Quantifying soil microbial effects on plant species coexistence: a conceptual synthesis

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Running head: Soil microbial effects on plant coexistence
Last rendered: February 28, 2024

Abstract

Soil microorganisms play a critical role in shaping the biodiversity dynamics of plant communities. These microbial effects can arise through direct mediation of plant fitness by pathogens and mutualists, and over the past two decades, numerous studies have shined a spotlight on the role of dynamic feedbacks between plants and soil microorganisms as key determinants of plant species coexistence. Such feedbacks occur when plants modify the composition of the soil community, which in turn affects plant performance. Stimulated by a theoretical model developed in the 1990s, a bulk of the empirical evidence for microbial controls over plant coexistence comes from experiments that quantify plant growth in soil communities that were previously conditioned by conspecific or heterospecific plants. These studies have revealed that soil microbes can generate strong negative to positive frequency-dependent dynamics among plants.

Even as soil microbes have become recognized as a key player in determining plant coexistence outcomes, the past five years have seen a renewed interest in expanding the conceptual foundations of this field. New results include re-interpretations of key metrics from classic two-species models, extensions of plant-soil feedback theory to multispecies communities, and frameworks to integrate plant-soil feedbacks with processes like intra- and inter-specific competition. Here, I review the implications of theoretical developments for interpreting existing empirical results, and highlight proposed analyses and designs for future experiments that can enable a more complete understanding of microbial regulation of plant community dynamics.

Keywords

multispecies coexistence, mutualists, mycorrhiza, pathogens, plant-soil feedback, theory-data integration, soil microbiome

> The environment is not a structure imposed on living beings from the outside but is in fact a creation of those beings. Just as there is no organism without an environment, there is no environment without an organism.
>
> Richard Lewontin
> *The Organism as the Subject and Object of Evolution*

Introduction

Like all organisms, plants simultaneously respond to and shape their environment. One aspect of the environment that is especially dynamic is the microbial community in the soil. Plants can actively alter the structure of the soil community, for example by secreting root exudates that promote the growth of some microbes over others. Plants can also affect the soil community more passively, for example by creating leaf litter that favors certain decomposing microbes over others. The soil community is itself a heterogeneous entity, comprising a diversity of microbes that can interact with plants directly as mutualists or pathogens, or indirectly by regulating nutrient dynamics and other soil properties in their role as decomposers. Through these complex networks of interactions, soil microbes likely play an important role in structuring biodiversity and community dynamics in all terrestrial ecosystems (Van Der Heijden et al., 2008).

One plant community outcome for which there is growing interest and evidence of microbial regulation is that of plant species coexistence. A hallmark of this research has been a tight integration of theory and experiment (e.g. Bever et al., 1997; Kulmatiski et al., 2011; Stein and Mangan, 2020). Theory suggested a streamlined experimental design for quantifying microbial effects on plant coexistence (Bever et al., 1997), and through meta-analysis of numerous such experiments, we now know that microbes can affect plant coexistence outcomes in a wide range of ecosystems (Crawford et al., 2019). Coexistence-promoting negative feedbacks most strongly arise among plant pairs that are distantly related, associate with similar mycorrhiza, and interact in soils to which they are native (Crawford et al., 2019), but this negative feedback is seldom strong enough to overcome the fitness imbalances between plants that microbes simultaneously generate (Yan et al., 2022). As a result, soil communities by themselves are unlikely to explain observed coexistence in plant communities, and building on simple pairwise pot experiments to understand how these effects play out in nature remains a challenge. To help foster continued interplay between theoretical and empirical research as we address this challenge, I use this Synthesis as an opportunity to review recent theoretical advances and their implications for empirical work.

Pairwise plant coexistence under soil microbial feedbacks

Experimental research on soil microbial regulation of plant species coexistence was catalyzed by the theoretical framework of Bever et al. (1997), which evaluates microbial effects on the dynamics of two plant species. In this model, each plant population grows exponentially at a rate determined by the composition of the soil microbial community. The composition of the soil community, in turn, is determined by the composition of the plant community, along with the strength of each species' conditioning effect. These interactions gives rise to feedbacks in the plant-soil system, such that the growth rate (fitness) of each plant species depends on its own frequency in the system. A formal model description is available in the original publication (Bever et al., 1997) and in Appendix S1. Briefly, the model follows the the dynamics of two plant species 1 and 2, and the distinct soil microbial communities A and B that each species cultivates (Fig. 1A). The rate at which plant 1 conditions the soil towards community A is set to 1, and the relative rate at which plant 2 conditions the soil towards B is denoted v. The effects of microbial community A on the growth rate of plants 1 and 2 are denoted m_{1A} and m_{2A}, respectively, and m_{1B} and m_{2B} capture the effect of microbial community B on plants 1 and 2. Positive values of m_{iX} indicate that plant species i perform better in soils with microbial community X than in soils without this microbial community; negative values indicate that plant i is suppressed by microbial community X (Fig. 1A-B).

Bever et al. (1997) presented two key insights about this model that set the stage for the design and analysis of subsequent empirical studies of microbially mediated plant coexistence. First, the authors showed that whether microbes drive positive or negative feedback in plant population dynamics is captured by the sign of a metric termed I_S:

$$I_S = (m_{1A} + m_{2B}) - (m_{1B} + m_{2A}) \qquad \text{(Eqn. 1)}$$

Positive feedback arises when microbial communities benefit their conditioning plant species more than they benefit the other species, or when microbes hurt the conditioning plant less than they hurt the other plant. Mathematically, this requires that $m_{1A} + m_{2B} > m_{1B} + m_{2A}$. In nature, positive feedback is more likely among pairs of ectomycorrhizal plant species than among plants that associate with arbuscular mycorrhiza (Bennett et al., 2017; Teste et al., 2017; Van Nuland et al., 2023). On the other hand, negative feedback arises when conditioned soil communities benefit the conditioning species less than the other plant (or hurt the conditioning species more than the other plant). In nature, negative feedback is likely driven by the accumulation

of host-specific soil pathogens, especially including fungi and oomycetes (Crawford et al., 2019; Domínguez-Begines et al., 2021), but it can also arise when conditioned soil microbes increase plant growth, provided that soil microbes benefit the conditioning plant less than they benefit the other plant (Bever, 2002). Positive feedback hinders plant diversity, because microbes provide a relative advantage to whichever species is more frequent in the community. Negative feedback promotes diversity, because microbes provide an advantage to whichever species is rare, allowing it to rise in frequency and avoid extinction (Fig. 1C-D). Subsequent descriptions of this model further extended the implications of I_S for species coexistence, as in Bever (2003):

> "When the interaction coefficient is positive ($I_S > 0$), the soil community dynamics generate net positive feedback on plant growth and the competing plant species do not coexist. When the interaction coefficient is negative ($I_S < 0$), the soil community dynamics generate net negative feedback on plant growth, and, as a result the competing plant species do coexist."

The second key contribution of Bever et al. (1997) was a clear explanation of the steps necessary for quantifying I_S empirically. This experimental design builds on important features of the parameters m_{iX}, and of the interaction coefficient I_S. Recall that in this model, microbes only affect the rate of exponential population growth for the two plant species (Fig. 1B-C). Assuming that biomass accumulation dynamics of individual plants mirror the population growth process, and provided that all plants were exposed to the soil community for an equal amount of time, one can estimate the m parameters with the log-transformed biomass of plants grown in different soil microbial contexts: $m_{iX} = \log(B_{iX}) - \log(B_{i0})$. Here, B_{iX} is the biomass of plant i in soil community X, and B_{i0} is plant i's biomass in reference (unconditioned) soil. In fact, Bever et al. (1997) showed that the data requirements for quantifying I_S simplify even further. Due to the arrangement of the m_{iX} terms, empirical quantification of I_S only requires biomass data of plants grown with a conspecific- or heterospecific-conditioned soil community; growth in unconditioned soils cancels out altogether:

$$I_S = [\overbrace{(\log(B_{1A}) - \cancel{\log(B_{10})})}^{m_{1A}} + \overbrace{(\log(B_{2B}) - \cancel{\log(B_{20})})}^{m_{2B}}] - [\overbrace{(\log(B_{1B}) - \cancel{\log(B_{10})})}^{m_{1B}} + \overbrace{(\log(B_{2A}) - \cancel{\log(B_{20})})}^{m_{2A}}]$$

Building on this insight, Bever et al. (1997) proposed a two-phased empirical design that yields all the necessary B_{iX} terms for quantifying I_S. This design has been described in detail elsewhere (e.g. Bever et al., 2012), and is summarized in Fig. S.1.

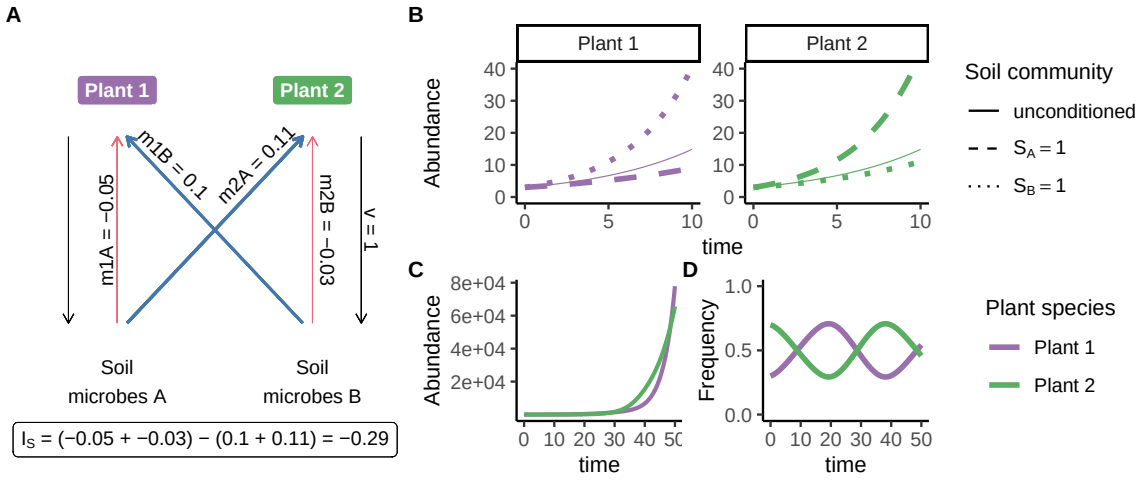

Fig 1: Schematic and simulated model dynamics from Bever et al. (1997)'s canonical framework for plant-soil feedback.
A. The model simulates the dynamics of two plant species (1 and 2) that cultivate distinct soil communities (A and B). Both plant species have some growth rate in unconditioned soils (set to 0.16 for the simulations in panels B-D), which is increased or decreased depending on the state of the microbial community, as described by the arrows (e.g. when the soil only reflects microbial community A, plant 1's growth rate decreases by 0.05, and plant 2's growth rate increases by 0.11). Following Eqn. 1, microbes generate $I_S < 0$ (negative feedback) for this set of parameters. **B.** Plant population dynamics when each species is growing separately in soils that are unconditioned (thin solid line), wholly conditioned by Plant 1 ($S_A = 1$, dashed line), or wholly conditioned by Plant 2 ($S_B = 1$, dotted line). Note that these scenarios are only illustrative and not biologically plausible dynamics - for example, as plant 1 grows, it should become impossible for the soil state $S_B = 1$ to persist, as plant 1's conditioning effects become evident. **C.** When both plants grow together, the soil community dynamically changes between $S_A = 1$ and $S_B = 1$, as determined by the plant composition. Both plants experience exponential growth, at a rate determined by the composition of the soil. In this simulatation each species' abundance periodically rises above the other's. **D.** The relative abundance (frequency) of each plant species. Microbes promote coexistence in this system by generating neutral oscillations. Model simulations were conducted with `deSolve::ode()` (Soetart et al. 2010) and visualized with Tidyverse packages (Wickham et al. 2019) in `R` v. 4.3.2 (R Core team 2023)

Limits to inferring coexistence from $I_S < 0$

While the insights from Bever et al. (1997) have enabled a vast body of empirical work (synthesized most recently in Crawford et al., 2019; see also Kulmatiski et al., 2008; Bever et al., 2012), several recent studies have highlighted limitations to inferring microbially mediated plant coexistence on the basis of negative feedback alone (Ke and Miki, 2015; Kandlikar et al., 2019; Broekman et al., 2019; Beckman et al., 2023). The main takeaway

from this work is that while $I_S < 0$ is a necessary condition for coexistence in the Bever et al. (1997) model, stabilizing effects of microbes do not *guarantee* long-term plant coexistence (Fig. 2). Part of the issue is that additional information that is not captured in I_S is required for accurate inferences of coexistence. This is not a new result per se: the original analysis and interpretation of I_S operates within the assumption that the soil microbes do not harm (or benefit) one species substantially more than the other (see pp. 563 of Bever et al. (1997)). However, in practice, this assumption is rarely tested, and the renewed clarity that one species can exclude the other despite $I_S < 0$ represents a departure from the longstanding interpretation that the sign of this metric reflects whether or not microbes drive species coexistence. I discuss theoretical metrics and experimental designs that help overcome this assumption in the following section.

Bever et al. (1997)'s analysis also builds on the assumption that both species condition the soil community with roughly equal strengths ($v \approx 1$). While explicit tests of this assumption are scarce, recent results raise questions about its generality. For example, low-abundance non-native species can have outsized effects on soil microbial communities (Peltzer et al., 2009), which points to substantial interspecific variation in soil conditioning strength. Moreover, Chen et al. (2019) found that variation in the rates at which tree species accumulate pathogenic vs. mutualistic (ectomycorrhizal) soil fungi explains variation in the observed strength of conspecific negative density-dependence. While the magnitude of v does not change the coexistence criteria in Bever et al. (1997) model (see Appendix S1), strong asymmetries in conditioning strengths have important implications for the system's temporal dynamics. For example, for a given set of m_{iX} parameters that should result in coexistence, $v \gg 1$ or $v \ll 1$ result in extended periods of dominance by one species (Fig. S.2). This increases the risk of stochastic extinction of the rare species. Very few studies have systematically evaluated the consequences of varying conditioning strengths on the feedback process (but see Ke and Levine (2021)), and further theoretical and empirical evaluation of microbial conditioning dynamics should yield fruitful insights (see also Chung (2023)).

How to more thoroughly evaluate plant coexistence with soil feedbacks?

Given that $I_S < 0$ does not guarantee plant coexistence in the Bever et al. (1997), what other information can help generate more reliable inferences? At least two analytical approaches address this question, yielding complementary insights. Both approaches are detailed in Appendix S1 and summarized here. The first approach was outlined in the

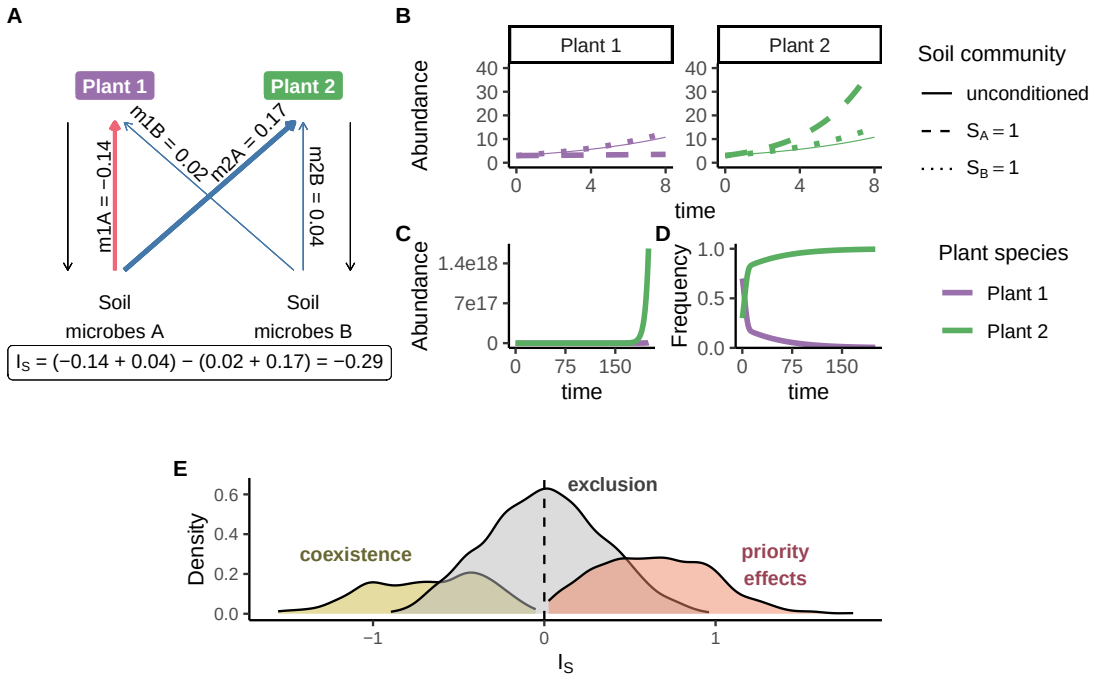

Fig 2: Soil microbes can drive plant species exclusion even when they generate negative feedback.

textbf A. In this simulation, plant 1's performance is suppressed by its own microbial community A, but boosted by microbial community B. On the other hand, plant 2's performance is increased by either conditioned community. The m terms yield the same negative I_S as in Fig. 1. **B.** Population growth dynamics for the two plants when soil is entirely conditioned by one plant or the other. **C.** When the two plants grow together, plant 2 has a higher rate of exponential growth than plant 1 at all times. **D.** Due to differences in the rates of exponential growth, the gulf in the two species' relative frequencies grows until the system is effectively entirely dominated by plant 2, and plant 1's frequency is nearly zero. **E.** The result shown in panels A-D is not exceptional: when microbes drive negative feedback ($I_S < 0$), the two plant species coexist in only about half of the simulation runs; in the other half, only one species persists. While coexistence is never possible under positive feedback ($I_S > 0$), inferring plant dyanamics on the basis of I_S alone obscures the fact that in some cases, microbes give rise to frequency-dependent priority effects (species that is initally more abundant excludes the other), while in other cases, the same plant wins regardless of its initial frequency. Values of m_{iX} were drawn from a uniform distribution (minimum value: -0.5, maximum value: 0.5). The density graph summarizes outcomes from 2000 simulation runs, which were generated with `rootSolve::runsteady()` (Soetart and Herman 2009; Soetart 2009).

original model analysis, but has received little empirical attention. This approach proceeds by identifying parameter combinations that allow for equilibrium conditions that are both feasible (meaning that all players are present with frequency > 0) and neutrally stable (meaning that perturbations to the equilibrium do not cause the system to collapse to monodominance). A second approach for identifying coexistence outcomes in the Bever et al. (1997) model was implemented in Kandlikar et al. (2019), and builds on the mutual invasibility requirement for pairwise species coexistence (Turelli, 1978; Chesson and Ellner, 1989; Grainger et al., 2019). Applying the invasion criterion to the Bever et al. (1997) model means that the plants can coexist if each species can successfully establish a foothold into an equilibrium monoculture of the other plant (and its corresponding soil community). Each species' population growth rate as it begins (or fails) to establish in its competitor's monoculture is its "low-density growth rate", or LDGR. (This term is more commonly called the "invasion growth rate" in the coexistence literature, but given the potential confusion between this abstract property and the separate process of ecological invasions by non-native plants, where soil microbes can also play an important role, I follow Lavorel and Chesson (1995) and Hallett et al. (2023) in using the term "low-density growth rate"). For the Bever et al. (1997) model, the LDGR for each species is given by the following:

$$\text{LDGR}_{1\to2} = m_{1B} - m_{2B} \quad \text{and} \quad \text{LDGR}_{2\to1} = m_{2A} - m_{1A}$$

Here, $\text{LDGR}_{1\to2}$ is the growth rate of plant 1 in a monoculture of plant 2, and vice-versa for $\text{LDGR}_{2\to1}$. Coexistence requires that each species have a positive LDGR, meaning that the following inequalities should be true:

$$m_{2B} < m_{1B} \quad \text{and} \quad m_{1A} < m_{2A} \tag{Eqn. 2}$$

As shown in Appendix S1, this is identical to the coexistence requirements identified through the feasibility analysis in Bever et al. (1997), and it mirrors the well-established criteria for two-species coexistence in a Lotka-Volterra competition model.

Evaluating Eqn. 2 is enough for evaluating whether or not species can coexist in the Bever et al. (1997) model, but further decomposing the LDGRs can yield useful insights into the biological basis for coexistence outcomes. Specifically, following the approach described in Chesson (2000) and Chesson (2018), one can further decompose LDGRs into two terms. One term captures the degree to which the soil communities increase (or decrease) the LDGR of both species, thereby favoring (or disfavoring) coexistence. The

second term captures the degree to which the microbial communities disproportionately favor one plant species over the other, thereby increasing the LDGR of one species and decreasing the LDGR for the other. Kandlikar et al. (2019) derived these terms for Bever et al. (1997)'s model which, following convention (Chesson, 2000, 2018), are termed as the microbially mediated "stabilization" and "fitness difference", respectively. Whether or not species can coexist is determined by the balance of these two effects. Specifically, coexistence requires the following to be true:

$$\overbrace{-\frac{1}{2}((m_{1A}+m_{2B})-(m_{2A}+m_{1B}))}^{\text{stablization}} > \text{abs}\left(\overbrace{\frac{1}{2}(m_{1A}+m_{1B})-\frac{1}{2}(m_{2A}+m_{2B})}^{\text{fitness difference}_{1,2}}\right) \quad \text{(Eqn. 3)}$$

Algebraically, the expression above is equivalent to Eqn. 2 (see Box S1.2 in Appendix S1). When this inequality is met, both species have positive LDGRs. Alternately, when microbes primarily act to destabilize plant interactions (stabilization $<$ 0 and abs(stablization) $>$ abs(fitness difference)), both species have negative LDGRs, and microbes give rise to frequency-dependent priority effects (either species can form a monoculture, but the two species cannot coexist (Yan et al., 2022; Zou and Rudolf, 2023)). When fitness differences overwhelm the strength of (de)stabilization, one species has negative LDGR, and the other has a positive LDGR. In this case, microbes drive exclusion of the species with negative LDGR.

Evaluating microbial effects on the basis of the (de)stabilization and fitness differences provides valuable insight into how their net effects arise. For example, the accumulation of species specific pathogens favors stabilization, but host-specific pathogens can nevertheless drive exclusion if one plant suffers more from its pathogens than the other (strong fitness differences). On the other hand, when plants are equally susceptible to pathogens, even a small amount of host specificity can promote stable plant coexistence. Moreover, framing soil microbial effects in terms of the degrees to which they generate stabilization and fitness differences unlocks the potential to integrate soil microbes into a broader theoretical framework that is actively being applied for studying how plant coexistence is mediated by pollinators (Lanuza et al., 2018; Johnson et al., 2022), seed consumers (Petry et al., 2018), foliar pathogens (Uricchio et al., 2019), facilitation (Bimler et al., 2018), and a host of other abiotic and biotic processes.

Implications for empirical studies

As with I_S, the complete coexistence criterion in Eqn. 3 is simply a linear combination of the four m_{iX} terms that capture microbial effects on plant performance. In principle, this might suggest that evaluating coexistence requires the same data as is required for quantifying I_S. However, in practice, evaluating coexistence requires more information. This distinction has to do with the role that plant performance in reference (uncultivated) soils plays in determining m_{iX}. As shown above, plant biomass in reference soil cancels out of the equation for I_S. This is also true for calculating stabilization; indeed, stabilization is simply equal to $-\frac{1}{2}I_S$. However, plant growth in reference soil does not cancel out of the fitness difference expansion:

$$\text{fitness difference}_{1,2} = \frac{1}{2}[\overbrace{\log(B_{1A}) - \log(B_{10}))}^{m_{1A}} + \overbrace{\log(B_{1B}) - \log(B_{10}))}^{m_{1B}}] - \frac{1}{2}[\overbrace{\log(B_{2A}) - \log(B_{20}))}^{m_{2A}} + \overbrace{\log(B_{2B}) - \log(B_{20}))}^{m_{2B}}]$$

The trivial implication of this result is that experiments aiming to infer plant coexistence in the Bever et al. (1997) model should include an additional response phase treatment in which plants are grown with a reference soil community (Kandlikar et al., 2019; Beckman et al., 2023). However, theory alone does not provide an unambiguous guide for defining the "correct" reference soil to use in an experiment. The original parameter descriptions only define the reference soil by negation, as soil *without* a conditioning history of either focal plant (Bever et al., 1997). In principle, this definition could apply equally well to any soils where the focal species have not grown. Kandlikar et al. (2021) suggest that the ideal reference soil for experiments reflects the microbial community that would exist in the relevant field system when the focal plant species are absent. Alternatively, Beckman et al. (2023) suggest soils conditioned by plants that associate with different mycorrhizal types or that have different geographic origins than the focal species as potential references. However, such soils are unlikely to include even low abundances of specialist pathogens or mutualists that the focal species might encounter in nature, which could affect the estimation of fitness differences and stabilization. When studies replace a specific conditioning phase and instead inoculate response phase pots with soils from adults in the field, soil from bare patches devoid of vegetation may be an appropriate reference. Many past studies included controls of plants growing in sterilized soils, but such soil is not an appropriate reference for studies aiming to isolate the *effects of the conditioning/feedback process*

itself (Abbott et al., 2021). This is because the consequences of microbial feedbacks arise from differences in plant performance with a species-specific soil community vs. performance in soil that does not reflect the conditioning effect of the focal plant species. Thus, comparisons of growth in conditioned vs. sterile soils conflate the presence of a microbial community with the process of plant conditioning. Nevertheless, as I discuss later in this manuscript (see Fig. 3), plant growth in sterile soils provides an important baseline for studies aiming to quantify the coexistence consequences of soil microbes generally, rather than the conditioning/response process specifically (see also Yan et al., 2022; Ke and Wan, 2023).

It is worth noting although the importance of reference soil growth is underscored by its prominence in the fitness difference calculation, the choice of reference soil also affects empirical estimates of I_S. For example, conditioning soils from a reference that contains low densities of the focal species' specialist pathogens can drive stronger stabilization (if the specialist pathogens proliferate during the conditioning phase) than conditioning from a reference that is completely lacking in specialist pathogens. In other words, all two-phase studies are built on implicit choices of a reference soil state. When the goal is to evaluate coexistence, plant growth in this same baseline soil community should be used to estimate B_{i0}. Preserving the reference soil community during the conditioning phase presents methodological challenges, as microbial communities are dynamic entities whose members grow and die (Abbott et al., 2021). Thus, future studies that couple reference soil treatments with assays of microbial activity/composition (especially approaches that also quantify microbial abundances (Tkacz et al., 2018)), and/or include carefully designed controls to evaluate the effects of such microbial dynamics will help paint a more complete picture of how soil communities shape plant coexistence.

The specification of Bever et al. (1997)'s model also has implications for the analysis of data from two-phased plant–soil feedback studies. As explained above, the canonical approach for evaluating coexistence consequences of microbes is through comparisons of plant growth in different soil contexts (e.g. $m_{1A} = \log(\text{biomass}_{1A}) - \log(\text{biomass}_{10})$). There is some ambiguity in the literature about the importance of log-transforming biomass measurements in such analyses.[1] Some authors omit this step entirely (or omit it from the reported methods, e.g. Bauer et al. (2017)), while some employ other transformations (e.g. square root transformation, Smith and Reynolds (2015)). When

[1]Note: A previous version of this manuscript mistakenly suggested that Dudenhöffer et al. (2022)'s analysis featured a double-log transformation. These authors avoided the double-log through a back-transformation step that I had overlooked.

log-transformation *is* reported, it is often justified on the basis of the statistical properties (skewness) of the data (e.g. Duell et al., 2023). While ensuring that the appropriate data transformations are applied prior to model fitting is of course essential, log-transforming biomass data from plant-soil feedback experiments before calculating I_S serves more than just a statistical purpose. A key but implicit assumption to parameterizing the Bever et al. (1997) model with individual plant biomass data is that plant growth during the response phase of experiments is an exponential process, mirroring the exponential population growth of the underlying population dynamics model. Assuming that the final biomass value is the result of an exponential growth process, log-transforming the final biomass enables comparisons of the *rates* of biomass accumulation (Blackman, 1919) - i.e., the biomass analogs of the exponential population growth rate parameters m_{iX}. Moreover, whether or not microbial impacts on individual plant growth translate into corresponding effects on long-term population dynamics remains unclear. Such mismatch between microbial effects on biomass vs. population dynamics can arise for at least two reasons. First, while it is true that large plants generally achieve higher demographic fitness than do smaller conspecifics (Younginger et al., 2017), examples abound of species for which differences in biomass are poor predictors of fitness (reviewed in Fridley, 2017). Recent empirical results also suggest that microbial effects vital rates related to growth, survival and reproduction can be largely uncorrelated (Dudenhöffer et al., 2018; Chung et al., 2023b), which further complicates inferences of long-term dynamics from measurements of plant biomass. Thus, theoretical and empirical efforts to more thoroughly incorporate microbial effects on key life history processes are likely to yield important insights.

Soil microbial feedbacks in more diverse plant communities

Studies of plant coexistence are often motivated by diverse communities, but microbial mediation of plant coexistence is usually evaluated among species pairs. While pairwise analyses provide important insights, extending these results to interpret microbial effects on diverse plant systems can be challenging (Barabás et al., 2016; Levine et al., 2017). Several studies have addressed this gap through extensions to the classic two-species plant-soil feedback model. An early advance was that of Kulmatiski et al. (2011), who developed a model of three plant species and showed that the additional complexity of such a system can yield routes to coexistence that are not identified from pairwise analyses. For example, cyclic plant dynamics can arise even when each species performs better in its own soil community than in other species' soil (i.e. $m_{1A} > \{m_{1B}, m_{1C}\}$) – an outcome that seem-

ingly contradicts the two-species coexistence criteria (Eqn. 2). More recently, Miller et al. (2022) extended the classic plant-soil feedback model to an arbitrary number of species and found that without any additional assumptions beyond those in Bever et al. (1997), robust coexistence of more than two species is virtually impossible. While it is possible to identify precise parameter sets yield oscillatory coexistence in this n-species model, this coexistence is fragile: minuscule perturbations to plant frequencies or to parameters cause the system to collapse to low-diversity (1 or 2 species). They conclude that stable multi-species coexistence is unlikely without accounting for other processes that regulate the dynamics of plants or of soil microbes. One such source of regulation is to more thoroughly integrate plant-microbe interactions and plant competition into a unified framework, a topic I return to in a following section.

Another potential source of regulation is through incorporating density-dependence in the microbial dynamics. This approach was implemented for two-species systems in Eppinga et al. (2006) and Aguilera (2011), and further extended to a multi-species plant system by Mack et al. (2019). This analysis identified a range of pathways through which microbes can enable multispecies plant coexistence, ranging from strict negative feedback to strict intransitivity in the system. Building on this model, Eppinga et al. (2018) analytically derived an n-species analogue of the pairwise stabilization metric termed I_C. As with I_S, negative values of I_C predict negative community-wide feedback, which is necessary for all n species persist in the system (see Appendix S2). Similar caveats also apply: while coexistence of all species is promoted by $I_C < 0$, negative community feedback does not guarantee coexistence. Importantly for empirical application, quantifying I_C only requires a complete performance matrix (i.e. all combinations of B_{iX}), the likes of which are generated from fully-factorial pairwise plant-soil feedback studies of >2 species.

Implications for empirical studies

To date, the vast majority of experiments interested in evaluating microbial effects in diverse communities have done so by inferring system-wide feedback from contrasts of pairwise I_S at the species level (statistical summary of all I_S values involving each focal species (Mangan et al., 2010; Bauer et al., 2015)), or whole-community level (Pizano et al., 2019; Stein and Mangan, 2020; Dudenhöffer et al., 2022). While such statistical averaging of pairwise coefficients seems promising, theory suggests that inferring multi-species effects from such calculations comes with pitfalls (Barabás et al., 2016; Spaak and Schreiber, 2023)

that have not yet been formally evaluated in the context of plant-soil feedback. The theoretical advances in Eppinga et al. (2018) suggest a robust alternative that is also frictionless, in that it does not require changing the two-phase design (Fig. S.1). Specifically, in systems where the model's assumptions regarding self-regulation of microbial dynamics are expected to apply, quantifying community-wide feedback through I_C provides a theoretically justified measure of microbial feedbacks on multispecies plant community structure. Moreover, doing so only requires the same information necessary to quantify species- or community-average I_S, and can yield surprising results. For example, Dudenhöffer et al. (2022) find that soil microbes most strongly *stabilize* pairwise plant coexistence under drought, but quantifying I_C for species triplets suggest that microbes most strongly *destabilize* multispecies systems under drought (Fig. S.3 and Appendix S2).

Such analyses point to the value of future studies linking data with theoretically rigorous metrics of multispecies coexistence dynamics for advancing our understanding microbial regulation of plant dynamics in diverse systems.

Contextualizing plant-microbe interactions relative to plant-plant interactions

Plant–microbe interactions are one of many processes that simultaneously structure plant communities. Thus, while models and experiments that isolate the soil conditioning/response process help establish the *potential* role of soil microbes in regulating plant communities, quantifying their contributions to plant coexistence in nature requires contextualizing their effects relative to those of other processes. Apart from their effects on plants' intrinsic fitness – the primary focus of plant–soil feedback studies – soil microbes can also affect plant coexistence and community dynamics by altering the nature of plant interactions with herbivores (Koricheva et al., 2009), pollinators (Barber and Soper Gorden, 2015), and con- and hetero-specific neighbors (Lekberg et al., 2018). Projecting the long-term consequences of such interactive effects on plant coexistence requires careful coupling of experimental data with population dynamics models. For example, consider Bever (2003)'s integration of the classic plant–soil feedback process (Bever et al., 1997) into a system of plants that also interact via Lotka-Volterra competition. As detailed in Appendix S3, this relatively simple extension implies subtle changes in the assumptions about the effect that microbes have on plant intrinsic growth rates – assumptions that also change the empirical estimation and interpretation of the m_{iX} parameters. Specifically, while the m_{iX} parameters in the 1997 model represent direct (additive) effects of microbes on plants' baseline growth rates in unconditioned soils, the

specification of the 2003 model means that the corresponding parameters represent the *proportional* (multiplicative) effects of microbes on baseline growth. Thus, m_{iX} terms in this model have different units than in the 1997 model, and estimating these parameters from empirical data requires scaling microbial effects relative to the baseline growth ($m_{iX} = \frac{B_{iX} - B_{i0}}{B_{i0}}$, see Appendix S3 for details).

More fundamentally, contextualizing microbial effects relative to those of other processes requires us to use modelling frameworks that reflect the diversity of pathways through which microbes impact plant communities in nature. One such possibility is that the effect of the microbial community scales with changes in the abundance (or density) of microbes, rather than changes in relative frequency. Empirical studies suggest that such density-dependent microbial effects may be common among fungal or oomycete pathogens (Liang et al., 2016; Lamichhane et al., 2017). In these communities, if both focal plant species are present at low abundances, then their cultivated soil microbes would also be expected at low abundances and thus exert only weak effects on plant growth. This is difficult to envisage in the feedback framework due its constraint that $S_A + S_B = 1$, meaning that if plant 1's microbes are rare, then plant 2's microbes are automatically dominant. Modeling how the absolute densities of microbes (rather than relative frequencies) affect plant population dynamics can help overcome some of these limitations (Kandlikar et al., 2019; Ke and Wan, 2020). These abundance-based frameworks also help more directly capture scenarios in which microbial effects on plant dynamics arise primarily by changing the nature of density-dependence, as has been shown to be the case for some ectomycorrhizal fungi, which benefit some plant hosts by reducing the competitive effects from neighbors rather than by increasing plants' intrinsic fitness per se (e.g. Liang et al., 2021). Importantly, although these changes to the feedback framework come with some cost of empirical tractability, the most relevant parameters can nevertheless be quantified from pot experiments tracking plant growth without explicit measurements of microbe dynamics (see Fig. 3, Ke and Wan (2020), and Ke and Wan (2023) for details).

Further departures from the feedback framework, which implies a strict correspondence between the number of plant species and microbial communities, also yield important insights. For example, tracking plant species' interactions with different types of mutualistic vs. harmful microbes can yield a more predictive understanding of conditions under which soil microbes contribute to coexistence vs. species replacement (Jiang et al., 2020; Schroeder et al., 2020). Integrating the role of soil microbes as mutualists, pathogens, and decomposers into a mechanistic framework for resource competition is

also a compelling a path towards understand the relative importance of microbes on biodiversity maintenance in nature (Chung et al., 2023a). Parameterizing such models requires experiments that carefully manipulate the abundance of different types of microbes and/or manipulate relevant abiotic factors like nutrient availability. These experiments are likely impractical in most field systems – especially in systems where the microbial communities themselves remain poorly understood. Nevertheless, insights from a few such studies in relatively tractable systems may enable a more mechanistic and generalizable understanding of how microbes shape plant communities across natural contexts.

Implications for empirical tests

Evidence that soil microbial effects scale up to structure whole plant communities largely comes from studies that correlate outcomes from feedback experiments to properties like species' relative abundance (meta-analyzed by Reinhart et al., 2021), community stability (Chung et al., 2019), or productivity (Forero et al., 2022). While such work provides compelling evidence for the importance of soil microbes, the lack of an integrative framework for studying their effects stymies our ability to make sense of seemingly contradictory results. For example, species whose performance is more strongly suppressed by conspecific-conditioned soil communities tend to be less abundant on the landscape in some systems (Klironomos, 2002; Mangan et al., 2010), but the opposite pattern arises elsewhere (Corrales et al., 2016; Maron et al., 2016). In yet other systems, feedback strength and abundance are unrelated (Reinhart, 2012). A unified framework that integrates microbial effects with other processes structuring plant communities can offer useful insights for making sense of the diversity of patterns observed in nature. For example, explicitly integrating plant-soil feedbacks and resource competition suggests that soil microbes drive plant dynamics most strongly when nutrients are less limiting; microbial effects are unlikely to affect plant competition when resource dynamics are slow (Kandlikar et al., 2019). Qualitatively, such a result is consistently with Corrales et al. (2016)'s conclusion that effects of slow soil nitrogen cycling override any negative plant-soil feedbacks in driving the monodominance of an ectomycorrhizal tree in a tropical montane forest. Such congruence between theoretical and empirical conclusions points to the potential value of studies that directly integrate experimental data and demographic models for projecting how microbes shape the dynamics of natural plant communities.

As mentioned in the previous section, empirically quantifying the interactive role of plant–microbe interactions and other processes will require experimental treatments

beyond those in the classic two-phase design (Fig. 3). The particular design and analysis of these experiments will vary depending on the scope of which microbes' effects are being evaluated (e.g. is the goal to quantify the effects of soil microbes as a whole, or of the conditioning process specifically?), which demographic processes are affected by microbes (e.g. do microbes primarily affect intrinsic growth rates, density dependence, or both processes?), and whether the goal of the study is to evaluate long-term pairwise coexistence or a different outcome (e.g. do microbes enable coexistence, vs. do microbes help stabilize plant dynamics?). For example, studies that are focused on experimentally evaluating the role of soil of soil microbes in shaping conspecific density dependence specifically rather than coexistence more broadly can focus their efforts on the comparisons labelled C.i, D.i, and E.i in Fig. 3. If such a study were to find strong positive effects of neighbors in comparison D.i but negative effects of neighbors in C.i, this would indicate that environmental microbes contribute to intraspecific facilitation. On the other hand, studies aiming to evaluate the contribution of soil microbes to pairwise coexistence among species that also compete with one another would require the full complement of comparisons in Fig. 3. In this case, comparisons C.i and C.ii would measure intra- and inter-specific competition without microbes, while D.i/D.ii and E.i/E.ii would measure intra- and inter-specific competition environmental and conditioned microbes, respectively. Whether one needs to include individual plant growth in sterile, live, and conditioned soils, or if only one of these is required, depends on whether soil microbes are expected to only affect density-dependence, or also affect intrinsic growth. Data from such studies can be used to parameterize population dynamics models that enable long-term predictions of pairwise coexistence under different microbial contexts (e.g. Chung and Rudgers, 2016; Van Nuland et al., 2023). The rapidly developing toolkit for evaluating multispecies coexistence dynamics (e.g. Song et al., 2018) also provides a promising avenue for building towards a more comprehensive understanding of how microbes shape the dynamics of diverse plant communities. As studies scale up to include more experimental treatments necessary for parameterizing such models, ensuring that the observed patterns are consistent with model assumptions and that uncertainty in parameter estimates is properly propagated to long-term conclusions should remain a priority (Terry and Armitage, 2023).

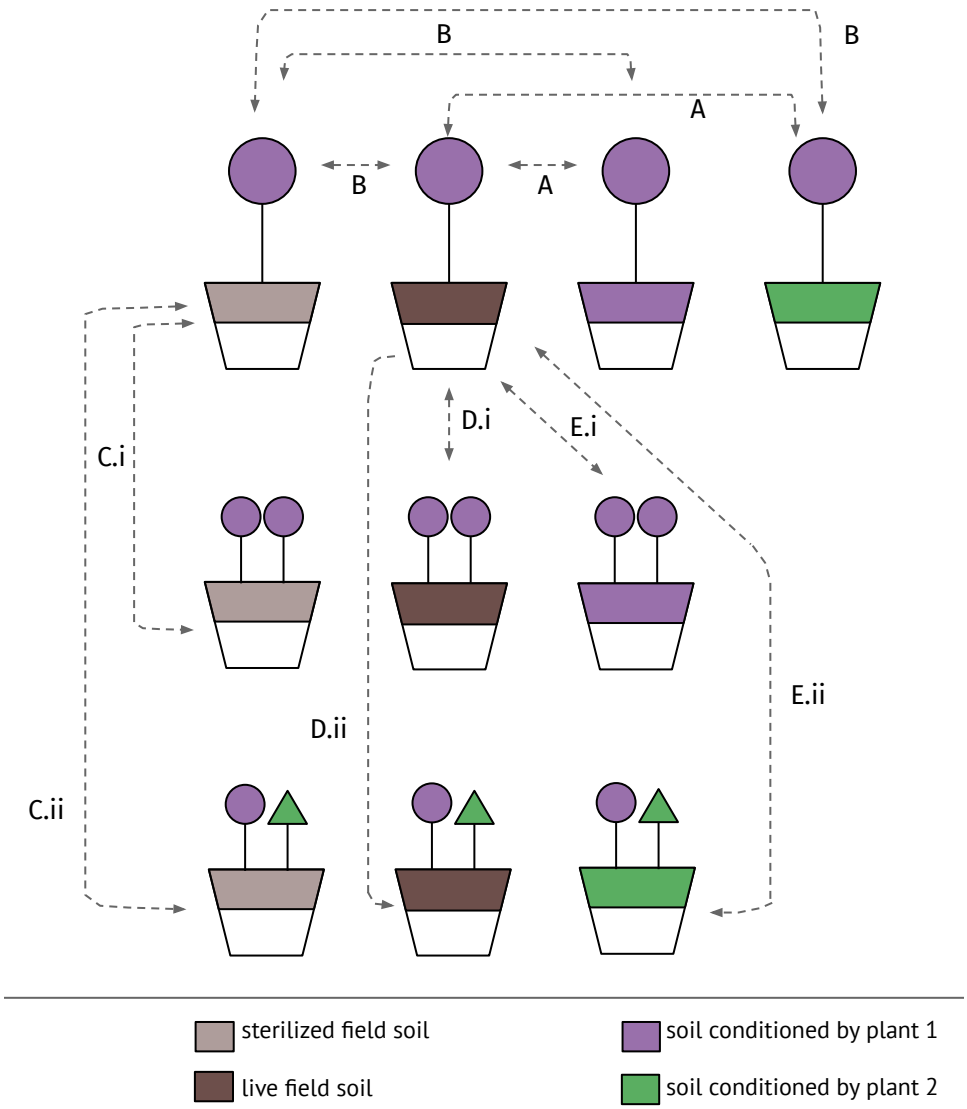

Fig 3: Potential design of a pot experiment that yields a more complete understanding of how microbes shape plant interactions.
Arrows labelled **A** fall under the purview of the classic pairwise feedback framework; these comparisons help predict coexistence when plants only interact with one another through the soil community. Arrows **B** provide insight on how the whole microbial community - and not just the conditioning process - shapes coexistence. Arrows **C, D**, and **E** quantify plant-plant interactions (both intra- and interspecific) in the absence of microbes, in the absence of the conditioning process, and when microbes are present and conditioned, respectively. Differences in arrows C-E can be used to infer how direct plant interactions and soil microbes jointly shape coexistence outcomes. For simplicity this figure only illustrates the soil treatments for one plant species; similar soil treatments are also required with plant 2 as the focal species for evaluating coexistence. Note that this design differs from the 'minimal design' of Ke and Wan (2020) by including individual plant growth in different soil backgrounds; these treatments can be omitted if microbes are thought to only affect the nature of density dependence rather than plants' intrinsic growth. As highlighted in Ke and Wan (2023), additional density treatments may be required to evaluate the nature of density dependence in some systems.

Conclusion

Soil microbes play a key role in the dynamics of all terrestrial ecosystems. A tight integration of theory and experiments over the past few decades has enabled rapid and sustained progress in our understanding of how soil microbes shape plant species coexistence. The theoretical advances reviewed here point to three areas of empirical research that should yield important insights:

1. While we now know that soil microbes can drive positive or negative feedback in a wide range of ecosystems, existing evidence also suggests that any such negative feedback rarely results in long-term coexistence (Yan et al., 2022). Evaluating the conditions under which soil microbes themselves give rise to pairwise *coexistence* (versus exclusion or priority effects) remains an open question.

2. While statistical averaging of pairwise metrics can provide useful insights into microbial effects in diverse communities, theory shows that such analyses come with some pitfalls. Eppinga et al. (2018)'s analytically-derived community-wide stabilization metric can be parameterised with data from fully factorial feedback studies, and doing so has the potential to yield insights into microbial effects on multispecies systems that are masked in pairwise analyses.

3. Designing pot experiments with treatments informed by theoretical models that integrate soil microbial effects with those of other processes like resource competition (e.g. Ke and Wan, 2020, 2023) will enable a more complete understanding of the conditions under which soil microbial effects scale up to affect plant community structure.

Continuing the interplay between theory and data is critical not only to improve our fundamental understanding of how soil microbes shape plant coexistence, but also promises to generate actionable insights into the role of soil microbes in pressing environmental challenges like invasive species management habitat restoration.

Acknowledgements

I thank Xinyi Yan, Po-Ju Ke, and Madeline Cowen for feedback (and much-needed encouragement) on this manuscript. Conversations with Karen Abbott, Priyanga Amarasekare, Gyuri Barabas, Adriana Corrales, Stan Harpole, Nathan Kraft, Meghna

Krishnadas, Jonathan Levine, Marcel Vaz, and Yadugiri VT have contributed to my understanding of plant-microbe interactions. Thanks also to Meghna Krishnadas for supporting my application to the AJB Synthesis Committee, to Jan Dudenhöffer, Richard Ita and members of Daijiang Li's lab for feedback, and to the editors and reviewers for comments that helped improve this work. Finally, thanks to sDiv, the Synthesis Centre of iDiv (DFG FZT 118, 202548816), for funding the pPSF working group, where I met many of the colleagues listed above.

Author contributions

G.S.K: Conceptualization; Writing - original draft; Writing - review & editing.

Data availability

No data were used in this manuscript. Code for rendering all figures and manuscript documents is available at https://gitlab.com/gklab/ajb-synthesis-public.

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Supplemental Figures

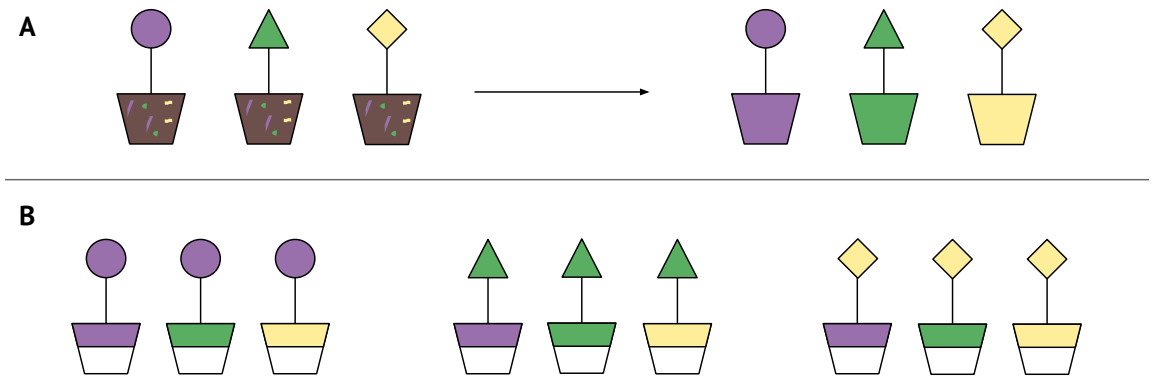

Fig S.1: Schematic of the two-phase feedback experimental design. A. In the first phase of the experiment, individuals (or monocultures) of each species are grown in soils that are identical at the beginning of the experiment. Over time, the plants grow, and the soil microbial community changes to reflect each species' unique conditioning effect (represented by distinct soil colors). **B.** In the second phase of the experiment, individuals of each species are grown, this time soils conditioned by conspecifics or by heterospecifics in the previous phase. A small volume of the conditioned inoculum is added to pots that primarily contain a common sterilized background soil (often <= 10% of the total soil volume in the pot is live conditioned inoculum, and the rest is bulk sterilized soil). Thus, soils should only differ in terms of their microbial community, and any nutritional differences that arise during the conditioning phase should not have a stong effect on plant growth in the response phase.

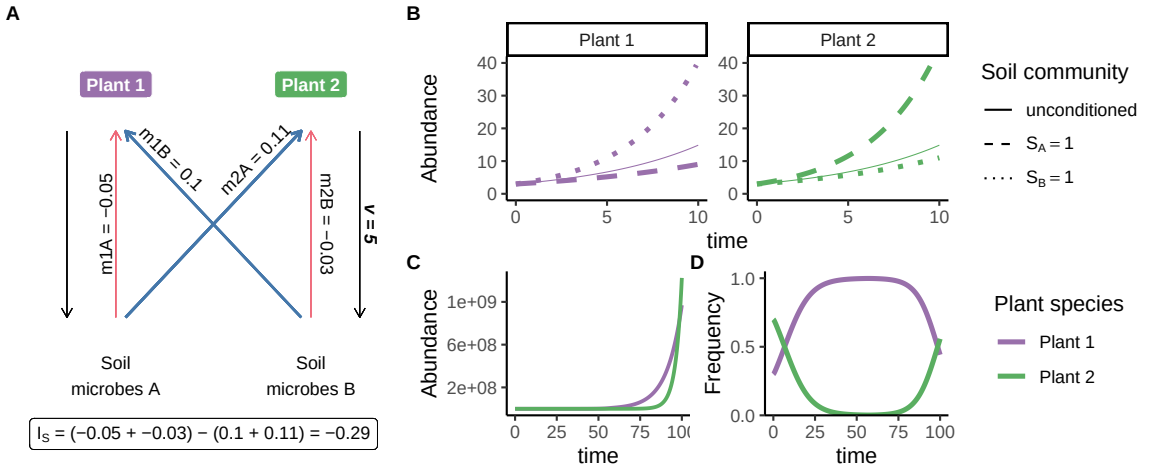

Fig S.2: Variation in species' conditioning strengths affects the temporal dynamics of species coexistence A. This simulation uses identical miX parameters as in Fig. 1 of the main text, but now, $v = 5$, which means that plant 2 conditions the soil towards S_B more strongly than does plant 1 towards S_A. **B.** Population growth dynamics for the two plants when soil is entirely conditioned by one plant or the other; this is identical to Fig. 1B. **C.** When the two plants grow together, both plants have periods when they overtake the other in abundance, but there is an extended period of time when plant 1 is substantially more abundant than plant 2 - punctuated by brief periods during which plant 2 overtakes plant 1 in abundance **D.** Due to differences in the rates of exponential growth of the species over extended periods of time, the gulf in the two species' relative frequencies grows until the system appears to be effectively entirely dominated by plant 1. Only over long periods of time does it become evident that plant 2 can rebound in abundance.

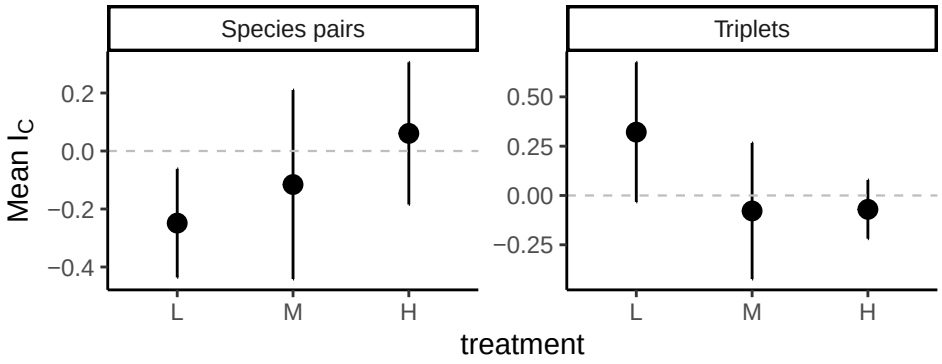

Fig S.3: Microbial stabilization of species pairs and triplets under low, medium, and high watering regimes. This figures shows results from an analysis estimating Eppinga et al. (2018)'s I_C, the multi-species analog of the pairwise interaction metric I_S, using data from Dudenhöffer et al. (2022). As in the original publication, we find that among species pairs, microbes exert stronger stabilization under drought ("low watering") than under high-watering regimes. However, among species triplets, the trend is reversed, with microbes generating slightly positive (destabilizing) feedbacks under drought, and slight negative (stabilizing) feedback under high-watering. Analysis details are available in Supplement S3, as are similar figures for 4 to 8 species communities that can be assembled from Dudenhöffer et al. (2022)'s study; these show that the the result shown for triplets here generaly extends to more diverse communities as well.

Appendix S1: Conditions for coexistence in the classic plant-soil feedback model

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This appendix begins with a overview of dynamics model from Bever et al. (1997), including detailed steps to convert the underlying exponential growth equations for plants and microbes into equations for tracking changes in plant and microbe frequencies. After describing the model, I outline two approaches for identifying the conditions that allow long-term persistence of both plant species in this model. Note that throughout this appendix, I use N to denote state variables that reflect abundances, and F to denote frequency. The subscripts 1 and 2 refer to the plant species, and the subscripts A and B refer to their associated soil communities.

Model description

The Bever et al. (1997) framework begins by considering a system comprising two plant species whose populations grow exponentially at a rate determined by the composition of the soil microbial community:

$$\frac{dN_1}{dt} = W_1 N_1 \quad \text{and} \quad \frac{dN_2}{dt} = W_2 N_2 \tag{S1.1}$$

W_i, the per-capita population growth rate of species i, is determined by the relative frequency of each microbial community (F_A and F_B), and by the effect of each microbial community on plant i (m_{iA} and m_{iB}):

$$W_i = m_{iA} F_A + m_{iB} F_B \tag{S1.2}$$

Here, the two m terms have the units of $\frac{1}{\text{microbe frequency} * \text{time}}$. F_A and F_B represent the relative frequency of each microbial community, rather than their absolute abundance. Thus, $F_A + F_B = 1$, and Eqn. S1.2 can also be written as $W_i = m_{iA} F_A + m_{iB}(1 - F_A)$, and W_i has units of $\frac{1}{\text{time}}$. Substituting this into the plant dynamics equation (S1.1) gives the full equations for plant population dynamics:

$$\frac{dN_1}{dt} = N_1(m_{1A} F_A + m_{1B}(1 - F_A)) \quad \text{and} \quad \frac{dN_2}{dt} = N_2(m_{2A} F_A + m_{2B}(1 - F_A)) \tag{S1.3}$$

The abundance of soil microbial communities N_A and N_B also experiences exponential growth, with the rate of growth determined by the relative frequency of each plant[2]:

$$\frac{dN_A}{dt} = N_A \frac{N_1}{N_1 + N_2} \quad \text{and} \quad \frac{dN_B}{dt} = vN_B \frac{N_2}{N_1 + N_2} \tag{S1.4}$$

The parameter v defines how strongly soil microbial community B accumulates with plant 2, relative to how strongly soil community A accumulates with plant 1.

Recognizing that plant population growth rates depend on the composition of the microbial community, which in turn depend on the relative frequency of each plant, we can express the system in terms of plant frequencies. This lets us simplify from the two equations in S1.3, to one equation for the frequency of plant 1 ($F_1 = \frac{N_1}{N_1+N_2}$):

$$\frac{dF_1}{dt} = F_1(1 - F_1)[(m_{1A} - m_{2A})F_A + (m_{1B} - m_{2B})(1 - F_A)] \tag{S1.5}$$

By definition, $F_2 = 1 - F_1$, and $\frac{dF_2}{dt} = -\frac{dF_1}{dt}$.

Similarly, from the equations for tracking change in soil community abundance (Eqns. Equation S1.4), we can derive equations for the change in the frequency of microbial community ($F_A = \frac{N_A}{N_A+N_B}$):

$$\frac{dF_A}{dt} = F_A(1 - F_A)(F_1 - v(1 - F_1)) \tag{S1.6}$$

By definition, $F_B = 1 - F_A$, and $\frac{dF_B}{dt} = -\frac{dF_A}{dt}$.

Deriving Eqn. S1.5 from Eqn. S1.3, and deriving Eqn. S1.6 from Eqn. S1.4 requires application of the quotient rule. To make this derivation more accessible, I provide detailed steps in Box S1. After Box S1, I outline two complementary ways to evaluate the conditions for coexistence in this model (via evaluating feasibility and stability of equilibria, or via evaluating the low-density growth rates).

[2]Note that on p. 563 of Bever et al. (1997), the authors write (using slightly different notation) that $dN_A/dt = N_A N_1$, implying that the growth rate of microbial community A depends on the *abundance* rather than *frequency* of plant 1. I believe this was a typo.

Box S1: Deriving the equation for plant frequency dynamics from exponential growth equations

This box details the steps for expressing plant and soil microbial frequency dynamics (Eqns S1.5 and S1.6) from the exponential growth models (Eqns S1.3 and S1.4).

Plant frequency dynamics To derive the plant frequency dynamics equation, we first define F_1 as the relative abundance of plant 1: $F_1 = \frac{N_1}{N_1+N_2}$. Our goal now is to derive the equation for change in F_1 over time: $\frac{dF_1}{dt}$.
We proceed by applying the quotient rule (for $h(x) = \frac{f(x)}{g(x)}$, $h'(x) = \frac{f'(x)g(x)-g'(x)f(x)}{g(x)^2}$) to get

$$\frac{dF_1}{dt} = \frac{d\frac{N_1}{N_1+N_2}}{dt} = \frac{\frac{dN_1}{dt}(N_1+N_2) - N_1(\frac{dN_1}{dt}+\frac{dN_2}{dt})}{(N_1+N_2)^2}$$

Recalling that $\frac{dN_1}{dt} = N_1(m_{1A}F_A + m_{1B}F_B)$ and $\frac{dN_2}{dt} = N_2(m_{2A}F_A + m_{2B}F_B)$, we can rewrite the equation as follows:

$$\frac{dF_1}{dt} = \frac{N_1(m_{1A}F_A + m_{1B}F_B)}{N_1+N_2} - \frac{N_1(N_1(m_{1A}F_A + m_{1B}F_B) + N_2(m_{2A}F_A + m_{2B}F_B))}{(N_1+N_2)^2}$$

Recalling that by definition, $F_1 = \frac{N_1}{N_1+N_2}$ and $F_2 = \frac{N_2}{N_1+N_2}$, this equation simplifies as follows:

$$\frac{dF_1}{dt} = F_1[(m_{1A}F_A + m_{1B}F_B) - F_1(m_{1A}F_A + m_{1B}F_B) - F_2(m_{2A}F_A + m_{2B}F_B)]$$

Combining the first two terms in the square brackets gives:

$$\frac{dF_1}{dt} = F_1[(1-F_1)(m_{1A}F_A + m_{1B}F_B) - F_2(m_{2A}F_A + m_{2B}F_B)]$$

Now, recognizing that $(1-F_1) = F_2$, we can simplify this to:

$$\frac{dF_1}{dt} = F_1[F_2[(m_{1A}F_A + m_{1B}F_B) - (m_{2A}F_A + m_{2B}F_B)]]$$

Moving F_2 outside the brackets, recognizing that $F_2 = 1 - F_1$, and recognizing that $F_B = (1-F_A)$ gives the frequency dynamics equation as stated in Eqn. 2 of Bever et al. (1997) (see also Eqn. S1.5 above):

$$\boxed{\frac{dF_1}{dt} = F_1(1-F_1)[(m_{1A}-m_{2A})F_A + (m_{1B}-m_{2B})(1-F_A)]}$$

continued on next page

Soil frequency dynamics

Next, we derive the microbial frequency dynamics (Eqn S1.6) from the equations for change in microbial abundance (Eqn S1.4). As above, we first define F_A as the relative abundance of soil community A: $F_1 = \frac{N_A}{N_A+N_B}$. Our goal now is to derive the equation for change in F_A over time: $\frac{dF_A}{dt}$.
As above, applying the quotient rule yields:

$$\frac{dF_A}{dt} = \frac{d\frac{N_A}{N_A+N_B}}{dt} = \frac{\frac{dN_A}{dt}(N_A+N_B) - N_A(\frac{dN_A}{dt}+\frac{dN_B}{dt})}{(N_A+N_B)^2}$$

Recalling from above that $\frac{dN_A}{dt} = N_A F_1$ and canceling terms gives:

$$\frac{dF_A}{dt} = \frac{N_A F_1}{N_A+N_B} - \frac{N_A(N_A F_1 + vN_B F_2)}{(N_A+N_B)^2}$$

Recognizing that $F_A = \frac{N_A}{N_A+N_B}$, and expanding out the second term, we can rewrite the equation as follows:

$$\frac{dF_A}{dt} = F_A F_1 - \frac{F_A(N_A F_1)}{N_A+N_B} - \frac{F_A(vN_B F_2)}{N_A+N_B}$$

Once again recognizing that $F_A = \frac{N_A}{N_A+N_B}$, we can further simplify the equation:

$$\frac{dF_A}{dt} = F_A F_1 - F_A^2(F_1) - vF_A F_B(F_2)$$

Factoring out F_A gives

$$\frac{dF_A}{dt} = F_A(F_1 - F_A F_1 - vF_B F_2)$$

We can further factor out F_1 in the parenthetical term to rewrite the equation:

$$\frac{dF_A}{dt} = F_A(F_1(1-F_A) - vF_B F_2)$$

Recognizing that $1 - F_A = F_B$, we can write:

$$\frac{dF_A}{dt} = F_A(F_1 F_B - vF_B F_2) = \boxed{F_A(1-F_A)[F_1 - v(1-F_1)]}$$

This is the same as Eqn. 3 in Bever et al. (1997), and Eqn. S1.6 above.

Evaluating coexistence by analysing the feasibility and stability of equilibrium points

The first approach to deriving the conditions necessary for coexistence of the two plant species involves identifying the conditions under which the model's equilibria are both *feasible* and *stable*. Feasible equilibrium points mean that all the components of the system (in this case, the two plant species and their associated microbial communities) are present in the system at equilibrium; stability means that slight perturbations from the equilibrium do not push the system towards exclusion of one plant or the other. This approach builds on the insight that for two-species Lotka-Volterra models, feasible equilibria that are locally stable guarantee coexistence (Goh, 1976).

Identifying the equilibrium conditions

The first step in this analysis is to find the equilibrium points of the model. To do so, we set Eqns. S1.5 and S1.6 equal to zero. We can start by evaluating the plant dynamics equation:

$$\frac{dF_1}{dt} = F_1(1-F_1)[(m_{1A}-m_{2A})F_A + (m_{1B}-m_{2B})(1-F_A)] = 0$$

This condition is satisfied when $F_1 = 0$ or when $F_1 = 1$, which corresponds to cases in which the plant community is a monoculture of species 2 or 1 respectively. However, equilibrium can also arise when the third term (i.e. the term in square brackets) is equal to zero:

$$[(m_{1A}-m_{2A})F_A + (m_{1B}-m_{2B})(1-F_A)] = 0 \tag{S1.7}$$

Solving this for F_A shows that equilibrium is achieved when the following is true:

$$F_A^* = \frac{m_{2B}-m_{1B}}{m_{1A}-m_{2A}-m_{1B}+m_{2B}} = \frac{m_{2B}-m_{1B}}{I_S} \tag{S1.8}$$

Given that $dF_2/dt = -dF_1/dt$, Equation S1.8 also implies that $dF_2/dt = 0$.

For the whole system to be at equilibrium, the microbial communities also need to be at equilibrium:

$$\frac{dF_A}{dt} = F_A(1-F_A)[(F_1 - v(1-F_1)] = 0 \tag{S1.9}$$

As above, the microbial community can equilibrate when it comprises entirely of microbial community A or B, corresponding to $F_A = 1$ or $F_A = 0$, respectively. The community is also at equilibrium when the third term (in square brackets) is equal to zero:

$$F_1 - v(1 - F_1) = 0$$

Solving this for F_1 shows that equilibrium requires the following to be true:

$$F_1^* = \frac{v}{1+v} \tag{S1.10}$$

Identifying feasible equilibrium points

Having identified the equilibrium conditions (Eqns. S1.8 and S1.10) can now evaluate the conditions under which this equilibrium is *feasible*, i.e. what is required for the equilibrium frequency of both plants and microbes to be between 0 and 1 ($0 < F_A^* < 1$ and $0 < F_1^* < 1$).

For simplicity, we begin with F_1^*. The value of Eqn. S1.10 will be between 0 and 1 for any $v > 0$. In other words, so long as both plant species condition the soil community, this condition is satisfied.

Next we move to Eqns. S1.8. Two sets of conditions can allow for $0 < F_A^* < 1$:

> ***Condition 1***: The numerator and denominator of Eqn. S1.8 are both positive ($m_{2B} - m_{1B} > 0$ and $m_{1A} - m_{2A} - m_{1B} + m_{2B} > 0$), *and* the magnitude of the numerator is smaller than that of the denominator ($m_{2B} - m_{1B} < m_{1A} - m_{2A} - m_{1B} + m_{2B}$).[3]
>
> ***Condition 2***: The numerator and denominator of Eqn. S1.8 are both negative ($m_{2B} - m_{1B} < 0$ and $m_{1A} - m_{2A} - m_{1B} + m_{2B} < 0$), *and* the magnitude of the numerator is smaller than that of the denominator (abs$(m_{2B} - m_{1B}) <$ abs$(m_{1A} - m_{2A} - m_{1B} + m_{2B})$)

If either condition is met (along with the condition that $v > 0$), the system has a feasible equilibrium point at which all players (both plants and both microbes) are present in the system at a frequency between 0 and 1. If neither of these conditions is met (e.g. if $I_S < 0$ but $m_{2B} - m_{1B} > 0$), the system does not have an internal equilibrium; in other words, the system only has a boundary equilibrium corresponding to only one species being present in the system.

The next step for understanding the coexistence conditions in this model is to evaluate the dynamic stability of these equilibrium points.

[3] Note that due to algebra, if $m_{2B} > m_{1B}$ and $I_S > 0$, $m_{1A} > m_{2A}$ is implied; likewise, if $m_{2B} < m_{1B}$ and $I_S < 0$ (Condition 2) is satisfied, $m_{1A} < m_{2A}$ is implied.

Evaluating the dynamic stability of equilibrium points

While the above expressions (conditions 1 and 2, along with $v > 0$) capture the conditions necessary for the existence of feasible equilibrium points, long-term coexistence also requires that these points are dynamically stable (i.e. that the system recovers equilibrium from slight perturbations away from the equilibrium state, Goh (1976)).

We can evaluate the local stability of the equilibria by creating the Jacobian Matrix of the system, which is denoted **J**. The Jacobian matrix helps us evaluate whether or not a system that is at equilibrium returns to the equilibrium when it is perturbed slightly. Each element in **J** is the partial derivative of one of the dynamics equations (Eqns S1.5 and S1.6) with respect to one of the components:

$$\mathbf{J} = \begin{bmatrix} \frac{\partial \dot{F}_1}{\partial F_1} & \frac{\partial \dot{F}_1}{\partial F_A} \\ \frac{\partial \dot{F}_A}{\partial F_1} & \frac{\partial \dot{F}_A}{\partial F_A} \end{bmatrix}$$

Note that above, $\dot{F}_1 = \frac{dF_1}{dt}$, and $\dot{F}_A = \frac{dF_A}{dt}$. Taking the respective partial derivatives gives us the following expressions for the four elements of the matrix:

$$\begin{aligned} \frac{\partial \dot{F}_1}{\partial F_1} &= (1 - 2F_1)[(m_{1A} - m_{2A})F_A + (m_{1B} - m_{2B})(1 - F_A)] \\ \frac{\partial \dot{F}_1}{\partial F_A} &= F_1(1 - F_1)(m_{1A} - m_{2A} - m_{1B} + m_{2B}) = F_1(1 - F_1)I_S \\ \frac{\partial \dot{F}_A}{\partial F_1} &= F_A(1 - F_A)(1 + v) \\ \frac{\partial \dot{F}_A}{\partial F_A} &= [F_1 - v(1 - F_1)](1 - 2F_A) \end{aligned}$$

These four terms define the entries of the Jacobian matrix, which we can now evaluate at the system's equilibrium points to determine their local stability.

Recall from our analysis of Eqn. S1.7 that at equilibrium, $[(m_{1A} - m_{2A})F_A + (m_{1B} - m_{2B})(1 - F_A)] = 0$; thus, $\frac{\partial \dot{F}_1}{\partial F_1}$ also equals 0 at equilibrium.

Similarly, recall from the analysis of Eqn. S1.9 that $[F_1 - v(1 - F_1)] = 0$ at equilibrium; thus, $\frac{\partial \dot{F}_A}{\partial F_A}$ also equals zero at equilibrium.

The system's Jacobian evaluated at its equilibrium (F_1^*, F_A^*) thus simplifies as follows:

$$\mathbf{J}|_{F_1^*, F_A^*} = \begin{bmatrix} 0 & F_1(1 - F_1)I_S \\ F_A(1 - F_A)(1 + v) & 0 \end{bmatrix}$$

We can evaluate the local stability of the equilibrium points on the basis of the trace and determinant of the matrix **J** (Panvilov et al., 2021). The trace (tr) for a square matrix is the

sum of its diagonal entries, so $\text{tr}(\mathbf{J}|_{F_1^*,F_A^*}) = 0$.

Given that the trace of the matrix is zero, the equilibrium can have one of two properties:

1. The equilibrium is a "center equilibrium" if the determinant is positive (Panvilov et al., 2021). A center equilibrium implies that the system is neutrally stable, meaning that the system never returns to the equilibrium point itself after perturbation; it remains in a perpetual cycle. For our purposes, we interpret this as a coexistence equilibrium, because it implies that both species have cyclical dynamics of their frequency in the system.

2. The equilibrium is a saddle node if the determinant is negative (Panvilov et al., 2021). This means that once perturbed from equilibrium, the system continues moving away from the equilibrium (peturbations in favor of species 1 eventually lead to monodominance by species 1, and vice-versa for perturbations in favor of species 2).

Thus, whether or not any feasible equilibrium point corresponds to stable coexistence is determined by the sign of the determinant.

Recalling that the determinant of a generic two-by-two matrix $\begin{pmatrix} a & b \\ c & d \end{pmatrix}$ is equal to $(ad) - (bc)$, the determinant of J is as follows:

$$\det(\mathbf{J}|_{F_1^*,F_A^*}) = 0 - [\overbrace{(F_A(1-F_A)(1+v))}^{\text{term 1}} * \overbrace{(F_1(1-F_1)I_S)}^{\text{term 2}}]$$

Given that we are evaluating feasible equilibrium points where $0 < F_A, F_B < 1$, and $v > 0$, term 1 is always positive. Additionally, given that by definition at the feasible equilibrium $0 < F_1, F_2 < 1$, the sign of term 2 - and thus, the sign of the determinant as a whole - is determined by the sign of I_S. Specifically, negative values of I_S correspond to a positive determinant, while positive values of I_S correspond to a negative determinant.

Building on the two potential properties listed above, this means that the equilibrium is neutrally stable if $I_S < 0$, or is a saddle node if $I_S > 0$.

Combining the criteria for feasibility and stability

From the above analysis, we see that only the equilibrium points in which both species can coexist with neutral stability satisfy Condition 2 for feasible equilibria:

$$m_{2B} - m_{1B} < 0 \text{ and } m_{1A} - m_{2A} - m_{1B} + m_{2B} < 0.$$

Note that the above inequality implies that $m_{1A} < m_{2A}$. Thus, we can express the coexistence conditions simply as:

$$m_{2B} < m_{1B} \quad \text{and} \quad m_{1A} < m_{2A} \tag{S1.11}$$

Evaluating coexistence by analysing the requirements for mutual invasion

While the above approach derives the coexistence criteria by evaluating the conditions for local stability around feasible equilibria, one can also approach coexistence criteria by evaluating the conditions that allow mutual invasibility (Turelli, 1978; Chesson and Ellner, 1989; Grainger et al., 2019). As explained in the main text of the manuscript, this approach builds on the insight that coexistence requires that each species can gain a foothold (i.e. achieve a positive low-density growth rate, or LDGR) as it grows into an equilibrium monoculture of the other. Following Chesson (2000) and Chesson (2018), one can further decompose the LDGRs into two terms - one that captures the microbially mediated stabilization (which promotes both species' invasion growth rates, and thus favors coexistence), and a second term that captures the microbially mediated fitness difference (which benefits one plant's invasion growth rate but suppresses the other, and thus favors exclusion). The details of this analysis are provided in the appendix of Kandlikar et al. (2019), and summarized below.

We begin the analysis with Eqn. S1.5, which defines the dynamics of each plant's frequency in the system:

$$\frac{dF_1}{dt} = F_1(1-F_1)[(m_{1A}-m_{2A})F_A + (m_{1B}-m_{2B})(1-F_A)]$$

We first evaluate the case where the system is an equilibrium monoculture of plant 2 (and its corresponding soil community). Plant 1 and its soil community are absent, meaning that $F_1 = F_A = 0$. We can now quantify plant 1's per-frequency growth rate ($\frac{1}{F_1}\frac{dF_1}{dt}$) as follows:

$$\text{LDGR}_{1\to 2} = \frac{1}{F_1}\frac{dF_1}{dt} = (1-F_1)[(m_{1A}-m_{2A})F_A + (m_{1B}-m_{2B})(1-F_A)] \quad \text{(S1.12)}$$

Given that $F_1 = F_A = 0$, Eqn. S1.12 simplifies as follows:

$$\text{LDGR}_{1\to 2} = m_{1B} - m_{2B} \quad \text{(S1.13)}$$

Through a similar analysis of plant 2's growth into a monoculture of plant 1, we get the invasion growth rate of plant 2:

$$\text{LDGR}_{2\to 1} = m_{2A} - m_{1A} \quad \text{(S1.14)}$$

If both of these conditions are satisfied, both species have positive low-density growth rates and can coexist provided that the following is true. Thus, this analysis yields the coexistence criteria:

$$m_{1B} > m_{2B} \quad \text{and} \quad m_{2A} > m_{1A} \quad \text{(S1.15)}$$

The inequalities in Eqn. S1.15 are identical to those that we derived through the feasibility

analysis above Eqn. S1.11, showing the inherent complementarity of these two approaches. If our goal were to simply evaluate coexistence in the Bever et al. (1997) model, simply evaluating LDGRs is a perfectly valid ending: if both LDGRs are positive, the two species can coexist; if the LDGRs are of opposite signs, the species with a positive LDGR outomes the other; and if both LDGRs are negative, the species experience frequency-dependent priority effects such that either species can establish a monoculture, but both cannot coexist.

However, we can extend our analysis further to generate additional insights. Specifically, decomposing the LDGRs into microbially mediated stabilization and fitness differences allows us to integrate plant-microbe interactions into a wider body of work that seeks to understand how plant coexistence is structured by competition, pollinators, herbivores, etc. (see main text for citations to specific examples).

As explained in Chesson (2018) and in Appendix S1 of Kandlikar et al. (2019), the first step in this decomposition is to define the species-level average fitness. In the case of the Bever et al. (1997) model, we can define the average fitness of species 1 as its average growth rate at all possible soil states (from $F_A = 0$ to $F_A = 1$):

$$\text{fitness}_1 = \frac{\int_0^1 m_{1B} + (m_{1A} - m_{1B})F_A dF_A}{\int_0^1 dF_A} = m_{1B}F_A + \frac{m_{1A} - m_{1B}}{2}F_A^2\Big|_0^1 = \frac{m_{1A} + m_{1B}}{2}$$

Similarly, $\text{fitness}_2 = \frac{m_{2A}+m_{2B}}{2}$. With these definitions of species 1 and 2's average fitness, we can express each species' invasion growth rate as the sum of the fitness difference and stabilization:

$$\text{LDGR}_1 = \text{fitness difference}_{1,2} + \text{stabilization} \tag{S1.16}$$

$$\text{LDGR}_2 = \text{fitness difference}_{2,1} + \text{stabilization} \tag{S1.17}$$

Note that $\text{fitness difference}_{1,2}$ is simply the difference between species 1 and 2's average fitness as defined above:

$$\text{fitness difference}_{1,2} = (\overbrace{\frac{m_{1A} + m_{1B}}{2}}^{\text{plant 1 fitness}}) - (\overbrace{\frac{m_{2A} + m_{2B}}{2}}^{\text{plant 2 fitness}})$$

The order of the two terms is flipped for calculating $\text{fitness difference}_{2,1}$. Thus, in the absence of stabilization, only one species can have a positive invasion growth rate, and coexistence is not possible.

Above, we saw that $\text{LDGR}_{1\to2} = m_{1B} - m_{2B}$ (Eqn S1.13). Substituting this into Eqn. S1.16, we get:

$$m_{1B} - m_{2B} = (\frac{m_{1A} + m_{1B}}{2}) - (\frac{m_{2A} + m_{2B}}{2}) + \text{stabilization}$$

Algebra (detailed in Box S2) yields the expression for stabilization:

$$\text{stabilization} = -\frac{1}{2}(m_{1A} - m_{1B} - m_{2A} + m_{2B}) = -\frac{1}{2}I_S$$

For both species to have a positive LDGR, the strength of stabilization should exceed the absolute value of the fitness difference[4]:

$$\text{stabilization} > abs(\text{fitness difference})$$

When fitness differences exceed stabilization, only the species with the higher fitness can invade into a monoculture of the other; this corresponds to species exclusion.

Negative stabilization (destabilization) suppresses each species' LDGR. If it does so to the point that neither species has a positive LDGR, the system experiences priority effects: whichever species is present at a higher frequency will dominate, and the species with initially low frequencies eventually gets excluded.

Box S2: Deriving the stabilization term

Above, we saw that the $\text{LDGR}_{1\to2}$ can be expressed as follows:

$$\text{LDGR}_{1\to2} = m_{1B} - m_{2B} = (\frac{m_{1A} + m_{1B}}{2}) - (\frac{m_{2A} + m_{2B}}{2}) + \text{stabilization}$$

We can rewrite this as follows:

$$m_{1B} - m_{2B} = \frac{1}{2}m_{1A} + \frac{1}{2}m_{1B} - \frac{1}{2}m_{2A} - \frac{1}{2}m_{2B} + \text{stabilization}$$

Moving the terms to the left of the equal sign to the right, and moving stabilization to the left gives

$$-\text{stabilization} = \frac{1}{2}m_{1A} - \frac{1}{2}m_{1B} - \frac{1}{2}m_{2A} + \frac{1}{2}m_{2B}$$

This equation simplifies to the expression for stabilization:

$$\boxed{\text{stabilization} = -\frac{1}{2}(m_{1A} - m_{1B} - m_{2A} + m_{2B})}$$

[4] the absolute value of $(\text{fitness difference})_{1,2}$ equals that of $(\text{fitness difference})_{2,1}$, so subscripts are not required

The decomposition also applies to $\text{LDGR}_{2\to1}$
While we derived stabilization from plant 1's LDGR, we can show that this applies equally well to plant 2's low density growth:

$$\text{LDGR}_{2\to1} = \text{fitness difference}_{2,1} + \text{stabilization}$$

Substituting the expressions for $\text{fitness difference}_{2,1}$ and stabilization gives us:

$$\text{LDGR}_{2\to1} = \frac{m_{2A} + m_{2B}}{2} - \frac{m_{1A} + m_{1B}}{2} - \frac{1}{2}(m_{1A} - m_{1B} - m_{2A} + m_{2B})$$

Through algebra, we recover Eqn. S1.17 as above:

$$\text{LDGR}_{2\to1} = m_{2A} - m_{1A}$$

The coexistence criteria in terms of stabilization/fitness difference is equivalent to that from the LDGR analysis
Finally, we can show that the coexistence criteria expressed as "stabilization > abs(fitness difference)" is equivalent to the criteria in Eqn. S1.15.
Recall the coexistence criteria in terms of stabilization and fitness difference:

$$\overbrace{-\frac{1}{2}((m_{1A} + m_{2B}) - (m_{2A} + m_{1B}))}^{\text{stablization}} > \text{abs}\left(\overbrace{\frac{1}{2}(m_{1A} + m_{1B}) - \frac{1}{2}(m_{2A} + m_{2B})}^{\text{fitness difference}_{1,2}}\right) \tag{S1.18}$$

By dividing though by $-\frac{1}{2}$, this can be rexpressed as follows:

$$m_{1A} + m_{2B} - m_{2A} - m_{1B} < \text{abs}(m_{1A} + m_{1B} - m_{2A} - m_{2B})$$

To accounting for the absolute value function on the right, this inequality can be written as two separate inequalities:

$$m_{1A} + m_{2B} - m_{2A} - m_{1B} < m_{1A} + m_{1B} - m_{2A} - m_{2B} \tag{S1.19}$$

$$m_{1A} + m_{2B} - m_{2A} - m_{1B} > -m_{1A} - m_{1B} + m_{2A} + m_{2B} \tag{S1.20}$$

Cancelling like terms in Eqn. S1.19 gives $m_{1B} > m_{2B}$, and doing the same in Eqn. S1.20 $m_{1A} > m_{2A}$. Together, these are identical to Eqn. S1.15.

Appendix S2: Quantifying the community-wide stabilization metric I_C with empirical data

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With some modifications to the nature of soil microbial dynamics, Mack et al. (2019) and Eppinga et al. (2018) extended the two-species feedback model of Bever et al. (1997) to evaluate microbial effects on coexistence in multi-species plant communities. Details of this multispecies model derivation and analysis are provided in the original publications. In this appendix, I demonstrate a practical application of quantifying the feedback metric from Eppinga et al. (2018) using empirical data from Dudenhöffer et al. (2022).

By analyzing an n-species plant-soil feedback model, Eppinga et al. (2018) showed that whether microbes generate positive or negative feedback is determined by the sign of the metric I_C, which serves as a community-wide analog of the two-species term I_S. Extending from the notation of the two-species model used in the main text, plant species are denoted $1, 2, \ldots, n$, and the corresponding microbial communities are denoted $A, B, \ldots, X$. The effect of a given microbial community x on plant i is denoted m_{ix}. One can arrange the m terms into an interaction matrix $\mathbf{A}$:

$$\mathbf{A} = \begin{bmatrix} m_{1A} & m_{1B} & \ldots & m_{1X} \\ m_{2A} & \ldots & \ldots & m_{2X} \\ \ldots & \ldots & \ldots & \ldots \\ m_{nA} & \ldots & \ldots & m_{nX} \end{bmatrix}$$

One can use this interaction $\mathbf{A}$ to calculate the community-wide stabilization I_C as follows:

$$I_C = (-1)^n \sum_{j=1}^{n} \det \mathbf{A}_j \tag{S2.21}$$

Here, det represents the matrix determinant, and $\mathbf{A_j}$ denotes the interaction matrix A with the j'th column replaced with a vector of 1s. Note that in two-species systems ($n = 2$), $I_C = I_S$, as detailed in Box S2.1.

The main text presents the caveats of using I_S to predicting pairwise species coexistence. Such caveats also exist for $I_C < 0$. While negative values of I_C indicate negative feedback (stabilizing effects on community dynamics), they do not guarantee that all species can coexist. In addition to $I_C < 0$, community-wide coexistence also requires that each species can persist at non-zero frequency at equilibrium:

$$0 < \hat{P}_i = \frac{\det \mathbf{A}_i}{(-1)^n \sum_{j=1}^{n} \det \mathbf{A}_j} < 1 \tag{S2.22}$$

For the same reason that growth in reference soil is essential for calculating pairwise fit-

ness differences (see Main Text), such data is also required for quantifying the equilibrium frequency.

Box 1: Correspondence between I_C and I_S when $n = 2$

The interaction matrix for two species is as follows:

$$\mathbf{A} = \begin{bmatrix} m_{1A} & m_{1B} \\ m_{2A} & m_{2B} \end{bmatrix}$$

Following Eqn. S2.21 above, I_C for this 2-species system (I_C) is calculated as follows:

$$I_C = (-1)^2 \sum_{j=1}^{2} \det A_j = (-1)^2 \left(\det \begin{pmatrix} 1 & m_{1B} \\ 1 & m_{2B} \end{pmatrix} + \det \begin{pmatrix} m_{1A} & 1 \\ m_{2A} & 1 \end{pmatrix} \right) \quad \text{(S2.23)}$$

Given that $\det \begin{pmatrix} a & b \\ c & d \end{pmatrix} = ad - bc$, Eqn. S2.23 simplifies as:

$$I_C = (-1)^2((1 * m_{2B} - m_{1B} * 1) + (m_{1A} * 1 - 1 * m_{2A}))$$

Through algebra, this simplifies to $I_C = m_{2B} - m_{1B} + m_{1A} - m_{2A}$, which is equivalent to the pairwise I_S.

Quantifying I_C with empirical data

This subsection provides `R` code for calculating I_C from the data collected for Dudenhöffer et al. (2022)'s study, which evaluated how drought affects plant-soil feedback outcomes.

Note: The goal of this code is not to be universally applicable in its current form to all datasets; rather, this code can merely serve as a starting point for future studies aiming to evaluate community-wide stability with I_C. The code below makes a number of simplifying assumptions (Box S2) which may not be appropriate in other contexts.

Assumptions embedded in the code

- Microbial effects on plant performance arise primarily through modification of plant biomass (survival not impacted; note that this diverges from Dudenhöffer et al. (2022)'s original analysis)
- In cases where an estimate of B_{ix} was unable, I use the average value of B_{ix} from all other pots in the same environmental (watering) treatment.

```r
library(tidyverse)
library(readxl)
library(osfr) # for downloading dataset

# Download dataset if it is not available
if(!("data_PSF_response_phase.xlsx" %in% list.files())) {
  osf_retrieve_file("https://osf.io/nx2e6") %>%
    osf_download()
}

psf_data <- read_xlsx("data_PSF_response_phase.xlsx")

# Structure of the dataset
colnames(psf_data)
```

```
[1] "block"     "soil"      "treatment" "species"   "part"      "bm"
[7] "dead"
```

```r
unique(psf_data$block) # There are sterile soils in this; we can filter them
```

```
 [1] "A"  "B"  "C"  "D"  "E"  "F"  "G"  "H"  "I"  "S1" "S2" "S3"
```

```r
table(psf_data$dead)/2
```

```
   0    1
2081  223
```

```r
# There are >200 dead plants; for now we can set aside
# microbial effects on mortality and focus instead on growth
# This differs from the authors of this study, but is consistent
# with lots of other work on PSF.
# For now, we can just assign dead plants to have the mean biomass
# across other replicates of the same species/soil/treatment combo.

# Data reformatting
interaction_matrices <-
  psf_data %>%
   # Change the species names to be in sentence case i.e. "AT" becomes "At"
  mutate(soil = str_to_sentence(soil),
         species = str_to_sentence(species)) %>%
  # filter out sterile soils treatment - not relevant for I_C
  filter(!str_detect(block, "S")) %>%
  # group by the relevant categories
  group_by(block, soil, treatment, species) %>%
  # Right now, biomass is separated agb/bgb;
```

```
    # This chunk combines the two into whole-plant biomass ("combined_bm")
    summarize(combined_bm = sum(bm),
              dead = max(dead)) %>%
    ungroup() %>%
    # Next, we replace NAs (biomass of dead plant) with mean values of that group
    # NOTE that this is not a unviersally good choice; but needed to do something
    # like this here because if any one entry of the matrix A is missing,
    # that matrix cannot be used for calculating I_C.
    group_by(soil, treatment, species) %>%
    mutate(combined_bm = ifelse(dead ==1, NA, combined_bm),
           combined_bm = ifelse(dead == 1,
                                mean(combined_bm, na.rm = T),
                                combined_bm)) %>%
    # filter out dead individuals
    select(-dead) %>%
    # calculate log biomass
    mutate(combined_bm = log(combined_bm)) %>%
    # make treatment into a factor vector, with levels L/M/H
    mutate(treatment = as_factor(treatment),
           treatment = fct_relevel(treatment, c("L", "M", "H"))) %>%
    ungroup() %>%
    # Now, we can work within each treatment & block to make interaction matrices.
    group_by(treatment, block) %>%
    arrange(treatment) %>%
    nest() %>%
    # The next chunk uses the biomass values B_{ij} and makes an
    # interaction matrix (A) for each replicate block/treatment combo
    mutate(interaction_matrix =
             map(data,
                 ~pivot_wider(.x,
                              # row is a species and each column is a soil type:
                              names_from = soil,
                              values_from = combined_bm) %>%
                   column_to_rownames('species') %>%
                   as.matrix()))

  # We can look at this new object:
  interaction_matrices
```

```
# A tibble: 27 x 4
# Groups:   treatment, block [27]
   block treatment data              interaction_matrix
   <chr> <fct>     <list>            <list>
 1 A     L         <tibble [64 x 3]> <dbl [8 x 8]>
 2 B     L         <tibble [64 x 3]> <dbl [8 x 8]>
 3 C     L         <tibble [64 x 3]> <dbl [8 x 8]>
 4 D     L         <tibble [64 x 3]> <dbl [8 x 8]>
```

```
 5 E     L         <tibble [64 x 3]> <dbl [8 x 8]>
 6 F     L         <tibble [64 x 3]> <dbl [8 x 8]>
 7 G     L         <tibble [64 x 3]> <dbl [8 x 8]>
 8 H     L         <tibble [64 x 3]> <dbl [8 x 8]>
 9 I     L         <tibble [64 x 3]> <dbl [8 x 8]>
10 A     M         <tibble [64 x 3]> <dbl [8 x 8]>
# i 17 more rows
```

```r
# We can look at what an interaction matrix looks like:

# This is the interaction matrix for Block A, low water treatment:
interaction_matrices %>%
  filter(block == "A", treatment == "L") %>%
  pull(interaction_matrix) %>% pluck(1) %>% round(., 2)
```

```
      At    Bi    Rc    Rh    Sh    Sn    Ss    Vb
At -1.33 -1.51 -0.89 -0.61 -1.69 -0.90 -0.67 -1.97
Bi -1.45 -3.86 -2.70 -0.31 -4.34 -4.42 -3.00 -2.60
Rc -1.31 -1.26 -0.87 -1.90 -4.02 -1.66 -1.14 -1.01
Rh -0.42 -0.85 -1.46 -0.94 -4.96 -1.12 -0.59 -1.43
Sh -2.90 -2.54 -2.02 -2.47 -3.73 -2.26 -0.49 -3.69
Sn -1.04 -3.44 -1.43 -1.96 -1.26 -1.39 -1.93 -0.80
Ss -1.41 -1.60 -1.85 -1.38 -3.32 -2.60 -1.16 -1.82
Vb -0.47 -0.77  0.06 -0.97 -3.61 -0.84 -1.01 -1.42
```

```r
# Conceptually it is similar to Fig. 2A from the paper, but note that this matrix
# is for Block A only; that one averages from across blocks (and also accounts
# for microbial effects on mortality).
```

Now that we have made the interaction matrices (1 matrix per block, per treatment), we can use this matrix to calculate the I_C for every possible 2, 3, 4, 5, 6, 7, and 8 species combination. That will represent the I_C for a given community, in a given treatment, in a given block. We can then summarize over different blocks to get a mean I_C for each community in each treatment.

```r
# To make calculations easier, we can write a function that calculates
# I_C for all possible subcommunities, gien a complete interaction matrix:

Ic_for_all_subs <- function(intmat) {

  # 1. Helper function: Given a species combination, make a submatrix
  make_submatrix <- function(intmat, indices) {
    to_return <- apply(indices, 2, function(x) intmat[x,x], simplify = F)
    names(to_return) <- apply(indices, 2, function(x)
      paste(rownames(intmat)[x], collapse=""))
    to_return
  }
```

```
  # 2. Helper function: Given an interaction matrix, calculate I_C
  Ic <- function(intmat) {
    # 2.1. make a variable that holds species number
    nsp = ncol(intmat)

    # 2.2. Define a sub-helper function for making matrices A_j
    # This function replaces the j'th column
    # in the interaction matrix (intmat) with a column of 1s
    make_Aj_mat <- function(intmat, j) {
      temp_mat <- intmat # Define a temporary holder matrix
      temp_mat[,j] <- 1  # Return the j'th column with 1
      return(temp_mat)   # return the holder matrix
    }

    # 2.3. Make Aj vectors using the sub-helper function above
    Ajs <- map(1:nsp, ~make_Aj_mat(intmat, .x))
    # 2.4. Calculate determinants of all Aj matrices
    dets <- map_dbl(Ajs, det)
    # 2.5. Calculate IC
    ((-1)^nsp)*(sum(dets))
  }


  # 3. Helper function: Given a list of submatrices, calculate their IC
  # This function returns a vector; each element in the vector is I_C
  make_Ic_vec <- function(submats) {
    map_dbl(submats, Ic)
  }

  # 4. Define the number of species (total), all possible 2:n species combinations,
  # and make all possible sub-matrices of 2:n species using Helper Fn 1 above.
  nsp <- nrow(intmat)
  possible_combns <- map(2:nsp, ~combn(nsp, .x))
  submats <- map(possible_combns, ~make_submatrix(intmat, .x))

  # 5. calculate Ic for all submatrices
  all_Ics <- map(submats, make_Ic_vec)
  all_Ics
}



# We can now use this function to calculate all ICs:
# Here, we use the interaction_matrices object and make a new column
# called all_Ics; each element in this column will have all
# possible I_C values for a given matrix.
```

```
interaction_matrices_with_ICs <-
  interaction_matrices %>%
  mutate(all_Ics = map(interaction_matrix, Ic_for_all_subs))

head(interaction_matrices_with_ICs)
```

```
# A tibble: 6 x 5
# Groups:   treatment, block [6]
  block treatment data              interaction_matrix all_Ics
  <chr> <fct>     <list>            <list>             <list>
1 A     L         <tibble [64 x 3]> <dbl [8 x 8]>      <list [7]>
2 B     L         <tibble [64 x 3]> <dbl [8 x 8]>      <list [7]>
3 C     L         <tibble [64 x 3]> <dbl [8 x 8]>      <list [7]>
4 D     L         <tibble [64 x 3]> <dbl [8 x 8]>      <list [7]>
5 E     L         <tibble [64 x 3]> <dbl [8 x 8]>      <list [7]>
6 F     L         <tibble [64 x 3]> <dbl [8 x 8]>      <list [7]>
```

```
# The first entry has all I_Cs for Block A/treatment L:
# (This will be a list; the first element in the list is a vector
# of the two-species I_Cs; the second element is a vector of the 3-species
# I_Cs, and so on)

# Two species I_C (AKA I_S), only printing first 10
interaction_matrices_with_ICs$all_Ics[[1]][[1]][1:10]
```

```
      AtBi        AtRc        AtRh        AtSh        AtSn        AtSs
-2.23727667  0.00289922 -1.24613067 -0.46826601 -0.78187924 -0.41424075
      AtVb        BiRc        BiRh        BiSh
-0.30827442 -0.76536237 -3.64484659 -0.71182094
```

```
# I_S for triplets,  only printing first 10
interaction_matrices_with_ICs$all_Ics[[1]][[2]][1:10]
```

```
    AtBiRc     AtBiRh     AtBiSh     AtBiSn     AtBiSs     AtBiVb     AtRcRh
-0.3814381 -2.8975229 -2.4155463  5.8255029 -0.8931710 -0.6285068  1.9405044
    AtRcSh     AtRcSn     AtRcSs
-1.0305773  0.6521919  0.4319539
```

We now have a value of I_C for every $n = 2, 3.., 8$ species combination in each block/treatment combination. There are various ways one can summarize this information; for simplicity, I will just summarize the mean value of pairwise I_C, triplet I_C, … 8-species I_C in each treatment.

```
interaction_matrices_with_ICs %>%
  # This next mutate call takes the big list of Ics and splits the
  # information into columns for 2, 3,..8 species communities
```

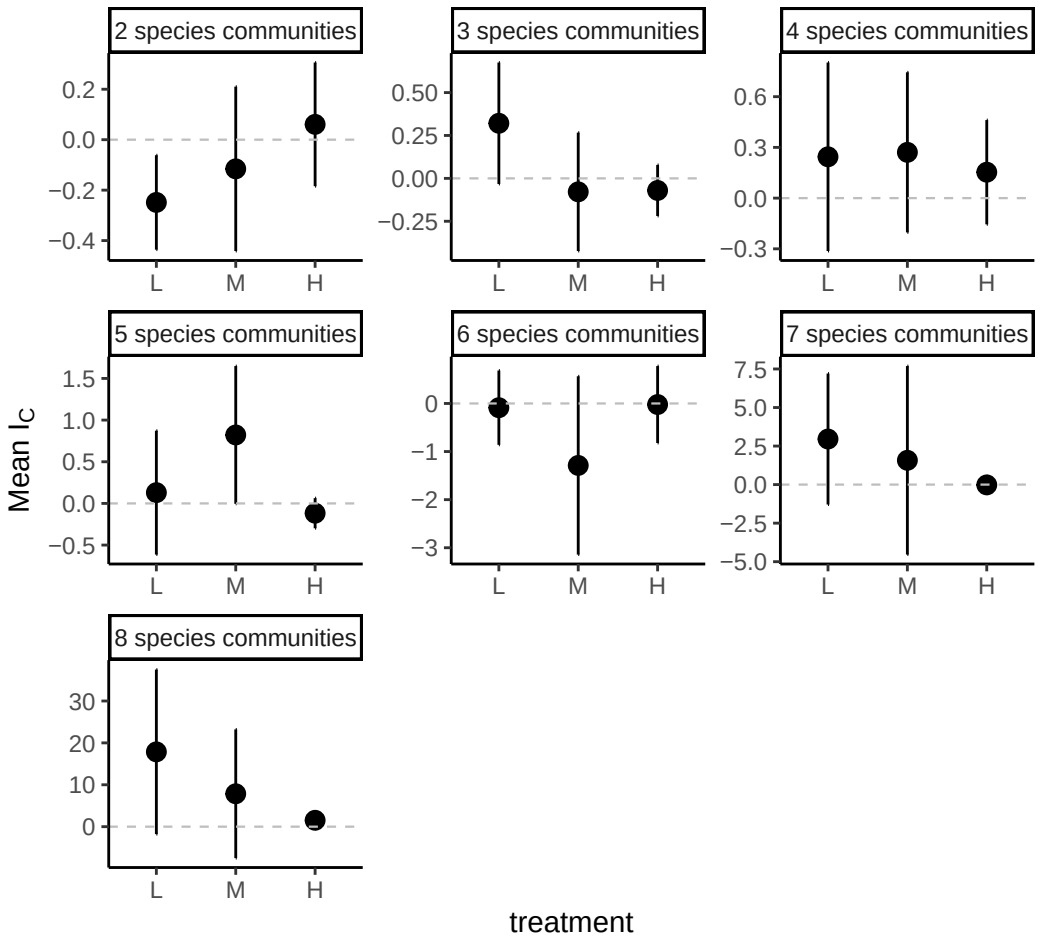
```
mutate(coms2 = map(all_Ics, ~pluck(.x,1)),
       coms3 = map(all_Ics, ~pluck(.x,2)),
       coms4 = map(all_Ics, ~pluck(.x,3)),
       coms5 = map(all_Ics, ~pluck(.x,4)),
       coms6 = map(all_Ics, ~pluck(.x,5)),
       coms7 = map(all_Ics, ~pluck(.x,6)),
       coms8 = map(all_Ics, ~pluck(.x,7))) %>%
# data managing: we can get rid of a few things and only focus on the IC columns
select(-data,  -interaction_matrix, -all_Ics) %>%
unnest(c(treatment, block)) %>%
# At this step, we get the mean value of $I_C$ for each n-species community
mutate(across(coms2:coms8, ~map_dbl(.x, mean))) %>%
# Clean out some columns that we don't need
select(block, treatment, coms2:coms8) %>%
# Calculate mean and SD of IC for each community size in each treatment
group_by(treatment) %>%
# Get the mean, standard deviation, and replicates per calculation
summarise(across(coms2:coms8, mean, .names = "{.col}_mean"),
          across(coms2:coms8, sd, .names = "{.col}_sd"),
          across(coms2:coms8, length, .names = "{.col}_nreps")) %>%
# Clean out some unsed columns
select(-(coms2_nreps:coms7_nreps), nreps = coms8_nreps) %>%
# Reshape the data in two steps:
# First, pivot it longer so that each sd/mean ends up on its own row
pivot_longer(coms2_mean:coms8_sd) %>%
# Then, clean up the names and pivot it wider so that mean/sd are in different columns
separate(name, into = c("which_comm", "which_value"), sep = "_") %>%
pivot_wider(names_from = which_value, values_from = value) %>%
# calculate SEM as sd/sqrt(n)
mutate(sem = sd/sqrt(nreps)) %>%

# NOTE: uncomment the following lines to make the Main Text Fig. S3;
# which focuses only on two- and three-species communities
# filter(which_comm %in% c("coms2", "coms3")) %>%
# mutate(which_comm = ifelse(which_comm == "coms2", "Species pairs", "Triplets")) %>%

mutate(which_comm = case_when(which_comm == "coms2" ~ "2 species communities",
                              which_comm == "coms3" ~ "3 species communities",
                              which_comm == "coms4" ~ "4 species communities",
                              which_comm == "coms5" ~ "5 species communities",
                              which_comm == "coms6" ~ "6 species communities",
                              which_comm == "coms7" ~ "7 species communities",
                              which_comm == "coms8" ~ "8 species communities")) %>%

ggplot(aes(x = treatment, y = mean, ymin = mean-sem*2, ymax = mean+sem*2)) +
geom_point(size = 3) +
```

```
  geom_errorbar(width = 0) +
  facet_wrap(.~which_comm, scales = "free") +
  ylab(latex2exp::TeX("Mean $I_C$")) +
  geom_hline(yintercept = 0, linewidth = 0.4, linetype = "dashed", color = "grey") +
  theme_classic()
```




```
# ggsave(filename = "figures/figS4.pdf", width = 5, height = 2)
```

Appendix S3: Derivation and implications of Bever (2003)'s model for plant–soil feedback among competing plants

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Bever (2003) presented the first modeling framework for integrating plant–soil feedback with the effects of direct competition among plants. One of the key results from this analysis was that sufficiently strong negative plant–soil feedback can enable coexistence of species pairs where the competitive dynamics by themselves result in exclusion.

In this Appendix, I briefly explain the derivation of this model, and focus on some implications of its specification for empirical applications. A more complete analysis of this model is presented in the original publication and in Revilla et al. (2013).

In the Bever (2003) model, the effects of plant–soil feedback and plant competition are integrated into a population dynamics model as follows:

$$\frac{dN_1}{dt} = r_1 N_1 (1 + m_{1A} S_A + m_{1B} S_B - \frac{N_1 + c_{12} N_2}{K_1}) \tag{S3.1}$$

Following the original parameter definitions, N_i is the abundance of plant i, r_i is the intrinsic population growth rate of plant i in the absence of soil conditioning (units: $\frac{1}{\text{time}}$), m_{iX} is the effect of microbial community X on plant species i (units: $\frac{1}{\text{microbe frequency}}$), K_i is plant i's carrying capacity in the absence of conditioning (units: abundance), and c_{ji} is the per-capita competitive effect of plant i on plant j, relative to the strength of plant j's intraspecific competitive effect (units: unitless).

While this model is in principle a simple extension of Bever et al. (1997)'s exponential growth model to incorporate intra- and interspecific competition, the specific formulation of the model implies subtle but important changes in our assumptions of how microbes alter plant population dynamics. A practical example helps illustrate the distinction.

Recall from Appendix 1 that in the Bever et al. (1997) model, the composition of the soil community directly (additively) increases or decreases the intrinsic growth rate of the plants. Thus, for example, the realized per-capita growth rate of plant 1 when growing alone (i.e. in soil entirely conditioned by plant 1, such that $S_A = 1$) is:

$$\text{Realized growth rate of plant 1 in soil A (1997 model)} = r_{1,\text{unconditioned soil}} + m_{1A} \tag{S3.2}$$

where r_1 is plant 1's growth rate in unconditioned soil.

In contrast, we can evaluate how soil microbes affect plant growth in the Bever (2003) model. To recreate a similar scenario of plant 1 growing alone in conspecific-conditioned soil, we set $S_A = 1$, and both plant densities to zero (i.e. $N_1 = N_2 = 0$). With these values, the per-capita growth rate of plant 1 is:

$$\begin{aligned}\text{Realized growth rate of plant 1 in soil A (2003 model)} &= r_{1,\text{unconditioned soil}}(1 + m_{1A}) \\ &= r_{1,\text{unconditioned soil}} + m_{1A} \times r_{1,\text{unconditioned soil}} \quad \text{(S3.3)}\end{aligned}$$

In other words, the specification of microbial effects in Eqn. S3.1 implies that the composition of the soil community causes a *proportional* increase or decrease in the intrinsic growth rate of the plant species, rather than an additive increase as in the exponential growth model. Thus, for a plant that grows in unconditioned soil at a rate of $r_{1,\text{unconditioned soil}} = 0.5$, a microbial effect of $m_{1A} = 0.2$ implies that it grows at a rate of $r_{1,\text{soil A}} = 0.7$ in the 1997 model, but $r_{1,\text{soil A}} = 0.6$ in the 2003 model.

The difference in model specification also has implications for how one analyzes experimental data, based on whether the goal is to parameterize the exponential growth model of Bever et al. (1997) or the competition model of Bever (2003). As explained in the main text and in Appendix 1, m_{iX} terms can be simply calculated as the difference in log-biomass of plants in conditioned vs. unconditioned soils, without any additional scaling (i.e. $m_{iX} = \log(B_{iX}) - \log(B_{i0})$). However, Eqn. S3.3 implies that when using these same data to parameterize the 2003 model, scaling by the growth rate in unconditioned soil becomes essential:

$$m_{iX} = \frac{\log(B_{iX}) - \log(B_{i0})}{\log(B_{i0})}$$