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E-Article

The Temporal Dimension of Plant-Soil Microbe Interactions: Mechanisms Promoting Feedback between Generations

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ABSTRACT: Soil microbes can influence plant competitive outcomes by stabilizing plant community dynamics or mediating plant competitive hierarchies. Which effect dominates depends on whether microbial effects can extend beyond the focal conditioning individual. While it is well known that microbial effects can extend to other individuals through space, we lack an explicit theoretical understanding of the factors that regulate their spread to other individuals in subsequent generations. Here, we examine how the commonly assumed stabilizing effects of host-specific pathogens in fact depend on two factors that allow microbial effects to be cross-generational—which plant demographic vital rate is influenced by microbes and the conditioning and decay rates of soil microbial communities. With a novel patch occupancy model that incorporates the transition of soil states following plant colonization and mortality, we show that host-specific pathogens enable plant coexistence when they suppress conspecific plant colonization of empty patches but contribute to competitive hierarchies when they modify only the mortality and fecundity of the conditioning plant individual. In a series of model extensions, we further demonstrate that these latter microbial effects can still promote coexistence, but only when microbial communities decay slowly following plant death, thereby allowing microbial effects to be cross-generational. Our study calls for further empirical work quantifying the demographic rates most affected by soil microbes as well as the timescales of conditioning and decay.

Keywords: coexistence, competitive hierarchy, decay rate, demographic process, Janzen-Connell hypothesis, plant-soil feedback.

Introduction

Reciprocal interactions between plants and soil microbes are increasingly recognized as a process shaping the structure of plant communities (Bever et al. 2010; van der Putten et al. 2013). These interactions are commonly studied under the framework of plant-soil feedback, a line of research that emphasizes the plant's ability to condition and cause species-specific changes in soil microbial communities that will feed back onto plant performance (Bever et al. 1997; Bever 2003). Theory suggests that soil microbes can influence plant competitive outcomes through two distinct channels (Stump and Comita 2018; Kandlikar et al. 2019; Ke and Wan 2020). On the one hand, soil microbes can stabilize plant dynamics and maintain plant community diversity by favoring species that drop to low abundance (Chung and Rudgers 2016; Siefert et al. 2019). On the other hand, soil microbes can favor a particular plant species over its competitors by influencing competitive hierarchies. The resulting competitive imbalances create variation in species' relative abundance (Klironomos 2002; Mangan et al. 2010) and, more generally, drive competitive exclusion. Given the two opposing effects of soil microbes, the next step is understanding how the biology of plant-soil microbe interactions predicts the relative importance of microbially mediated stabilization versus competitive hierarchies.

Host specificity of soil microbes has been recognized as one key factor determining how soil microbes influence plant competitive outcomes (Ke and Wan 2020). In particular, following the Janzen-Connell hypothesis (Janzen 1970; Connell 1971), host-specific pathogens are commonly thought to promote diversity and stabilize competitive dynamics in plant communities. Across various plant functional groups and ecosystems, studies have shown that plants generally perform worse when grown in soils conditioned by conspecifics, presumably because of the accumulation of host-specific pathogens (Kulmatiski et al. 2008; Crawford et al. 2019). Demographic models parameterized with this type of empirical data have further shown that negative effects of host-specific pathogens give species an advantage when rare, thereby maintaining plant diversity (Petermann et al. 2008; Chung and Rudgers 2016).

Importantly, such stabilization emerges because plant individuals harm other individuals of their own species

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through negative microbial effects more than they harm other individuals of other species (Chesson 2000). If, instead, a plant individual cultivates a pathogenic community that simply harms that conditioning individual itself, soil pathogens act as a factor controlling that plant's vital rates but cannot stabilize competitive dynamics; there is no opportunity for the conditioned pathogens to influence the fate of other plant individuals. Indeed, the dominant theory showing stabilization by plant-soil feedback achieves this effect by modeling a spatially well-mixed system, where plants contribute to a pool of pathogens whose negative effects influence all plant individuals in the system (Bever et al. 1997; Bever 2003). Building on these results, subsequent theoretical studies have explored the implications of spatially local negative microbial effects and shown that the spatial scale of microbial effects can influence plant competitive outcomes (Molofsky et al. 2002; Mack and Bever 2014; Stump and Chesson 2015).

While the role of the spatial extent in determining the consequences of plant-soil feedback for competitive dynamics is well established, the role of the temporal dimension is only beginning to be explored (e.g., Wubs et al. 2019; Hannula et al. 2020; De Long et al. 2021). Better understanding this latter dimension is critical because microbial effects can extend beyond conditioning individuals not only in space but also through time. This principally occurs when individuals affect other individuals in subsequent generations. Indeed, empirical approaches for measuring plant-soil microbe interactions acknowledge this temporal dimension when they measure an individual plant's response to soils previously conditioned by other individuals (Wubs and Bezemer 2018). However, existing theoretical studies often lack explicit details of the key factors that will determine the cross-generational extent of plant-soil feedback (Schroeder et al. 2020; Greenspoon and Wadhawan 2021)—namely, models rarely specify which demographic process is affected by pathogens (Bever 2003; Revilla et al. 2013), and some further assume that microbial dynamics equilibrate instantaneously compared with the dynamics of their plant counterparts (Bever et al. 2012; Kandlikar et al. 2019; Ke and Wan 2020). A deeper theoretical understanding of the temporal dimensions of plant-soil feedback requires exploring the two factors that determine how microbial effects transfer between plant generations—(1) the plant demographic process affected by soil microbes and (2) the accumulation and decay rates of microbial effects.

Soil pathogens affect various stages of plant demography, including seed survival (Dalling et al. 1998), seedling recruitment (Augspurger 1984), plant biomass growth (Mangan et al. 2010), and adult mortality (Roy et al. 2014; Bever et al. 2015). Depending on which plant demographic vital rate they affect, some pathogens are more likely to influence subsequent plant generations than others (Chu and Adler 2015). For example, empirical work suggests that some pathogens impact the performance of the plant individual conditioning the soil, while others may affect the demographic rates of subsequent generations (Hannula et al. 2020; De Long et al. 2021). Therefore, the demographic context of plant-soil microbe interactions represents one pathway through which microbial effects can become cross-generational. However, empirical studies mostly quantify microbial effects by measuring the biomass growth of individual plants (Lekberg et al. 2018; Crawford et al. 2019; but see Dudenhöffer et al. 2018), and classic models typically abstract multiple plant demographic rates into a single growth parameter affected by soil microbes (Bever et al. 1997; Bever 2003; Revilla et al. 2013). As a result, the demographic context of plant-soil microbe interactions is often ambiguous, and how it influences microbially mediated stabilization remains understudied.

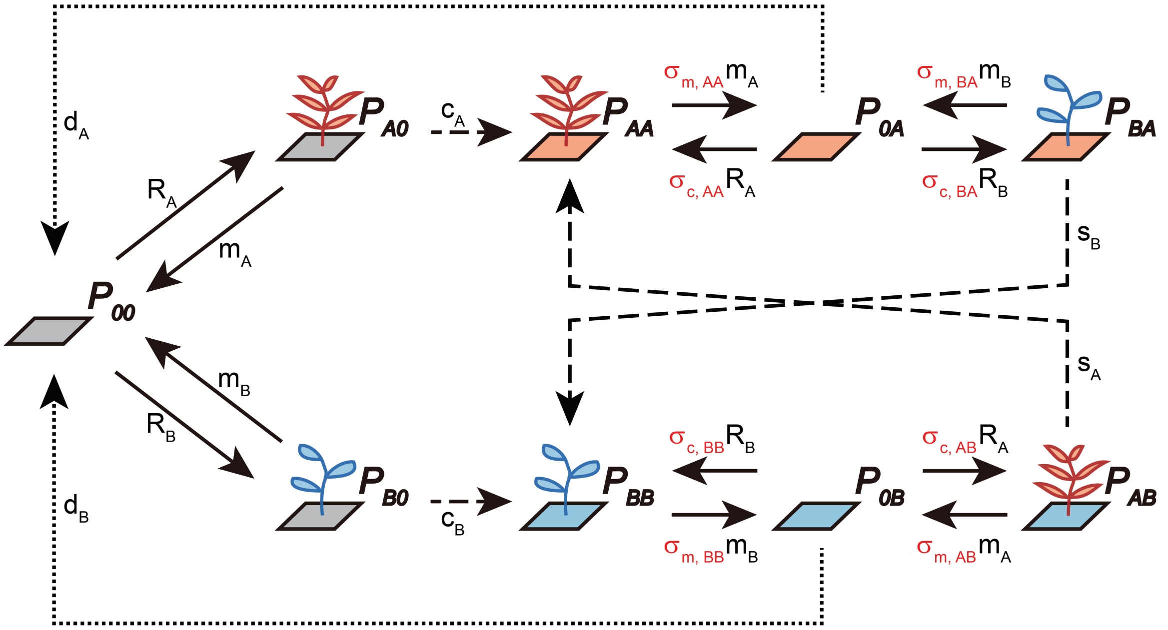
The other key controls over how plant-soil microbe interactions extend between generations is the rate of soil conditioning by colonizing plants as well as the rate of microbial community decay when plants turnover. Theoretical studies often assume that the conditioning and decay of soil microbial communities happen instantaneously following plant colonization and death (Bever et al. 2012; Kandlikar et al. 2019; Ke and Wan 2020). However, this assumption is at odds with empirical studies, which show that the buildup and collapse of microbial communities is a gradual process, calling for a more realistic representation when modeling microbial dynamics (Umbanhowar and McCann 2005; Jiang et al. 2020; Schroeder et al. 2020). Importantly, the decay rate of microbial effects provide another pathway that allows plant-soil feedback to become cross-generational, but this relationship is obscured when assuming instantaneous microbial dynamics. Moreover, the temporal scale necessary for microbial effects to be cross-generational may depend on the demographic context of plant-soil microbe interactions. The temporal scale of microbial effects therefore represents another factor that predicts how soil microbes influence plant competitive outcomes.

In this study, we explore how the temporal dimension of plant-soil feedback—namely, the demographic context as well as the rates of microbial conditioning and decay—predict the degree to which host-specific pathogens stabilize plant competitive interactions or drive competitive hierarchies. We hypothesize that the effects of these two factors on competitive outcomes depends on whether they enable microbial effects to extend between plant generations. To evaluate this hypothesis, we develop a novel patch occupancy model that formulates the stepwise ecological processes involved in plant-soil microbe interactions: plant colonization of local sites, development of soil microbial effects via soil conditioning, plant death followed by the release of sites with a microbial legacy, and the recolonization or decay of conditioned sites (see fig. 1). Moreover, the patch occupancy modeling framework decomposes plant population growth process into various demographic stages, allowing us to study the consequences of different plant demographic responses to soil pathogens. Although the model can be applied to various microbial functional groups that interact with plants in various ways, here we focus on host-specific pathogens to exemplify how the temporal dimensions of plant-soil microbe interactions affect plant competitive outcomes. Specifically, we ask: Do host-specific pathogenic effects on different demographic rates (e.g., seedling colonization versus adult fecundity) lead to different competitive outcomes, and what type of soil conditioning and decay are required for microbial effects on different demographic rates to extend to individuals in subsequent generations? In a series of analytically tractable model extensions, we specify the mechanisms that allow microbial effects to be cross-generational and thereby stabilize plant interactions.

Model

General Patch Occupancy Model for Plant-Soil Microbe Dynamics

Here, we first introduce our general patch occupancy model for studying plant-soil microbe dynamics and then demonstrate how different demographic effects of host-specific pathogens can be incorporated. Our model assumes that the landscape can be divided into an infinite number of sites, each being the size of a single plant individual. In our model, plant individuals can colonize only empty sites (i.e., replacement competition, sensu Yu and Wilson 2001) and cannot displace established individuals from the sites



* $R_A = r_A(P_{A0} + \sigma_{f,AA} P_{AA} + \sigma_{f,AB} P_{AB})$; $R_B = r_B(P_{B0} + \sigma_{f,BA} P_{BA} + \sigma_{f,BB} P_{BB})$

Figure 1: Patch occupancy model for studying the dynamics of plant-soil microbe interactions. Our model tracks the transition between sites that belong to different plant-soil microbe states, indicated in the figure by various combinations of differently colored plants and soil patches (i.e., orange colors: plant *A* and its associated soil microbes; blue colors: plant *B* and its associated soil microbes). We use the notation P_{ij} to indicate sites that are now colonized by plant species *i* but have soil microbes associated with plant species *j* as a result of previous soil conditioning. Here, *i* and *j* can take values of *A*, *B*, or 0, where $i = 0$ indicates sites that are not colonized by plants (i.e., only soil patch) and $j = 0$ indicates sites that have no recent plant-conditioning history (i.e., gray soil patch). Solid arrows represent state changes resulting from plant colonization and death (with rates R_i and m_i, respectively). Here, R_i equals $r_i(P_{i0} + P_{iA} + P_{iB})$ for the colonization model and the mortality model, whereas R_i equals $r_i(P_{i0} + \sigma_{f,iA}P_{iA} + \sigma_{f,iB}P_{iB})$ for the fecundity model; r_i is the colonization rate of plant *i*. Dashed arrows represent state changes resulting from soil conditioning by plants (with rates c_i and s_i). Dotted arrows represent state changes resulting from the decay of microbial communities (with rates d_i). Red symbols represent how soil microbes modify three different plant demographic vital rates: the colonization rate of seedlings ($\sigma_{c,ij}$), the mortality rate of established individuals ($\sigma_{m,ij}$), and the fecundity of established individuals ($\sigma_{f,ij}$).

that they occupy (e.g., as in Tilman 1994). We characterize sites by their plant-soil microbe state, using the notation P_{ij} to indicate sites that are now occupied by plant species i but have soil microbes associated with plant species j because of previous soil conditioning. We consider competition between two plant species, plants A and B. Therefore, i and j can take values of A, B, or 0, where $i = 0$ indicates sites that are not colonized by plants and $j = 0$ indicates sites that have no recent plant conditioning history. For example, P_{00} represents unoccupied sites without plant-specific microbial communities; P_{A0} represents sites occupied by plant A but soil microbes are yet to be conditioned into any plant-specific state; P_{AA} indicates that plant A is growing on sites with soil microbes specific to plant A; P_{0A} represents sites that are currently unoccupied but have soil microbes that were associated with plant A. At the landscape scale, P_{ij} represents the proportion of sites belonging to a particular plant-soil microbe state, and its dynamics, dP_{ij}/dt, summarizes the processes of plant colonization and death.

Unconditioned sites can be colonized by the two plant species. This causes the transition from P_{00} to P_{A0} or P_{B0}. The proportion of sites belonging to these three unconditioned soil states have dynamics that can be described by the following equations:

$$\frac{dP_{00}}{dt} = -r_A P_{AX} P_{00} - r_B P_{BX} P_{00} + m_A P_{A0} + m_B P_{B0} + d_A P_{0A} + d_B P_{0B}, \tag{1}$$

$$\frac{dP_{A0}}{dt} = r_A P_{AX} P_{00} - m_A P_{A0} - c_A P_{A0}, \tag{2}$$

$$\frac{dP_{B0}}{dt} = r_B P_{BX} P_{00} - m_B P_{B0} - c_B P_{B0}. \tag{3}$$

The first two terms in equation (1) (and correspondingly the first term in eqq. [2] and [3] with opposite sign) represent transitions from P_{00} to P_{i0} ($i = A$ or B) due to plant colonization. The rate of propagule production by plant species i depends on the plant's colonization rate, r_i, and the total proportion of sites occupied by the plant, P_{iX} ($= P_{i0} + P_{iA} + P_{iB}$, i.e., plant i on all possible soil types). This term is denoted as R_i in figure 1 and is then multiplied by the proportion of unoccupied sites to give the production rate of newly colonized sites. The third and fourth terms in equation (1) (and correspondingly the second term in eqq. [2] and [3] with opposite sign) describe the rate at which sites become vacant as a result of plant death, with m_i being plant-specific mortality rates. These two terms represent the death of plants before they could condition the soil. The final two terms in equation (1) describe the decay (at rate d_i) of plant-specific microbial communities in sites that are no longer occupied, P_{0i} (see eqq. [8] and [9]). Last, the conditioning of plant-specific microbial communities (at rate c_i) is described by the third term in equations (2) and (3). Here, c_i represents a plant's ability to condition microbial communities.

Once plants are established in previously unconditioned sites, they will begin to condition the soil to form its specific microbial community, assuming that microbial communities associated with different plants are distinct from each other. In the model, this is captured by the transition of P_{A0} and P_{B0} into P_{AA} and P_{BB}, respectively. This necessary transition from P_{i0} to P_{ii} formalizes the fact that conditioning of soil microbes is not an instantaneous process but instead proceeds at rates specific to different plant species (Hoeksema et al. 2010; Knelman et al. 2012). Following the death of plant individuals, sites become unoccupied but have a remaining microbial legacy, denoted as P_{0A} and P_{0B}, and are available for subsequent colonization by plant propagules. These sites may be recolonized by either conspecifics (i.e., P_{AA} and P_{BB}) or heterospecifics (i.e., P_{BA} and P_{AB}). The dynamics of these occupied sites with a conditioned soil microbial community are as follows:

$$\frac{dP_{AA}}{dt} = c_A P_{A0} + r_A P_{AX} P_{0A} + s_A P_{AB} - m_A P_{AA}, \tag{4}$$

$$\frac{dP_{BB}}{dt} = c_B P_{B0} + r_B P_{BX} P_{0B} + s_B P_{BA} - m_B P_{BB}, \tag{5}$$

$$\frac{dP_{BA}}{dt} = r_B P_{BX} P_{0A} - s_B P_{BA} - m_B P_{BA}, \tag{6}$$

$$\frac{dP_{AB}}{dt} = r_A P_{AX} P_{0B} - s_A P_{AB} - m_A P_{AB}. \tag{7}$$

The first term in equations (4) and (5) represents the increase in these occupied and conditioned sites due to soil conditioning (i.e., from the last term of eqq. [2] and [3]). The second term in equations (4) and (5), as well as the first term in equations (6) and (7), represents the increase in these plant-soil microbe states due to the recolonization of unoccupied but conditioned sites, P_{0j}. Similar to previous equations, the increase rate of newly colonized sites P_{ij} is the product of propagule production, $r_i P_{iX}$ (i.e., R_i in fig. 1), and available sites, this time P_{0j}. The third term in equations (4) and (5) (and correspondingly the second term in eqq. [7] and [6] with opposite sign) represents the transition of soil microbial state. This happens when plants recolonize sites that were previously conditioned by heterospecifics and are now imposing their own conditioning effects, turning the state from P_{AB} to P_{AA} and from P_{BA} to P_{BB}. We assume that interactions with members of the original heterospecific microbial community slow the invasion of microbes associated with the new plant individual (Kurkjian et al. 2021). As a result, the conditioning rate on a previously conditioned site, s_i, is slower than c_i, as it involves both the disassembly of the original microbial community and the establishment of plant i's microbial community. Finally, the last term in equations (4)–(7) represents plant death on conditioned soil, which turns P_{AA} and P_{BA} to P_{0A} with rates m_A and m_B, respectively (i.e., the first two terms in eq. [8]). The same dynamics apply to the transition of sites from P_{BB} and P_{AB} to P_{0B} (i.e., the first two terms in eq. [9]).

The dynamics of conditioned but unoccupied sites, P_{0A} and P_{0B}, follow the dynamics of other plant-soil microbe states. In particular, the proportion of P_{0A} and P_{0B} increase as a result of plant death and decrease as they are recolonized, which can be described by the following equations:

$$\frac{dP_{0A}}{dt} = m_A P_{AA} + m_B P_{BA} - r_A P_{AX} P_{0A} - r_B P_{BX} P_{0A} - d_A P_{0A}, \tag{8}$$

$$\frac{dP_{0B}}{dt} = m_B P_{BB} + m_A P_{AB} - r_B P_{BX} P_{0B} - r_A P_{AX} P_{0B} - d_B P_{0B}. \tag{9}$$

The final term in equations (8) and (9) represents the decay of microbial communities, turning P_{0i} back to P_{00} (i.e., the final two terms in eq. [1]) with a decay rate specific to each microbial community, d_i. We assume that microbial communities only decay in unoccupied sites because of the lack of plant-derived resources, such as root exudates. Importantly, the existence of an unoccupied state with only soil microbes (i.e., a legacy plant-soil microbe state) formalizes the fact that soil microbial communities may not die off instantaneously with plant death but instead can be long-lasting and affect the performance of future colonizing individuals.

Effects of Soil Microbes on Plant Demographic Vital Rates

Soil microbes can affect various plant demographic vital rates throughout a plant's life span (Bever et al. 2015; Dudenhöffer et al. 2018). Taking advantage of the stepwise formulation of our patch occupancy model, we assume that soil microbes inhabiting conditioned soils can affect three different plant demographic vital rates: the colonization rate of seedlings, the mortality rate of established adult individuals, and the fecundity of established adult individuals (fig. 1). In this study, we simulate dynamics for the full model (including microbial effects on all three demographic vital rate) as well as for three separate models, each of which allows microbes to affect only a single plant vital rate—colonization, mortality, or fecundity. Below we explain how these microbial effects on various plant vital rates are incorporated into our general patch occupancy framework.

First, soil microbes may affect the establishment of seedlings, an effect mostly studied in the context of the Janzen-Connell hypothesis (Janzen 1970; Connell 1971). This effect of soil microbes modifies the recolonization rate of propagules on conditioned but unoccupied soils (i.e., the second term in eqq. [4] and [5]; the first term in eqq. [6] and [7]; corresponding terms in eqq. [8] and [9]). In particular, recolonization by conspecifics, $r_A P_{AX} P_{0A}$ and $r_B P_{BX} P_{0B}$, are multiplied by $\sigma_{c,AA}$ and $\sigma_{c,BB}$, respectively. Similarly, recolonization by heterospecifics, $r_B P_{BX} P_{0A}$ and $r_A P_{AX} P_{0B}$, are multiplied by $\sigma_{c,BA}$, and $\sigma_{c,AB}$, respectively. Here, we use the parameter $\sigma_{c,ij}$ to represent the effects that soil microbes associated with plant j have on propagules of plant i, with subscript c indicating effects on colonization. A value less than 1 represents a detrimental microbial effect of soil j, consistent with the pathogenic effects studied here (values greater than 1 would represent facilitation). See equations (S1a)–(S1i) and figure S1 in appendix A (figs. S1–S7 and apps. A–C are available online) for the specific equations of this model, which we will call the "colonization model."

Second, soil microbes may affect the mortality of established host individuals (e.g., Roy et al. 2014; Bever et al. 2015). In our model, this effect of soil microbes modifies plant mortality rates when growing in soils with a conditioning history (i.e., the last term in eqq. [4]–[7]; corresponding terms in eqq. [8] and [9]). In particular, terms representing plant death on conspecific-conditioned soils, $m_A P_{AA}$ and $m_B P_{BB}$, are multiplied by $\sigma_{m,AA}$ and $\sigma_{m,BB}$, respectively. Similarly, plant death on heterospecific-conditioned soils, $m_A P_{AB}$ and $m_B P_{BA}$, are multiplied by $\sigma_{m,AB}$ and $\sigma_{m,BA}$, respectively. We use the parameter $\sigma_{m,ij}$ to capture the effects of plant j's soil microbes on plant i, with subscript m indicating effects on plant mortality. Since $\sigma_{m,ij}$ directly modifies the plant's mortality rate, a value greater than 1 results in greater mortality and therefore represents a detrimental microbial effect (a value less than 1 represents a facilitative effect). See also equations (S2a)–(S2i) and figure S2 in appendix A for the specific equations of this model, which we will call the "mortality model."

Finally, soil microbes can modify plant population growth rate through affecting reproduction. This effect is closest to that quantified in most empirical studies if one assumes a linear scaling between an individual's biomass growth and fecundity. We assume that soil microbes affect reproduction by causing the propagule production rate of plant A to be more complicated than the simple multiplication of r_A and its total occupancy (i.e., R_A in fig. 1 is no longer $r_A(P_{A0} + P_{AA} + P_{AB})$, as in previous models). Instead, this production rate depends on the soil in which plant individuals are growing, that is, $r_A(P_{A0} + \sigma_{f,AA} P_{AA} + \sigma_{f,AB} P_{AB})$. Similarly, the propagule production rate for plant B becomes $r_B(P_{B0} + \sigma_{f,BA} P_{BA} + \sigma_{f,BB} P_{BB})$. In equations (S3a)–(S3i), this microbially mediated propagule production rate for plant i is denoted as $r_i\phi_i$. We use the parameter $\sigma_{f,ij}$ to represent how soil microbes of plant j modify the fecundity of plant i, and a value less (greater) than 1 means that a plant's fecundity is suppressed (enhanced) in the presence of soil microbes. We will call this specific model the "fecundity model" (see eqq. [S3a]–[S3i] and fig. S3 in app. A for specific equations).

Results

Plant Demographic Rate Affected by Soil Microbes Predicts Consequences for Competitive Outcome

We first simulate the competitive dynamics for the full model, where soil microbes affect all three demographic rates (i.e., seedlings' colonization rate and adult individuals' mortality rate and fecundity). We set the parameters such that plant B is the superior competitor in the absence of soil microbial effects because of its lower mortality (i.e., $r_A = r_B$ but $m_B < m_A$). We consider the case where soil microbes are host-specific pathogens (Kulmatiski et al. 2008; Crawford et al. 2019), a case where past studies predict effects that are purely stabilizing. Without loss of generality, we set heterospecific microbial effects to be neutral (i.e., $\sigma_{k,AB}$ and $\sigma_{k,BA} = 1$ for all three demographic rates; k is one of c, m, or f), whereas conspecific microbial effects are set to be detrimental ($\sigma_{c,ii}$ and $\sigma_{f,ii} < 1$ while $\sigma_{m,ii} > 1$). Numerical simulations with different parameter combinations are performed in the C language using the fourth-order Runge-Kutta method, and simulated plant competitive outcomes are further visualized using R version 3.6.1 (scripts underlying the results have been deposited in the Dryad Digital Repository; https://doi.org/10.5061/dryad.0cfxpnw20; Ke and Levine 2021).

After simulating plant competition for numerous sites across the landscape, we summarize the competitive outcome in a two-dimension parameter space of c_A and c_B, the soil conditioning rates for the two species. The soil conditioning rate determines how strongly the plant experiences detrimental microbial effects, thereby influencing the competitive outcome (fig. 2*A*). Specifically, in the full model, plant A excludes plant B when the harmful effects of soil pathogens on plant B quickly accumulate (fig. 2*B*); the two plant species coexist at an intermediate value of plant B's soil conditioning rate (fig. 2*C*); finally, plant B excludes plant A when the pathogenic effect influencing its performance accumulate slowly (fig. 2*D*).

To study how the demographic context of plant-soil microbe interactions influences the relative importance of microbially mediated stabilization versus competitive hierarchies, we further simulate the competitive dynamics for three separate demographic models, where the microbes affect colonization, mortality, and fecundity, respectively. Specifically, in each of the three demographic models, only one set of microbial effects operates (i.e., only one of $\sigma_{c,ii}$, $\sigma_{m,ii}$, or $\sigma_{f,ii}$ was not equal to 1). We find that when host-specific pathogens influence the seedling colonization rate of empty patches (i.e., the colonization model), detrimental microbial effects are strongly stabilizing—the two plant species coexist above a minimum conditioning rate for plant B (fig. 3*A*). The stabilizing effects in this model arise because host-specific pathogens suppress the recolonization of conspecific individuals more than heterospecific individuals. Hence, as the occupancy of a plant species increases, the proportion of unoccupied sites with its host-specific pathogen also increases, hindering its recruitment. This provides its competitor an opportunity to increase in their occupancy. Host-specific pathogens in this model thereby generate negative frequency-dependent community dynamics that stabilize plant coexistence.

However, when host-specific pathogens increase the mortality rate (i.e., the mortality model) or decrease the fecundity (i.e., the fecundity model) of established host individuals, varying soil conditioning rates changes the plants' competitive hierarchy (fig. 3*B*, 3*C*). In these two models, we see dynamics that are similar to that of the full model—the plant species with the faster conditioning rate becomes the inferior competitor because it experiences the detrimental microbial effects more strongly (although coexistence is still possible under some parameter combinations; see below). The strong effects of host-specific pathogens on plant competitive hierarchies in the mortality- and fecundity-based models emerge because microbes directly modify the mortality rate and fecundity of the conditioning plant individual that is growing in the conditioned soil. That is, microbes determine the mortality and fecundity of the conditioning individual and essentially become part of the individual's trait.

Soil Decay Rates Allowing Cross-Generational Microbial Effects That Promote Coexistence

To further understand how microbially mediated stabilization and competitive hierarchies operate, we analyze simplified versions of the model that vary in their assumptions about the soil conditioning and decay process (i.e., the temporal extent of microbial effects; fig. 4). These simplifications allow us to study the system's behavior through invasion growth rates, generating predictions that are independent of the specific set of parameters.

We first consider a simplified model where both the conditioning and the decay of soil microbial communities are assumed to occur infinitely fast, and therefore P_{00} and P_{ii} directly and instantaneously transition between one another following the colonization and death of plant individuals (fig. 4*A*). Once conditioned, we assume that

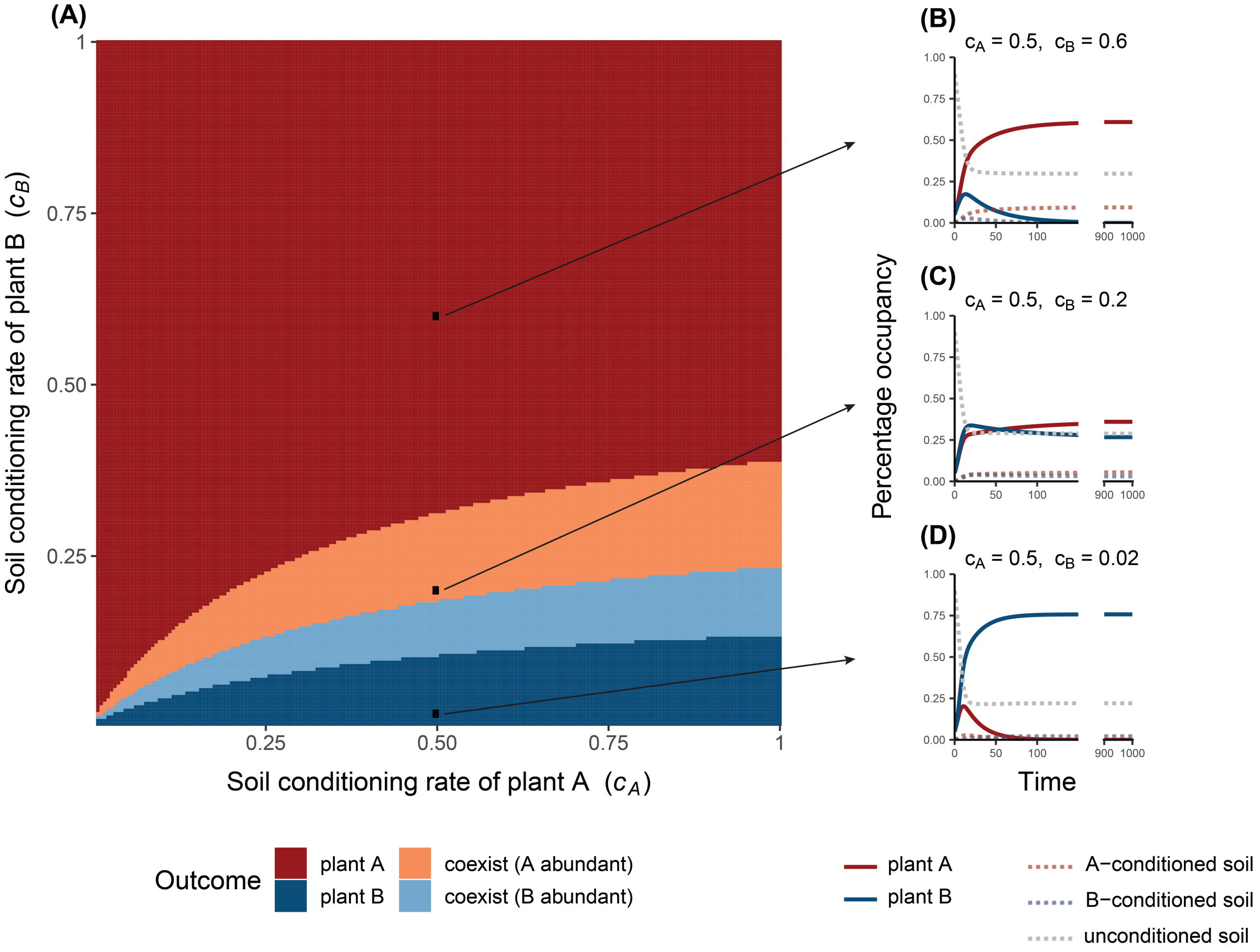


Figure 2: Effects of varying plant-specific soil conditioning rate, c_A and c_B, on plant competitive outcome when host-specific pathogens influence all three demographic rates (i.e., the full model, where plant colonization, mortality, and fecundity are all affected). *A*, Different competitive outcomes in the soil-conditioning rate (c_A–c_B) parameter space. *B–D*, Time series showing different competitive outcomes, spanning from plant *A* dominating (*B*), to two plants coexisting (*C*), to plant *B* dominating with slower conditioning rate of plant *B* (*D*). Lines show the trajectories of different patch states (red solid line: plant *A* on all soil types, $P_{A0} + P_{AA} + P_{AB}$; blue solid line: plant *B* on all soil types, $P_{B0} + P_{BA} + P_{BB}$; gray dotted line: unoccupied and unconditioned soil, P_{00}; red dotted line: unoccupied soil with microbes associated with plant *A*, P_{0A}; blue dotted line: unoccupied soil with microbes associated with plant *B*, P_{0B}). Numerical simulations start with the majority of sites being unoccupied and unconditioned (i.e., $P_{00}(0) = 0.9$, $P_{A0}(0) = 0.05$, $P_{B0}(0) = 0.05$). Parameters for microbial effects: $\sigma_{c,AA} = 0.7$, $\sigma_{c,BB} = 0.5$, $\sigma_{m,AA} = 1.3$, $\sigma_{m,BB} = 1.5$, $\sigma_{f,AA} = 0.7$, $\sigma_{f,BB} = 0.5$. All heterospecific microbial effects are set to 1. Other parameters: $r_A = r_B = 0.5$, $m_A = 0.11$, $m_B = 0.1$, $d_A = d_B = 0.6$, $s_i = d_j \times c_i$.

host-specific pathogens negatively affect both the mortality and the fecundity of the conditioning plant individual. Invasion analysis (app. B, sec. B.1) shows that $(r_A\sigma_{f,AA})/(m_A\sigma_{m,AA})$ needs to be greater than $(r_B\sigma_{f,BB})/(m_B\sigma_{m,BB})$ for plant *A* to invade the monoculture of plant *B*, whereas the opposite is true for plant *B* to invade the monoculture of plant *A*. Since these two criteria cannot be fulfilled simultaneously, mutual invasibility—and therefore stable coexistence of the two plant species—cannot be achieved (fig. 4*D*). Instead, the plant with a higher realized fecundity to mortality ratio after accounting for microbial effects, $(r_i\sigma_{f,ii})/(m_i\sigma_{m,ii})$, dominates the community. Here, we can observe that soil microbial effects act as direct modifiers of a plant's innate mortality rate and fecundity, essentially becoming an "extended phenotype" (sensu Dawkins 1982) of the plant and not providing a pathway to plant coexistence. Similar conclusions can be derived from a second simplified model where the soil conditioning process does not proceed at infinitely fast rates but soil decay still occurs instantaneously (i.e., the inclusion of unconditioned states, P_{i0}; fig. 4*B*, 4*E*; see also app. B, sec. B.2). In sum, an infinitely fast decaying microbial effect removes the opportunities for coexistence observed in the mortality and fecundity model simulations with slower decay rates (fig. 3*B*, 3*C*).

A final simplified model can be used to show that pathogenic microbial effects on the colonization of conspecifics necessarily stabilize plant coexistence, even in the presence of microbially mediated competitive hierarchies through mortality and fecundity effects. We consider a model where the decay process of soil microbes does not proceed at infinitely fast rates (but soil conditioning occurs instantaneously; fig. 4*C*), which retains the legacy plant-soil microbe state, P_{0i}, and thereby gives pathogens the opportunity to affect nonfocal individuals via influencing the colonization process. Based on findings from prior simplified models, microbial effects on mortality and fecundity in this model should still contribute only to competitive exclusion. This is because successfully colonizing individuals instantaneously cultivate their own soil community and therefore cannot experience higher mortality (or lower fecundity) owing to the prior presence of conspecifics. Microbial effects on colonization, by contrast, provide the potential for stabilization. Indeed, invasion analysis (app. B, sec. B.3) shows that coexistence is not possible when pathogens do not limit conspecific more than heterospecific colonization ($\sigma_{c,AA}$ and $\sigma_{c,BB}$ also equal 1); under such a condition, the species with larger $(r_i\sigma_{f,ii})/(m_i\sigma_{m,ii})$ dominates. In this simplified model, coexistence is possible only when pathogens have stronger detrimental effects on the colonization of conspecific plants ($\sigma_{c,AA}$ and $\sigma_{c,BB} < 1$). Under such conditions, we can, for example, derive a critical soil decay rate, above which the detrimental microbial effects degrade too rapidly to limit the superior competitor from dominating but below which the two plants can coexist (fig. 4*F*; see also app. B, sec. B.3).

Importantly, by comparing across the three simplified models, we can highlight a general requirement for microbially mediated stabilization. That is, soil microbial effects need to have impacts that extend beyond the focal conditioning host individual. Since plants in our model only compete for empty sites, to fulfill this requirement soil microbial effects must outlive their host and remain as a legacy effect in order to impact nonhost individuals

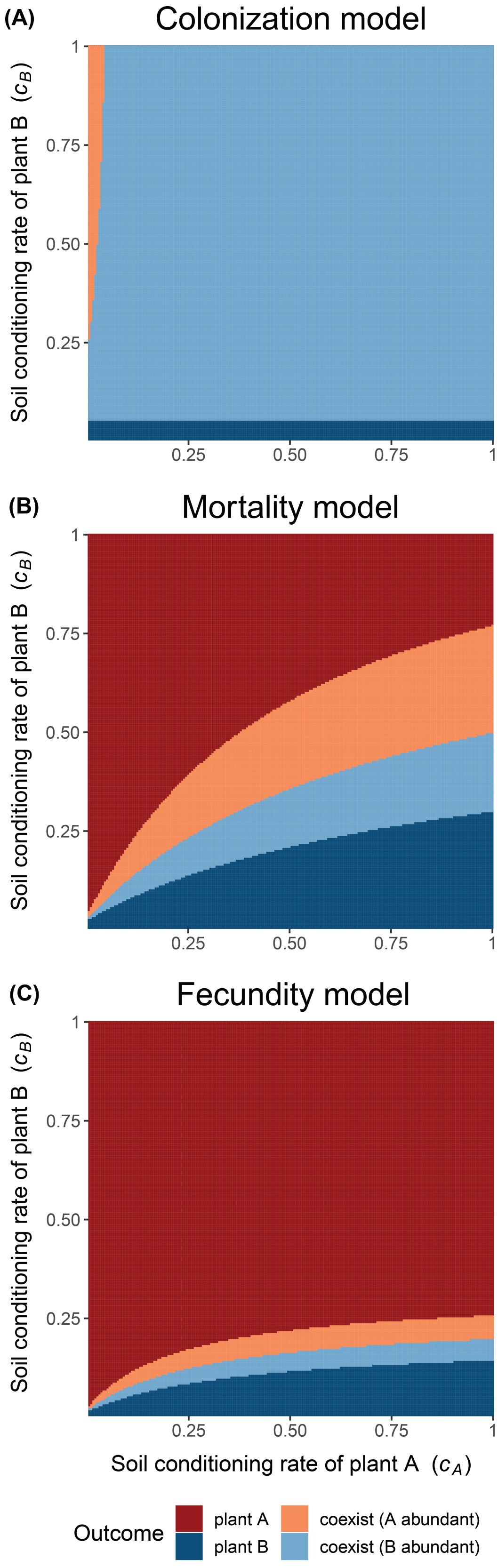


Figure 3: Effects of varying plant-specific soil conditioning rate, c_A and c_B, on plant competitive outcome for the three separate demographic models: the colonization model (*A*), the mortality model (*B*), and the fecundity model (*C*). Grid colors indicate different competitive outcomes. Soil microbes in these three models are assumed to be host-specific pathogens, and the detrimental conspecific microbial effects are stronger for plant *B*: $\sigma_{c,AA} = 0.7$, $\sigma_{c,BB} = 0.5$ (*A*); $\sigma_{m,AA} = 1.3$, $\sigma_{m,BB} = 1.5$ (*B*); and $\sigma_{f,AA} = 0.7$, $\sigma_{f,BB} = 0.5$ (*C*). All heterospecific microbial effects are set as 1. See figure 2 for other parameter values.

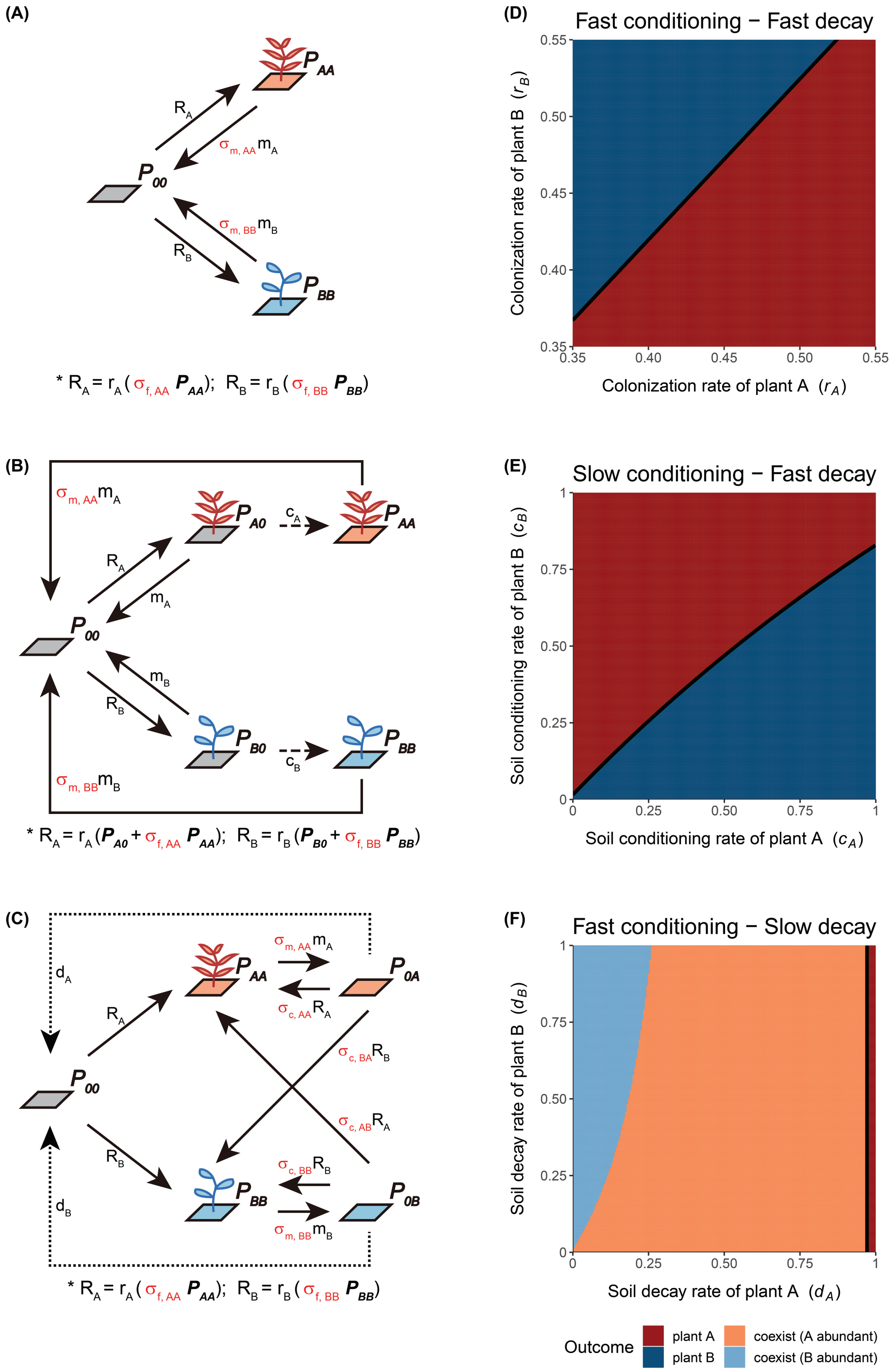


Figure 4: Simplified patch occupancy models that vary in their assumptions about the dynamical rates of soil microbial communities: both conditioning and decay proceed at infinitely fast rates (*A*), only the decay process proceeds infinitely fast (*B*), and only the conditioning process proceeds infinitely fast (*C*). *A*–*C* show flow diagram for each simplified model, with soil microbial effects highlighted in red (see also fig. 1 for notation and parameter definition). *D* and *E* illustrate the effects of soil microbes on plant competitive hierarchies, whereas *F* illustrates the potential for plant coexistence when the model incorporates legacy plant-soil states. We varied plant colonization rate r_A and r_B in *D*, soil conditioning rate c_A and c_B in *E*, and soil decay rate d_A and d_B in *F*. Black solid lines in *D*–*F* are invasion boundaries derived from analytical analyses in appendix B, whereas grid colors indicate simulated competitive outcomes under different parameter combinations. Parameters used in these simulations: $r_A = r_B = 0.5$, $m_A = 0.11$, $m_B = 0.1$, $\sigma_{m,AA} = 1.3$, $\sigma_{m,BB} = 1.5$, $\sigma_{f,AA} = 0.5$, $\sigma_{f,BB} = 0.5$, $\sigma_{c,AA} = 0.5$, $\sigma_{c,BB} = 0.5$, $\sigma_{c,AB} = \sigma_{c,BA} = 1.0$.

(i.e., operate at a longer temporal scale). This is why coexistence is possible in the final simplified model, where individuals harm the colonization of conspecifics through microbial effects (fig. 4*F*); by definition, this is a cross-generational effect. This is also why coexistence is not possible in the first two simplified models (fig. 4*D*, 4*E*)—the impacts of host-specific pathogens are confined to the conditioning host individual and can only alter plant competitive hierarchy because their effects immediately decay following plant death. This contrasts with the formation of legacy soil states allowing coexistence in the mortality- and fecundity-based simulation models (fig. 3*B*, 3*C*), where soil conditioning lasts beyond the death of the conditioning individual and is not instantaneously erased by the new colonizing individual.

This general rule indicates that microbially mediated stabilization is driven by both the demographic rate affected by soil microbes and the decay rate of microbial effects, a result illustrated in figure 5. Here, for our three separate demographic models, we perform simulations across the c_A–c_B parameter space (i.e., as in fig. 3) with different underlying values of soil decay rate, d_A and d_B, and summarize the proportion of different competitive outcomes. When microbial effects decay slowly following plant death (i.e., decreasing d_A and d_B), the strong effects of soil microbes on plant competitive hierarchies in the mortality and fecundity models are greatly ameliorated (fig. 5*B*, 5*C*). On the other hand, the opportunity for coexistence in the colonization model remains high under different soil decay rates (fig. 5*A*). This is because, as noted in the prior paragraph, soil microbial effects in the colonization model, by definition, are cross-generational, since they influence the recolonization process of future seedlings, whereas in the mortality- and fecundity-based models, microbial effects rely on their slow decay in order to become cross-generational. A similar pattern can be observed when microbial effects are no longer constrained locally but instead operate at a spatial scale larger than the individual (see app. C and fig. S7 for a spatial analog of the temporal mechanism).

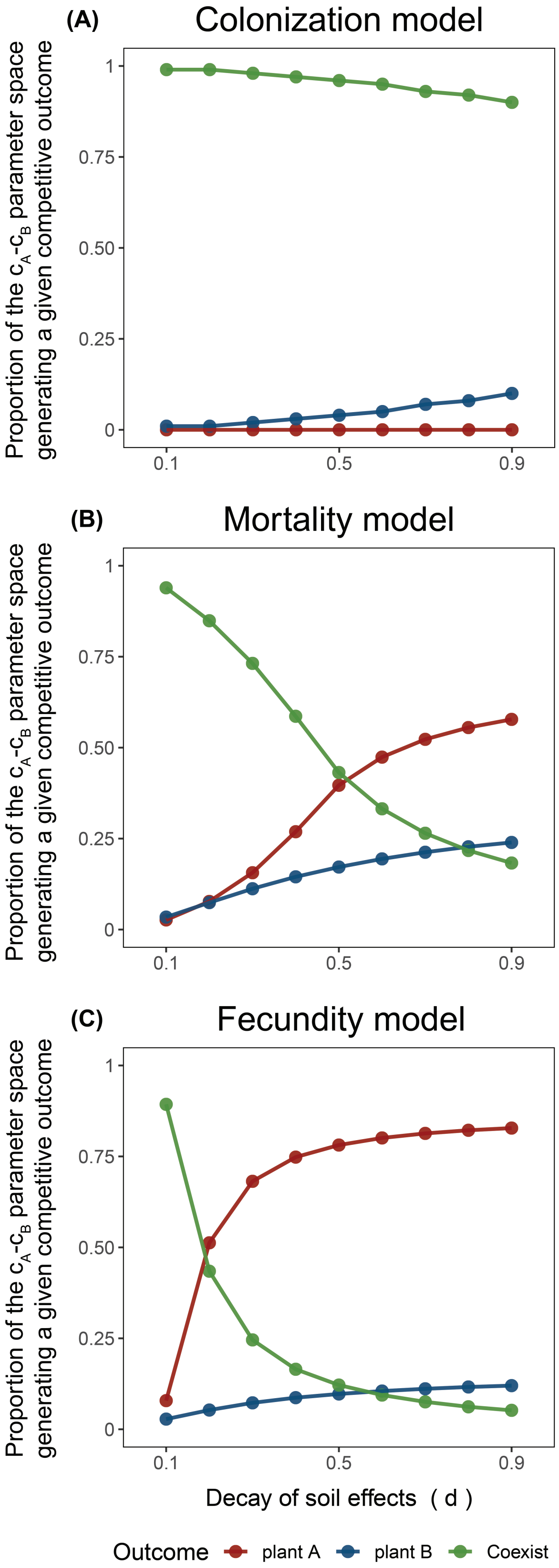


Figure 5: Plant competitive outcome when soil microbial effects decay at different rates for the three separate demographic models: the colonization model (*A*), the mortality model (*B*), and the fecundity model (*C*). The *X*-axis indicates the decay rate of both microbial effects (i.e., d_A and d_B), with larger values representing faster decay. The *Y*-axis indicates the percentage of different competitive outcomes when c_A and c_B are varied under specific values of decay rate (i.e., when performing the simulation in fig. 3 under different values of d_A and d_B). See figure 2 for other parameter values.

Discussion

Soil microbes can contribute to the coexistence of two plant species by driving stabilizing dynamics or favor species exclusion by structuring plant competitive hierarchies (Kandlikar et al. 2019; Ke and Wan 2020). To promote coexistence, the negative effects of host-specific pathogens need to extend beyond the conditioning individual. We show that this can happen when factors regulating the temporal dimension of plant-soil microbe interactions cause microbial effects to be cross-generational. Specifically, microbially mediated stabilization can be realized if soil microbes affect the recruitment probability of newly arrived seedlings (fig. 3), if they act as a temporal legacy effect to influence future colonizing individuals' demography (fig. 5), or if they affect spatially adjacent plant individuals (fig. S7). On the other hand, microbially mediated competitive hierarchies dominate when soil microbes primarily affect the mortality rate and fecundity of the conditioning individual, especially when the decay of microbial effects following plant death is fast (figs. 4, 5).

Our patch occupancy modeling framework provides the opportunity to specify which vital rate is affected by soil microbes, thereby allowing us to dissect the demographic details of plant-soil microbe interactions (fig. 1). Although past studies have proposed that host-specific pathogens can promote plant coexistence, here we show that their effects depend on which demographic rate is affected. For example, while host-specific pathogens that negatively influence a plant's colonization rate can effectively promote coexistence, those that negatively influence a plant's fecundity also have substantial effects on plant competitive hierarchies (fig. 3). This result indicates that when modeling plant-soil microbe interactions (e.g., with simplified models, such as the Lotka-Volterra framework), one should think carefully about which parameter is affected by soil microbes (e.g., intrinsic growth rates or competition coefficients; Bever 2003; Revilla et al. 2013). By capturing the different plant demographic responses to soil microbes, our framework presents one step toward more mechanistically modeling plant-soil microbe interactions. Our results also call for empirical studies to examine the effects of soil microbes on different demographic vital rates—for example, seedling survival rate—in addition to the commonly measured plant biomass performance (Teste et al. 2017; Hazelwood et al. 2021).

We also highlight that dynamical rates of the soil microbial community play an essential role in determining plant competitive outcomes. Instead of using a single growth parameter to summarize the dynamics of soil microbes, we echo recent calls for modeling microbial community dynamics more mechanistically and consider soil conditioning and decay as separate processes (Umbanhowar and McCann 2005; Jiang et al. 2020; Schroeder et al. 2020). The buildup of a plant's specific microbial community depends on a combination of plant traits, such as the quantity and quality of plant root exudates (Knelman et al. 2012; Ke et al. 2015), and microbial traits, such as the ability of microbes to be revived from dormancy (Lennon and Jones 2011). Empirically, the soil conditioning rate can be characterized by monitoring microbial community composition in chronosequences (Dinnage et al. 2019; Ke et al. 2021) or longitudinal data (Gao et al. 2019). In general, we show that plants experience stronger microbial effects if the microbial community develops at a faster rate, which contributes to competitive hierarchies if plant mortality and fecundity are the primary affected demographic rates (figs. 2, 3). This result corroborates findings in other recent models (Kandlikar et al. 2019; Ke and Wan 2020) and is supported by recent empirical evidence. For example, Chen et al. (2019) showed that tree species with higher accumulation rates of soil pathogens suffered more from conspecific negative density dependence (see also Liu et al. 2015).

The decay rate of soil microbial communities, which determines the temporal extent of microbial effects, is rarely explicitly considered in classic models of plant-soil microbe interactions (e.g., Bever et al. 1997). Here, we demonstrate the importance of the soil-decaying process: although the soil conditioning rate determines how strongly microbes contribute to competitive hierarchies in the mortality- and fecundity-based models, it is the soil decay rate that influences plants' opportunity to coexist (figs. 4, 5). In particular, if host-specific pathogenic effects are not retained long enough after plant death (i.e., fast decay of microbial effects) or if subsequent plant propagules do not arrive at a conditioned but vacant site soon enough (e.g., as a result of sparse spatial distribution of plant individuals), soil microbes may lose their ability to promote plant coexistence despite having strong host-specific detrimental effects. In addition to species coexistence, we believe that the interactive effects of soil decay rate and propagule pressure can influence other aspects of plant community assembly, such as restoration and recovery from disturbance. We therefore recommend studies focusing on these properties to account for the decay process of plant-soil microbe interactions (Zee and Fukami 2015; Nagendra and Peterson 2016).

Our model helps decipher the mechanism behind simulation-based models of plant-soil feedback by showing how microbially mediated stabilization and competitive hierarchies depend on the spatial-temporal scale of microbial effects (figs. 5, S7). For example, Teste et al. (2017) showed that plant diversity declined rapidly when only considering conspecific negative microbial effects but maintained at high levels when also including positive microbial effects conditioned by heterospecific individuals, thereby arguing that conspecific negative plant-soil feedback is not sufficient to maintain plant diversity. In their simulated conspecific scenario, the soil in which a plant grows is assumed to be influenced only by the current individual plant itself; however, the soil in their heterospecific scenarios is assumed to be influenced by the previous colonizing plant individual or neighboring plants. Therefore, we suggest that the low diversity in their conspecific scenario arises precisely because microbial effects were limited to the conditioning individual itself and were not allowed to propagate through time and space. Another example comes from Mack and Bever (2014), who showed that the relationship between plants' feedback strength and their relative abundance is stronger when microbial effects operate locally. In light of our results, this pattern can be expected because localized microbial effects mainly modify plant competitive hierarchies, which is an important determinant of species' relative abundance (Chisholm and Muller-Landau 2011).

The results presented here also have implications for experiments quantifying the effects of soil microbes on plant competitive outcomes. Two-phase experiments of plant-soil feedback typically include a training phase immediately followed by a response phase, where plants condition the soil microbial community in the former and respond to the soil modification in the latter (Bever et al. 1997; Brinkman et al. 2010). Often, researchers interpret the observed negative microbial effect as a stabilizing force that promotes plant coexistence (Crawford et al. 2019). Our model suggests that if the measured plant response is seedling survival (e.g., Swamy and Terborgh 2010; Teste et al. 2017), the estimated effects of host-specific pathogens indeed imply the strength of microbially mediated stabilization due to its underlying cross-generational nature. However, if the measured response is plant biomass (with an assumed relationship between plant biomass and fecundity), then the estimated microbial effects may instead represent a competitive imbalance, and the potential for microbially mediated stabilization resides in the spatiotemporal scale of the microbial effects (figs. 5, S7). The decay rate of microbial effects can then be quantified by performing the experiment with various time lags between the training and response phases or with soil inocula collected at different time points during the decay process (e.g., plant individuals that died at different years or fields abandoned for different amount of time; van de Voorde et al. 2012). We believe that considering the decay rate of soil microbial effects helps bridge the gap between experimental results and how plant-soil feedback operates in the field.

Our model considers the scenario where plants compete only for sites that were left empty after plants die (Yu and Wilson 2001). However, plants also directly interfere with the performance of one other and, at the extreme, replace established individuals (e.g., as modeled in the classic competition-colonization trade-off; Tilman 1994), a type of competition worth further investigation. We speculate that if colonists can replace established individuals (which have modified the soil community), the necessity of a slow decay rate may be of less importance because soil microbes can now influence the nonfocal plant that colonizes (Pacala and Rees 1998); the unique role of colonization effects in our models is also likely to be weaker. Future models can also expand our framework to consider more complex interactions between the spatial and temporal aspects of plant-soil feedback. For example, studies have shown that the strength of plant-soil feedback varies with the density of conditioning plants (van de Voorde et al. 2012). It might be interesting to study plant competitive dynamics when soil conditioning and decay rates are influenced by the density of neighboring plants in a spatially explicit framework (e.g., the microbial community may have a slower decay rate if the focal site is surrounded by conspecific neighbors).

Future studies can integrate more complicated microbial community dynamics into our modeling framework by exploring the soil decaying process in closer detail and by considering different microbial functional groups (e.g., decomposers and mycorrhizal fungi). The decay rate of microbial effects is related to the resistance of microbial communities against disturbance, which, at the species level, depends on microbial traits, such as stress tolerance and plasticity (Shade et al. 2012). Some pathogenic fungi can perform saprophytic growth on dead plant material (Hoitink and Boehm 1999; Bonanomi et al. 2010). In such a scenario, the microbial community trajectory during the decaying process may simply be the reverse of its conditioning process, and the resulting impact on plant performance is simply a pathogenic effect that becomes weaker through time. Alternatively, the functional composition of microbial communities may vary through time after plant death, therefore regressing to the unconditioned state via an alternative community trajectory different from that during its buildup. For example, the microbial community may become progressively dominated by decomposers due to the input of recalcitrant dead plant material, thereby affecting plant performance via local nutrient availability (Hannula et al. 2017; Veen et al. 2019). These microbial community dynamics can be incorporated into our model by adding additional soil microbial states that interact with plants in various ways (e.g., facilitate plant performance), as well as explicitly considering the interplay between various plant-soil feedback mechanisms (Miki et al. 2010; Ke and Miki 2015).

In this study, we identify key biological aspects of plant-soil microbe interactions that contribute to plant coexistence and those that structure plant competitive hierarchies. In the language of modern coexistence theory, these two effects correspond to increasing niche and fitness differences, respectively (Chesson 2000; Letten et al. 2017). Overall, we demonstrate that microbially mediated stabilization operates when the demographic details and the dynamical rates of plant-soil microbe interactions allow microbial effects to be cross-generational. Based on our results, we advocate for empirical studies that identify the plant demographic vital rate most affected by soil microbes (Dudenhöffer et al. 2018) and that track the changes in microbial effects following plant death or disturbance (Nagendra and Peterson 2016). Theoretical models considering plant-soil microbe interactions across multiple plant life stages should be explored (Ke and Miki 2015), and the framework developed here can also be combined with others that explicitly consider disturbances (e.g., the competition-colonization trade-off). Only by placing microbial effects on the correct demographic process and temporal scale can we better predict their effects on plant competitive outcomes in their natural context.

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Statement of Authorship

P.-J.K. and J.M.L. conceived the study, P.-J.K. conducted the study, and P.-J.K. and J.M.L. wrote the manuscript.

Data and Code Availability

Computer scripts supporting the results are archived in the Dryad Digital Repository (https://doi.org/10.5061/dryad.0cfxpnw20; Ke and Levine 2021).

Literature Cited

Augspurger, C. K. 1984. Seedling survival of tropical tree species: interactions of dispersal distance, light-gaps, and pathogens. Ecology 65:1705–1712.

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

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

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

Bever, J. D., T. G. Platt, and E. R. Morton. 2012. Microbial population and community dynamics on plant roots and their feedbacks on plant communities. Annual Review of Microbiology 66:265–283.

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

Bonanomi, G., V. Antignani, M. Capodilupo, and F. Scala. 2010. Identifying the characteristics of organic soil amendments that suppress soilborne plant diseases. Soil Biology and Biochemistry 42:136–144.

Brinkman, E. P., W. H. van der Putten, E.-J. Bakker, and K. J. F. Verhoeven. 2010. Plant–soil feedback: experimental approaches, statistical analyses and ecological interpretations. Journal of Ecology 98:1063–1073.

Chen, L., N. G. Swenson, N. Ji, X. Mi, H. Ren, L. Guo, and K. Ma. 2019. Differential soil fungus accumulation and density dependence of trees in a subtropical forest. Science 366:124–128.

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

Chisholm, R. A., and H. C. Muller-Landau. 2011. A theoretical model linking interspecific variation in density dependence to species abundances. Theoretical Ecology 4:241–253.

Chu, C., and P. B. Adler. 2015. Large niche differences emerge at the recruitment stage to stabilize grassland coexistence. Ecological Monographs 85:373–392.

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

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

Crawford, K. M., J. T. Bauer, L. S. Comita, M. B. Eppinga, D. J. Johnson, S. A. Mangan, S. A. Queenborough, et al. 2019. When and where plant-soil feedback may promote plant coexistence: a meta-analysis. Ecology Letters 22:1274–1284.

Dalling, J. W., S. P. Hubbell, and K. Silvera. 1998. Seed dispersal, seedling establishment and gap partitioning among tropical pioneer trees. Journal of Ecology 86:674–689.

Dawkins, R. 1982. The extended phenotype. Oxford University Press, Oxford.

De Long, J. R., R. Heinen, R. Jongen, S. E. Hannula, M. Huberty, A. M. Kielak, K. Steinauer, and T. M. Bezemer. 2021. How plant–soil feedbacks influence the next generation of plants. Ecological Research 36:32–44.

Dinnage, R., A. K. Simonsen, L. G. Barrett, M. Cardillo, N. Raisbeck-Brown, P. H. Thrall, and S. M. Prober. 2019. Larger plants promote a greater diversity of symbiotic nitrogen-fixing soil bacteria associated with an Australian endemic legume. Journal of Ecology 107:977–991.

Dudenhöffer, J.-H., A. Ebeling, A.-M. Klein, and C. Wagg. 2018. Beyond biomass: soil feedbacks are transient over plant life stages and alter fitness. Journal of Ecology 106:230–241.

Gao, C., L. Montoya, L. Xu, M. Madera, J. Hollingsworth, E. Purdom, R. B. Hutmacher, et al. 2019. Strong succession in arbuscular mycorrhizal fungal communities. ISME Journal 13:214–226.

Greenspoon, P., and K. Wadhawan. 2021. Colonization limitation of specialized enemies reduces species richness. Theoretical Ecology 14:1–8.

Hannula, E. S., R. Heinen, M. Huberty, K. Steinauer, J. R. De Long, R. Jongen, and M. T. Bezemer. 2020. Persistence of plant-mediated microbial soil legacy effects in soil and inside roots. bioRxiv, https://doi.org/10.1101/2020.10.15.340620.

Hannula, S. E., E. Morriën, M. de Hollander, W. H. van der Putten, J. A. van Veen, and W. De Boer. 2017. Shifts in rhizosphere fungal community during secondary succession following abandonment from agriculture. ISME Journal 11:2294–2304.

Hazelwood, K., H. Beck, and C. Timothy Paine. 2021. Negative density dependence in the mortality and growth of tropical tree seedlings is strong, and primarily caused by fungal pathogens. Journal of Ecology 109:1909–1918.

Hoeksema, J. D., V. B. Chaudhary, C. A. Gehring, N. C. Johnson, J. Karst, R. T. Koide, A. Pringle, et al. 2010. A meta-analysis of context-dependency in plant response to inoculation with mycorrhizal fungi. Ecology Letters 13:394–407.

Hoitink, H., and M. Boehm. 1999. Biocontrol within the context of soil microbial communities: a substrate-dependent phenomenon. Annual Review of Phytopathology 37:427–446.

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

Jiang, J., K. C. Abbott, M. Baudena, M. B. Eppinga, J. A. Umbanhowar, and J. D. Bever. 2020. Pathogens and mutualists as joint drivers of host species coexistence and turnover: implications for plant competition and succession. American Naturalist 195:591–602.

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

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

Ke, P.-J., and J. M. Levine. 2021. Data from: The temporal dimension of plant-soil microbe interactions: mechanisms promoting feedback between generations. American Naturalist, Dryad Digital Repository, https://doi.org/10.5061/dryad.0cfxpnw20.

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

Ke, P.-J., and J. Wan. 2020. Effects of soil microbes on plant competition: a perspective from modern coexistence theory. Ecological Monographs 90:e01391.

Ke, P.-J., P. C. Zee, and T. Fukami. 2021. Dynamic plant–soil microbe interactions: the neglected effect of soil conditioning time. New Phytologist, https://doi.org/10.1111/nph.17420.

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

Knelman, J. E., T. M. Legg, S. P. O'Neill, C. L. Washenberger, A. González, C. C. Cleveland, and D. R. Nemergut. 2012. Bacterial community structure and function change in association with colonizer plants during early primary succession in a glacier forefield. Soil Biology and Biochemistry 46:172–180.

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

Kurkjian, H. M., M. J. Akbari, and B. Momeni. 2021. The impact of interactions on invasion and colonization resistance in microbial communities. PLoS Computational Biology 17:e1008643.

Lekberg, Y., J. D. Bever, R. A. Bunn, R. M. Callaway, M. M. Hart, S. N. Kivlin, J. Klironomos, et al. 2018. Relative importance of competition and plant–soil feedback, their synergy, context dependency and implications for coexistence. Ecology Letters 21:1268–1281.

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

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

Liu, Y., S. Fang, P. Chesson, and F. He. 2015. The effect of soil-borne pathogens depends on the abundance of host tree species. Nature Communications 6:10017.

Mack, K. M., and J. D. Bever. 2014. Coexistence and relative abundance in plant communities are determined by feedbacks when the scale of feedback and dispersal is local. Journal of Ecology 102:1195–1201.

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

Miki, T., M. Ushio, S. Fukui, and M. Kondoh. 2010. Functional diversity of microbial decomposers facilitates plant coexistence in a plant-microbe-soil feedback model. Proceedings of the National Academy of Sciences of the USA 107:14251–14256.

Molofsky, J., J. D. Bever, J. Antonovics, and T. J. Newman. 2002. Negative frequency dependence and the importance of spatial scale. Ecology 83:21–27.

Nagendra, U. J., and C. J. Peterson. 2016. Plant-soil feedbacks differ in intact and tornado-damaged areas of the southern Appalachian Mountains, USA. Plant and Soil 402:103–116.

Pacala, S. W., and M. Rees. 1998. Models suggesting field experiments to test two hypotheses explaining successional diversity. American Naturalist 152:729–737.

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

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

Roy, B. A., H. M. Alexander, J. Davidson, F. T. Campbell, J. J. Burdon, R. Sniezko, and C. Brasier. 2014. Increasing forest loss worldwide from invasive pests requires new trade regulations. Frontiers in Ecology and the Environment 12:457–465.

Schroeder, J. W., A. Dobson, S. A. Mangan, D. F. Petticord, and E. A. Herre. 2020. Mutualist and pathogen traits interact to affect plant community structure in a spatially explicit model. Nature Communications 11:2204.

Shade, A., H. Peter, S. D. Allison, D. Baho, M. Berga, H. Bürgmann, D. H. Huber, et al. 2012. Fundamentals of microbial community resistance and resilience. Frontiers in Microbiology 3:417.

Siefert, A., K. W. Zillig, M. L. Friesen, and S. Y. Strauss. 2019. Mutualists stabilize the coexistence of congeneric legumes. American Naturalist 193:200–212.

Stump, S. M., and P. Chesson. 2015. Distance-responsive predation is not necessary for the Janzen–Connell hypothesis. Theoretical Population Biology 106:60–70.

Stump, S. M., and L. S. Comita. 2018. Interspecific variation in conspecific negative density dependence can make species less likely to coexist. Ecology Letters 21:1541–1551.

Swamy, V., and J. W. Terborgh. 2010. Distance-responsive natural enemies strongly influence seedling establishment patterns of multiple species in an Amazonian rain forest. Journal of Ecology 98:1096–1107.

Teste, F. P., P. Kardol, B. L. Turner, D. A. Wardle, G. Zemunik, M. Renton, and E. Laliberté. 2017. Plant-soil feedback and the maintenance of diversity in Mediterranean-climate shrublands. Science 355:173–176.

Tilman, D. 1994. Competition and biodiversity in spatially structured habitats. Ecology 75:2–16.

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

van de Voorde, T. F., W. H. van der Putten, and T. M. Bezemer. 2012. The importance of plant–soil interactions, soil nutrients, and plant life history traits for the temporal dynamics of *Jacobaea vulgaris* in a chronosequence of old-fields. Oikos 121:1251–1262.

van der Putten, W. H., R. D. Bardgett, J. D. Bever, T. M. Bezemer, B. B. Casper, T. Fukami, P. Kardol, et al. 2013. Plant–soil feedbacks: the past, the present and future challenges. Journal of Ecology 101:265–276.

Veen, C., E. Fry, F. ten Hooven, P. Kardol, E. Morriën, and J. R. De Long. 2019. The role of plant litter in driving plant-soil feedbacks. Frontiers in Environmental Science 7:168.

Wubs, E. R. J., and T. M. Bezemer. 2018. Temporal carry-over effects in sequential plant–soil feedbacks. Oikos 127:220–229.

Wubs, E. R. J., W. H. van der Putten, S. R. Mortimer, G. W. Korthals, H. Duyts, R. Wagenaar, and T. M. Bezemer. 2019. Single introductions of soil biota and plants generate long-term legacies in soil and plant community assembly. Ecology Letters 22:1145–1151.

Yu, D. W., and H. B. Wilson. 2001. The competition-colonization trade-off is dead; long live the competition-colonization trade-off. American Naturalist 158:49–63.

Zee, P. C., and T. Fukami. 2015. Complex organism–environment feedbacks buffer species diversity against habitat fragmentation. Ecography 38:370–379.

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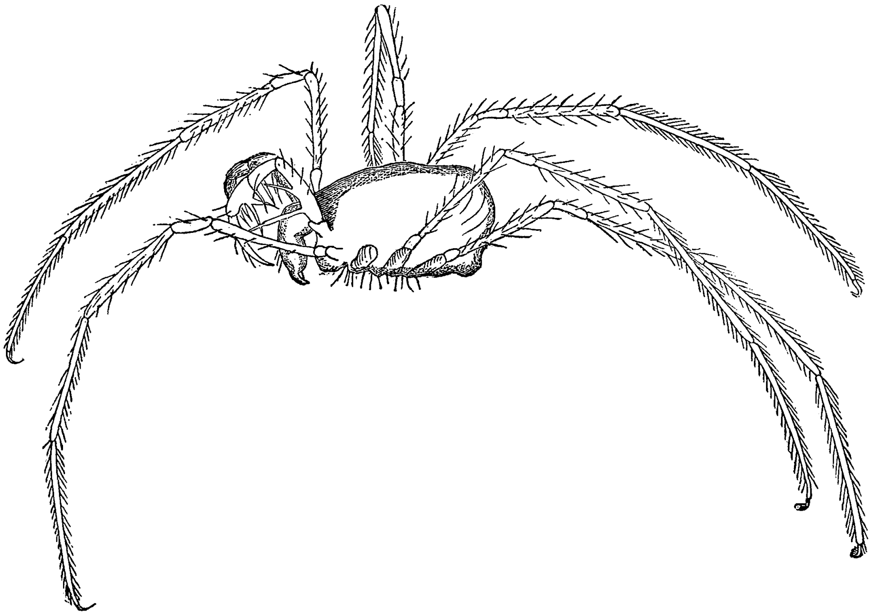

“The family of Harvest men is represented by a small white form, described by Tellkampf under the name of *Phalangodes armata* [figured] but now called *Acanthocheir armata* Lucas. The body alone is but half a line long, the legs measuring two lines.” From “The Mammoth Cave and Its Inhabitants” by A. S. Packard Jr. (*The American Naturalist*, 1871, 5:739–761).