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IDEA AND PERSPECTIVE

Winning and losing with microbes: how microbially mediated fitness differences influence plant diversity

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Abstract

Interactions between plants and soil microbes can strongly influence plant diversity and community dynamics. Soil microbes may promote plant diversity by driving negative frequency-dependent plant population dynamics, or may favor species exclusion by providing one species an average fitness advantage over others. However, past empirical research has focused overwhelmingly on the consequences of frequency-dependent feedbacks for plant species coexistence and has generally neglected the consequences of microbially mediated average fitness differences. Here we use theory to develop metrics that quantify microbially mediated plant fitness differences, and show that accounting for these effects can profoundly change our understanding of how microbes influence plant diversity. We show that soil microbes can generate fitness differences that favour plant species exclusion when they disproportionately harm (or favour) one plant species over another, but these fitness differences may also favor coexistence if they trade off with competition for other resources or generate intransitive dominance hierarchies among plants. We also show how the metrics we present can quantify microbially mediated fitness differences in empirical studies, and explore how microbial control over coexistence varies along productivity gradients. In all, our analysis provides a more complete theoretical foundation for understanding how plant–microbe interactions influence plant diversity.

Keywords

Coexistence, competition, mutualisms, pathogens, plant-soil feedback, rhizosphere.

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INTRODUCTION

Interactions between plants and soil microbes are widespread and consequential for plant performance (Selosse *et al*. 2015; Peay 2016). Over the past two decades, ecologists have begun to quantify the complex ways in which these interactions can influence plant competition and community dynamics (van der Putten *et al*. 1993; van der Heijden *et al*. ; Bever *et al*. 2012). The soil microbial community has been implicated in regulating a number of ecological processes. Negative frequency dependent growth in plant populations driven by the soil microbial community can help maintain plant diversity in various communities including old fields (Pendergast *et al*. 2013), Mediterranean shrublands (Teste *et al*. 2017), and tropical forests (Mangan *et al*. 2010). Spatial variation in the soil microbial community can lead to variation in plant productivity (van der Heijden *et al.*) and can influence the outcome of plant restoration (Wubs *et al*. 2016). Interactions between plants and soil microbes have also been shown to influence plant succession and species invasions (Inderjit & van der Putten 2010). Nevertheless, predicting the influence of soil microbes on the diversity and dynamics of natural plant communities remains a challenge.

Empirical research has highlighted two general avenues by which soil microbes can modify plant community dynamics. First, differential responses of plant species to soil microbes can contribute to negative frequency dependent plant population dynamics that can promote diversity (Mangan *et al*. 2010; Bever *et al*. 2015). Many studies find that plants grow less vigorously in soil harboring a microbial community cultivated by conspecific individuals than in soil harboring a microbial community cultivated by heterospecific individuals (reviewed in Kulmatiski *et al*. 2008). Moreover, plant species that experience more negative microbial effects in greenhouse experiments tend to be less abundant in natural communities (Klironomos 2002; Mangan *et al*. 2010; Kempel *et al*. 2018, but see Maron *et al*. 2016), suggesting a link between the strength of these interactions and plant abundance. Our ability to project the influence of plant-microbe interactions in stabilising coexistence has been both facilitated and motivated by a theoretical framework developed in Bever *et al*. (1997) and Bever (2003) (Box 1) which summarises the effect of microbial feedbacks in a metric termed I_S. In the context of modern coexistence theory (Chesson 2000), plant-microbe interactions that generate frequency-dependent feedback loops have a "*stabilising*" (negative feedbacks) or "*destabilising*" (positive feedbacks) effect on the plant community.

The second avenue through which the soil microbial community can influence plant community dynamics is by driving the replacement of plant species, especially during succession or invasion. In a seminal study, for example, van der Putten *et al*. (1993) found that succession in foredune communities might be driven by the low susceptibility of late-succession plant species to the pathogenic microbes that accumulate in soils colonised by early-succession plants. Plant-microbe interactions can similarly exacerbate plant invasions when invasive

Box 1: Bever's model of pairwise plant-soil feedback

Here, we summarise the pioneering plant-soil feedback framework developed in Bever *et al.* (1997) and Bever (2003), and briefly review its use in empirical research. The Bever framework considers the effects of microbes in a system in which each of two plant species 1 and 2 cultivates a particular microbial community denoted A and B respectively. The aggregate soil microbial community depends on the relative abundance and influence of each plant species. These interactions can generate a frequency-dependent plant-soil feedback via a two-step process. First, as a plant population grows in proportion, the microbial community becomes more similar to that plant's characteristic community. Second, the altered soil community influences the performance of both plant species at a rate m. The effects of each microbial community on the plant species that cultivates it (i.e. the effect of microbe community A on plant 1 and of microbe community B on plant 2, denoted m_{1A} and m_{2B} respectively) are termed "direct feedbacks". The effects of each microbial community on the other plant (i.e. the effect of microbe community A on plant 2 (m_{2A}) and of microbe community B on plant 1 (m_{1B})) are termed "indirect feedbacks". Bever *et al.* (1997) showed that microbes can stabilise plant dynamics when they exert more negative (or less positive) direct feedbacks than indirect feedbacks, resulting in a negative value for the metric they termed I_S. Bever (2003) extended the framework to show that microbial feedbacks could dictate the outcome of community dynamics even when there is simultaneous plant competition (Fig. 1b).

Bever *et al.* (1997) show that the degree to which the system is stabilised (negative frequency dependent dynamics between the plant species) or destabilised (positive frequency dependence) is given by the following:

$$I_S = m_{1A} - m_{2A} - m_{1B} + m_{2B}$$

This term measures the degree to which the microbial community cultivated by each plant harms the competitor more than the cultivating plant (or favors the cultivating plant over its competitors). Negative I_S causes negative frequency dependent dynamics (tendency towards coexistence), while positive I_S means positive frequency dependent dynamics (tendency towards priority effects). Bever *et al.* (1997) also showed that in addition to a negative I_S, stable coexistence requires that the microbes cultivated by each plant species influence the cultivating species more negatively (or less positively) than the other plant species ($m_{1A} < m_{2A}$ and $m_{2B} < m_{1B}$). Revilla *et al.* (2013) later developed a metric termed J_S, which generalises I_S to describe the sign of microbial feedbacks when the plant species are unequal competitors.

Part of the reason behind the lasting influence of the plant-soil feedback theory is that Bever (1994) and Bever *et al.* (1997) outlined a two-phase experimental approach to estimate the microbial effects relevant to I_S that remains a gold-standard (Pernilla Brinkman *et al.* 2010; Bever *et al.* 2012). In the first phase of these experiments, plants of each focal species are grown in sterilised soil containing a field-collected inoculum. In the second phase, plants from all focal species are grown in sterilised soil that is inoculated with a microbial community cultivated either by conspecifics or by one of the other focal species. The biomass of plants grown on previously cultivated soils is generally used to estimate the four m terms to calculate I_S for each species pair (e.g. Fitzsimons & Miller 2010; Smith & Reynolds 2015; Bauer *et al.* 2017).

Although I_S incorporates the effects of both microbial communities on both plant species, relatively few empirical studies motivated by Bever's framework quantify all four components of the pairwise stabilisation term directly (Smith-Ramesh & Reynolds 2017). Considerably more plant-soil feedback studies evaluate individual (rather than pairwise) negative feedbacks by measuring the growth of one or a few focal plant species in soil harboring a conspecific-cultivated microbial community and in soil harboring a microbial community cultivated by other plant species. For example, negative values of a log-response ratio $\left(\ln\left(\frac{\text{biomass}_{\text{conspecific microbes}}}{\text{biomass}_{\text{heterospecific microbes}}}\right)\right)$ indicate lower plant growth in soils with conspecific-cultivated microbial communities than in soils with heterospecific-cultivated microbial communities (corresponding to $m_{1A} - m_{1B} < 0$ in Bever's framework), resulting in negative individual feedback for the focal species (Reinhart 2012; Baxendale *et al.* 2014; Pfennigwerth *et al.* 2017; Teste *et al.* 2017). Although it is true that all else being equal, a more negative individual feedback suggests a diversity-maintaining role for microbes, it should be clear that assessing the net stabilising effects of plant-microbe interactions on plant diversity requires simultaneously assessing their effects across both plant species. Moreover, as we show in the main text, focusing only on the stabilising effects of plant microbe interactions and not comparing these stabilising effects to microbially mediated plant fitness differences can lead to false conclusions regarding the influence of soil microbes on plant diversity.

species are less susceptible than native plant species to soil-borne pathogens in the exotic range (Reinhart *et al.* 2003; Callaway *et al.* 2004; Inderjit & van der Putten 2010). While in all of these examples, the plant-microbe interactions will inevitably cause some frequency dependent dynamics, if one averages over the range of plant species frequencies in these systems, one species (often the late-succession or invasive species) is on average less sensitive to the harmful effects of cultivated soil biota than the other. Following Chesson (2000), we term such average differences among plants in their susceptibility to soil-borne pathogens or in the benefits they accrue from below-ground mutualists as "*microbially mediated fitness differences*". Importantly, in Chesson's framework, these fitness differences are an abstraction, analogous to competitive ability, that reflect species performances across the full range of conditions they can experience; they are not per-capita growth rate differences as might be expected from conventional uses of the term "fitness" (Chesson 2018).

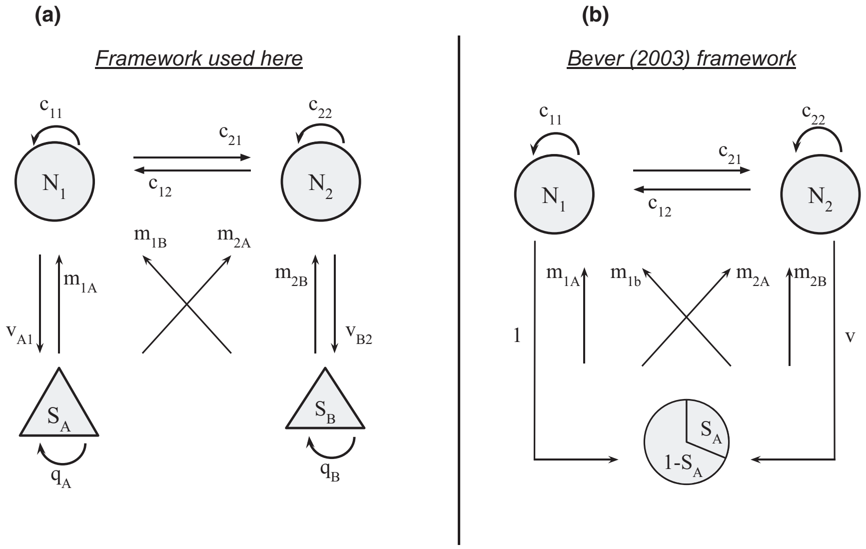

Figure 1 (a) A schematic of the framework we use to model plant-microbe interactions. Plants N_1 and N_2 compete via Lotka-Volterra competition (c's) and via their interactions with microbes A and B. As in Bever's classic plant-soil feedback models, plant species 1 cultivates soil microbial community A, and plant species 2 cultivates microbial community B. In this model, S_A and S_B denote the density of microbes A and B respectively. Plants 1 and 2 cultivate microbial communities A and B at a per-capita rate v_{A1} and v_{B2}, respectively, and each microbial community has a per-capita effect on each plant species (m terms). (b) The classic framework for plant-microbe interactions occuring among competing plant species as described in Bever (2003). Plants compete via Lotka-Volterra competition (c's) and via their interactions with soil microbes. Microbes A represent the microbial community characteristic of plant 1's soil, and microbes B represent the microbial community characterstic of plant 2's soil. S_A and S_B denote the proportion of of microbes A and B in the soil, so that $S_A + S_B = 1$. The rate at which plant 2 cultivates microbes B, relative to the rate at which plant 1 cultivates microbes A, is denoted v.

The net effect of soil microbes on plant diversity depends both on the extent to which they stabilise or destabilise plant interactions due to frequency-dependent feedbacks, and on the extent to which they give one species an average fitness advantage. In the extreme, microbial interactions that have stabilising effects on plant coexistence can nonetheless drive species exclusion if they also generate plant fitness differences to an extent that exceeds their stabilising influence. A similar result was shown by Bever *et al.* (1997), who found that plant species pairs whose interactions are stabilised by microbes (negative I_S) could fail to coexist if the microbial communities overwhelmingly favor one plant species (Box 1). Still, the original analysis in Bever *et al.* (1997) and subsequent theoretical analyses and extensions of the model (Bever 2003; Kulmatiski *et al.* 2011; Revilla *et al.* 2013; Eppinga *et al.* 2018) focus primarily on the frequency-dependent stabilising or destabilising effects of microbes, with less attention paid to microbially mediated fitness differences.

Empirical studies have also tended to emphasise the positive or negative frequency-dependency arising from plant-microbe interactions and have typically ignored the effects of microbially mediated fitness differences (reviewed in Ke & Miki 2015; but see Chung & Rudgers 2016; Siefert *et al.* 2019). It is therefore difficult to draw inferences regarding the total or net effects of soil microbes on plant species diversity from many empirical plant–soil feedback studies. Part of the problem relates to our lack of a theoretically justified metric for the microbially mediated fitness differences, analogous to the metric I_S for quantifying frequency-dependent effects. Only with such a metric can we more accurately infer the effects of soil microbes on plant species diversity by analysing the interplay between their (de)stabilising effects and the fitness differences they generate.

Here, we use theory to explore how plant-microbe interactions can generate fitness differences between competitors, and derive a metric essential for quantifying the effect of such interactions on plant diversity. To do so, we first define the microbially mediated fitness differences in Bever's classic plant-soil feedback model, a difference that favours one plant over the other and thereby counterbalances the stabilising or destabilising effects of soil microbes. We then explore the biological processes that can contribute to these fitness differences by expanding the classic plant-soil feedback model to include a greater range of soil microbial dynamics. Through a series of scenarios, we illustrate how not accounting for microbially mediated fitness differences can lead to erroneous conclusions about how microbes influence plant diversity. Lastly, we show how our model relates to a much larger body of work in coexistence theory that allows us to predict, for example, how the importance of plant-microbe interactions changes along productivity gradients. In the discussion we explain how the fitness differences identified here can be quantified in empirical studies and propose avenues of research to give a more complete picture of how soil microbes shape plant diversity.

MICROBES DRIVE A FITNESS DIFFERENCE BETWEEN PLANTS IN THE CLASSIC PLANT-SOIL FEEDBACK MODEL

We begin by analysing the model of plant-soil feedbacks among competing plants from Bever (2003) to develop a metric that quantifies microbially mediated fitness differences. The following analysis also applies to the original competition-implicit model in Bever *et al.* (1997) (Appendix S1). Bever (2003) models two plant species N_1 and N_2 that interact via Lotka-Volterra competition and via their effects on soil microbial communities A and B. With some minor notational changes from Bever (2003), the dynamics of plant densities N are as follows:

$$\frac{1}{N_1}\frac{dN_1}{dt} = g_1(1 - c_{11}N_1 - c_{12}N_2 + m_{1A}S_A + m_{1B}S_B) \quad (1)$$

where g_1 represents the intrinsic growth rate of plant species 1 in the absence of competitors and microbial effects, and c_{11} and c_{12} represent the intra- and interspecific per-capita competitive effects on plant 1, respectively. The microbial community characteristic of plant 1's soil is denoted A, and the microbial community characteristic of plant 2's soil is denoted B. S_A denotes the proportional effect of plant 1 on the composition of the soil microbial community, and the proportional effect of plant 2 on the soil microbial community, denoted S_B, is equal to $1 - S_A$. m_{1A} is the growth of species 1 on soil containing only microbial community A minus its growth on uncultivated soil (Bever *et al.* 1997); an analogous definition exists for m_{1B}. Positive values of m_{1A} or m_{1B} indicate higher plant performance in the presence of cultivated microbes, while negative values of m_{1A} or m_{1B} indicate lower plant performance in the presence of cultivated microbes. The proportions S_A and S_B therefore scale the microbial effects on plant growth.

In Bever's model, the rate of change in S_A depends on the relative frequency of plants 1 and 2, and on the relative degree to which plant 2 versus plant 1 cultivate their characteristic soil microbial community, with this relative degree denoted v:

$$\frac{dS_A}{dt} = S_A(1 - S_A)\left(\frac{N_1}{N_1 + N_2} - v\frac{N_2}{N_1 + N_2}\right) \quad (2)$$

We focus on the effects of plant–microbe interactions on plant dynamics by assuming that the intra- and inter-specific competitive effects of each plant species are equal (i.e. $c_{12} = c_{22}$ and $c_{21} = c_{11}$; see Appendix S1 for the coexistence criteria when this assumption is violated). With this assumption, the per-proportion growth rate of plant species 1 when invading a system with plant species 2 at equilibrium, denoted IGR_1, is as follows (see Appendix S1 for derivation):

$$\mathrm{IGR}_1 = g_1(m_{1B} - m_{2B})$$

This shows that the invasion growth rate of plant 1 is determined by the relative effect of the resident plant 2's soil microbial community (i.e. microbial community B) on each plant species. Note that g_1, the growth in the absence of microbes, simply scales the relative effects of the resident microbial community on the two plant species. Assuming g_1 is positive, it has no effect on the sign of the invasion growth rate and is therefore irrelevant to the mutual invasibility condition. Following Chesson (2000), we can express the scaled (IGR_1/g_1) invasion growth rate IGR'_1 as the sum of the microbially mediated fitness difference and the stabilising effects of plant-microbe interactions:

$$\mathrm{IGR}'_1 = (\mathrm{fitness}_1 - \mathrm{fitness}_2) + \mathrm{stabilisation}$$

As Bever *et al.* (1997) have shown, microbial interactions stabilise plant coexistence when microbes more strongly suppress (or more weakly promote) the growth of their cultivating plant species than of the other plant. In the Chesson-type decomposition of the invasion growth rate, the stabilisation due to microbes, which contributes to both species' invasion growth rates, is as follows (Appendix S1):

$$\mathrm{stabilisation} = -\frac{1}{2}I_S = -\frac{1}{2}(m_{1A} - m_{1B} - m_{2A} + m_{2B}) \quad (3)$$

Recall that m_{1A} is the difference between species 1's growth with soil microbial community A and its growth in uncultivated soil. Given that m_{1B} is the difference between species 1's growth with microbial community B and its growth on the same uncultivated soil, $m_{1A} - m_{1B}$ is independent of growth on uncultivated soil (Appendix S1). Thus, as noted by Bever *et al.* (1997), the degree to which microbes stabilise plant interactions is not affected by the growth of plants in uncultivated soils, simplifying experimental parameterisations of I_S. This result also makes intuitive sense, since I_S describes the average consequences of plants growing with soil microbes cultivated by one plant species versus another; growth on uncultivated soil is irrelevant to this problem. As in Bever's past work, negative frequency dependent dynamics (negative I_S) increase invasion growth rates, and positive frequency dependent dynamics (positive I_S) decrease invasion growth rates. However, as we explain next, the net effect of plant-microbe interactions on plant diversity will depend on whether their stabilising effect exceeds the fitness difference they generate.

The microbially mediated average fitness of plant 1 is determined by the average degree to which the two microbial communities A and B benefit or harm plant 1 (Appendix S1):

$$\mathrm{fitness}_1 = \frac{1}{2}(m_{1A} + m_{1B}) \quad (4)$$

An analogous expression exists for plant 2. When microbial communities A and B are on average more pathogenic or less mutualistic towards one plant species than another, they generate a fitness difference:

$$\mathrm{fitness\ difference} = \frac{1}{2}(m_{1A} + m_{1B} - m_{2A} - m_{2B})$$

Importantly, proper parameterisation of the microbially mediated fitness difference requires measuring plant growth on uncultivated soil, something that is not required for determining the stabilising effect (I_S). Following from the definition of each m term as the growth G on cultivated (subscripted A or B) versus uncultivated (subscripted O) soils (e.g. $m_{1A} = G_{1A} - G_{1O}$, Bever *et al.* (1997)), the fitness difference can be calculated as follows:

$$\mathrm{fitness\ difference} = \left(\frac{1}{2}(G_{1A} + G_{1B}) - G_{1O}\right) - \left(\frac{1}{2}(G_{2A} + G_{2B}) - G_{2O}\right) \quad (5)$$

The fitness difference can therefore be interpreted as the difference between species 1 and 2 in how much their growth benefits or suffers, on average, from the soil microbial community cultivated by the two competitors. This benefit or harm is measured with reference to growth on uncultivated soil (G_{1O} or G_{2O}, depending on the focal plant species).

In the absence of stabilisation, the invasion growth rate is positive for only one species, and coexistence is impossible. When microbial stabilisation of plant dynamics is sufficiently large to overcome the fitness disadvantage of the weaker plant, microbial interactions can cause both plants to have positive invasion growth rates and therefore coexist. This condition is equivalent to the feasibility criteria from Bever *et al.* (1997) stating that stable coexistence is possible when I_S is negative and the effects of each microbial community are more negative (or less positive) on the species that cultivates it than on the other plant (i.e. $m_{1A} < m_{2A}$ and $m_{2B} < m_{1B}$; Appendix S1). In sum, soil microbes enhance plant coexistence with negative values of I_S, but also mediate an average fitness difference that favors the exclusion of one plant species.

A CLOSER EVALUATION OF MICROBIAL EFFECTS ON PLANT FITNESS DIFFERENCES

A deeper understanding of the microbial interactions that drive plant fitness differences can come from a fuller exploration of the dynamics of soil microbes. Following Eppinga *et al.* (2006), we expand the microbial population dynamics in Bever's framework to model the density (rather than frequency) of the two soil microbial communities (Fig. 1a). Increasing the range of microbial dynamics possible in the model admittedly makes the theory less easily parameterised with soil training experiments, but allows us to include a greater range of soil microbial dynamics that can favor one plant over another. We can then see how these dynamics are encapsulated within the inter- and intraspecific competitive coefficients underlying coexistence or exclusion, and what assumptions need to be made to yield versions of the model that are more easily parameterised. Moreover, by removing some of the constraints on microbial dynamics in the original formulation of the plant-soil feedback model, we can derive stabilisation and fitness difference terms that integrate the effects of both plant competition and microbial feedbacks, and formally link the model to broader coexistence theory. As we show in the final section of this paper, doing so allows us to explore, for example, how resource availability influences the importance of plant-microbe interactions for competitive outcomes.

In our expanded model, plant dynamics still follow eqn. 1, but we now model the density S of soil microbial communities A and B that are cultivated by plant species 1 and 2 respectively, and suffer from density-dependent mortality:

$$\frac{1}{S_A}\frac{\mathrm{d}S_A}{\mathrm{d}t} = v_{A1}N_1 - q_A S_A \qquad (6)$$

An analogous equation exists for S_B. This model assumes that species 1 cultivates soil microbial community A at a constant per-capita rate v_{A1}, and that the density of A declines due to density-dependent mortality, q_A (Stevens & Holbert 1995; Woody *et al.* 2007). Following classic plant-soil feedback theory, S_A and S_B denote densities of the unique microbial communities cultivated by plant species 1 and 2 respectively. In this framework, the densities S_A and S_B can vary independently of each other– they are no longer proportions constrained to sum to 1, and S_B can no longer be expressed as $1 - S_A$(Fig. 1a). Although the two microbial communities S_A and S_B may directly interact with each other in natural systems, we assume in the main text that these interactions do not significantly affect the overall microbial dynamics (see Appendix S2 for a model that includes microbial competition). As this model is coupled to the plant dynamics in eqn. 1, the m terms in the plant dynamics equation are now interpreted as the per-capita effect of each microbial community on plant growth. The units and definitions of the parameters are summarised in Table S2.1.

These changes to the microbial dynamics equations increase the range of behaviour the model is capable of producing relative to the original Bever models, but they inevitably make the model less coupled to the two-phase experiments that so nicely parameterise Bever's model (Box 1). However, as we show in the following scenarios and in the discussion, many insights provided from the model developed here apply regardless of whether one begins with a frequency-based framework or our extended version.

To evaluate microbial effects on plant dynamics in terms of fitness differences that favor one plant over the other, and niche differences that stabilise their interaction by favouring species that drop to low density, we assume that microbial dynamics operate on a faster time scale than the plants. This assumption is consistent with the general expectation that microbes have shorter generation times and faster dynamics than their plant hosts (Bever *et al.* 2012; but see Treseder & Lennon 2015). With this separation of timescale assumption, the per-capita effect of plant j on plant i, which is used to calculate the degree of niche overlap and the magnitude of the fitness difference, is termed α_{ij} and is expressed as follows (see Appendix S2 for derivation):

$$\alpha_{ij} = \left(c_{ij} - \frac{m_{iX}v_{Xj}}{q_X}\right) \qquad (7)$$

where X=A when j=1, and X=B when j=2. This expression shows that two processes influence the per capita effect of plant j on plant i. First, plant j harms plant i through direct competition (c_{ij}) independent of the soil microbial community. Second, plant j can cultivate a microbial community X that affects plant i's population growth. The sign of this effect depends on whether the microbial community cultivated by plant j is on average beneficial for plant i (with positive m's that weaken the total per capita suppression) or suppressive (with negative m's that increase the per capita suppression). The strength of this effect is determined by how strongly the microbes grow with plant j (v_{Xj}), how strongly the microbes affect plant i (m_{iX}), and how well the microbes survive in the soil (q_X). The effect of plant j on plant i due to competition alone or due microbial interactions alone can be assessed by setting the other mechanism equal to zero. For example, in the absence of competition ($c_{ij} = 0$), the per capita suppression of plant species i by species j is simply determined by the degree to which plant species j promotes a microbial community that harms species i.

When the cultivated microbial community has a net positive effect on a plant species $\left(\frac{m_{iX}v_{Xj}}{q_X} > 0\right)$, there is the potential for net facilitation ($\alpha_{ij} < 0$). For example, plant 2 may facilitate plant 1 when the microbial community it cultivates (community B) is more beneficial for plant 1 than plant 2's competitive suppression of plant 1 (i.e. $c_{12} < \frac{m_{1A} v_{B2}}{q_B}$, resulting in $\alpha_{12} < 0$). Such interspecific facilitation generally makes coexistence a non-issue. When only one plant species is facilitated, coexistence simply requires that the species being facilitated limits itself more than it limits the other species ($\alpha_{21} < \alpha_{11}$ in this example). When both plant species facilitate one another, coexistence is assured. We therefore focus the remainder of this paper on cases where the net effects of plants on neighbors are negative, meaning interspecific competition is stronger than any microbially mediated interspecific facilitation (i.e., $c_{12} > \frac{m_{1B} v_{B2}}{q_B}$ and $c_{21} > \frac{m_{2A} v_{A1}}{q_A}$). Similarly, because species can never indefinitely facilitate themselves (which would lead to unbounded growth), we also assume net negative intraspecific interactions. These conditions are automatically satisfied when microbe effects (m_{iX}) are themselves negative.

The relative strength of interspecific and intraspecific suppression determines the degree of niche overlap ρ as follows (Chesson 2013):

$$\rho = \sqrt{\frac{\alpha_{12}\alpha_{21}}{\alpha_{11}\alpha_{22}}} \tag{8}$$

This term reflects the degree to which the two plant species limit heterospecifics versus conspecifics. There is complete niche overlap (ρ=1) when each plant species equally affects the growth of con- and heterospecifics. The niche difference is simply the complement of the niche overlap ($1-\rho$). In this model, two types of biological differences can stabilise coexistence by reducing niche overlap. First, species differences that drive stronger intra- than interspecific competition ($c_{11} > c_{21}$ and $c_{22} > c_{21}$) can stabilise coexistence. Second, microbial interactions can stabilise coexistence when the microbial community cultivated by each plant is on average more harmful (or less beneficial) to the cultivating species than to the other plant. The stabilisation due to competition alone (ρ^{comp}) or due to microbial interactions alone (ρ^{micr}) can be assessed by setting the microbial or competition terms, respectively, equal to zero in eqn. 7. Assuming symmetry in all parameters except the microbial effects on plants, the niche overlap term ρ has a nearly identical interpretation to I_S in Bever's framework: strong conspecific and weak heterospecific microbial suppression drive a negative plant-soil feedback indicated by negative values of I_S, and they drive low niche overlap (ρ<1) in our framework.

Whether species coexist is determined both by the degree of niche overlap, and by their average fitness differences. The ratio of the two species' geometric mean suppression by intraspecific and interspecific individuals determines their fitness difference κ_2/κ_1 as follows (Godoy & Levine 2014):

$$\frac{\kappa_2}{\kappa_1} = \sqrt{\frac{\alpha_{11}\alpha_{12}}{\alpha_{22}\alpha_{21}}} \tag{9}$$

The fitness difference reflects the relative degree to which each species is influenced by competition and microbial interactions, irrespective of which plant cultivates the microbes. Fitness differences are large when species differ in their sensitivity to competition, as explained in Chesson (2000) and Godoy & Levine (2014), or when they differ in their sensitivity to the microbial community. As above, the fitness differences generated by competition alone (${\kappa_2/\kappa_1}^{comp}$) or by microbial interactions alone (${\kappa_2/\kappa_1}^{micr}$) can be calculated by setting the other process equal to zero in eqn. 7.

Coexistence depends on small niche overlap (a large niche difference) relative to the fitness differences as follows:

$$\rho < \frac{\kappa_2}{\kappa_1} < \frac{1}{\rho} \tag{10}$$

Algebra shows that this inequality is equivalent to the well-known condition from two-species coexistence in Lotka-Volterra competition models, which requires that intraspecific competition is stronger than interspecific competition (i.e. $\alpha_{21} < \alpha_{11}$ and $\alpha_{12} < \alpha_{22}$, Appendix S2, and the two species equilibrium exhibits the same stability properties). Species with large fitness differences (κ_2/κ_1 further from 1) can coexist only when there is low niche overlap ($\rho \rightarrow 0$); conversely when species have high niche overlap, coexistence is only possible if the two species have very similar ecological fitness (κ_2/κ_1 close to 1, Fig. 2a). Microbial interactions can also drive positive frequency dependence leading to a priority effect when they cause net intraspecific suppression to be weaker than interspecific suppression, resulting in ρ>1; stable coexistence is impossible in such cases.

It is important to note here that the terms describing plant-microbial interactions are essential to determine the interaction terms α, which in turn determine both niche overlap and fitness difference. Thus, the microbial influence on plant species diversity will result from effects on both the niche overlap and the fitness difference.

WHY MICROBIALLY MEDIATED FITNESS DIFFERENCES MATTER

We now elaborate three scenarios that demonstrate why quantifying microbially mediated fitness differences is important for understanding how soil microbes influence plant coexistence. Rather than forging new theoretical results (see Bever 2003; Revilla *et al.* 2013; Eppinga *et al.* 2018), each of these scenarios aims to make obvious for empiricists measuring only I_S that the microbially mediated fitness difference is an equally important metric for inferring microbial effects on coexistence.

Our three scenarios include one in which microbes favor exclusion even when they cause negative plant-soil feedback, one in which microbes favor coexistence even when they cause no plant-soil feedback, and one in which microbes promote diversity in multi-species plant communities despite favoring exclusion among pairs. The parameter values used in each of these scenarios are presented in Appendix S3.

Scenario 1: Microbes favor exclusion even when they cause negative plant-soil feedback

We first consider a scenario (points labelled S1 in Fig. 2a) where measuring the microbially mediated fitness difference would be key to properly inferring that the net effect of microbes is to favor plant species exclusion. The results of

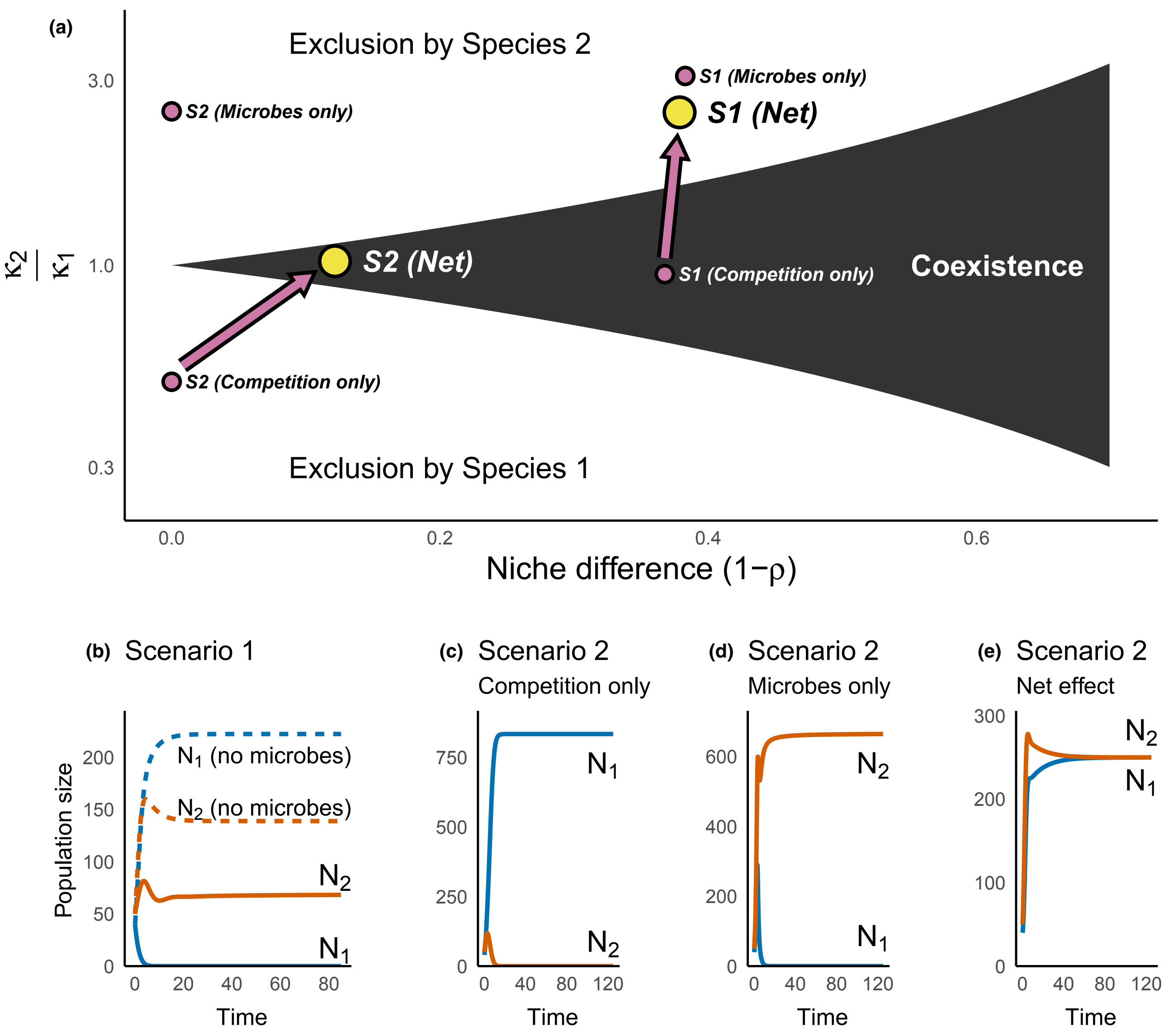

Figure 2 (a) Coexistence is possible when stabilising effects between species are stronger than the fitness difference between them, i.e. when the inequality $\rho < \kappa_2/\kappa_1 < 1/\rho$ is satisfied. Arrows indicate the change in net fitness and niche differences due to plant-microbe interactions in Scenarios S1 and S2. (b) In Scenario **S1**, plants coexist when microbial effects are set to zero (dashed lines). The plant-interactions further stabilise this interaction; however, the net effect of microbes is to drive the exclusion of N_1 (solid lines) due the large fitness difference they generate. (c–e) In Scenario **S2**, neither competition nor microbial interactions alone stabilise coexistence among the plant species (c and d). However, when both mechanisms occur simultaneously, they promote coexistence both by equalising fitness and driving a niche difference (e).

this scenario also follow from the feasibility criteria of Bever *et al.* (1997), though this earlier result was not expressed in terms of microbially mediated fitness differences. We consider a plant species pair that can coexist in the absence of microbial effects due to stronger intraspecific than interspecific competition (dashed lines in Fig. 2b). The plant-microbial interactions in this scenario further stabilise the system ($\rho^{micr} = 0.617$).

However, in this scenario, microbes also have the effect of more strongly suppressing plant 1 than plant 2, causing a substantial fitness difference ($(\kappa_2/\kappa_1)^{micr} = 3.086$) that overcomes their stabilising effect. Indeed, when competition and plant-microbe interactions act together, plant 1 is excluded from the system because its microbial interactions give it such low fitness. Thus, contrary to the conclusion from analysing microbe effects on niche differentiation alone, properly predicting that the net effect of microbial interactions is to drive the exclusion of species 1 (solid lines in Fig. 2b) requires measuring the microbially mediated fitness difference as well.

Scenario 2: Microbes promote coexistence even without generating negative plant-soil feedback

Next, we consider a scenario (points labelled S2 in Fig. 2a) that highlights how measuring microbially mediated fitness differences is key to inferring the interactive effects of competition and plant-microbe interactions. The model developed here and its associated measure of the niche difference (eqns 7 and 8) not only allows us to more precisely define the basis of microbially mediated fitness and niche differences, but also to quantify the effects of new stabilising mechanisms that are more difficult to resolve under the Bever framework. For example, it is well known that a competition-defense trade-off can create opportunities for plant coexistence beyond the stabilising opportunities from each mechanism alone (Holt *et al.* 1994; Mordecai 2011). This tradeoff can also involve plant-microbe interactions (Bever *et al.* 2015; Laliberté *et al.* 2015; Lekberg *et al.* 2018).

We consider a system in which plant species differences in their sensitivity to competition drive a competitive fitness difference in favor of plant 1 ($\kappa_2/\kappa_1{}^{comp} = 0.5$), and there is no competition-mediated stabilisation ($\rho^{comp} = 1$). Thus, in the absence of microbial interactions, competition would cause the exclusion of plant 2, the inferior competitor (Fig. 2c). However, there is a tradeoff such that plant 1, the stronger competitor, is more sensitive to pathogenic soil microbes. By also assuming that the two plants have complete microbial niche overlap, microbes drive a fitness difference in favor of plant 2 ($\kappa_2/\kappa_1{}^{micr} = 2.5$) and provide no stabilisation ($\rho^{micr} = 1$). Thus, independent of competition, plant-microbe interactions simply favor the exclusion of plant 1 (Fig. 2d).

However, when the effects of competition and plant-microbial interactions are considered simultaneously, it becomes clear that microbes in fact promote coexistence in this system (Fig. 2a and e). Two processes contribute to this outcome. First, competitive and microbial interactions jointly equalise plant fitness ($\kappa_2/\kappa_1{}^{net} = 1.025$), as species 1 has superior competitive ability but suffers more from microbes, and vice-versa for species 2. Second, competitive and microbial interactions reduce net niche overlap from 1 to $\rho^{net} = 0.878$ (Fig. 2a). In other words, although plant–microbial interactions alone do not create a negative plant–soil feedback that stabilises plant coexistence in this scenario, their interplay with plant competition provides an additional axis for niche differentiation that promotes species diversity in this system (Chesson & Kuang 2008). This scenario provides another example of how the total effects of soil microbes on diversity in natural plant communities can only be understood by studying microbially mediated stabilisation and fitness differences relative to those caused by other ecological process like competition.

Scenario 3: Microbially mediated fitness differences can help maintain plant diversity in multispecies systems through indirect effects among competitors

As in the previous two scenarios, most theoretical and empirical plant–soil feedback research has focused on the effects of plant–microbial interactions on pairwise plant competition (but see Eppinga *et al.* (2018) for an *n*-species version of I_S that incorporates the structure of the feedback network). Our next scenario illustrates that while inferring the effects of soil microbes from the pairwise stabilisation and fitness differences they generate might obscure their role in influencing plant diversity in systems of more than two species, this role can be understood from the network of pairwise fitness differences. To explore such a multispecies system, we extend eqns 1 and 6 to model the interactions between three plant species and the microbial communities they each cultivate (Appendix S3). Importantly, the inequality in eqn. 9 (or the equivalent condition that each species suppress itself more than it suppresses the other) no longer fully explains coexistence in this multispecies model (Barabás *et al.* 2016), though lower values of α_{ij}/α_{jj} generally favor diversity (Chesson 2018). In other words, evaluating the stabilisation and fitness differences that microbes mediate between each species pair might not predict whether they promote plant diversity across the entire system, because the outcome of any given pairwise interaction can be modified by the indirect effects of microbes cultivated by other plant species.

For this scenario, we examine a system of three species where microbially mediated pairwise fitness differences can promote multispecies coexistence by creating an intransitive dominance hierarchy (i.e. no single species has a fitness advantage over all others, May & Leonard 1975; Soliveres *et al.* 2018), a condition which was recently explored by Eppinga *et al.* (2018). We parameterise the system such that each plant's microbial community gives the cultivating species a fitness advantage over one other species in the system. Specifically, the interactions with soil microbes generate an ecological "rock-paper-scissors" dynamic (Allesina & Levine 2011; Gallien *et al.* 2017) in which plant 1 has an advantage over plant 2, plant 2 an advantage over plant 3, and plant 3 an advantage over plant 1. In this scenario, microbial interactions also stabilise the interaction between each pair, but this stabilising effect is not sufficient to overcome any of the pairwise fitness differences they generate (Fig. S3.1). Thus, for any given plant species pair, the microbially mediated fitness differences drive exclusion (Fig. 3b–d). Nonetheless, by evaluating the dynamics of this system when all three plant species are present, it becomes clear that the indirect effects of the microbially mediated fitness differences in this scenario in fact create an intransitive loop that allows coexistence of all three species (Fig. 3a).

In the present parameterisation, all three plant species coexist even when the soil microbial community drives exclusion among any given pair, but one can also construct scenarios in which the network of microbially mediated fitness differences reduces diversity in multispecies systems even when microbial stabilisation allows each individual species pair to coexist (Appendix S3). In general, accurately predicting whether soil microbes favour or hinder plant diversity in speciose systems from studies of pairwise plant interactions is a difficult task, one that will be made more tractable by interpreting microbial effects on the stability of plant interaction networks in diverse communities (Barabás *et al.* 2016; Levine *et al.* 2017; Eppinga *et al.* 2018).

INTEGRATING PLANT–MICROBE INTERACTIONS INTO BROADER COEXISTENCE THEORY GENERATES USEFUL PREDICTIONS

As demonstrated in the three scenarios of the prior section of this paper, the plant–microbe interaction model developed here allows us to integrate our work into a large body of theory regarding the coexistence of species competing for resources and interacting via organisms at other trophic levels.

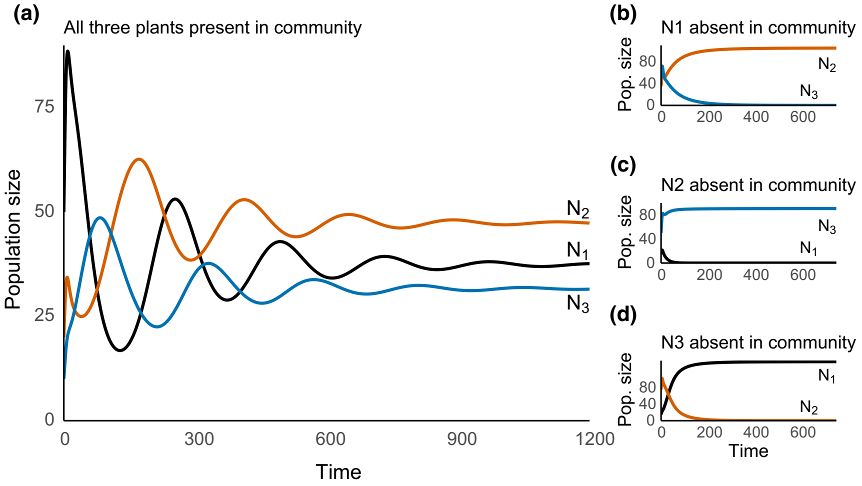

Figure 3 When plant-microbe interactions drive intransitive dominance hierarchies among plants, they can promote diversity in multispecies plant communities (panel a) even when they do not allow any species pair to coexist (panels b–d). The position of the three species pairs in the fitness difference/niche difference landscape is presented in Fig. S3.1 (Appendix S3).

This allows us to model a wide range of ecological scenarios– for example, one can modify the multispecies model used in Scenario 3 to decompose the effects of the soil microbial community as a whole into the effects of particular microbial taxa or guilds (Appendix S4). As the last section of this paper, we demonstrate the value of integrating plant-microbe feedbacks with broader coexistence theory by considering a model of explicit resource competition and plant-microbe interactions that we use to make theoretically justified predictions regarding the relative importance of microbial interactions across a productivity gradient.

Recent advances in coexistence theory have made it clear that the effects of density dependence arising from trophic interactions are symmetric to those of resource competition, and that the relative importance of each mechanism to determining the diversity of a given guild depends on a variety of ecological conditions (Chesson & Kuang 2008). These insights can be extended to provide a theoretical basis for understanding the relative importance of plant-microbe interactions and competition in natural communities. To do so, we unite the effects of explicit resource competition and plant–microbe interactions into a single model with plants as the focal guild consuming resources and interacting with microbes (Fig. 4a). For simplicity, the effects of microbes on plant growth in our model operate independently of plant resource uptake; models in which plant–microbe interactions directly influence the nature of plant resource uptake also yield valuable insights (Umbanhowar & McCann 2005; Jiang *et al.* 2017). The plant-microbe interactions in this model follow exactly from the previous model (eqns 1 and 6 Following MacArthur (1970) and Chesson & Kuang (2008), we model resources l that accumulate logistically with a low-density growth rate of r_l until they reach a resource carrying capacity of $1/s_l$. Plants consume resources at a rate u and convert resources into plant population growth. Equations and analyses for this model are presented in Appendix S5.

Assuming that both resource and microbe dynamics occur more rapidly than plant dynamics (MacArthur 1970; Chesson & Kuang 2008), the per-capita suppression of plant species i by species j in this model (α'_{ij}) is as follows (see Appendix S5 for derivation):

$$\alpha'_{ij} = \left(\overbrace{\sum_{l} \frac{u_{il}u_{jl}}{s_l r_l}}^{\text{resource competition effect}} - \overbrace{\frac{m_{iX}v_{Xj}}{q_X}}^{\text{microbe effect}} \right) \tag{11}$$

shows that the strength of resource competition depends on the rate of resource consumption (u's) and on the nature of resource dynamics in the system (s_l and r_l). When plants i and j consume entirely distinct resources, the left term is equal to zero, and plant j's interaction with plant i is determined only via the effect of the soil microbial community it cultivates. However, when plant species overlap in resource consumption, their overall interaction is determined jointly by resource competition and the microbial community each plant cultivates. As in the interaction term for the previous model (eqn. 7), the sign and strength of microbial effects is determined by the rate at which plant j cultivates microbes that affect the growth of plant i. The niche overlap ρ and fitness differences κ_2/κ_1 in this model are calculated in the same way as in the previous analysis (eqns. 8 and 9 respectively) (Chesson 2013).

Importantly, this model, a simple extension of Chesson & Kuang (2008), can be used to make theoretically justified predictions regarding the relative contribution of resource competition and plant-microbe interactions to the outcome of plant competition as a function of site productivity (r_l). In this model formulation, the interspecific interaction parameters α', and ultimately the net niche overlap ρ, are more strongly driven by the degree to which plants overlap in their resource use in low-productivity communities (i.e. low values of r_l). By

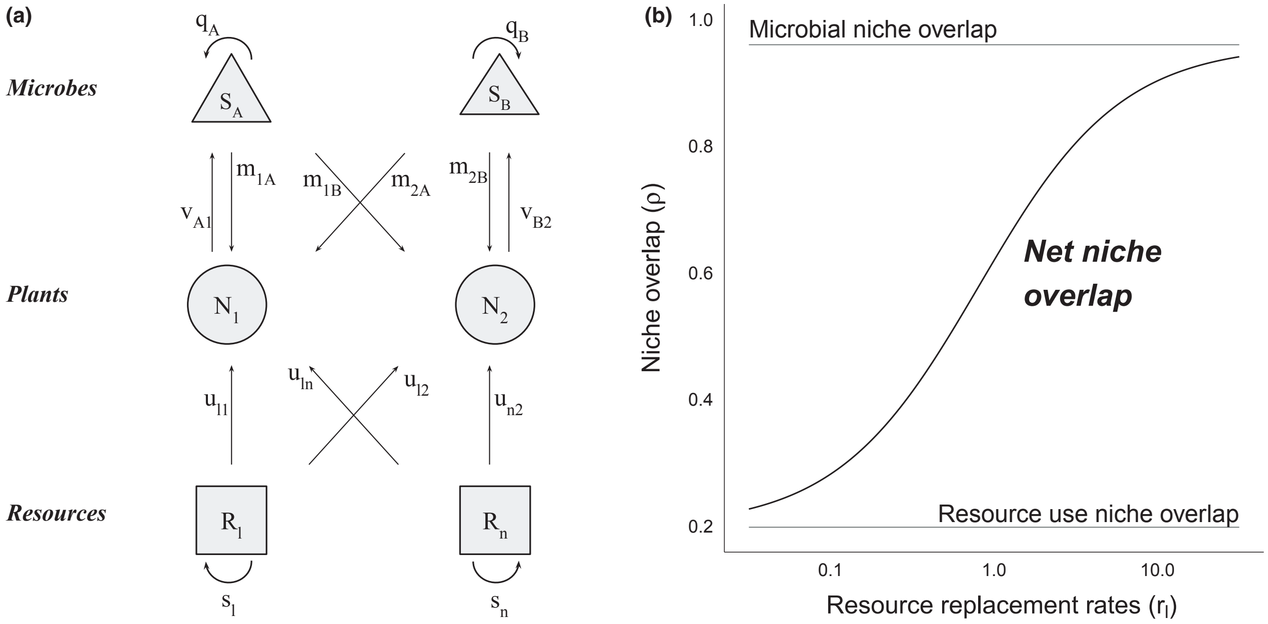

Figure 4 (a) Schematic of a model with explicit resource competition. Plant-microbe interactions (upper two trophic levels) are modeled as in Fig. 1a. Populations of plants 1 and 2 grow as they take up resources l. The u terms denote the per-capita resource uptake rates of each resource by each plant. Resources are modeled as experiencing logistic growth with a low-density growth (replacement) rate of r_l until they are saturated at the carrying capacity $1/s_l$. See Appendix S5 for dynamics equations. (b) The net niche overlap between plants represents the joint influence of the niche overlap due to shared resource consumption and the niche overlap due to shared microbial interactions. The resource use niche overlap exerts a relatively strong influence on the net ρ when resource replacement rates are low; at higher levels of resource replacement rate, the net ρ is more strongly influenced by the niche overlap due to microbial interactions.

contrast, in productive communities (high r_l), species interactions are more strongly influenced by the soil microbial communities, and these interactions strongly determine the net niche overlap (Fig. 4b). A similar result can be derived for the fitness differences (Fig. S5.1 in Appendix S5). Moreover, the qualitative result that microbial niche differences more strongly influence net niche overlap at high resource levels than at low resource levels also holds in systems in which microbial effects on plants (i.e. the m terms) themselves shift from being mutualistic in low-resource environments, to pathogenic in high-resource environments (Revillini *et al.* 2016, Figure S5.2). This result is not due to changes in resource niche overlap along the gradient– in our analysis, the niche overlap due to resource competition is just as high in productive sites as in low-productivity sites. Rather, this model predicts that when resources are less limiting, resource competition more weakly affects plant community dynamics. It is important to note that this result is in part due to our formulation of a model in which the direct microbial effects on plant-plant interactions operate separately from plant resource uptake (i.e. microbes do not directly change plant resource uptake dynamics), as a result of which the productivity term r_l appears only in the denominator of the resource competition component of eqn. 11.

DISCUSSION

Plant–microbe interactions can drive a fitness difference that provides one plant species an average fitness advantage over the other in pairwise competition. These fitness differences arise from differences in plant species' ability to tolerate the pathogenic soil microbes or benefit from the mutualistic soil microbes cultivated by different plant species. We show that ignoring microbially mediated fitness differences and only considering the stabilising or destabilising effects of plant-microbe interactions, as is frequently done in empirical analyses, can lead to erroneous conclusions regarding the total effects of soil microbes on plant diversity. With an extension of Bever *et al.* (1997)'s pioneering theoretical framework of plant-soil feedbacks, we show that the degree to which soil microbes can drive plant coexistence or exclusion is influenced by the relative sensitivity of each plant to the microbial communities, as well as the rate at which each plant influences the growth of persistent soil microbial communities. Finally, we show that modelling microbial dynamics in terms of their density allows us to organise, interpret, and predict the effects of microbes in light of a large body of coexistence theory that considers the drivers of coexistence among consumer-resource communities.

We focus our discussion on the implications of our theoretical results for empirical work testing how interactions between plants and soil microbes influence plant diversity. To do so, we first show how microbially mediated plant fitness differences can be quantified in typical plant-soil feedback experiments. We then discuss some limitations to the standard experimental approach used in these studies. Last, we suggest avenues for future research to integrate insights from our theoretical work and develop a more complete understanding of how soil microbes influence plant diversity.

Empirically measuring the microbially mediated plant fitness difference

Our plant–soil feedback model with microbial density dynamics shows that microbial effects on plant diversity depend on microbe dynamics terms that are difficult to measure empirically (e.g. the v and q terms in eqn. 6). Thus, we expect that until it becomes more feasible to quantify these microbial dynamics parameters, most empirical studies of plant-soil feedback will continue to use the two-phase approach (Box 1) to parameterise Bever's microbe frequency-based framework. Nevertheless, the conceptual insights we derive from our microbial density-based model apply to the interpretation of these empirical studies. Moreover, our analysis suggests that variation in microbial community dynamics can be consequential to determining the effects of soil microbes on plant diversity, and that empirically testing assumptions regarding microbial dynamics that are implicit in the standard two-phase experimental approach should help refine our understanding of how plant-microbial interactions influence plant species diversity. For example, assumptions about how each plant species favors its microbial community can be tested with greenhouse experiments capturing the temporal dynamics of plant-soil feedbacks (e.g. Hawkes *et al*. 2012; Wubs & Bezemer 2017; Bezemer *et al*. 2018) and with more refined measurements of microbial population dynamics now possible with advances in DNA sequencing and cell counting technologies (e.g. Quantitative Microbiome Profiling (Vandeputte *et al*. 2017)).

Regardless of whether one begins with the model of Bever (2003) (or Bever *et al*. (1997)) or a more complex version like the one we develop here, our analyses show that empirically quantifying the microbially mediated fitness difference is an essential step for understanding the full effects of soil microbes on plant coexistence. Doing so is rather straightforward following eqn. 5. One simply needs the growth of both plant competitors on soils cultivated by both plants and on a reference uncultivated soil, as noted in the text before eqn. 5. Thus, at a minimum, soil feedback experiments following the two-phase approach with an additional uncultivated soil treatment during the second phase provide the necessary empirical data for parameterising both the stabilisation term and the microbially mediated fitness difference. With such information, one can compare the magnitude of the stabilisation term ($-\frac{1}{2}I_S$) to the microbially mediated fitness difference (eqn. 5).

Recommendations for future empirical plant-soil feedback studies

One limitation of the classic plant-soil feedback experimental design (Box 1) is that the coexistence consequences of soil microbes are not clear without contextualising microbially mediated fitness differences within those generated by competition or other ecological processes. For example, soil microbes can favour plant diversity (reduce the degree of niche differentiation required for coexistence) even when they generate no negative frequency dependence if they simply give a fitness advantage to a weak resource competitor. Indeed, in Scenario 2, the joint effect of competition and plant–microbe interaction was to stabilise plant interactions even when neither mechanism alone promotes coexistence. Similarly, whether microbially mediated fitness differences quantified in soil feedback studies actually reduce diversity in nature will depend on whether they ameliorate or augment fitness differences based on plant competitive ability. Although this competitive information is not frequently quantified in empirical plant-soil feedback studies, evidence is accumulating that plant species experience trade-offs between competitive ability and susceptibility to soil pathogens or mutualists (Laliberté *et al*. 2015; Lekberg *et al*. 2018). This suggests that soil microbes might indeed frequently promote plant diversity in nature by equalising competitive fitness differences.

We therefore echo recent calls (Smith-Ramesh & Reynolds 2017; Lekberg *et al*. 2018) for experiments that explicitly investigate the joint effects of plant-microbe interactions and resource competition in nature. The niche and fitness difference terms we derive from our density-based model of plant-microbe interactions (eqns. 6-8) provide a foundation for future studies that couple population dynamics models with greenhouse and field experiments (Hart *et al*. 2018) to more thoroughly assess the influence of soil microbes on plant diversity.

When should microbes most strongly influence plant diversity?

The final goal of our analysis was to show that modelling microbial population dynamics in terms of their absolute abundance can allow us to apply insights from a vast body of ecological theory to understanding the role of plant-microbial interactions in shaping plant diversity. Specifically, we explored how the relative importance of plant-microbe interactions and resource competition changes along a productivity gradient, a topic for which a number of authors have recently posed hypotheses (van der Putten *et al*. 2016; Smith-Ramesh & Reynolds 2017; Lekberg *et al*. 2018). These hypotheses are generally motivated by empirical observations of variation in the effect sizes of competition and plant-microbe interactions on the growth of individual plants at different sites. However, the consequences of such variation in plant growth for the population dynamics of competing species are difficult to evaluate without a theoretical model (Chesson & Huntly 1997; Chase *et al*. 2002; Hart & Marshall 2013). Our analysis of one such model shows that even when the strength of competitive and microbial interactions is held constant, the relative importance of plant-microbe interactions for plant dynamics increases with productivity (Fig. 4b, Fig. S5.1). We encourage future modelling efforts to incorporate observed variation in the direction and strength of plant-microbe interactions across productivity gradients into plant population dynamics models, as well as the potential for microbes to directly mediate plant resource uptake. Such models and associated empirical studies will refine our understanding of the relative importance of soil microbes in shaping natural plant communities.

While tremendous progress has been made by treating the soil microbial community cultivated by plants as a black box, our ability to predict the consequences of plant-microbe interactions to the dynamics of natural plant communities will also improve with a more mechanistic understanding of how the population dynamics and effects of individual components of the microbial community (e.g. pathogens, mutualists, saprophytes) vary across environments (van der Putten *et al.* 2016; Bennett & Klironomos 2018; Lekberg *et al.* 2018). A growing number of studies are building this understanding by performing experiments that involve modifying targeted components of the microbial community across resource gradients (e.g. Jiang *et al.* 2018), but it is difficult to evaluate results from these studies in the context of plant-soil feedback theory and the paired two-phase experimental approach, which focus on the effects of the whole microbial community cultivated by each plant species.

In this paper we followed classic plant-soil feedback theory to define the soil communities A and B in our density-based model as the unique microbial communities cultivated by plants 1 and 2. However, the modelling framework we use here can be easily extended to evaluate the coexistence consequences of particular groups of microbes. To do so, one can define the S terms in eqn. 5 as the density of individual microbial taxa or guilds, and extend the model to any n number of such microbial groups. Such models can be used, for example, to evaluate the coexistence consequences of mutualistic microbes that can be cultivated by any plant species but to which plant species vary in their response (Appendix S4). Parameterising such models is challenging, and beyond the elegant simplicity of the two-phase feedback experimental approach. Integrating the dynamics and effects of particular components of the microbial community to better understand when these interactions can most strongly influence plant community dynamics will require studies that combine careful experimental methods and modern molecular technology to embrace the complex nature of these plant-microbial interactions.

CONCLUSION

Ecologists have learned a great deal regarding the importance of soil biota for plant coexistence since the pioneering work of Bever *et al.* (1997). Here, we have identified the conditions under which microbes can favor one plant species over others, and this simple result has important implications for how we interpret the results of empirical investigations of feedbacks between plants and the soil microbial community. Analysing empirical data in ways that quantify both the stabilising effects of plant–microbe interactions and their effect on frequency-independent fitness differences should be a top priority to improve our understanding of how soil microbes influence plant diversity. In addition, along with Eppinga *et al.* (2018), our work also suggests that the focus on pairwise approaches in the plant-soil feedback literature might obscure an important role for soil microbes in maintaining diversity in multispecies plant communities. More generally, we expect that our understanding of the net effects of microbes on plant diversity will improve with future studies that couple experimental approaches to population dynamics models capturing the many ways soil microbes can influence plant diversity.

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AUTHORSHIP

GSK conceived the problem with NJBK and JML. GSK led the research with JML and all authors provided input. GSK wrote the manuscript with JML and all authors contributed to revisions.

DATA ACCESSIBILITY STATEMENT

The zenodo archive of the github repository is here: https://zenodo.org/record/2857243#.XOeMNB5lB-E.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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