rates. For example, when pathogens increase host mortality, the host's R* will also increase (Figure 2a). On the other hand, many below-ground microbial mutualists benefit host survival, either via increased tolerance to environmental stress or protection from pathogens (Kumar & Verma, 2018; Olanrewaju et al., 2017). There is also evidence of host-specific root endophytes decreasing the P requirement of legume *Ornithopus* species relative to *Trifolium*, potentially due to reduced C demand and P availability compared with the alternative treatment, which was an AMF inoculation (Jeffery et al., 2018).

Microbe-mediated changes in R* for a given resource are empirically measurable (see Section 6), and could lead to changes in coexistence outcomes. For example, protective mycorrhizae interacting with an inferior competitor could decrease its R* due to lowered mortality rate, potentially shifting the outcome from exclusion to coexistence. How much a protective mutualism decreases mortality also depends on abiotic context, leading to testable hypotheses. For example, the survival benefits of symbiosis with an *Epichloë* fungal endophyte for a native grass host were highest in locations with the lowest precipitation (Afkhami et al., 2014). This interaction suggests that the relative decrease in R* for this native grass would be the strongest in contexts of low water supply.

6 | FUTURE DIRECTIONS TO LINK THEORY AND OBSERVATION

Our synthesis identifies new research directions to understand the role of microbial functions in plant competition. First, how can we measure the components of resource ratio theory for plants? Second, how can we isolate microbial contributions to those components? Past work has approximated R* by allowing plant monocultures to draw down a major resource until its concentration in the soil is constant (at R*) (Dybzinski & Tilman, 2007). Supply rates, however, are more challenging to measure in a plant–soil system, and are often approximated by nutrient availability at the beginning of the experiment (Dybzinski & Tilman, 2007), or more directly by measuring mineralization rates (Menge et al., 2009). Finally, total resource consumption can be approximated by multiplying plant biomass and tissue resource concentration (Dybzinski & Tilman, 2007). Or, it could be possible to use change in tissue stoichiometry to monitor the change in consumption vector angle. Given the number of moving parts, a good starting point for empiricists could be the single resource scenario, where dynamics are controlled by only R* and other components can be ignored (Figure 2a). This provides an entry point for experiments to verify model predictions before moving on to consider plants' consumption and requirements for other limiting resources.

Empirical approaches exist to manipulate and quantify the influence of plant–soil microbe interactions on components of the resource ratio theory, with the ultimate goal of parameterizing a mechanistic model. For example, inoculation and exclusion experiments could isolate microbe effects on resource ratio components. While there is no perfect method to manipulate the presence or absence of microbial mutualists versus pathogens versus decomposers, established size-based and biocide methods can come close. To target the presence of AMF, researchers can inoculate whole AMF communities using spore extraction from field soils and pair it with a background microbial wash of a smaller size fraction as a control (Schnitzer et al., 2011). A gradient of increasingly small cell size restrictions can create a series of subset communities, which can be mapped to known microbial traits (Wagg et al., 2021; Zanne et al., 2020). Size-based exclusion can also be used in the field with colonization barriers using different-sized mesh (Chung et al., 2019). In addition to inoculating with specific microbial cultures, selective biocides are also available to remove target specific pathogen groups, such as fungal versus oomycete pathogens, in competition and feedback experiments (Domínguez-Begines et al., 2021; Liu et al., 2022). While not as naturalistic, recent developments in 'EcoFAB' flow-through root chambers allow potential for mechanistic experiments where plant–soil microbe interactions can be studied in close to chemostat conditions with constant resource supply (Gao et al., 2018). Finally, 'omics-based correlative approaches have potential, but rely on future improvements in quantitative microbiome profiling and functional annotation. As annotations in microbial metagenomics and metatranscriptomics become more robust, it may be possible to link snapshots of microbiome composition to resource function (Knight et al., 2018; Shakya et al., 2019; Taş et al., 2021).

We have highlighted just a few ways that soil microbes affect plant coexistence, but future work should consider the full diversity of microbe-mediated impacts on plant niches. Microbes can modify niche elements for plant resource competition (Peay, 2016), microbes can be limiting factors themselves (Koffel et al., 2021), or they can function as competitors of plants for nutrients (Orwin et al., 2011). Furthermore, one microbial functional group could simultaneously modify many elements of coexistence (Table 1). For example, pathogens can affect coexistence by changing host resource consumption, yet the literature has primarily focused on pathogen-mediated host coexistence via effects on mortality. A logical extension of our framework would consider how altered abiotic contexts, such as temperature or soil moisture, could change how multiple microbes alter not just one, but all components of the resource ratio theory. Finally, recognizing the roles of specific microbial functional groups also makes it possible to study their interactions which, in theory, can lead to a wider range of possible dynamics than previously appreciated (Jiang et al., 2020).

7 | CONCLUSIONS

The microbial black box has served us well. However, we now have the theory and technology to open it up using mechanistic approaches. Our framework generates specific, testable hypotheses that can guide future theories and experiments in a tractable way. Characterizing specific mechanisms by which microbial mutualists, decomposers, and pathogens affect plants is the critical next step in understanding how plant–soil microbe interactions mediate coexistence. Here, we used resource ratio theory as an example to demonstrate how a clear understanding of microbial function can help us predict microbial effects on plant communities under varying environmental contexts. Combining plant and microbial ecology with plant physiological ecology and ecological stoichiometry could advance our empirical understanding of mechanisms that underlie microbe-mediated plant competition and coexistence. Ultimately, a shift away from phenomenological indices will promote a better understanding of plant–soil microbe interactions in the context of other coexistence mechanisms and environmental change.

AUTHOR CONTRIBUTIONS

All authors worked together to conceive and develop the ideas. Anny Chung took the lead in writing the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

ACKNOWLEDGEMENTS

This work was supported by NSF DEB-1655522 to Adler and Chung, start-up funds from the University of Georgia and NSF DEB-2105482 to Chung, and Taiwan MOE Yushan scholar program 111V1010-2 and MOST 111-2621-B-002-001-MY3 to Ke.

CONFLICT OF INTEREST STATEMENT

Anny Chung is an Associate Editor of the *Journal of Ecology* but took no part in the peer review and decision-making processes for this paper. The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

No novel data are associated with this manuscript.

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How to cite this article: Chung, Y. A., Ke, P.-J., & Adler, P. B. (2023). Mechanistic approaches to investigate soil microbe-mediated plant competition. *Journal of Ecology*, *111*, 1590–1597. https://doi.org/10.1111/1365-2745.14156