CONCEPTS AND SYNTHESIS

EMPHASIZING NEW IDEAS TO STIMULATE RESEARCH IN ECOLOGY

Effects of soil microbes on plant competition: a perspective from modern coexistence theory

Po-Ju Ke [1,3] and Joe Wan [1,2]

[1]*Department of Biology, Stanford University, Stanford, California 94305-5020 USA*
[2]*Institute of Integrative Biology, Department of Environmental Systems Science, ETH Zürich, 8092 Zürich, Switzerland*

Abstract. Growing evidence shows that soil microbes affect plant coexistence in a variety of systems. However, since these systems vary in the impacts microbes have on plants and in the ways plants compete with each other, it is challenging to integrate results into a general predictive theory. To this end, we suggest that the concepts of niche and fitness difference from modern coexistence theory should be used to contextualize how soil microbes contribute to plant coexistence. Synthesizing a range of mechanisms under a general plant–soil microbe interaction model, we show that, depending on host specificity, both pathogens and mutualists can affect the niche difference between competing plants. However, we emphasize the need to also consider the effect of soil microbes on plant fitness differences, a role often overlooked when examining their role in plant coexistence. Additionally, since our framework predicts that soil microbes modify the importance of plant–plant competition relative to other factors for determining the outcome of competition, we suggest that experimental work should simultaneously quantify microbial effects and plant competition. Thus, we propose experimental designs that efficiently measure both processes and show how our framework can be applied to identify the underlying drivers of coexistence. Using an empirical case study, we demonstrate that the processes driving coexistence can be counterintuitive, and that our general predictive framework provides a better way to identify the true processes through which soil microbes affect coexistence.

Key words: equalizing mechanisms; fitness difference; Janzen-Connell hypothesis; mutualism; niche difference; pathogens; plant–soil feedback; stabilizing mechanisms.

INTRODUCTION

Ecologists have long invoked resource partitioning to explain the coexistence of competing species (Gause 1934, Tilman 1982), yet differences in resource use cannot fully account for plant diversity (Silvertown 2004). As a result, plant community ecologists have broadened their focus beyond plant–plant competition to address how interactions between trophic levels can affect plant coexistence (Chesson 2008, Mordecai 2011, Cardinaux et al. 2018, Lanuza et al. 2018). Growing evidence suggests that plants can influence the performance of both conspecifics and competitors by modifying soil microbial communities, an effect commonly studied under the framework of plant–soil feedbacks (Bever et al. 1997,

Bever 2003). Differences in the way competing plants interact with soil microbes might promote plant coexistence (Bever 2003, Chung and Rudgers 2016). Alternatively, soil microbes could favor certain plants over their competitors, creating variation in species' relative abundance (Klironomos 2002, Mangan et al. 2010) and invasion success (Reinhart and Callaway 2006, Ke et al. 2015).

The wide range of plant–soil microbe interactions makes it difficult to draw general conclusions about their effects on plant communities. In some systems, soil microbial communities may be predominantly harmful to plants due to high pathogen prevalence, while in other systems, beneficial microbes such as mycorrhizal fungi may play a more important role. Moreover, the impacts of soil microbes depend on their degree of host specificity. For example, pathogens can promote plant coexistence if they are host specific (Bell et al. 2006, Yamazaki et al. 2008, Bagchi et al. 2010) but may reduce plant

[3] E-mail: pojuke@stanford.edu

diversity if a single species suffers greater attack (Mordecai 2011). On the other hand, mycorrhizal fungi can hinder plant coexistence if the dominant species has greater mycorrhizal dependence (Urcelay and Díaz 2003), but may promote coexistence if they benefit not only their hosts but also their hosts' competitors (Bever 2002). Further adding to this complexity, plant–soil microbe interactions do not operate in isolation: their effect on coexistence must be considered within the context of plant–plant competition for limiting resources such as light and soil nutrients (Callaway et al. 2004, Casper and Castelli 2007, Shannon et al. 2012, Crawford and Knight 2017). Indeed, variability in experimental results suggests that the relative importance of plant–soil microbe and plant–plant interactions may be highly system specific (Lekberg et al. 2018). Because of the context dependency of soil microbial interactions, an important question remains: what are the general conditions under which soil microbes promote plant coexistence?

To synthesize the diverse roles that plant–soil microbe interactions play in plant communities, we draw on modern coexistence theory (Chesson 1990, 2000, 2008). This framework uses two quantitative components to link species differences to competitive outcomes. Niche differences summarize mechanisms that promote coexistence, such as differences in resource use (Chesson 1990) or parasitism (Chesson 2008). These prevent competitive exclusion by giving each species an advantage when it is rare. On the other hand, fitness differences, such as differences in reproductive output or environmental tolerance, determine the ability of one species to exclude its competitor. Thus, modern coexistence theory classifies processes mediating coexistence into two general categories: equalizing mechanisms, which decrease fitness differences between species, and stabilizing mechanisms, which increase niche differences between species (Chesson 2000, Adler et al. 2007, HilleRisLambers et al. 2012). Since coexistence requires the niche difference to be greater than the fitness difference between the two species, the two components form a common currency for understanding how mechanisms simultaneously affect coexistence. Moreover, niche and fitness differences can be calculated for mathematical models (Chesson 2008) as well as experimental results (Godoy and Levine 2014, Gross et al. 2015, Kraft et al. 2015), providing a quantitative link between empirical results and theoretical perspectives.

Taking advantage of the strengths of modern coexistence theory, we provide a unified framework that predicts and classifies the effects of soil microbes on plant coexistence. We begin by presenting a theoretical framework for modeling interactions between plants and soil microbes (*Modeling plant–soil microbe interactions*). In this section, we summarize previous theoretical treatments of plant–soil microbe interactions and outline a new mathematical model that links this field of research to the empirical and experimental tools of modern

coexistence theory. In particular, we highlight the derivation of niche and fitness differences from the underlying plant–soil microbe demographic model. In the next section, we demonstrate how this model can be used to understand the outcome of plant–soil microbe interactions in diverse contexts (*Synthesizing microbial effects on plant coexistence*). Here, we apply the model to four soil-microbe-mediated scenarios drawn from the empirical literature and simulate their impacts on plant coexistence. Synthesizing the results, we provide a general classification of soil microbial effects that clarifies: (1) when soil microbes stabilize plant coexistence, (2) when soil microbes equalize plant fitness, and (3) how soil microbes affect the importance of plant–plant competition. Finally, we show how our framework can guide empirical studies (*Applying modern coexistence theory to plant–soil microbe interaction experiments*). To do so, we propose experimental designs that efficiently quantify the full set of plant–plant and plant–soil microbe interactions. In a case study, we then apply our framework to existing experimental data and show how it uses the context of plant competition to identify the plant–soil microbe interactions most important for coexistence.

Modeling Plant–Soil Microbe Interactions

A brief overview of past modeling achievements

We begin by summarizing previous theoretical work on plant–soil interactions to clarify the rationale behind our model. In the first theoretical investigation of the role of soil microbes in plant coexistence, Bever et al. (1997) showed that plant-induced changes in the soil microbial community can promote coexistence if these changes negatively affect the growth rate of the plant relative to that of its competitors. The model underlying this result focuses on plant and microbe frequencies (i.e., relative abundances): plant populations grow exponentially at rates determined by the frequencies of soil microbial communities, and coexistence conditions can be derived from the equations for plant frequencies. This approach allowed Bever et al. (1997) to define an "interaction coefficient," I_s, whose sign is mathematically a necessary (but not sufficient) criterion for plant coexistence (Revilla et al. 2013, Ke and Miki 2015). Bever et al. (1997) used this index to categorize the overall effects of soil microbes: when plants only interact with each other through their soil microbes, coexisting plants have a negative I_s and are said to be experiencing "negative plant–soil feedback."

The model of Bever et al. (1997) served as a starting point for subsequent theoretical studies (reviewed in Bever et al. 2010, Ke and Miki 2015), including spatially explicit treatments (Eppinga et al. 2006), frameworks explicitly representing soil nutrients (Umbanhowar and McCann 2005), and multispecies models (Kulmatiski et al. 2011, Eppinga et al. 2018). Moreover, this

theoretical treatment stimulated a productive line of empirical investigation (Kulmatiski et al. 2008, van der Putten et al. 2013). Since the interaction coefficient in Bever et al. (1997) can be calculated by comparing plant performance in conspecific (home) and heterospecific (away) soils, it has allowed researchers to identify the direction of soil microbe-mediated feedbacks in a variety of systems (reviewed in Bever et al. 2010, 2015, van der Putten et al. 2013).

Subsequent work has addressed restrictions of the original approach. First, some follow-up work replaced the frequency-dependent microbial effects of the original model with density-dependent effects, which may be more appropriate for certain guilds of microbes (Umbanhowar and McCann 2005, Eppinga et al. 2006). Second, studies have incorporated more realistic plant population dynamics into the model. Originally, Bever et al. (1997) focused on the effects of soil microbes by assuming no self-limitation or competition in the plant populations. As a result, the original model cannot predict coexistence in systems where plants experience asymmetric competition. Bever (2003) added Lotka-Volterra-type density-dependent plant competition to the original frequency-based plant–soil feedback model; Revilla et al. (2013) later analyzed this model and derived indexes corresponding to the original I_s in Bever et al. (1997). Nonetheless, these results have not provided a way to empirically predict the competitive outcome of combined plant–soil microbe and plant–plant interactions.

Model

We build upon these previous models of reciprocal plant–soil microbe interactions to provide a theoretical model that (1) represents a more general set of plant–microbe and plant–plant interactions, (2) allows us to quantify niche and fitness differences, and (3) can be applied to predict competitive outcomes from greenhouse measurements of plant population dynamics. In contrast to the approach in Bever (2003), which mixes frequency-dependent microbial effects with density-dependent plant–plant competition, we choose to consistently adopt density units. This approach has previously been used to model a variety of soil microbes, and is compatible with experimental approaches that measure per-capita effects of competitors on plants.

Our model adapts and generalizes the approach of Eppinga et al. (2006) by considering mutualistic soil microbes in addition to pathogens. Like most models of plant–soil interactions, it does not explicitly consider variability in time or space. The model tracks the densities of two competing plants and their associated soil microbes (summarized visually in Fig. 1a): N_A and N_B represent the density of competing plant species A and B, respectively, while S_A and S_B represent the total density of each plant's root-associated soil microbial community. Each soil microbial community grows logistically with intrinsic growth rate g_A or g_B toward its carrying capacity k_A or k_B:
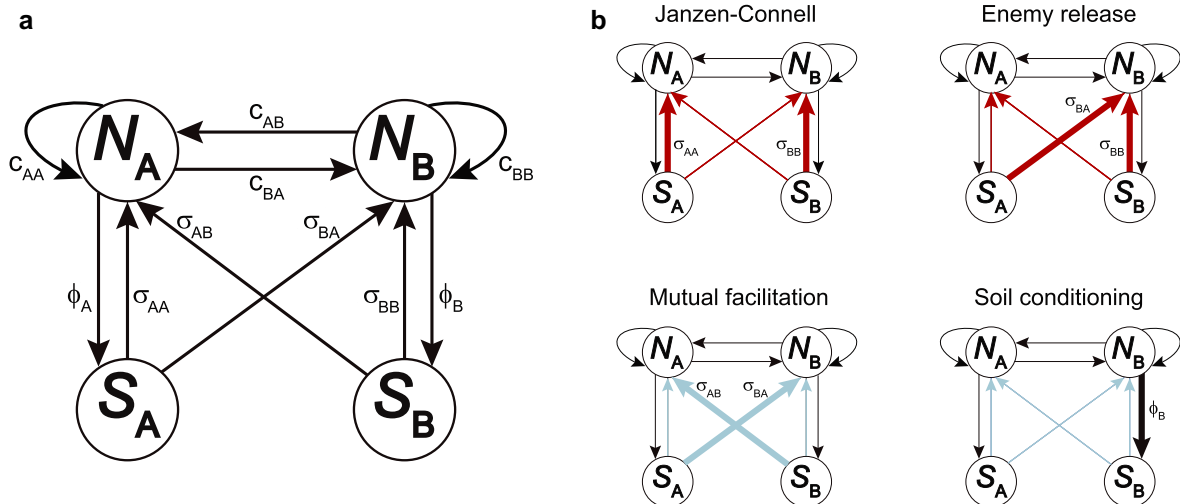
Fig. 1. Conceptual framework for the plant–soil microbe interaction model. (a) The model describes the dynamics of two plants (N_A and N_B) and the total density of their associated soil microbial communities (S_A and S_B), considering both plant–plant competition (c_{ij}) and plant–soil microbe interaction (σ_{ij}). All arrows are labeled with corresponding model parameters; see section *Model* for parameter definitions. (b) The four interaction scenarios analyzed in this study: Janzen-Connell (top left, varying σ_{AA} and σ_{BB}); enemy release (top right, varying σ_{BA} and σ_{BB}); mutual facilitation (bottom left, varying σ_{AB} and σ_{BA}); and differential soil conditioning (bottom right, varying ϕ_B). Parameters varied in each scenario are highlighted with thick arrows. Soil microbial effects in the Janzen-Connell and enemy release scenario are pathogenic ($\sigma_{ij} < 0$, dark red arrows), whereas in the mutual facilitation and differential soil conditioning scenario, they are mutualistic ($\sigma_{ij} > 0$, light blue arrows). Default parameter values are provided in Appendix S4: Table S1.

$$\frac{dS_A}{dt} = g_A S_A \left(1 - \frac{S_A}{k_A}\right) \tag{1}$$

$$\frac{dS_B}{dt} = g_B S_B \left(1 - \frac{S_B}{k_B}\right). \tag{2}$$

Since the soil microbial community relies on resources that are supplied by plants (e.g., litter inputs, root exudates, or roots for direct colonization), we let the carrying capacity of the soil microbial community increase linearly with host plant density: $k_i = \phi_i \times N_i$, where i = A or B. The parameter ϕ_i represents the ability of a plant individual to condition its soil microbes by supplying litter inputs or root exudates. As a result, when the host plant population increases, the carrying capacity of soil microbes also increases. In this respect, our model is similar to a recent model by Kandlikar et al. (2019), which assumed that the per-capita growth rate of soil microbes increases linearly with plant density but decreases due to density-dependent mortality.

Plant populations N_A and N_B grow at rates determined both by plant–plant competition and by the effects of soil microbes. As in the Lotka-Volterra competition model, the population growth of plants in the absence of competitors or microbes is given by the intrinsic growth rates r_A and r_B. Plant–plant interaction is measured by c_{ij}, the linear effect of plant j on plant i. We build on this classic model by incorporating direct interaction between plants and soil microbial communities: σ_{ij}, the soil microbe interaction coefficient, gives the linear effect of the microbial community specific to plant j on plant i (see Eppinga et al. 2006 and Aguilera 2011 for nonlinear functional response). Note that unlike in the model of Bever (2003), here c_{ij} and σ_{ij} have the same density-based units. Accordingly, plant population dynamics are described as follows:

$$\frac{dN_A}{dt} = r_A N_A (1 + c_{AA} N_A + c_{AB} N_B + \sigma_{AA} S_A + \sigma_{AB} S_B) \tag{3}$$

$$\frac{dN_B}{dt} = r_B N_B (1 + c_{BA} N_A + c_{BB} N_B + \sigma_{BA} S_A + \sigma_{BB} S_B). \tag{4}$$

For our purpose, we assume that plant–plant interactions are competitive ($c_{ij} < 0$, thus hereafter referred as plant–plant competition), where a more negative c_{ij} represents stronger competition. On the other hand, each species-specific soil microbial community may be either detrimental ($\sigma_{ij} < 0$) or beneficial ($\sigma_{ij} > 0$) to each plant. A more negative σ_{ij} represents a stronger detrimental effect of a soil microbial community on a plant, whereas a more positive σ_{ij} represents a greater beneficial effect. Since σ_{ij} represents the entire effect of a microbial community, it may summarize a variety of microbial guilds. Thus, on the whole, each specific microbial community may be considered to have a net

---

Box 1. Separating the stabilizing and equalizing components

To calculate the components of modern coexistence theory, we applied separation of timescales by assuming that soil microbe dynamics were sufficiently fast compared to plant population dynamics and that all dynamics occurred near equilibrium. In particular, this means that soil microbes reach their plant-determined carrying capacities without any time lag and die instantly when the host plant dies. Under these conditions, we reduced our model (Eqs. 1–4) to a two-species Lotka-Volterra model (see Appendix S2), with the following interaction coefficients:

$$\alpha_{ij} = c_{ij} + \sigma_{ij} \phi_j. \tag{5}$$

Here, α_{ij} represents the net competitive effect of species j on i and i and j = A or B. Importantly, we can observe that net competition consists of two terms: (1) plant–plant competition not related to soil microbes, c_{ij}, and (2) soil microbial effects, summarized as $\sigma_{ij}\phi_j$. We assumed that plant–plant interactions are competitive ($c_{ij} < 0$) and plant–soil microbe interactions can be either detrimental ($\sigma_{ij} < 0$) or beneficial ($\sigma_{ij} > 0$). Note that, when microbes have no effect on plants (σ_{ij} or $\phi_i = 0$), the model simplifies to pure Lotka-Volterra competition. In addition, if the soil microbes have a very strong positive effect, α_{ij} becomes greater than zero and the plant populations grow toward infinite population size without other regulatory forces.

After transforming the model, we quantified niche overlap and fitness ratio between the two plants using formulas derived specifically for two-species Lotka-Volterra models (Chesson 1990, 2013, Chesson and Kuang 2008). Under this formalization, stabilizing mechanisms represent processes that decrease niche overlap (ρ, or increase niche difference, $1 - \rho$). Here, ρ is the magnitude of difference in inter- to intraspecific interaction coefficients, i.e., $\rho = \sqrt{\alpha_{BA}\alpha_{AB}/\alpha_{AA}\alpha_{BB}}$. Equalizing mechanisms, on the other hand, represent processes that reduce the fitness ratio, which is defined as $\frac{f_B}{f_A} = \sqrt{\alpha_{AA}\alpha_{AB}/\alpha_{BB}\alpha_{BA}}$. Following these definitions, we derived the niche overlap and fitness ratio between N_A and N_B as:

$$\rho = \sqrt{\frac{(c_{BA} + \sigma_{BA}\phi_A)(c_{AB} + \sigma_{AB}\phi_B)}{(c_{AA} + \sigma_{AA}\phi_A)(c_{BB} + \sigma_{BB}\phi_B)}} \tag{6}$$

$$\frac{f_B}{f_A} = \sqrt{\frac{(c_{AA} + \sigma_{AA}\phi_A)(c_{AB} + \sigma_{AB}\phi_B)}{(c_{BB} + \sigma_{BB}\phi_B)(c_{BA} + \sigma_{BA}\phi_A)}}. \tag{7}$$

pathogenic ($\sigma_{ij} < 0$) or mutualistic effect ($\sigma_{ij} > 0$) relative to the case where no plant-specific soil conditioning occurs. Additionally, we note that our model is able to represent shared soil microbial associates through their net effect on σ_{ij} (see Appendix S1, where we derive Eqs. 3, 4 from a model that explicitly represents microbial species).

Quantifying the components of modern coexistence theory

Modern coexistence theory provides a general method to quantify the stabilizing and equalizing components of coexistence for a variety of models (Chesson 2003, Barabás et al., 2018). The formulas for these components in the Lotka-Volterra model of competition (Chesson 1990, 2013, Chesson and Kuang 2008) can be used in cases where environmental variability is not the primary focus. To take advantage of this theory, we applied separation of timescales to transform our model into the standard Lotka-Volterra form. In particular, we assumed that the dynamics of soil microbes were sufficiently fast compared to those of the plants (see Box 1 and Appendix S2 for detailed derivation and interpretation). While we focus here on our general theoretical framework, we note that timescale separation can be applied to derive niche overlap and fitness ratio for a variety of models of plant–soil microbe interactions (Appendix S1).

A key feature in our mathematical derivation is the phenomenological interaction coefficient, α_{ij} (i.e., the competition coefficient of the Lotka-Volterra appoximation, Eq. 5 in Box 1). This coefficient represents the total per-capita effect of each plant species on its conspecifics or heterospecifics, summarizing the combined effect of plant–plant competition (c_{ij}) and soil microbes (σ_{ij}). As α_{ij} corresponds to the interaction coefficients measured by plant competition experiments, this result links our framework to existing experimental methods for quantifying the modern coexistence theory components. After transforming the model, we used the formulas from Chesson (2008) to quantify niche overlap and fitness ratio between the two species. Doing so, we were able to examine how plant–plant competition and soil microbial effects interactively determine coexistence.

SYNTHESIZING MICROBIAL EFFECTS ON PLANT COEXISTENCE

In this section, we demonstrate how our model can be applied to predict the effect of soil microbes, and show that the two components of modern coexistence theory synthesize a diverse set of microbial processes that affect plant coexistence. We begin by applying the formulas for niche overlap and fitness ratio (Box 1) to study four plant–soil microbe interaction scenarios, each representing a well-documented empirical example of how soil microbes can influence plant performance. In each case,

we determine whether soil microbes promoted or prevented coexistence, and whether this effect was mediated by niche, fitness, or both components. Generalizing these results, we then present a small set of categories that can predict how a large number of soil microbe-mediated processes affect plant coexistence.

Simulating different plant–soil microbe interaction scenarios

As shown in Fig. 1b, we considered the following scenarios: (1) a Janzen-Connell scenario, where both plants experience increasingly negative conspecific microbial effects driven by host-specific pathogens (Janzen 1970, Connell 1971); (2) an enemy release scenario, where negative microbial effects on one plant are alleviated (Keane and Crawley 2002, Reinhart and Callaway 2006); (3) a mutual facilitation scenario, where the beneficial mycorrhizal fungus hosted by each plant has an increasingly positive effect on the competitor of its host (Bever 2002); and (4) a differential soil conditioning scenario, where one plant allocates more photosynthetic products to support a greater population of beneficial microbes (Norby et al. 1987, Zheng et al. 2015). Fig. 1b summarizes these scenarios using thick arrows to highlight each set of characteristic parameters. Together, the four scenarios encompass a wide array of microbial functional groups, ranging from pathogens to mutualists and from specialists to generalists. See also Table 1 for a list of other scenarios that can be considered using our modeling framework.

For each of the four scenarios, we ran simulations to quantify how varying soil microbial effects (i.e., the magnitude of σ_{ij} or ϕ_i; see Fig. 3 and Appendix S4: Table S1 for parameter values) affected overall competitive outcomes. We visualized these results on the parameter space of niche difference and fitness ratio (Box 2). Although varying effect strengths always impacted both of these components (arrows of Fig. 3), the effect of some scenarios was primarily mediated by a single mechanism. The Janzen-Connell (Fig. 3a) and mutual facilitation (Fig. 3c) scenarios always increased niche differences, but their effects on fitness ratio were smaller and inconsistent. Thus, in these scenarios, soil microbes acted as a stabilizing mechanism. On the other hand, enemy release (Fig. 3b) primarily affected the fitness ratio; thus, soil microbes in this scenario primarily had an equalizing effect, promoting coexistence when they benefited the inferior competitor. Finally, both mechanisms were important in the soil conditioning case (Fig. 3d).

To understand the interaction between plant–soil microbe interactions and plant–plant competition, we simulated each of the four scenarios with different strengths of plant–plant competition, c_{ij}, producing the different-colored arrows in Fig. 3. We varied one of the

four c_{ij} at a time while keeping the other three fixed (see Fig. 3 and Appendix S4: Table S1 for parameter values). The range of niche differences and fitness ratio generated by different values of c_{ij} then indicates the importance of plant–plant competition in determining competitive outcome. We showed that the effect of the illustrated coefficients could be either reduced (Fig. 3a) or amplified (Fig. 3b–d) by soil microbial effects, suggesting the need to consider interactions between plant–plant and plant–soil microbe interactions. However, for other coefficients, plant–soil microbe interactions did not alter the qualitative importance of plant–plant competition (Appendix S4: Figs. S1–S4). In general, these interactive effects only occurred for the forms of plant–plant competition (c_{ij}) corresponding to the soil microbial effects (σ_{ij}) varied by the plant–soil microbe interaction scenario. Below, we detail the simulation results for each of our four scenarios.

Janzen-Connell scenario.—According to the Janzen-Connell hypothesis, a classic mechanism of natural enemy-mediated coexistence, species build up high densities of host-specific natural enemies near parent trees (Augspurger and Kelly 1984). We focused on a version of this mechanism mediated by soil pathogens, corresponding to the negative plant–soil feedbacks measured in both temperate (Bennett et al. 2017) and tropical (Mangan et al. 2010) forest systems. In the simulation, plants cultivated soil pathogen communities that were only slightly harmful to the non-cultivating species ($\sigma_{AB} = -0.4$, $\sigma_{BA} = -0.5$). Beginning with $\sigma_{AA} = \sigma_{BB} = -0.32$ (weaker than interspecific effects), we strengthened the impact of both soil pathogen communities on their cultivating plants until both parameters reached -6.0 (much stronger than interspecific effects).

This promoted coexistence primarily by increasing niche difference between the competing plant species: in other words, soil microbes acted primarily as a stabilizing mechanism. Nonetheless, varying Janzen-Connell strength also affected fitness ratio, which was sometimes enough to change the identity of the dominant competitor (Fig. 3a, $c_{AA} = -1$), but this effect was small relative to the change in niche difference and varied depending on plant–plant competition. As the negative effect of host-specific pathogens increased, intraspecific plant–plant competition (c_{AA} and c_{BB}) became less important in determining overall competitive outcome. This can be seen in Fig. 3a, where the changes in fitness ratio and niche difference caused by changing c_{AA} decreased with intensifying soil microbial effects. However, we did not observe a similar effect for interspecific competition (c_{AB} and c_{BA}), which remained qualitatively important for determining fitness ratio regardless of Janzen-Connell strength (Appendix S4: Fig. S1).

Enemy release scenario.—Enemy release occurs when species experience decreased pressure from natural enemies in their introduced range. While release from

species-specific natural enemies has received greater attention, the effect also encompasses decreased pressure from generalist natural enemies (Keane and Crawley 2002); here, we considered both kinds of natural enemies. Inspired by evidence that plants are less negatively affected by soil pathogens in their introduced ranges (Reinhart and Callaway 2006), we considered an introduced species (plant B) competing with a native species (plant A). Beginning with a scenario where soil pathogen communities affect both plants ($\sigma_{AA} = \sigma_{AB} = -0.5$; $\sigma_{BA} = \sigma_{BB} = -2.0$), we alleviated the effect of both pathogen communities on B by making σ_{BA} and σ_{BB} less negative until $\sigma_{BA} = \sigma_{BB} = 0$ (representing complete enemy release).

The enemy release scenario had a strong effect on fitness ratios: as plant B became increasingly released from enemy effects, its fitness increased relative to that of its competitor. In the case examined here, this allowed the two plants to coexist. More generally, such an effect should be expected to promote coexistence if it benefits the inferior competitor to an intermediate degree (Appendix S4: Fig. S2). Enemy release had a smaller effect on niche difference, and the direction of this effect varied according to c_{BA} (different arrows in Fig. 3b). As the impact of natural enemies on plant B decreased, its sensitivity to plant–plant competition (c_{BA} and c_{BB}) became increasingly important for determining fitness ratio and niche difference (shown for c_{BA} in Fig. 3b). In contrast, the remaining coefficients (c_{AB} and c_{AA}, representing the sensitivity of plant A to plant–plant competition) did not produce this interactive effect (Appendix S4: Fig. S2).

Mutual facilitation scenario.—While much work on microbe-mediated plant coexistence has focused on pathogens, Bever (2002) proposed that conditioning of mutualist communities can promote plant coexistence if each plant's conditioning favors its competitors (i.e., causes plants to facilitate one another). Beginning with a scenario where the soil mutualist communities benefited their cultivating hosts ($\sigma_{AA} = \sigma_{BB} = 0.5$) but not their hosts' competitors ($\sigma_{AB} = \sigma_{BA} = 0.0$), we increased the degree of mutual facilitation (σ_{AB} and σ_{BA}) until each soil community was much more beneficial to non-host plants than to its own host ($\sigma_{AB} = \sigma_{BA} = 2.0$).

Like the Janzen-Connell scenario, the mutual facilitation scenario always increased niche difference between the two competitors; in some cases, this was enough to result in coexistence. Additionally, mutual facilitation affected fitness ratio, but the direction of these changes was inconsistent (different arrows in Fig. 3c). Increasing mutual facilitation amplified the effect of interspecific plant–plant competition (c_{AB} and c_{BA}), but not that of intraspecific competition (c_{AA} and c_{BB}), on fitness ratio and niche difference (shown for c_{AB} in Fig. 3c; see also Appendix S4: Fig. S3). Thus, though the Janzen-Connell and mutual facilitation scenarios both increased niche difference, they interacted differently with plant–plant competition.

<div style="border:1px solid">

Box 2. Visualizing the niche difference–fitness ratio parameter space

In our model, niche difference $(1 - \rho)$ and fitness ratio (f_B/f_A) predict the outcome of plant competition. Thus, we use the parameter space defined by the two components to visualize competitive dynamics between the two plant species. Here, we use Fig. 2 as an illustrative example to demonstrate how to interpret our results. The solid linear and dotted curvilinear black lines denote the boundary where fitness ratio is equal to niche overlap (ρ) and the inverse of niche overlap $(1/\rho)$, respectively. These two boundaries partition the parameter space into four distinct regions, representing different outcomes of competition. If the two species differ too greatly in fitness relative to their niche difference, one species outcompetes the other (upper and lower white regions). When the niche difference is positive, stable coexistence occurs if the fitness ratio is not too extreme (right gray region). When niche difference is negative, priority effects may occur (left gray region), where community composition depends on which plant arrives first (Ke and Letten 2018).

The pathways shown in Fig. 2 illustrate how soil microbes might alter competitive outcomes. For example, soil microbes may promote coexistence by primarily affecting niche difference (a stabilizing mechanism, arrow a in Fig. 2) or fitness ratio (an equalizing mechanism, arrow b Fig. 2). Soil microbes may also flip the competitive hierarchy by changing the identity of the dominant competitor (arrow c in Fig. 2). Note that since microbe-mediated parameters make up part of the phenomenological interaction coefficients (Eq. 5), varying their strength simultaneously affects both niche difference and fitness ratio. The only exception is the special case where a pair of σ_{ij} coefficients are varied in a way that maintains the value of Eq. 6 or Eq. 7. In general, however, plant–soil interactions should predominantly affect either the stabilizing or equalizing component depending on the interaction network between plants and soil microbes (*Synthesizing microbial effects on plant coexistence*).

</div>

Differential soil conditioning.—Differences in the strength of soil microbial effects on plants may also be mediated by differences in plants' ability to cultivate soil microbial communities. For instance, the amount of fixed carbon provided by plants to their mycorrhizal mutualists may vary depending on the environmental context (Norby et al. 1987, Zheng et al. 2015) and on plant competitive strategy (Hoeksema et al. 2010). We considered a pair of competing plants, each cultivating a mutualist community $(\sigma_{AA} = 0.5; \sigma_{AB} = 0.25; \sigma_{BB} = 0.20; \sigma_{BA} = 0.10)$. We began by giving both
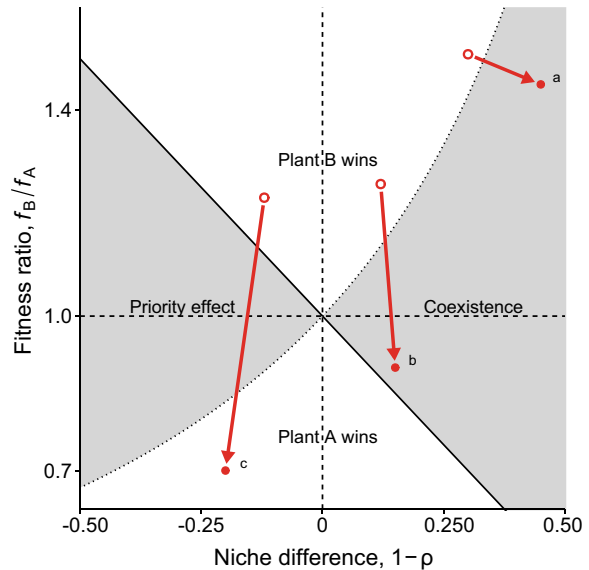

Fig. 2. Potential effects of soil microbes on the outcome of plant competition, visualized on the parameter space of niche difference $(1 - \rho,$ x-axis) and fitness ratio $(f_B/f_A,$ y-axis). The solid and dotted lines represent the boundaries where f_B/f_A equals ρ or $1/\rho$, respectively. The right and left gray shaded areas indicate the regions where coexistence or priority effects occur, respectively; the top and bottom white areas indicate where plant B or A is dominant, respectively. The red arrows demonstrate how soil microbes may alter the outcome of competition by (a) acting primarily as a stabilizing mechanism, (b) acting primarily as an equalizing mechanism, or (c) changing the identity of the dominant competitor. Open and solid circles represent competition in the absence or presence of soil microbes, respectively.

plants equal conditioning ability, represented by the microbial carrying capacity $\phi_A = \phi_B = 0.025$. We then increased the ability of plant B to condition its soil community by increasing ϕ_B up to 2.5.

Depending on plant–plant competition parameters, increased soil conditioning by plant B could either promote or prevent coexistence, an effect mediated by both fitness and niche components (Fig. 3d). Mathematically, this context-dependent result occurs because changing the conditioning ability of B affects the invasion growth rate of plant A, but not that of plant B (Appendix S3). Examining the interaction of plant–plant competition parameters with soil conditioning, we found that soil conditioning increased the importance of plant B's competitive effect $(c_{AB}$ and c_{BB}; shown for c_{AB} in Fig. 3d) but did not change the qualitative importance of plant A's competitive effect $(c_{BA}$ and c_{AA}; Appendix S4: Fig. S4).

A general categorization of soil microbial effects

The above simulations illustrate that interactions between plants and soil microbes can have diverse effects on coexistence. Some mechanisms primarily affected
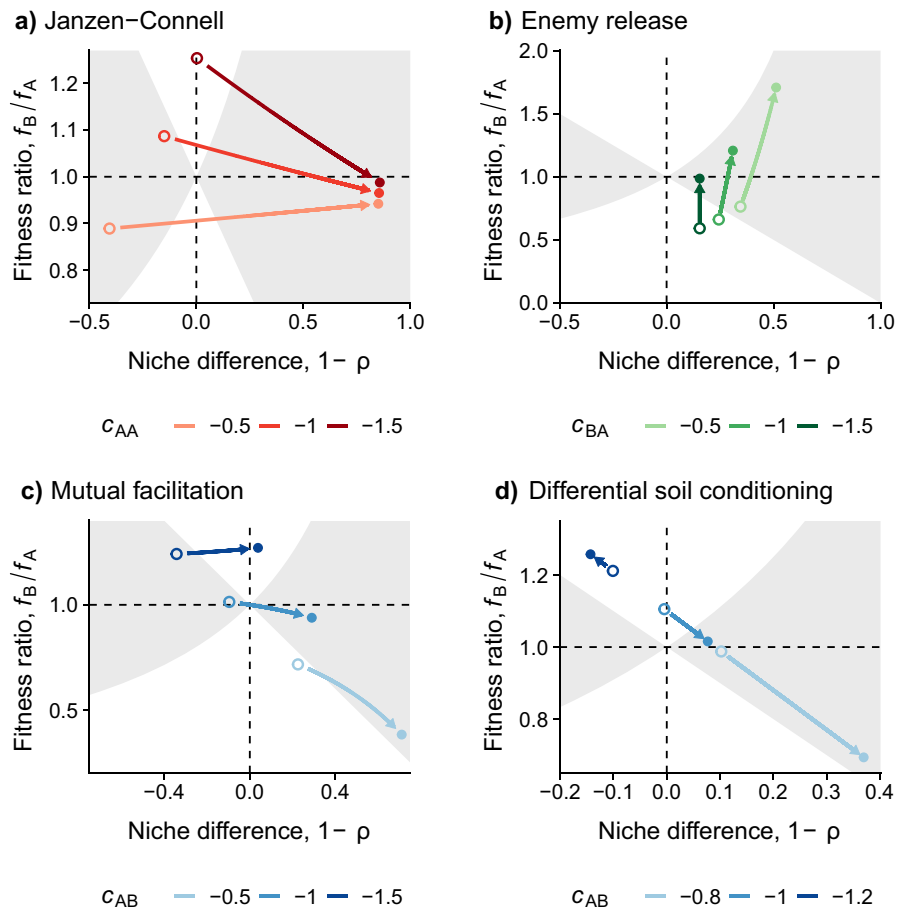
FIG. 3. Examples of how plant–soil microbe interactions and plant–plant competition together determine competition outcome. Four plant–soil microbe interaction scenarios were considered: (a) Janzen-Connell (varying σ_{AA} and σ_{BB}), (b) enemy release (varying σ_{BA} and σ_{BA}), (c) mutual facilitation (varying σ_{AB} and σ_{BA}), and (d) differential soil conditioning (varying ϕ_B). For each scenario, arrows show how niche difference ($1-\rho$, x-axis) and fitness ratio (f_B/f_A, y-axis) changed as we varied the strength of soil microbial effects (σ_{ij} and ϕ_i) from weakest (open circles) to strongest (solid circles). To demonstrate its interactive effect with plant–plant competition, this trajectory is shown for different strengths of plant–plant competition (c_{ij}) ranging from weak (light colors) to strong (dark colors). Plant–plant competition coefficients that were shown here for each scenario are (a) c_{AA}; (b) c_{BA}; (c) c_{AB}; and (d) c_{AB}. In panels a–c, c_{ij} was varied between −0.5, −1.0, and −1.5, whereas in panel d, c_{ij} was varied between −0.8, −1.0, and −1.2. See Appendix S4 for other plant–plant competition coefficients (Appendix S4: Figs. S1–S4) and default parameter values (Appendix S4: Table S1).

niche differences, others affected fitness, and still others acted through a combination of the two components; moreover, each mechanism interacted differently with plant–plant competition. Given these diverse results, how can we synthesize existing perspectives into a unified understanding of how soil microbes influence plant coexistence?

Our study provides a general framework for integrating a diverse set of plant–soil microbe interactions with plant–plant competition. In Table 1, we show how the effects of a microbe-mediated process on niche and fitness differences, as well as its impact on the relative importance of plant–plant competition, can be predicted using an understanding of which interactions are being modified. We identify four ways a process can affect the plant–microbe interaction network, representing each

possible pair of plant–soil microbe interactions σ_{ij} (column I). Within each category of network effects, we contrast processes that increase the overall negative interaction among plants (i.e., making α_{ij}, the total per-capita effect of one plant on another, more negative) with those that decrease the overall negative interaction (column II). In other words, we consider whether the indirect effect of microbe intensifies or mitigates negative interaction among plants. Importantly, these changes are not specific to pathogens or mutualists: for instance, an increase in a plant's overall negative impact can result from strengthening the effect of pathogens or from weakening the effects of mutualists.

Based on this general categorization, the effect of a process on the underlying interaction network determines whether it primarily affects niche or fitness (column

TABLE 1. General framework for understanding how soil microbes affect plant coexistence through their effects on niche and fitness differences.

I. Which interactions does the process affect?	II. How does the process modify plants' negative effects on each other?	III. Primary effect on coexistence	IV. Effects on the relative importance of plant–plant competition	V. Example mechanisms
a. Both microbes' effects on the host (σ_{ii}, σ_{jj})	Increases negative interaction	Increases niche difference	Decreases role of intraspecific competition (c_{ii}, c_{jj})	**Janzen-Connell (host-specific) pathogens**
	Decreases negative interaction	Decreases niche difference	Increases role of intraspecific competition (c_{ii}, c_{jj})	Host-specific mutualists
b. Both microbes' effects on non-hosts (σ_{ij}, σ_{ji})	Increases negative interaction	Decreases niche difference	Decreases role of interspecific competition (c_{ij}, c_{ji})	Pathogen spillover
	Decreases negative interaction	Increases niche difference	Increases role of interspecific competition (c_{ij}, c_{ji})	**Mutual facilitation,** pathogen specificity
c. Both microbes' effects on plant i (σ_{ij}, σ_{ii})	Increases negative interaction	Decreases fitness of plant i	Decreases role of i's sensitivity to competition (c_{ii}, c_{ij})	Increased sensitivity to pathogens
	Decreases negative interaction	Increases fitness of plant i	Increases role of i's sensitivity to competition (c_{ii}, c_{ij})	**Enemy release,** increased benefits from mutualists
d. Microbe i's effects on both plants (σ_{ii}, σ_{ji}; or ϕ_i)	Increases negative interaction	Not consistent; affects j's invasion growth	Decreases role of i's competitive effect (c_{ii}, c_{ji})	Pathogen conditioning
	Decreases negative interaction	Not consistent; affects j's invasion growth	Increases role of i's competitive effect (c_{ii}, c_{ji})	**Mutualist conditioning**

Notes: Processes are categorized according to (I) the types of interactions they affect and (II) whether they intensify or mitigate overall plant interaction. Accordingly, we predict how each category affects (III) niche and fitness differences and (IV) the interactive effect of processes. Finally, (V) we give examples of mechanisms for each category.

III) and predicts which forms of plant–plant competition (c_{ij}) will change in importance for coexistence (column IV). In both cases, the direction of these changes depends on whether a process increases or decreases the overall negative interaction among plants. Thus, our framework can be applied to predict the effects of various soil microbe-mediated processes considered in the empirical literature (column V), including the four focal scenarios simulated in this study (shown in bold type).

Soil microbes and stabilizing niche differences.—Our findings confirm that soil microbes can promote plant coexistence by favoring each plant when it is rare, an effect frequently discussed in the literature (Bever et al. 1997, Bever 2003, Hart et al. 2003, Ke and Miki 2015). This effect, often termed negative plant–soil feedback Bever et al. (1997), corresponds to the niche difference component of modern coexistence theory. Our approach shows that this occurs when a microbe-mediated process causes the negative impact of a plant on conspecifics to increase (type a in Table 1; e.g., Janzen-Connell scenario, Fig. 3a) or that on its competitors to decrease (type b in Table 1; e.g., mutual facilitation scenario, Fig. 3c). This result is in accordance with those from the exponential model of Bever et al. (1997), which showed that both pathogens and mutualists may promote plant coexistence. Our application of modern coexistence theory

adds to this classic perspective by linking it to the broader empirical literature on plant coexistence and providing a more thorough exploration of the contexts under which soil microbes affect coexistence.

This perspective synthesizes a diverse range of stabilizing and destabilizing soil microbial processes from the literature. We confirm that species-specific soil pathogens indeed promote coexistence by increasing niche differences, thus acting as a stabilizing mechanism (Petermann et al. 2008). We also note that stabilization is not unique to soil pathogens: mutualists can stabilize coexistence if they also confer their mutualistic benefits to their host plant's competitors (Bever 1999, 2002). In contrast to the case of mutual facilitation, we also predict that host-specific soil mutualists can lead to priority effects by increasing niche overlap, thus acting as a destabilizing mechanism (sensu Fukami et al. 2016). Empirical evidence of such positive feedbacks comes from systems where arbuscular mycorrhizal plants compete with ectomycorrhizal plants (McGuire 2007, Bennett et al. 2017, Kadowaki et al. 2018). Accordingly, we suggest that experimental approaches informed by modern coexistence theory may further elucidate links between mycorrhizal strategy and plant community dynamics.

Despite similar stabilizing effects, different soil microbial processes may have different effects on the importance of plant–plant competition, an aspect not

CONCEPTS AND SYNTHESIS

captured by the original Bever et al. (1997) model and its I_s index. For example, while host-specific pathogens contribute to stabilization and can overwhelm the effect of intraspecific plant–plant competition (Fig. 3a), interspecific competition remains important in determining the degree of stabilization required for coexistence (Appendix S4: Fig. S1). This prediction emphasizes the importance of considering interspecific competition when studying conspecific negative density dependence (LaManna et al. 2017). In other cases (e.g., mutual facilitation), microbe-mediated processes may amplify the role of certain forms of plant–plant competition (here, interspecific competition). This is in line with empirical findings that mycorrhizal fungi can intensify plant competition for light (Facelli et al. 1999) by modifying the shoot-to-root ratio of plants (Veresoglou et al. 2012). Such differences between scenarios, despite their similar stabilizing effect, highlight the importance of considering soil microbial effects within the context of plant–plant competition (Callaway et al. 2004, Casper and Castelli 2007, Shannon et al. 2012, Crawford and Knight 2017, Peay 2018). Here, we suggest that further categorizing plant–soil microbe interactions with our framework provides concrete predictions of how the two processes interact (Table 1).

The need to consider soil microbial effects on fitness.—In addition to their frequently cited stabilizing role, soil microbes may also affect the fitness of competing plants (Mordecai 2011). However, this aspect of soil microbial effects is often overlooked in frequency-based models (but see Kandlikar et al. (2019) for how to quantify the effect of soil microbes on plant fitness differences for the classic Bever model). Supporting the notion that niche and fitness differences are not independent (Letten et al. 2017, Barabás et al. 2018), we found that soil microbes always affected fitness (Fig. 3). Mathematically, this occurs because changing any soil microbial coefficient always affects both ρ and f_2/f_1 (Box 1). Furthermore, fitness is sometimes key to predicting coexistence: when a process alters the sensitivity of one plant to both microbial communities, its effect on coexistence is primarily mediated by equalizing mechanisms (type c in Table 1; e.g., enemy release scenario). In some cases, soil microbes promote coexistence if they benefit the plant with lower fitness to an intermediate degree (Fig. 3b); in other cases, the effects of soil microbes on fitness can lead to competitive exclusion despite their stabilizing effects (Fig. S2b). In a recent study, Kandlikar et al. (2019) also showed, for a variety of theoretical models, that studying "microbially mediated fitness differences" is critical for understanding plant coexistence. Observed trade-offs between plant–plant competition and responsiveness to mutualists (Grman 2012) or defense against soil pathogens (Rasmann et al. 2011) may thus promote coexistence by acting as equalizing mechanisms.

As in other scenarios, these microbe-mediated processes may affect the importance of plant–plant competition for plant fitness. For instance, fitness differences generated by intraspecific plant competition were erased by host-specific pathogens in the Janzen-Connell scenario (Fig. 3a), but were not affected in the mutual facilitation scenario (Appendix S4: Fig. S3). Another example comes from the enemy release scenario: we predict that, as an invader (here, plant B) becomes increasingly released from enemies, its sensitivity to competition (c_{BA} and c_{BB}) will become increasingly important for determining competitive outcome (Appendix S4: Fig. S2). This prediction has practical implications: when considering the invasive potential of an enemy-released exotic plant, for instance, it may be particularly important to evaluate its sensitivity to plant–plant competition. That is, in the presence of enemy release, the most successful invaders should be those with the highest tolerance of competition from natives (least negative c_{BA}), rather than those with the strongest negative impact on natives (most negative c_{AB}). In summary, the different effects of soil microbes on plant fitness, a crucial determinant of coexistence highlighted in modern coexistence theory, emphasize the importance of the competitive context in which plant–soil microbe interactions occur.

Though some processes are primarily equalizing or stabilizing, we also identify a set of processes where both effects must be considered (type d in Table 1). Namely, when a mechanism varies a single soil community's effect on both plants (e.g., differential soil conditioning scenario, Fig. 3d), its effect on coexistence is mediated by both niche difference and fitness ratio. This occurs because a soil microbial community can only affect the invasion growth of the non-cultivating plant. Thus, it affects both niche difference and fitness ratio, and the direction of these effects varies depending on plant–plant competition.

Many biologically relevant processes belong to this category. For instance, pathogens vary in their virulence (Reinhart et al. 2010) and plants' ability to condition mutualists may vary due to environmental conditions (Norby et al. 1987, Zheng et al. 2015). Under these cases, it is not possible to draw a general conclusion on the effect of soil microbes on plant coexistence because the direction of these effects are context dependent. To further decipher the role of soil microbes in these processes, we emphasize the need for empirical work to directly measure the strength of both plant–plant and plant–soil microbe interactions.

APPLYING MODERN COEXISTENCE THEORY TO PLANT–SOIL MICROBE INTERACTION EXPERIMENTS

Our framework demonstrates the importance of the interaction between soil microbial effects and plant–plant competition. Given the complexity highlighted above, how can empirical work effectively evaluate the

role of soil microbes? In this section, we outline an approach that quantifies all plant–plant and plant–soil microbe interactions for a pair of competing plants. We then use data from an existing study (Aguilera et al. 2017) to demonstrate how our framework can identify which plant–microbe interactions drive coexistence in empirical systems.

Recommendations for empirical experimental design

Comparing the performance of plants grown individually to plants grown in competition is already a standard approach for inferring phenomenological interaction coefficients (Hart et al. 2018). These interaction coefficients correspond to the α_{ij} of our model, which can be partitioned into terms representing plant–plant competition and the effect of soil microbes. Thus, growing plants in soil where conditioning has not occurred allows the researcher to calculate the plant–plant competition coefficients, and comparing these to the corresponding coefficients in conditioned soil gives the plant–soil microbe term. With this information, it is then possible to apply our quantitative framework.

Nonetheless, existing experimental designs for measuring the effect of soil microbes do not provide enough information to fully quantify plant–soil microbe and plant–plant interactions. In Fig. 4, we highlight two experimental designs that are commonly implemented for the purpose of quantifying soil microbial effects and plant–plant competition. One design, which we term "fixed density intra/inter" (Fig. 4a; different soils are represented by different colors), subjects a focal plant to either intra- or interspecific competition in different soil environments (Petermann et al. 2008). Although this design explicitly considers competition, it lacks data on the growth responses of single individuals in the absence of any competition. Thus, at its best, it can only provide an estimation of the difference between intra- and interspecific competition for each species (i.e., the relative magnitudes of α_{ii} and α_{ij}). Another design, referred here and elsewhere as "multiple/single" (Fig. 4b), compares the growth a focal species alone to its growth with a heterospecific competitor in different soil environments (Shannon et al. 2012, Crawford and Knight 2017). Although it may seem less comprehensive than the intra/inter design, this design in fact provides the density treatment necessary for estimating interspecific competition (i.e., α_{ij}). What is missing here is the growth response of the focal species when growing with conspecifics (i.e., an estimation of α_{ii}). The above two experimental designs quantify aspects of soil microbial effects, but it is difficult to directly link these data to modern coexistence theory. While Kandlikar et al. (2019) laid out the necessary treatments to characterize niche and fitness differences mediated by soil microbes, a more comprehensive experimental design is needed to study the effects of plant–microbe interactions within the context of plant–plant competition.

Here, we propose the minimal setup that is required to quantify the effects of both plant–plant and plant–microbe interactions on plant coexistence (see also Hart et al. 2018 for similar design). This minimal design combines elements of the two common setups and is capable of estimating intra- and interspecific competition under different soil types (Fig. 4c). This need not be as daunting as it may sound, since not all treatments are necessary. Many combinations, such as growing multiple individuals of the same focal species in heterospecific soils (e.g., two red diamond plants in soil conditioned by the blue circle plant; Fig. 4a), are not relevant to the invasion perspective of modern coexistence theory. The critical insight is that we must quantify a focal plant's response to competitors in the competitor-conditioned soil. For example, we should quantify the red diamond plant's intraspecific
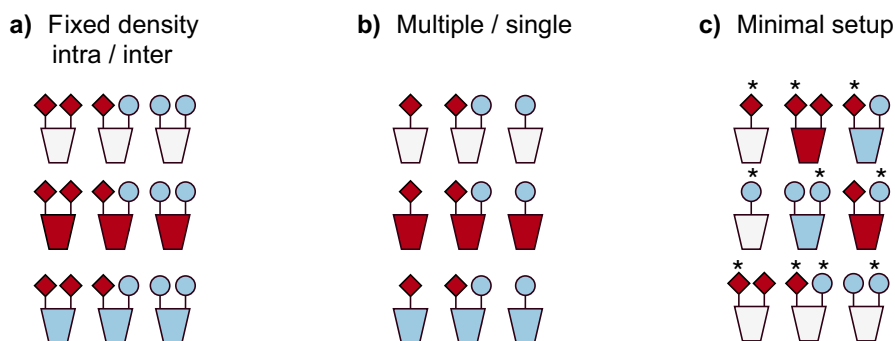

FIG. 4. Experimental designs to quantify the effects of soil microbes on plant competitive outcome. (a) Fixed-density intra/inter designs consisting of growing the focal plant in either intra- or inter-specific plant–plant competition; (b) multiple/single designs consisting of growing the focal plant either with or without interspecific plant–plant competition; (c) minimal experimental setup. Pots with different colors represent soils with different conditioning history: no conditioning history or sterile soil (white); conditioned by the red diamond plant (dark red); conditioned by the blue circle plant (light blue). In the minimal setup, competition coefficients can be calculated from measurements of the plants marked with asterisks *.

competition by measuring its performance when it competes with conspecifics in conspecific soil (Fig. 4c, top center). To quantify how interspecific competition affects the red diamond plant, we should instead measure its performance when it competes with the blue circle plant in soil conditioned by the blue circle plant (indicated in Fig. 4c, top right; asterisk indicates the individual to be measured). In order to fully include microbial effects in these competition measurements, performance under competition in conditioned soil should be compared to single-individual performance in a reference soil (i.e., soils without plant-specific microbial communities; single-plant pots in Fig. 4c). After calculating these effects, we can then partition the effect of soil microbes by comparing competitive effects to ones calculated for competition in a reference soil (bottom row in Fig. 4c).

There are multiple options for the reference soil, and it is important to recognize that different reference soils isolate different aspects of plant–soil microbe interactions. Two common choices are sterilized soil and unconditioned soil from a location where neither plant is present. Ultimately, the most appropriate reference soil depends on the system and research question. Comparing density treatments in conditioned soil to the same treatments in sterilized soils captures the effect of all soil microbes, since the reference soil should contain virtually no microbes. This might be a suitable choice for studies that wish to isolate the impacts of soil microbes and compare the strength of microbial effects to other processes (Chung and Rudgers 2016, which asked whether soil microbes promoted plant coexistence). One the other hand, unconditioned soils may harbor microbial propagules such as dormant spores (Lennon and Jones 2011) that could potentially affect the focal plant. Comparing treatments in conditioned soil to those in unconditioned soil therefore captures the conditioning ability of each plant. Although the natural history of some systems may suggest a natural choice for the unconditioned soil (e.g., bare sand for sand dunes undergoing primary succession), other systems may lack a reasonable option. Nevertheless, when selected properly, unconditioned soil can be an appropriate reference soil for certain research questions. For instance, soils conditioned by a native plant could be used to study how microbes impact competition between two simultaneously invading species.

We also note that by incorporating a small number of missing treatments, the two common experimental designs can be expanded to collect all necessary data: the "fixed density intra/inter" designs, for instance, are missing only the performance of single individuals in reference soil. Moreover, additional density treatments can be added to our minimal design to improve statistical fitting or detect nonlinear responses (e.g., higher order interactions). Whether the substantial work of these additional treatments (e.g., a response surface

design; Inouye 2001) is necessary depends on the research question. For example, the simplified density treatment may suffice for a study that aims to qualitatively predict competitive outcomes, whereas extra density treatments might be needed if a study is specifically concerned with quantitatively predicting community dynamics (Hart et al. 2018, Letten and Stouffer 2019).

Applying the conceptual framework: a case study

Though fully quantifying plant–plant and plant–microbe interactions does not require a large number of treatments, surprisingly few studies have collected all relevant data. One example of such data is given in Aguilera et al. (2017), where the authors studied how soil microbes affect *Lactuca sativa* and its closely related competitor *Lactuca serriola*, showing that the latter generates stronger negative soil feedback (i.e., it conditions a more pathogenic soil community). Below, we outline the experimental design of Aguilera et al. (2017) and describe how we extracted data to calculate niche and fitness differences. Using this data, we then apply our quantitative framework to infer the underlying microbe-mediated processes driving changes in competitive outcome.

Aguilera et al. (2017) grew a single focal individual of each species with four conspecific or heterospecific competitors. They also grew one single individual of each species alone with no background competitors, creating a density gradient (i.e., zero vs. four) of competitors. Moreover, this planting scheme was conducted using either sterilized or live soil. After nine weeks of growth, the plants were harvested for biomass measurements. The authors present biomass data for plant i growing with competitors of plant j in either sterile or live soil (Figure 1 of Aguilera et al. 2017). We denote these biomass measurments as $M_{i,j,\text{sterile}}$ and $M_{i,j,\text{live}}$, respectively, where i and j can refer to *L. sativa*, abbreviated "sat," or to *L. serriola*, abbreviated "ser." They also presented an index measuring the severity of competition, defined as the log ratio between the performance of the single-growing individual (hereafter, $M_{i,0,\text{sterile}}$) and that of an individual grown under competition (Figure 2 of Aguilera et al. 2017).

Using the density and soil sterilization treatments from Aguilera et al. (2017), we calculated the full set of interaction coefficients required by our framework. Depending on a study's measure of plant fitness and its assumptions about plant demography, these coefficients can be calculated in several ways (Weigelt and Jolliffe 2003). For the Aguilera et al. (2017) data set, we assumed that each plant's reproductive ability was proportional to its biomass and calculated the interaction coefficient between plants i and j as the per-capita effect of j on biomass of i, relative to the biomass of i when grown individually. To obtain this value in the presence of microbial effects, we compared
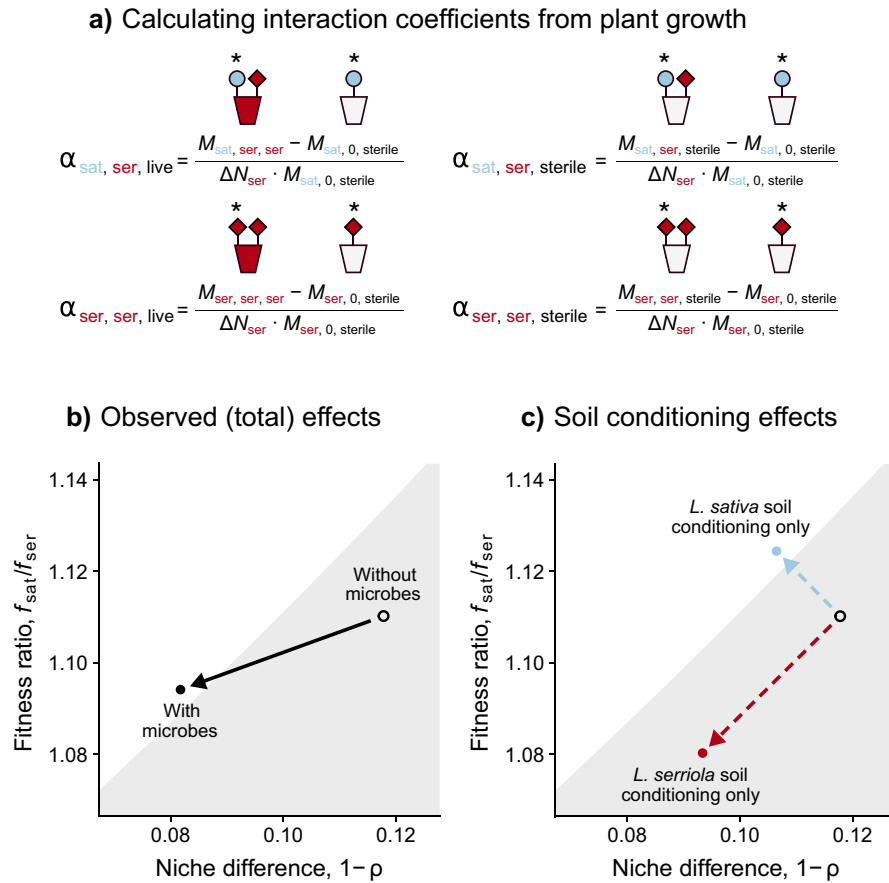
a) Calculating interaction coefficients from plant growth

$$\alpha_{\text{sat, ser, live}} = \frac{M_{\text{sat, ser, ser}} - M_{\text{sat, 0, sterile}}}{\Delta N_{\text{ser}} \cdot M_{\text{sat, 0, sterile}}}$$

$$\alpha_{\text{sat, ser, sterile}} = \frac{M_{\text{sat, ser, sterile}} - M_{\text{sat, 0, sterile}}}{\Delta N_{\text{ser}} \cdot M_{\text{sat, 0, sterile}}}$$

$$\alpha_{\text{ser, ser, live}} = \frac{M_{\text{ser, ser, ser}} - M_{\text{ser, 0, sterile}}}{\Delta N_{\text{ser}} \cdot M_{\text{ser, 0, sterile}}}$$

$$\alpha_{\text{ser, ser, sterile}} = \frac{M_{\text{ser, ser, sterile}} - M_{\text{ser, 0, sterile}}}{\Delta N_{\text{ser}} \cdot M_{\text{ser, 0, sterile}}}$$

b) Observed (total) effects

c) Soil conditioning effects

Fig. 5. Applying modern coexistence theory to understand the effects of soil microbes on plant competitive outcome using data from Aguilera et al. (2017) as a case study. (a) Calculating the competitive and soil microbial effects of *Lactuca serriola* (ser; dark red) on *Lactuca sativa* (sat; light blue) and *L. serriola*. $M_{i, j, k}$ represents the biomass of species i competing with species j in soil cultivated by species k (with $j = 0$ indicating no competitors and $k = s$terile if soils were sterilized); ΔN_j represents the density of competitors of species j. Above each biomass term, we illustrate the corresponding experimental treatment and mark the measured individual with an asterisk. The effects of *L. sativa* can be calculated the same way. (b) Predicted effect of soil microbes (open circles, without microbes; solid circles, with microbes) on the outcome of competition between *L. sativa* and *L. serriola*. Using competition coefficients calculated from empirical data, we applied our model to calculate niche difference and fitness ratio (see Box 2). The white region (upper left) indicates that *L. sativa* outcompetes *L. serriola*, whereas the gray region (lower right) indicates coexistence. (c) The impact of plant-specific conditioning effects on the competitive outcome between *L. sativa* and *L. serriola* (red arrows, only *L. serriola* soil conditioning effects; blue arrows, only *L. sativa* soil conditioning effects).

competition biomass in live soil to the single-individual biomass in sterile soil (Fig. 5a, left column):

$$\alpha_{i,j,\text{live}} = \frac{(M_{i,j,\text{live}} - M_{i,0,\text{sterile}})}{\Delta N_j \times M_{i,0,\text{sterile}}}$$

where ΔN_j represents the density of competitors of species j. Here, it is important to use single-individual biomass in sterile soil (i.e., $M_{i,0,\text{sterile}}$) in order to include the effects of soil microbes into the calculation of live interaction coefficient. This calculation assumes that the high density of background competitors conditioned the soil to its species-specific state (i.e., $M_{i,j,\text{live}}$ is effectively the biomass of i in competition with j in j's species-specific soil, $M_{i,j,j}$; in Fig. 5a, i = ser or sat and j = ser). We calculated interaction coefficients in the absence of

microbial effects by instead using the competition treatments in sterile soil (Fig. 5a, right column):

$$\alpha_{i,j,\text{sterile}} = \frac{(M_{i,j,\text{sterile}} - M_{i,0,\text{sterile}})}{\Delta N_j \times M_{i,0,\text{sterile}}}.$$

All required biomass measurements were digitized using Web Plot Digitizer version 4.1 (https://automeris.io/Web PlotDigitizer/). Mean biomass from competition treatments ($M_{i,j,\text{live}}$ and $M_{i,j,\text{sterile}}$) was obtained directly from Figure 1 of Aguilera et al. 2017. Since biomass of the single-individual treatments was not reported, we used the author's competition index (Fig. 2 of the original study) to back-calculate single-individual biomass in sterile soil ($M_{i,0,\text{sterile}}$) and took the average value for each species.

TABLE 2. Overall interaction coefficients calculated from Aguilera et al. (2017)

	$\alpha_{sat,sat}$	$\alpha_{sat,ser}$	$\alpha_{ser,sat}$	$\alpha_{ser,ser}$
Sterilized soil	−0.2418	−0.1380	−0.2368	−0.1736
Live soil	−0.2418	−0.1942	−0.2429	−0.2314
Microbial effect	−0.0	−0.0562	−0.0061	−0.0578

Note: Abbreviations are sat, *Lactuca sativa*; ser, *Lactuca serriola*.

Table 2 shows the interaction coefficients for sterile and live soils, as well as the contribution of soil microbes (i.e., the difference between $\alpha_{i,j,\text{sterile}}$ and $\alpha_{i,j,\text{live}}$). Examining changes in the interaction coefficients shows that the soil microbial community conditioned by *L. serriola* had a negative effect on both species, whereas the community conditioned by *L. sativa* affected only *L. serriola* and had a much weaker negative effect (Table 2). This agrees with the findings of the original study, which concluded that soil communities associated with *L. serriola* caused stronger negative feedbacks. Our framework adds to this perspective by showing how these changes affect plant coexistence. Taking advantage of the explicit demographic predictions of modern coexistence theory, we predicted that the two plants can coexist in sterile soil, but that soil microbes allow *L. sativa* to competitively exclude *L. serriola* (Fig. 5b). Visualizing the changes in niche and fitness difference indicated that soil microbes exerted a slight equalizing effect (by decreasing the fitness ratio between the two species), but this change was counteracted by a much stronger destabilizing effect.

Next, we separately considered the effect of each plant's soil community in order to identify which interactions were responsible for changes in coexistence (Fig. 5c). Our framework allowed us to selectively remove individual microbial interactions: starting with the full set of interactions, we set some of the coefficients to the values measured without microbes. Simulating competition with each species' conditioning effect "turned off" (Fig. 5c) showed that the strongly pathogenic *L. serriola* soil community created larger differences in fitness ratio and niche overlap, but only the *L. sativa* community was able to drive the exclusion of *L. serriola*. This counterintuitive result can be understood using our general framework (Table 1, type d: pathogen conditioning), which predicts that the stronger conditioning caused by *L. serriola* modifies both niche and fitness difference, but ultimately only affects the invasion growth of *L. sativa*. The exclusion of *L. serriola* instead reflects its own negative invasion growth, which according to our framework can only be affected by the pathogen conditioning caused by *L. sativa*. This exercise thus demonstrates that the soil microbial effects that determine coexistence may not be the ones with the largest magnitude. Because *L. serriola* was closer to being competitively excluded in sterile soil, the outcome of competition was more sensitive to changes in the interactions that affected its invasion growth rate. Thus, the smaller

effects of *L. sativa*'s soil nonetheless altered competitive outcome in this system.

In order to more rigorously identify the drivers of plant community dynamics, we call for future studies to experimentally quantify and interpret soil microbial effects through the perspective of modern coexistence theory. Rather than considering all interactions equally, our approach considers the context of plant–plant competition in order to identify the most important effects for coexistence. Using an experimental approach that quantifies both interspecific and intraspecific competition in soils with and without microbial effects, our method isolates the role of microbes. By modifying the strength of different interaction coefficients in a demographic model, we can then identify the specific mechanisms that are most important for coexistence.

CONCLUSION

As the field of plant community ecology expands to address the role of plant–soil microbe interactions in different natural systems, there is a growing need to unite these multiple lines of research (Mordecai 2011, Peay 2016). Modern coexistence theory provides a way to synthesize a variety of soil microbial effects and identify how they contribute to plant coexistence. Generalizing beyond the existing focus on soil pathogens, we apply this theory to show that both pathogens and mutualists can affect niche difference (i.e., stabilization) depending on their host specificity. Moreover, the theory shows that it is also important to consider how both types of microbes affect fitness differences between competing plants (i.e., equalization). Finally, since our framework predicts that coexistence is interactively determined by soil microbes and plant–plant competition, we suggest that future studies should simultaneously quantify both effects in order to accurately understand underlying drivers of coexistence.

We have shown that applying modern coexistence theory provides a valuable framework for experimentally testing of the role of soil microbes in plant coexistence. Here, we focus on aspects of the theory that have informed most experimental work, but we also note that this developing body of mathematical work continues to offer rigorous quantitative tools for understanding coexistence: for instance, in multi-species communities (Saavedra et al. 2017), in temporally or spatially variable environments (Ellner et al. 2019), and when facilitative interactions are critical (Bimler et al. 2018). While our current framework does not incorporate these processes, our use of a demographic model provides a useful starting point that can be extended to incorporate these recent theoretical developments. Indeed, there is a need to study the role of soil microbes in highly diverse plant systems (Johnson et al. 2012) and it is becoming clear that temporal variation and spatial processes such as microbial dispersal (Peay 2016) are crucial to soil microbial community dynamics. Thus, we urge plant ecologists

to place plant–soil microbe interactions into the broader context provided by general theory as they disentangle the forces structuring plant communities.

LITERATURE CITED

Adler, P. B., J. Hillerislambers, and J. M. Levine. 2007. A niche for neutrality. Ecology Letters 10:95–104.

Aguilera, A. G. 2011. The influence of soil community density on plant–soil feedbacks: an important unknown in plant invasion. Ecological Modelling 222:3413–3420.

Aguilera, A. G., S. Morey, M. Gammon, M. Jiang, S. Ramos, and R. Kesseli. 2017. Effect of plant–soil feedbacks on the growth and competition of *Lactuca* species. Plant Ecology 218:359–372.

Augspurger, C. K., and C. K. Kelly. 1984. Pathogen mortality of tropical tree seedlings: experimental studies of the effects of dispersal distance, seedling density, and light conditions. Oecologia 61:211–217.

Bagchi, R., T. Swinfield, R. E. Gallery, O. T. Lewis, S. Gripenberg, L. Narayan, and R. P. Freckleton. 2010. Testing the Janzen-Connell mechanism: pathogens cause overcompensating density dependence in a tropical tree. Ecology Letters 13:1262–1269.

Barabás, G., R. D'Andrea, and S. M. Stump. 2018. Chesson's coexistence theory. Ecological Monographs 88:277–303.

Bell, T., R. P. Freckleton, and O. T. Lewis. 2006. Plant pathogens drive density-dependent seedling mortality in a tropical tree. Ecology Letters 9:569–574.

Bennett, J. A., H. Maherali, K. O. Reinhart, Y. Lekberg, M. M. Hart, and J. Klironomos. 2017. Plant–soil feedbacks and mycorrhizal type influence temperate forest population dynamics. Science 355:181–184.

Bever, J. 1999. Dynamics within mutualism and the maintenance of diversity: inference from a model of interguild frequency dependence. Ecology Letters 2:52–61.

Bever, J. D. 2002. Negative feedback within a mutualism: host-specific growth of mycorrhizal fungi reduces plant benefit. Proceedings of the Royal Society B 269:2595–2601.

Bever, J. D. 2003. Soil community feedback and the coexistence of competitors : conceptual frameworks and empirical tests. New Phytologist 157:465–473.

Bever, J. D., K. M. Westover, and J. Antonovics. 1997. Incorporating the soil community into plant population dynamics: the utility of the feedback approach. Journal of Ecology 85:561–573.

Bever, J. D., I. A. Dickie, E. Facelli, J. M. Facelli, J. Klironomos, M. Moora, M. C. Rillig, W. D. Stock, M. Tibbett, and M. Zobel. 2010. Rooting theories of plant community ecology in microbial interactions. Trends in Ecology & Evolution 25:468–478.

Bever, J. D., S. A. Mangan, and H. M. Alexander. 2015. Maintenance of plant species diversity by pathogens. Annual Review of Ecology, Evolution, and Systematics 46:305–325.

Bimler, M. D., D. B. Stouffer, H. R. Lai, and M. M. Mayfield. 2018. Accurate predictions of coexistence in natural systems require the inclusion of facilitative interactions and environmental dependency. Journal of Ecology 106:1839–1852.

Callaway, R. M., G. C. Thelen, S. Barth, P. W. Ramsey, and J. E. Gannon. 2004. Soil fungi alter interactions between the invader *Centaurea maculosa* and North American natives. Ecology 85:1062–1071.

Cardinaux, A., S. P. Hart, and J. M. Alexander. 2018. Do soil biota influence the outcome of novel interactions between plant competitors? Journal of Ecology 106:1853–1863.

Casper, B. B., and J. P. Castelli. 2007. Evaluating plant–soil feedback together with competition in a serpentine grassland. Ecology Letters 10:394–400.

Chesson, P. 1990. MacArthur's consumer-resource model. Theoretical Population Biology 37:26–38.

Chesson, P. 2000. Mechanisms of maintenance of species diversity. Annual Review of Ecology, Evolution, and Systematics 31:343–366.

Chesson, P. 2003. Quantifying and testing coexistence mechanisms arising from recruitment fluctuations. Theoretical Population Biology 64:345–357.

Chesson, P. 2008. Quantifying and testing species coexistence mechanisms. Pages 119–164 in F. Valladares, A. Camacho, A. Elosegi, C. Gracia, M. Estrada, J. C. Senar, and J.-M. Gili, editors. Unity in diversity: reflections on ecology after the legacy of Ramon Margalef. Fundacion BBVA, Bilbao, Spain.

Chesson, P. 2013. Species competition and predation. Pages 223–256 in R. Leemans, editor. Ecological systems. Springer, New York, New York, USA.

Chesson, P., and J. J. Kuang. 2008. The interaction between predation and competition. Nature 456:235–238.

Chung, Y. A., and J. A. Rudgers. 2016. Plant–soil feedbacks promote negative frequency dependence in the coexistence of two aridland grasses. Proceedings of the Royal Society B 283:20160608.

Connell, J. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. Pages 298–312 in P. Den Boer and G. Gradwell, editors. Dynamics of populations. Centre for Agricultural Publishing and Documentation, Wageningen, The Netherlands.

Crawford, K. M., and T. M. Knight. 2017. Competition overwhelms the positive plant–soil feedback generated by an invasive plant. Oecologia 183:211–220.

Ellner, S. P., R. E. Snyder, P. B. Adler, and G. Hooker. 2019. An expanded modern coexistence theory for empirical applications. Ecology Letters 22:3–18.

Eppinga, M. B., M. Rietkerk, S. C. Dekker, and P. C. D. Ruiter. 2006. Accumulation of local pathogens: a new hypothesis to explain exotic plant invasion. Oikos 114:168–176.

Eppinga, M. B., M. Baudena, D. J. Johnson, J. Jiang, K. M. L. Mack, A. E. Strand, and J. D. Bever. 2018. Frequency-dependent feedback constrains plant community coexistence. Nature Ecology & Evolution 2:1403–1407.

Facelli, E., J. M. Facelli, S. E. Smith, and M. J. McLaughlin. 1999. Interactive effects of arbuscular mycorrhizal symbiosis, intraspecific competition and resource availability on *Trifolium subterraneum* cv. Mt. Barker. New Phytologist 141:535–547.

Fukami, T., E. A. Mordecai, and A. Ostling. 2016. A framework for priority effects. Journal of Vegetation Science 27:655–657.

Gause, G. F. 1934. The struggle for existence. Volume 102/103. Williams and Wilkins, Philadelphia, Pennsylvania, USA.

Godoy, O., and J. M. Levine. 2014. Phenology effects on invasion success: insights from coupling field experiments to coexistence theory. Ecology 95:726–736.

CONCEPTS AND SYNTHESIS

Grman, E. 2012. Plant species differ in their ability to reduce allocation to non-beneficial arbuscular mycorrhizal fungi. Ecology 93:711–718.

Gross, N., P. Liancourt, R. Butters, R. P. Duncan, and P. E. Hulme. 2015. Functional equivalence, competitive hierarchy and facilitation determine species coexistence in highly invaded grasslands. New Phytologist 206:175–186.

Hart, M. M., R. J. Reader, and J. N. Klironomos. 2003. Plant coexistence mediated by arbuscular mycorrhizal fungi. Trends in Ecology & Evolution 18:418–423.

Hart, S. P., R. P. Freckleton, and J. M. Levine. 2018. How to quantify competitive ability. Journal of Ecology 5:1902–1909.

HilleRisLambers, J., P. B. Adler, W. Harpole, J. M. Levine, and M. Mayfield. 2012. Rethinking community assembly through the lens of coexistence theory. Annual Review of Ecology, Evolution, and Systematics 43:227–248.

Hoeksema, J. D., et al. 2010. A meta-analysis of context-dependency in plant response to inoculation with mycorrhizal fungi. Ecology Letters 13:394–407.

Inouye, B. D. 2001. Response surface experimental designs for investigating interspecific competition. Ecology 82:2696–2706.

Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. American Naturalist 104:501–528.

Johnson, D. J., W. T. Beaulieu, J. D. Bever, and K. Clay. 2012. Conspecific negative density dependence and forest diversity. Science 336:904–907.

Kadowaki, K., S. Yamamoto, H. Sato, A. S. Tanabe, A. Hidaka, and H. Toju. 2018. Mycorrhizal fungi mediate the direction and strength of plant–soil feedbacks differently between arbuscular mycorrhizal and ectomycorrhizal communities. Communications Biology 1:196.

Kandlikar, G. S., C. A. Johnson, X. Yan, N. J. B. Kraft, and J. M. Levine. 2019. Winning and losing with microbes: how microbially mediated fitness differences influence plant diversity. Ecology Letters 22:1178–1191.

Ke, P.-J., and A. D. Letten. 2018. Coexistence theory and the frequency dependence of priority effects. Nature Ecology & Evolution 2:1691–1695.

Ke, P.-J., and T. Miki. 2015. Incorporating the soil environment and microbial community into plant competition theory. Frontiers in Microbiology 6:1066.

Ke, P.-J., T. Miki, and T.-S. Ding. 2015. The soil microbial community predicts the importance of plant traits in plant–soil feedback. New Phytologist 206:329–341.

Keane, R. M., and M. J. Crawley. 2002. Exotic plant invasions and the enemy release hypothesis. Trends in Ecology & Evolution 17:164–170.

Klironomos, J. N. 2002. Feedback with soil biota contributes to plant rarity and invasiveness in communities. Nature 417:67–70.

Kraft, N. J. B., O. Godoy, and J. M. Levine. 2015. Plant functional traits and the multidimensional nature of species coexistence. Proceedings of the National Academy of Sciences USA 112:797–802.

Kulmatiski, A., K. H. Beard, J. R. Stevens, and S. M. Cobbold. 2008. Plant–soil feedbacks: a meta-analytical review. Ecology Letters 11:980–992.

Kulmatiski, A., J. Heavilin, and K. H. Beard. 2011. Testing predictions of a three-species plant–soil feedback model. Journal of Ecology 99:542–550.

LaManna, J. A., R. T. Belote, L. A. Burkle, C. P. Catano, and J. A. Myers. 2017. Negative density dependence mediates biodiversity–productivity relationships across scales. Nature Ecology & Evolution 1:1107–1115.

Lanuza, J. B., I. Bartomeus, and O. Godoy. 2018. Opposing effects of floral visitors and soil conditions on the

determinants of competitive outcomes maintain species diversity in heterogeneous landscapes. Ecology Letters 21:865–874.

Lekberg, Y., et al. 2018. Relative importance of competition and plant–soil feedback, their synergy, context dependency and implications for coexistence. Ecology Letters 21:1268–1281.

Lennon, J. T., and S. E. Jones. 2011. Microbial seed banks: the ecological and evolutionary implications of dormancy. Nature Reviews Microbiology 9:119–130.

Letten, A. D., and D. B. Stouffer. 2019. The mechanistic basis for higher-order interactions and non-additivity in competitive communities. Ecology Letters 22:423–436.

Letten, A. D., P.-J. Ke, and T. Fukami. 2017. Linking modern coexistence theory and contemporary niche theory. Ecological Monographs 87:161–177.

Mangan, S. A., S. A. Schnitzer, E. A. Herre, K. M. L. Mack, M. C. Valencia, E. I. Sanchez, and J. D. Bever. 2010. Negative plant–soil feedback predicts tree-species relative abundance in a tropical forest. Nature 466:752–755.

McGuire, K. L. 2007. Common ectomycorrhizal networks may maintain monodominance in a tropical rain forest. Ecology 88:567–574.

Mordecai, E. A. 2011. Pathogen impacts on plant communities: unifying theory, concepts, and empirical work. Ecological Monographs 81:429–441.

Norby, R. J., E. G. O'Neill, W. G. Hood, and R. J. Luxmoore. 1987. Carbon allocation, root exudation and mycorrhizal colonization of *Pinus echinata* seedlings grown under CO_2 enrichment. Tree Physiology 3:203–210.

Peay, K. G. 2016. The mutualistic niche: mycorrhizal symbiosis and community dynamics. Annual Review of Ecology, Evolution, and Systematics 47:143–164.

Peay, K. G. 2018. Timing of mutualist arrival has a greater effect on *Pinus muricata* seedling growth than interspecific competition. Journal of Ecology 106:514–523.

Petermann, J. S., A. J. F. Fergus, L. A. Turnbull, and B. Schmid. 2008. Janzen-Connell effects are widespread and strong enough to maintain diversity in grasslands. Ecology 89:2399–2406.

van der Putten, W. H., et al. 2013. Plant–soil feedbacks: the past, the present and future challenges. Journal of Ecology 101:265–276.

Rasmann, S., T. L. Bauerle, K. Poveda, and R. Vannette. 2011. Predicting root defence against herbivores during succession. Functional Ecology 25:368–379.

Reinhart, K. O., and R. M. Callaway. 2006. Soil biota and invasive plants. New Phytologist 170:445–457.

Reinhart, K. O., T. Tytgat, W. H. van der Putten, and K. Clay. 2010. Virulence of soil-borne pathogens and invasion by *Prunus serotina*. New Phytologist 186:484–495.

Revilla, T. A., G. F. C. Veen, M. B. Eppinga, and F. J. Weissing. 2013. Plant–soil feedbacks and the coexistence of competing plants. Theoretical Ecology 6:99–113.

Saavedra, S., R. P. Rohr, J. Bascompte, O. Godoy, N. J. B. Kraft, and J. M. Levine. 2017. A structural approach for understanding multispecies coexistence. Ecological Monographs 87:470–486.

Shannon, S., S. L. Flory, and H. Reynolds. 2012. Competitive context alters plant–soil feedback in an experimental woodland community. Oecologia 169:235–243.

Silvertown, J. 2004. Plant coexistence and the niche. Trends in Ecology & Evolution 19:605–611.

Tilman, D. 1982. Resource competition and community structure. Princeton University Press, Princeton, New Jersey, USA.

Umbanhowar, J., and K. McCann. 2005. Simple rules for the coexistence and competitive dominance of plants mediated by mycorrhizal fungi. Ecology Letters 8:247–252.

Urcelay, C., and S. Díaz. 2003. The mycorrhizal dependence of subordinates determines the effect of arbuscular mycorrhizal fungi on plant diversity. Ecology Letters 6:388–391.

Veresoglou, S. D., G. Menexes, and M. C. Rillig. 2012. Do arbuscular mycorrhizal fungi affect the allometric partition of host plant biomass to shoots and roots? A meta-analysis of studies from 1990 to 2010. Mycorrhiza 22:227–235.

Weigelt, A., and P. Jolliffe. 2003. Indices of plant competition. Journal of Ecology 91:707–720.

Yamazaki, M., S. Iwamoto, and K. Seiwa. 2008. Distance- and density-dependent seedling mortality caused by several diseases in eight tree species co-occurring in a temperate forest. Plant Ecology 201:181–196.

Zheng, C., B. Ji, J. Zhang, F. Zhang, and J. D. Bever. 2015. Shading decreases plant carbon preferential allocation towards the most beneficial mycorrhizal mutualist. New Phytologist 205:361–368.

Supporting Information

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecm.1391/full

Data Availability

Code used for this study is available at https://github.com/pojuke/MCTbasedPSF and the public GitHub repository is permanently archived with Zenodo (https://doi.org/10.5281/zenodo.3355580).

Concepts and Synthesis