Time will tell: the temporal and demographic contexts of plant–soil microbe interactions

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Abstract

Soil microorganisms can have profound impacts on plant community dynamics and have received increasing attention in the context of plant–soil feedback. The effects of soil microbes on plant community dynamics are classically evaluated with a two-phase experimental design that consists of a conditioning phase, during which plants modify the soil microbial community, and a response phase, during which the biomass performance of plants is measured as their response to the soil modification. Predicting plant community-level outcomes based on these greenhouse experimental results implicitly assumes that plant–soil microbe interactions remain constant through time. However, a growing body of research points to a complex temporal trajectory of plant–soil microbe interactions, with microbial effects varying with the conditioning duration, plant development, and time since conditioning. Most previous studies also implicitly assume that measuring plant biomass performance alone adequately captures the most critical impacts soil microbes have on plant population dynamics, neglecting that soil microbes also govern other key demographic processes over the plant life cycle. Here, we discuss the relevance of these temporal and demographic dimensions of plant–soil microbe interactions when extrapolating experimental results and propose modeling frameworks that can incorporate the new empirical evidence. By integrating empirical and theoretical approaches, we provide a roadmap for more nuanced predictions of the long-term consequences of plant–soil microbe interactions in nature.

Keywords

conspecific negative density dependence, demographic models, Janzen–Connell hypothesis, microbial community, patch occupancy model, plant–soil feedback

I. Introduction

Plants interact with a diverse array of soil microbes, including mutualists, decomposers, and pathogens. These interactions can be bidirectional, with plants altering the composition of the soil microbial community, and the resulting changes in microbial community impacting subsequent plant performance in the conditioned soil (Bever, 1994, Bever et al., 1997, Bever, 2003). The study of plant–soil microbe interactions has its origin in agricultural science (Huang et al., 2013, van der Putten et al., 2013) and has been integrated into community ecology under the framework of plant–soil feedback (PSF). Since its introduction by Bever et al. (1997), studies have extensively discussed how plant–soil microbe interactions influence plant coexistence (Bever et al., 2010, Ke and Miki, 2015, Bever et al., 2015, Kandlikar, 2024). The PSF framework has also been used to explore how soil microbes affect patterns in the relative abundance of plant communities (Mangan et al., 2010, Reinhart et al., 2021), restoration success (Wubs et al., 2016, Koziol et al., 2018), plant invasion (Callaway et al., 2004, Suding et al., 2013), and the biodiversity–productivity relationship (Kulmatiski et al., 2012, Forero et al., 2021).

To characterize the direction and strength of plant–soil microbe interactions, most studies follow a two-phase experimental design aimed at capturing the two-way interactions between plants and soil microbes (Bever et al., 1997). The classic greenhouse experiment consists of a "conditioning" phase during which plants modify the soil microbial community, directly followed by a "response" phase during which plants of the same or other species respond to the conditioned soil community (Bever et al., 2010, Brinkman et al., 2010). This distinct two-phase design elegantly captures the necessary information for parameterizing the key terms in the classic plant–soil feedback model (Bever et al., 1997, 2012) and has enabled a strong empirical foundation of PSF research across ecosystems (Crawford et al., 2019, Yan et al., 2022). However, this approach implies a number of assumptions about the nature of plant–soil microbe interactions that do not align with our contemporary understanding of their dynamics. In particular, a growing number of studies have highlighted the importance of accounting for different temporal and demographic dimensions of plant–soil microbe interactions (Kardol et al., 2013, Gundale and Kardol, 2021, Chung, 2023). Such evidence should reshape both the design of experiments (e.g., how long should the conditioning phase last?) and the interpretation of their results (e.g., how do microbial

effects on early-life stage plant performance translate to population-level consequences?). In this paper, we focus on two key assumptions: first, the temporal assumption that microbial effects develop quickly during the conditioning phase and maintain constant strength over time; and second, the demographic assumption that plant biomass performance during the response phase reflects microbial impact on plant population growth.

The conditioning and response phases in two-phase experiments are typically conducted over short time frames (e.g., a few months), with the same time frame applied across all species despite potential life history and growth trajectory differences between the focal species. Field-based studies may also source conditioned soil microbial communities by collecting soil from individuals growing in the field, but the age of the conditioning plant is generally unknown. Both approaches implicitly assume that microbial effects develop relatively quickly and, perhaps more importantly, that these effects maintain constant strength throughout different plant developmental stages (Fig. 1a). This assumption is at odds with growing evidence that within a single plant generation, microbial communities undergo a continuous turnover (e.g., Edwards et al., 2018, Gao et al., 2019), and that their resulting effects on plant performance can vary based on the duration of plant conditioning and response phases (e.g., Hawkes et al., 2013, Bezemer et al., 2018, Lepinay et al., 2018; Fig. 1b). Moreover, it is often assumed that greenhouse-measured microbial effects manifest both spatially (i.e., affecting concurrently growing plants) and temporally (i.e., carrying over through time with little change in its impact; Ke and Levine, 2021). However, predictions made based on studies that conduct the response phase immediately following the conditioning phase neglect the potential consequences of time lags that occur in nature (Ou et al., 2024). Therefore, while experiments are understandably constrained by feasibility, explicit examination of the system's temporal context is critical to better predict how soil microbes shape natural plant communities.

The short-term nature of most experiments also constrains researchers to focus on a single plant demographic response that presumably reflects the most critical impact of the microbial community (Ke and Wan, 2023). The most frequently measured performance proxy is plant biomass, which is then used to calculate theoretically derived metrics to infer how soil microbes influence plant coexistence. For instance, the biomass of plants in conspecific- and

heterospecific-conditioned soils can be used to calculate the pairwise feedback metric that quantifies the frequency-dependent feedback loops generated by plant–soil microbe interactions (Bever et al., 1997). Negative frequency-dependence arises when both plants condition their soil microbes in a way that favors heterospecifics over conspecifics, thereby promoting plant coexistence (Crawford et al., 2019). In the context of the classic PSF model, where soil microbes drive plant community dynamics by changing plants' intrinsic growth rates (Bever et al., 1997), these metrics operate under the assumption that plant biomass performance is a proxy for plant population growth. However, soil microbes can also affect other demographic processes across the plant life cycle that are not captured simply by measuring plant biomass (e.g., changing seed and seedling survival rates or the nature of density-dependence among plants), potentially with opposing effects at different plant ontogenetic stages that lead to different coexistence predictions (Dudenhöffer et al., 2018, Dostálek et al., 2022). Integrating these different impacts, instead of making predictions based on microbial effects on any one life stage, is another challenge when predicting the long-term demographic consequences of soil microbes.

Here, we discuss the two critical assumptions regarding temporal and demographic aspects of plant–soil microbe interactions in nature. We aim to highlight the relevance of these assumptions when extrapolating greenhouse results, and outline future empirical and theoretical avenues to incorporate them. In particular, we advocate for a shift from using biomass-based performance indices to parameterizing patch occupancy models and plant demographic models with microbial effects. While these biologically important complications make experiments more logistically challenging, we argue that integrating the temporal and demographic details can better predict the outcome of plant–soil microbe interactions in their natural context.

II. Significant consequences of overlooking the temporal and demographic aspects of plant–soil microbe interactions

To motivate our thesis that explicitly evaluating the variation in microbial effects across time and across different life stages is important for predicting their consequences in nature, we first present a simple plant demographic model that illustrates the potential consequences of ignoring these

temporal dynamics. Specifically, we consider two annual plant species, N_1 and N_2, with dynamics described by the Beverton–Holt annual plant model:

$$N_{i,t+1} = \overbrace{s_i\,(1-g_i)\,N_{i,t}}^{\substack{\text{Survival of}\\ \text{ungerminated seeds}}} + \frac{\overbrace{\lambda_i g_i N_{i,t}}^{\text{Intrinsic fecundity of germinated seeds}}}{\underbrace{1+\alpha_{ii}g_iN_{i,t}+\alpha_{ij}g_jN_{j,t}}_{\text{Effect of neighbors}}},$$

with subscripts i and j indicating species 1 or 2. The first term represents the survival of ungerminated seeds, with g_i and s_i representing seed germination and survival rate, respectively (circular loop in Fig. 2A). The second term represents seed production and density-dependent interactions among germinated seeds, with λ_i, α_{ii} and α_{ij} representing intrinsic plant fecundity, intraspecific and interspecific competitive impact experienced by N_i, respectively (rightward arrows in Fig. 2A). As opposed to biomass-based metrics, this demographic model provides the opportunity to study microbial effects on five different demographic parameters (i.e., g_i, s_i, λ_i, α_{ii}, and α_{ij}). For short-term greenhouse studies comparing these demographic processes in conditioned versus sterilized soil, this model offers a way to predict the long-term effect of soil microbes on plant competitive outcomes.

As a case study, consider a scenario in which pathogenic microbes operate by harming one of these demographic processes for a given species. If a short-term greenhouse study were to suggest that the primary effects of the soil pathogen is to reduce species 1's seed survival (s_1) by 10% while leaving s_2 unaffected, the model would predict negligible impacts of the soil microbes on long-term plant community dynamics. This is illustrated in the left panel of Fig. 2B, as the grey lines (indicating species abundance under no pathogenic impact) and blue lines (indicating a pathogenic impact on species 1's seed survival) almost overlap completely. If instead the greenhouse study were to find that the pathogen decreases plant 1's intrinsic fecundity (λ_1) by 10%, the model predicts substantially lower population sizes for species 1 in the long-term ($\approx 18\%$ reduction in equilibrium abundance). This exercise highlights the importance of understanding where in the plant demographic cycle microbial effects arise, an aspect of plant–soil microbe interactions that is often overlooked when assuming a single performance measurement can predict demographic outcomes.

Further suppose that the pathogenic effects measured in the short-term greenhouse aggravate over time in the field, for example due to the gradual accumulation of soil pathogens across multiple generations (Diez et al., 2010, Day et al., 2015). The right panel of Fig. 2B depicts the competitive outcomes caused by different microbial effects assuming that the 10% decrease in s_1 and λ_1 after one generation intensified to an 80% decrease by the end of eight generations (i.e., 10% decrease after every generation). While the temporally-intensifying pathogenic effect on s_1 (blue lines) remained relatively insignificant, the pathogenic effect on λ_1 (orange lines) became so strong that it resulted in the exclusion of N_1. This simulation exercise demonstrates the consequence of neglecting the temporal dynamics of plant–soil microbe interactions, a realistic concern in nature that is often replaced by the simplifying assumption of a constant microbial effect in greenhouse experiments.

III. Dissecting different temporal dimensions of microbial effects

Studies on the temporal patterns of plant–soil microbe interactions have classically focused on its variation along plant succession, which typically involves plants with different traits or shifts in the external environment (Kardol et al., 2006, 2013, Bauer et al., 2015). However, temporal variation in plant–microbe interactions also occurs across shorter time scales because the conditioned soil microbial community and plant response both vary over time (Fig. 1B). Recognizing that plant–soil microbe interactions are not constant through time directly influences the experimental design and how we interpret experimental results. Moreover, this temporal variability may be a key mechanism behind the effects of phenological mismatch between plants and soil microbes (Peay, 2018, Rudgers et al., 2020). In this section, we review evidence of temporal variability and discuss mechanisms by which the impact of microbial communities on plant biomass performance varies with the duration of the conditioning and response phases (subsection III.1), as well as the time lag between consecutive generations (subsection III.2). We then discuss how to design experiments that tackle the temporal complexities observed in nature (subsection III.3). Note that for this section we focus on studies that measure plant biomass as the key performance proxy; we will discuss other demographic responses in section IV.

III.1 Temporal development during the conditioning and response phases

As the strength and direction of plant–soil microbe interactions depend on the timing of interactions, the duration of the conditioning and response phases influences the greenhouse-measured interaction strength. By compiling information on the experimental duration of studies included in two prominent meta-analyses (Crawford et al., 2019, Yan et al., 2022), we showed that the length of conditioning and response phases are short in most studies (Fig. 3). The median conditioning length is 3.5 months (n = 59 studies, after excluding 47 studies with field-collected soils) while that of the response phase is 3 months (n = 106 studies). Extrapolating from these experiments to predict the long-term consequences of soil microbes is based on the assumption that the relative impact of conspecific- and heterospecific-conditioned soils remains constant throughout plant development. The significance of overlooking the temporal development of plant–soil microbe interactions is exemplified when one considers plants with different life histories. For example, 20% of studies (21 out of 106) in Fig. 3 evaluated microbially mediated stabilization between plant species pairs comprised of one annual and one perennial species while implementing the same (usually short) experimental duration. This overlooks the potential for short- and long-lived plants to condition microbial communities at different rates, such that the same duration of soil conditioning may correspond to different developmental stages and microbial effects (Kulmatiski et al., 2017): the species-specific microbiome of a short-lived annual plant may be fully conditioned by the end of an experiment, whereas that of a long-lived perennial may require a longer conditioning time. Similarly, a short response phase may capture the full physiological response of an annual plant, while that of a perennial may vary with its ontogeny. This mismatch in temporal development patterns highlights the challenge of interpreting experimental results in the context of the focal system's natural history.

Compared to the classic two-phase design with a single fixed duration of soil conditioning (Fig. 4A), a few studies have grown plants in soils that were conditioned for different duration (red vertical arrow (i) in Fig. 4B). Studies have shown that the relative impact of conspecific- and heterospecific-conditioned soil on the responding individual can vary with the duration of soil conditioning. For example, Lepinay et al. (2018) found that after a brief conditioning period of two weeks, heterospecific soil had a more negative impact on *Rorippa austriaca* performance than

its conspecific soil. However, a longer duration of soil conditioning resulted in the opposite relationship: conspecific soil had an increasingly stronger negative impact peaking at six weeks of conditioning, whereas the negative effect of heterospecific soils diminished after four to eight weeks of conditioning. In a more natural setting, Ke et al. (2021) studied how the microbial impact varied with soil conditioning length by transplanting seedlings into field-conditioned soil collected under plant individuals of different ages. They found that the soil microbial community underwent continuous successional dynamics over the span of 20 years and three out of four species experienced negative microbial effects that intensified with longer conditioning time. Importantly, these results have crucial implications on the design of two-phase experiments: arresting soil conditioning at different time points causes the responding plant to encounter microbial communities with different compositions and functions, thereby giving rise to different plant–soil microbe interactions.

Previous experimental studies on the temporal dynamics of plant–soil microbe interactions have largely focused on the development of microbial effects across the lifespan of the responding individual, which is typically achieved by harvesting responding plants at various time intervals (Kardol et al., 2013, Gundale and Kardol, 2021; red diagonal arrow (ii) in Fig. 4B). For example, by sequentially harvesting seedlings at four time points spanning 19 months, Hawkes et al. (2013) showed that the microbial effect experienced by native plants became more negative through time, whereas the development patterns for invasive plants were more variable. Recent studies have also highlighted that other factors can modify the temporal pattern of microbial effects during the response phase (Dostál, 2021, Bezemer et al., 2018). For instance, harvesting twice every week for 11 weeks, Bezemer et al. (2018) showed that the negative effect of conspecific-conditioned soil experienced by *Jacobaea vulgaris* attenuated as plants became older; however, when grown together with a heterospecific competitor, the negative effect instead aggravated over time (but see Dostál, 2021 for a nonlinear pattern for three harvests spanning 13 months). Together, this empirical evidence provides a strong impetus to consider temporal variability in the response phase since harvesting an experiment at different endpoints can alter our understanding of the microbial effect.

The temporal development of plant–soil microbe interaction likely occurs due to shifts in the

composition and/or functionality of microbial communities as plants mature or enter different developmental stages (Chaparro et al., 2013, Dombrowski et al., 2016, Edwards et al., 2018, Hannula et al., 2019). Mechanisms underlying these shifts in soil microbial communities include physiological changes in nutrient allocation or root exudation across plant ontogenetic stages (Chaparro et al., 2013, Zhalnina et al., 2018), as well as an increase in immunity and antibiotic defense against pathogens as plants mature (Bulgarelli et al., 2013, Chaparro et al., 2013). Furthermore, alterations prompted by plants can lead to shifts in microbe–microbe interactions and the processes governing microbial community assembly (Barret et al., 2015, Herrera Paredes and Lebeis, 2016, Bittleston et al., 2021), all of which may trigger further responses in plant physiology via a complex interplay between mechanisms. Importantly, as conditioning and response processes operate simultaneously in nature, the same set of mechanisms apply to explain temporal patterns in both phases. For example, strengthening of immunity as plants mature can reduce pathogen abundance as the conditioning phase progresses (Bulgarelli et al., 2013); it can also reduce plant susceptibility to pathogens and alleviate negative microbial effects experienced by the plant as the responding individual matures. Similarly, mechanisms that reduce the abundance of beneficial microbes after soil conditioning (e.g., mature plants becoming less reliant on mutualistic partners) also act upon the responding individual to diminish the observed positive microbial effect. We will elaborate on necessary experiments to tease apart different temporal dimensions and mechanisms in the subsection III.3.

III.2 Alterations of microbial effects after plant death

One common implicit assumption in plant–soil feedback studies is that greenhouse-measured microbial effects manifest similarly on plants neighboring the focal individuals as on individuals that arrive and grow in the conditioned soil after the focal plant. However, whether microbial effects carry over through time and how long they persist remains an understudied temporal aspect of plant–soil microbe interactions. This question is especially important for systems with discrete growing seasons or dispersal limitation, where a temporal lag exists between the senescence of one plant (the conditioning individual) and the growth of another (responding) individual. This introduces a lag phase during which the conditioned soil is left unoccupied for an extended period

of time; processes such as litter decomposition, abiotic filtering, and stochastic drift may restructure the microbial community during such lags. Studies growing seedlings in soils collected from dead individuals (red vertical arrow (iii) in Fig. 4B) suggest that such lags can have distinct effects across different systems. For example, Esch and Kobe (2021) showed that the negative effects of soil from live *Prunus serotina* on the survival of conspecific seedlings faded away within one year after tree removal. Conversely, Bennett et al. (2023) showed that microbial communities from soils collected under dead and live adult *Populus tremuloides* trees had similar effects on conspecific seedlings. As an alternative to collecting soil from naturally occurring dead individuals, Ou et al. (2024) modified the two-phase experiment to include a six-month delay between the conditioning and response phase; their results suggest that the seasonal lag in Mediterranean annual plant systems changes the microbial community and their corresponding impact on plant coexistence. Below, we discuss the mechanisms that could either maintain or alter microbial effects when a temporal lag exists between consecutive generations.

Microbial effects could persist after active plant conditioning ceases due to the continued survival and functioning of the conditioned microbial community in the soil (Lennon and Jones, 2011, Pepe et al., 2018, Esch et al., 2021, Hannula et al., 2021). For example, Esch et al. (2021) found that the persisting pathogenic oomycetes collected from live versus dead tree stumps have similar negative effects on conspecific seedling survival. Similarly, Pepe et al. (2018) showed that arbuscular mycorrhizal fungi remain active and can spread from roots after host shoot removal. The maintenance of microbial activity can occur if root systems remain active after the removal of aboveground tissues or if the release of nutrients from dead belowground tissues mirrors exudates from living plants (Johansen and Jensen, 1996, Müller et al., 2013). Additionally, trophic flexibility (e.g., saprotrophic ability of certain pathogens; Bonanomi et al., 2010) and dormancy of soil microbes can allow the microbial communities to persist after the death of their host, enabling microbes to wait for the arrival of a new host (Lennon and Jones, 2011, Shade et al., 2012, Shemesh et al., 2023). In these cases, the succeeding (response) individual will experience a similar microbial effect despite the temporal lag in arrival timing, and predictions from immediate transplant experiments are relevant to natural systems.

However, various processes can cause the microbial community to change after plants stop

actively conditioning the soil, such that subsequent responding individuals encounter a different soil microbial community than that obtained in an immediate transplant scenario (Grove et al., 2015, Veen et al., 2019, Ou et al., 2024). The process of litter decomposition can introduce phyllosphere microbes to the soil (Fanin et al., 2021, Minás et al., 2021) and release chemicals and nutrients that shift microbial communities (Veen et al., 2021). Additionally, different causes of plant death (e.g., herbivory, fire, and disease) are often associated with further changes in abiotic factors, with potential effects on the composition and function of microbial communities. For example, canopy gaps caused by wind disturbances modify nearby light and moisture levels in a way that suppresses pathogens (Augspurger, 1984, Reinhart et al., 2010, Nagendra and Peterson, 2016). Finally, stochastic drift could decouple microbial community from plant conditioning influence if the soil remains uncolonized over an extended period of time due to plant propagule limitation. In these scenarios, immediate transplant experiments fail to capture the microbial effects experienced by the responding plant in nature.

III.3 Implications for experimental design

While an increasing number of studies have recognized the temporal dimensions of plant–soil microbe interactions, synthesizing the factors contributing to this variability, e.g., the life history of plants and functional groups of microbes involved, requires more targeted studies. Here, we recommend a path forward for understanding these context dependencies. First, the temporal settings of the experiment should guide our interpretation of the results. For instance, in Mediterranean plant communities where the growing season only lasts a few months, traditional experiments in which a short-term conditioning phase is immediately followed by the response phase may adequately reflect potential microbial effects on concurrently growing neighbors that unfold within one growing season. However, such a design may not be adequate to project microbial effects on population dynamics across years because it overlooks the temporal lag associated with the clear seasonality of plant growth in nature (Ou et al., 2024). Second, we encourage modification of the classic two-phase design (Fig. 4A) to reflect the temporal aspects of a focal plant–soil system in nature. For Mediterranean annual plant communities, mirroring the temporal dynamics of the natural system by incorporating a decay phase during which the conditioned soils are exposed

to a prolonged drought with no vegetative growth (red vertical arrow (iii) in Fig. 4B) may provide a better understanding of how soil microbes shape plant community dynamics across years (Ou et al., 2024). Moreover, researchers can build on long-term monitoring plots and historical information to account for variation in conditioning duration, host plant age, or time since host tree death. This approach may be especially applicable in studies that focus on long-lived plants, which often source field-conditioned soils for greenhouse experiments (44%; 47 out of 106 studies in Fig. 3). For example, Ke et al. (2021) estimated plant age with historical aerial photos and employed a chronosequence approach to study the influence of soil conditioning length. Other examples include using host tree size as a proxy of conditioning time (Chen et al., 2019) and utilizing chronosequences of abandoned fields or agricultural harvest times to study the persistence of microbial effects (van de Voorde et al., 2012, Esch and Kobe, 2021).

One can also design experiments that isolate a particular facet of temporal variability to help disentangle the mechanisms behind observed temporal patterns. Current studies on the temporal development of microbial effects typically employ sequential harvesting, where the observed temporal changes result from the combination of varying plant physiological responses and any changes to the soil community that are due to the effects of the responding plant itself (red diagonal arrow (ii) in Fig. 4B). To isolate the effects associated with changing soil microbial communities during soil conditioning, studies could plant seedlings of the same age in soils with different conditioning duration (red vertical arrow (i) in Fig. 4B). Alternatively, if the goal is to isolate the effects caused by changing plant physiology, an experiment could instead grow plants of different ages/sizes (kept in a relatively sterilized environment such as a Magenta box before transplanting) in soils with identical conditioning duration (red horizontal arrow (iv) in Fig. 4B). A recent study by Liu et al. (2024) utilized such experimental design to illustrate the importance of conditioning and response duration as well as the underlying mechanisms. In addition, mutants or cultivars with different developmental rates can also be used to separate the effects of plant developmental stage (e.g., vegetative growth or flowering) and age *per se* (Dombrowski et al., 2016). While the above scenarios are deliberately artificial, such experiments can provide important mechanistic insights into the observed temporal patterns of plant–soil microbe interactions.

While we have focused on changes happening over the course of a single plant-to-plant

replacement, these dynamics are closely related to other temporal patterns. One direction of research is how microbial effects build up over generations through multiple rounds of conditioning and response. A wealth of literature has explored the microbial changes underpinning reduced crop yield following repeated planting (i.e., soil sickness; reviewed in Huang et al., 2013) and the strengthening of conspecific microbial effects experienced by non-native plants after their introduction (Diez et al., 2010, Dostál et al., 2013; but see Day et al., 2015). The temporal scale of these studies typically spans hundreds of years. While this temporal pattern has been demonstrated by experiments using soils with conditioning histories that span multiple generations, few studies have generalized the traditional focus of single species to multiple species. In a unique greenhouse experiment consisting of two rounds of soil conditioning by different combinations of six plant species, Wubs and Bezemer (2018) demonstrated the complicated patterns arising from multiple rounds of soil conditioning. Future work can expand upon Wubs and Bezemer (2018) to study how the unique sequences of soil conditioning result in different plant–soil microbe interactions. Another tightly interconnected aspect is the demographic facet of plant–soil microbial interactions: as the responding individual matures, soil microbes can influence various demographic processes in addition to varying biomass responses. We elaborate on this in the next section.

IV. Assessing multiple demographic consequences of soil microbes

Most two-phase studies of plant–soil microbe interactions are designed to evaluate how different soil microbial contexts influence plant biomass performance. Experimentally, the implicit assumption is that individual biomass at the end of the experiment integrates all critical impacts of the microbial community and that variation in individual biomass growth is predictive of variation in population growth rates. This assumption corresponds well with the classic feedback model of Bever et al. (1997), where microbes regulate the intrinsic growth rate of an exponentially growing plant population. However, soil microbes can also alter other key demographic processes throughout the plant life cycle that are not directly correlated with biomass accumulation (e.g., seed germination and pollinator visitation in Dudenhöffer et al., 2018). Dostálek et al. (2022) demonstrated that it can be difficult to predict plant coexistence by using the microbial effect measured at a single life stage – while biomass performance suggests self-limitation of both *Bromus*

erectus and *Inula salicina*, including microbial effects on seed germination and fruit production suggests that both species in fact benefited from self-conditioned soil. Here, we highlight key studies that provide insights into microbial control over non-biomass plant demographic processes, with a particular focus on early life stage transitions.

IV.1 Microbial regulation of seed-to-seedling transition

Soil microbes can have drastic consequences on the early life stages of plants. While these effects can arise from microbial effects on distinct life history processes (i.e., seed survival, germination, and early seeding survival; Fig. 5), empirical studies often group them together given the logistical challenges of separating these effects in field settings. For example, when studying long-lived plants such as forest trees, repeated demographic censuses are often used to monitor seed-to-seedling transitions (e.g., Harms et al., 2000, Swamy et al., 2011). A large body of evidence for microbial effects on plant early life stages comes from field studies finding that fungicide applications alter patterns of seed and seedling demography (e.g., Bell et al., 2006, Bagchi et al., 2014, Krishnadas et al., 2018, Song and Corlett, 2022). Many of these studies are conducted to evaluate soil microbes as potential drivers of the Janzen–Connell hypothesis (Janzen, 1970, Connell, 1971)) and conspecific negative density-dependence (CNDD). These hypotheses suggest that the aggregation of host-specific enemies around adult plants reduces the survival probability of seedlings that disperse close to adults and under high conspecific densities. While evaluating the compound microbial effect across multiple early life stages can yield important insights, studies that isolate microbial effects on specific underlying demographic transitions (Fig. 5) can enable a nuanced and mechanistic understanding of microbial effects on plant population dynamics.

Soil-borne pathogens can cause substantial mortality at the seed stage across biomes (e.g., Kotanen, 2007, Sarmiento et al., 2017, Li et al., 2019). One system where the impact of fungal seed pathogens has been systematically dissected is that of pioneer tree species in neotropical forests, especially those in the genus *Cecropia*. As pioneer species whose seeds need to germinate quickly in response to new gap openings, these species produce seeds that can persist in the soil until the formation of nearby gaps. These seeds are vulnerable to pathogen attack during their time in the soil seed bank, and as a result, fungicide treatments can nearly double their survival and emergence

(Dalling et al., 1998, Gallery et al., 2010). Moreover, Dalling et al. (1998) found that seeds were more susceptible to pathogen attack in soils close to conspecific adults than in soils far from conspecifics, implicating soil pathogens as potential drivers of Janzen–Connell dynamics. Furthermore, recent advances have employed molecular methods toward understanding longstanding questions about pathogen host specificity. Zalamea et al. (2021) found that seeds of closely related *Cecropia* species harbor vastly distinct fungal communities, with species identity explaining substantially more variation than the seeds' location or their viability. Working with a more diverse group of pioneer tree species, Sarmiento et al. (2017) showed that while many fungi can grow on seeds of multiple plant species, their effects on seed mortality are highly species-specific. Together, this series of studies has highlighted soil-borne fungal seed pathogens as key microbial players in the dynamics of pioneer trees in tropical forests. While quantifying microbial effects on seed survival requires laborious methods (e.g., tetrazolium staining for testing seed viability; Sarmiento et al., 2017), a better understanding of these effects is critical given that seed limitation can be a bottleneck on plant population dynamics (Harper, 1977, Clark et al., 2007).

Soil microbes can also affect the rates and timing of germination. Such regulation primarily arises due to the production and/or metabolism of key germination-related phytohormones like gibberellins (reviewed in Keswani et al., 2022 and Bottini et al., 2004) or ethylene (reviewed in Ravanbakhsh et al., 2018 and Ishaq, 2017). While studies of how soil microbes regulate germination have historically focused on managed settings, evidence that microbes also affect germination in natural settings is now accumulating. In one of the few two-phase experiments focused on pairwise feedback effects on germination, Miller et al. (2019) found species-specific effects of conditioned microbes on germination. Specifically, the legume *Desmodium illinoense* achieved lower germination rates in conspecific-conditioned soils than in sterilized or heterospecific-conditioned soils, while germination of *Bromus inermis* and *Solidago canadensis* was unaffected by soil microbes. Across a large-scale microcosm experiment, Eldridge et al. (2021) found that soil bacterial and fungal communities help explain substantial variation in patterns of seed germination across nine plant species, suggesting a relationship between soil microbes and plant germination that is not explained simply by their shared responses to abiotic soil properties. Even when soil microbes do not affect overall rates of germination, they can alter the phenology of germination (Keeler and

Rafferty, 2022) which could either harm (e.g., if later germination reduces seedlings' performance due to competition; Orrock and Christopher, 2010) or benefit (e.g., if later germinants escape severe competition at the seedling stage or avoid abiotic stress; Leverett et al., 2018) population growth.

Finally, soil microbes also play a key role in determining the survival of seedlings after germination. The widespread role of mycorrhizal symbioses in promoting seedling survival and the potential for soil-borne pathogens to cause mortality among seedlings have been studied for decades and reviewed elsewhere (e.g., Gilbert, 2002, Horton and van der Heijden, 2008). Recent advances have focused on elucidating the relative role of harmful and beneficial soil microbes in driving seedling survival and establishment across different environmental contexts, including abiotic conditions (Bingham and Simard, 2011), the relative abundance of conspecific and heterospecific adults (Teste et al., 2017), and the functional groups of mycorrhizal fungi (Liang et al., 2016, Bennett et al., 2017). In addition to studies that directly track the fate of newly germinated seedlings in specific microbial contexts, studies that monitor the fate of older plant individuals also often speculate soil microbes as the underlying mechanism (e.g., CNDD studies on the survival of larger individuals; Comita et al., 2010). While, in comparison, the effect of soil microbes on seedling survival has rarely been the target variable in biomass-focused greenhouse experiments, recent studies have also started to quantify the contribution of this demographic process to microbe-mediated coexistence (Dudenhöffer et al., 2022, Chung et al., 2023, Pajares-Murgó et al., 2024).

IV.2 Microbial effects beyond early life stages

As seedlings establish and grow into reproductive adults, the soil microbial community continues to affect their performance in various ways not captured by experiments that focus only on plant biomass. While an exhaustive review of all such effects of soil microbes is beyond the scope of this study, we briefly highlight soil microbial regulation of flowering phenology and susceptibility to herbivores. Over the past decade, evidence of microbial regulation of flowering phenology across systems has become widespread (Lau and Lennon, 2012, Wagner et al., 2014, Igwe et al., 2021). Although the consequences of such phenological shifts at the population level are seldom

quantified, the few-day differences reported in these studies could in principle have drastic consequences for plant fitness, especially under abiotic stress when earlier flowering can be crucial to reproductive success and fitness (reviewed in Kazan and Lyons, 2016, O'Brien et al., 2021). The soil community can also regulate plant susceptibility to invertebrate herbivores (e.g., Howard et al., 2020, Pineda et al., 2020, Kalske et al., 2022), with such effects likely arising due to soil microbe-induced changes in leaf metabolomes or volatile organics (Kalske et al., 2022, Huberty et al., 2022). The consequences of microbe-mediated shifts in plant–herbivore interactions on insect population dynamics are becoming increasingly well-studied (reviewed in Shikano et al., 2017), but whether these changes affect plant population dynamics is less well established. Soilborne pathogens can also contribute to inter-specific and spatial variability in rates of adult tree mortality (Das et al., 2016). The integration of these microbial effects remains an ongoing challenge. In light of this, we propose that a promising approach is to combine experiments with system-specific models that can assess their long-term consequences on plant population dynamics.

IV.3 Implications for experimental design

While incorporating all aforementioned demographic impacts of soil microbes is logistically challenging, we also see a path forward. Current experimental studies of plant–microbe interactions often transplant pre-germinated seeds into conditioned soils, thereby neglecting the impact of soil microbes on seed survival and germination. Accordingly, a first step in enhancing our understanding of this phenomenon is for two-phase studies to plant ungerminated seeds and report germination rates along with the biomass performance and survival rates of germinated plants. Studies can employ statistical approaches (Dudenhöffer et al., 2022, Chung et al., 2023) or other population demographic models (David et al., 2019, Dostálek et al., 2022) to integrate the impact of microbes on multiple early stage transitions (see also section V.). Moreover, for short-lived plants, one can aim to follow the entire plant life cycle. For example, Dostálek et al. (2022) documented seedling establishment and biomass dynamics for two growing seasons, and recorded final fruit production of plants in different soil microbial backgrounds. While such an experiment is more challenging, the matrix population model parameterized by Dostálek et al. (2022), where soil microbes modulate transition probabilities across states, enables a more nuanced estimate of

microbial impact compared to solely relying on biomass-based metrics.

Compared to greenhouse-based plant–soil feedback studies that focus on biomass performance, CNDD studies using field census data are arguably more directly linked to population growth due to their emphasis on individual survival. However, observational CNDD studies can be limited as it can be challenging to attribute demographic patterns to soil microbes, and the impact of heterospecifics, which are necessary to infer coexistence outcomes, is sometimes overlooked. We propose that controlled experiments could complement census data for more mechanistic insights. For example, field-based biocide experiments have been used to identify soil microbes as key drivers of Janzen–Connell effects in seed and seedling mortality (Bell et al., 2006, Bagchi et al., 2010, Song and Corlett, 2022, Krishnadas and Comita, 2018). Furthermore, adding a reference treatment in randomly located field soil allows one to estimate frequency-independent microbial impacts on survival, aligning with recent studies that emphasize plant–soil microbe interactions within modern coexistence theory (Kandlikar et al., 2019, Ke and Wan, 2020). Greenhouse experiments can also be adapted to capture the density-dependent microbial effects implicit in CNDD studies. To this end, one can use field-conditioned soil from locations with varying adult densities or perform a pot experiment with varying seedling densities (Ke and Wan, 2023). These modifications in study design can help bridge the gap between microbial impacts inferred from experiments and field census data.

Finally, we argue that researchers should identify the demographic process that acts as a bottleneck for plant population growth in the focal system and prioritize studying the microbial impact on that specific demographic process. For example, in communities dominated by species with persistent seed banks, the microbial effect on seed survival may be particularly important. In systems where plant germination is highly constrained by soil-borne pathogens, germination success in soils with different conditioning histories should be measured. We also recognize that in some plant communities, individual biomass growth indeed correlates well with critical demographic processes. For annual plants, individual biomass at the time of peak flowering may reflect fecundity (Neytcheva and Aarssen, 2008, Younginger et al., 2017). For forest trees, since seedling survival beneath the forest canopy is often size-dependent (Chang-Yang et al., 2021), microbial effects that reduce seedling biomass lead to higher mortality and thus have a clear

demographic consequence on plant populations. However, while individual biomass can serve as a proxy for population growth in these particular systems, it is crucial to recognize that the underlying demographic process enabling this interpretation varies among systems.

V. Modeling frameworks for incorporating temporal and demographic aspects of plant–soil microbe interactions

As reviewed in the above sections, the strength and direction of plant–soil microbe interactions vary along different temporal dimensions and can influence various demographic processes. While empirical studies are essential for growing our understanding of these aspects, predicting their long-term consequences requires an integration of data with models of plant population dynamics. Therefore, we encourage studies to go beyond biomass-based inferences to demographic models that directly incorporate microbial effects. Developing suitable theoretical models for the focal plant–soil system and connecting them with empirical data is a pressing research direction. Below, we discuss two theoretical frameworks that are especially well-suited to incorporate the temporal and demographic components of plant–soil microbe interactions and highlight studies that have parameterized them with empirical data.

V.1 Patch occupancy models

Patch occupancy models represent a relatively straightforward framework for studying plant–soil microbe interactions (Pacala and Tilman, 1994, Mouquet et al., 2002). In this group of models, plants compete for unoccupied sites (patches) and the probability that a particular plant species establishes in a local site depends on the site's microbial legacy (Stump and Comita, 2018, Miller and Allesina, 2021, Ke and Levine, 2021). Such models can either be spatially implicit, which assumes that the landscape can be divided into an infinite number of patches and tracks the proportion of different plant–soil microbe states (e.g., Miller and Allesina, 2021, Ke and Levine, 2021), or spatially explicit, which considers a fixed-size arena and allows one to consider spatial proximity when modeling microbial impact (e.g., the diffusion of microbial effects from live individuals nearby; Bever et al., 1997, Mack and Bever, 2014, Bauer et al., 2015). Detailed formulation

aside, a common assumption in such models is that plants only indirectly influence each other by modifying soil microbial legacies. This assumption aligns well with two-phase experiments that grow individual plants in soils with different conditioning histories, and as such, patch occupancy models can be readily parameterized with biomass measurements from pot experiments (e.g., by assuming establishment probability scales with the relative biomass performance). Alternatively, patch occupancy models can also be parameterized with recruitment data from repeated censuses, thereby incorporating microbial effects on multiple early life stages (e.g., seed survival, germination, and seedling survival in Fig. 5; Krishnadas and Stump, 2021). Due to this connection with empirical data, patch occupancy models are commonly used in the PSF literature when studies wish to extrapolate predictions based on pairwise biomass-based metrics to multi-species communities (e.g., Mangan et al., 2010, Teste et al., 2017, Dudenhöffer et al., 2022).

The patch occupancy framework offers a pathway to effectively incorporate various temporal aspects of plant–soil microbe interactions (Fig. 1; see also an example in Box 1). This is because such models can treat different developmental stages of the soil microbial community as distinct states so that the transitions between states reflect the conditioning and decay rates of soil microbes. The explicit inclusion of microbial legacies in the form of an unoccupied but conditioned patch state differs from previous feedback models, which usually assume tight coupling between plants and microbes (Eppinga et al., 2018, Mack et al., 2019). For example, Ke et al. (2021) modified a previous model (Fukami and Nakajima, 2013) by making microbial effects vary with the duration of soil conditioning, which in turn influences the transient trajectory of community assembly. In another example, Ke and Levine (2021) used a spatially implicit model to show that the strength of stabilization driven by host-specific pathogens depends on how quickly the conditioning effects of plants erode. The above models directly track the changes of microbial impact on plants through time, and can thus be parameterized with the type of experiments mentioned in subsection III.3. Alternatively, one can build simulation-based models that explicitly track the population size of microbes at each local site, allowing the temporal development and decay of microbial effects to emerge naturally (Schroeder et al., 2020). However, such models are harder to parameterize with empirical data since they require detailed knowledge of microbial traits and population dynamics (Jiang et al., 2020).

V.2 Models incorporating multiple demographic processes

In contrast to patch occupancy models, which usually assume that microbes only impact the establishment process, one can also formulate models that directly consider distinct microbial impacts on distinct plant demographic processes. Such an approach, which can be difficult to implement due to the extensive amount of work required to obtain all parameters, may be particularly fruitful in demographically complex systems. Demonstrating the power of this approach, a series of studies (Mordecai, 2013a,b, 2015, Uricchio et al., 2019) integrated models and empirical observations to investigate how pathogens affect competition between native perennials and invasive annual grasses. The plant demography components of these models begin with an approach often used for annual plants: they track the yearly population of each species' seeds, which persist in the soil seed bank from previous years or are produced by reproductive-stage individuals, and capture the effect of plant competition through density-dependent decreases in seed production (Fig. 2A; see also section II. and Box 2). The authors then incorporated perennial demography by additionally tracking the number of adult perennials, reflecting successful seed germination and recruitment, as well as adult survival from the previous year. This model structure can flexibly incorporate the effect of microbes by allowing them to modify various demographic transitions; in particular, the authors focused on a soil-borne pathogen that reduces seed persistence and germination (Mordecai, 2013a). With a plant competition experiment and manipulations of pathogen densities, Mordecai (2013b) parameterized a model with density-dependent microbial effects and concluded that pathogen spillover promotes the persistence of perennial bunchgrasses. Subsequent work further demonstrated the adaptability of this framework: Mordecai (2015) showed that the plant life stage attacked by pathogens (i.e., seedlings or dormant seeds) and environmental variation jointly determined the coexistence of competing annual plants. In another application, Uricchio et al. (2019) combined field observations and experiments to parameterize an even more realistic model, considering multiple annual and perennial species and incorporating two additional microbial effects (i.e., the impacts of foliar pathogens on seedling survival and adult perennial fecundity).

In addition to integrating multiple microbial effects, a demographically explicit model can help identify the most critical microbial effect via simulations. For instance, in the annual–perennial

plant model in Uricchio et al. (2019), foliar pathogens have little impact but seed pathogens can have a more significant effect on perennial competitors in the system. Such a sensitivity analysis is particularly useful when models include many mechanistic parameters for microbial dynamics (e.g., Ke et al., 2015, Schroeder et al., 2020) and represents another reason why isolating microbial effects on specific demographic transitions can be enlightening. Even for models that do not explicitly incorporate microbial dynamics, identifying the bottleneck for population growth can provide insights for future studies and guide more targeted experiments. Using an integral projection model parameterized with long-term demographic data, Chu and Adler (2015) showed that feedback loops during the recruitment stage contributed most to plant coexistence compared to that during the growth and survival stages. The authors speculated this is due to the recruitment stage involving many demographic transitions that are susceptible to soil pathogens (Chu and Adler, 2015). In Box 2, with an annual–perennial plant model incorporating microbial effects as qualitative switches in parameter values, we also demonstrate how sensitivity analysis can help identify the relative importance of different microbial effects on the perennial plant. In sum, formulating demographic models not only allows smooth integration of the temporal and demographic dimensions of plant–soil microbe interactions but also provides an opportunity to explore their consequences in multi-species communities.

VI. Conclusion: moving forward with an empirical-theoretical feedback loop

Since its introduction to community ecology, the study of plant–soil microbe interactions has long been shaped by a tight link between empirical and theoretical approaches. By showing how empirically tractable greenhouse experiments can yield data to calculate theory-derived metrics, the approach from Bever et al. (1997) has motivated more than two decades of research to predict the long-term consequences of soil microbes (Crawford et al., 2019). To date, new studies continue to follow this integration, proposing new theories to capture different impacts of soil microbes as well as new experimental designs to quantify them (e.g., Kandlikar et al., 2019, 2021, Yan et al., 2022). Two key assumptions of this approach are that plant–soil microbe interactions follow a

simplified temporal trajectory, and that measuring microbial impact on plant biomass captures the population dynamic consequences of soil microbes. While such abstractions have helped make models generalizable, growing evidence has proven the relevance of the two knowledge gaps when predicting the role of soil microbes in natural communities (Chung, 2023). Explicit consideration of the temporal and demographic aspects not only leads to new research questions but also allows researchers to draw conclusions grounded on relevant experimental settings. As such, we see tremendous value in future efforts that aim to (1) develop theoretical models that can explicitly incorporate the temporal and demographic components of plant–soil microbe interactions, and (2) parameterize such models with corresponding observational data or experiments aimed at quantifying these past-missing components.

New modeling frameworks should be developed in order to incorporate the aforementioned temporal and demographic components. Here, we identify two paths moving forward. First, patch occupancy models can be used to study the temporal dimensions of plant–soil microbe interactions by tracking the transition between different soil microbial states, which impact the subsequent establishment of plants in that patch. This framework also echoes recent theoretical studies suggesting that competition for limited colonization sites generates more interpretable frequency-based dynamics for multi-species communities than do extensions of the classic pairwise feedback model (Miller et al., 2022). Second, instead of tracking species' occupancy frequency, one can also build demographic models that explicitly track plant population densities; this approach offers the opportunity to easily incorporate microbial effects on multiple plant demographic stages. We note that in practice, these modeling approaches are both flexible and can be used to answer more than one research question (e.g., decay dynamics and time-dependent feedback can also be built into a demographically explicit model; Senthilnathan and D'Andrea, 2023, Zou et al., 2024). Ultimately, the choice depends on the research question and the focal plant–soil system. For example, in systems with disturbances that may truncate soil conditioning at different timings (Nagendra and Peterson, 2016), or those with low propagule availability such that conditioned soils are not immediately recolonized, investigating the temporal dimension can provide great insights into the role of soil microbes in nature; this can also be done by simulations of time-discrete models (Zou et al., 2024) and individual-based models (Zee and Fukami, 2015). On the other hand,

when different soil microbes are known to impact different parts of the plant life cycle, integrating multiple microbial effects into a single demographic model may be more important.

While patch occupancy models can be parameterized with either biomass measurements (e.g., Mangan et al., 2010, Teste et al., 2017, Dudenhöffer et al., 2022) or census data (e.g., Stump and Comita, 2018), we caution that the model itself is agnostic to the demographic details of plant–soil microbe interactions and will encompass different microbial effects depending on the data used for parameterization (Fig. 5). For instance, Stump and Comita (2018) parameterized their patch occupancy model with CNDD patterns based on 5-year seedling survival (Comita et al., 2010), which correspond to microbial effects on the survival of established older seedlings. On the other hand, Krishnadas and Stump (2021) parameterized a similar model with CNDD patterns based on the seed-to-seedling transition, thereby representing microbial effects on recruitment and earlier life stages. Moreover, using different types of data to parameterize the model implies different assumptions on how microbial effects operate. In particular, using performance measurements from single-individual greenhouse experiments (e.g., Teste et al., 2017, Dudenhöffer et al., 2022) to parameterize a patch occupancy model implies that the plant community is driven by how soil microbes affect the density-independent growth rate of plant populations, whereas using CNDD patterns from observational census incorporates how soil microbes and other non-microbial mechanisms modify the nature of density dependence among plants.

Designing new experiments that provide the necessary information to parameterize the new plant demographic models of plant–soil microbe interactions is another frontier of research. Some models require experiments that are similar to current two-phase experiments. For instance, to depict temporal development patterns, one can repeat an experiment along naturally occurring variations in the duration of soil conditioning; to track multiple early life stage microbial effects, one can directly plant ungerminated seeds into cultivated soils. However, some microbial effects cannot be reliably estimated by classic two-phase experiments with a single-growing plant individual. For example, if microbes are expected to affect not only plant intrinsic growth rate but also the nature of density dependence among plants, then estimating microbial effects requires additional treatments beyond the classic two-phase design Recent studies linking plant–soil microbe interactions and coexistence theory specifically highlight this scenario where soil microbes influence the model's

density dependence parameters (Kandlikar et al., 2019, Ke and Wan, 2020, Zou et al., 2024), which require employing experiments that directly manipulate plant density and soil origin (Chung and Rudgers, 2016, Cardinaux et al., 2018). An empirical–theoretical feedback loop is also central to the design of such theory-driven experiments. For example, a proposed design based on the premise that plant–plant interactions are competitive (Ke and Wan, 2020) was challenged by the observation that facilitation is common, leading to a revised density gradient design with greater flexibility (Ke and Wan, 2023). Again, the optimal approach depends on feasibility and which research question can provide a fundamental understanding of the focal plant–soil system.

Recent census-based CNDD studies have introduced a promising approach to investigate how microbe-mediated plant demography interacts with the three temporal aspects, namely, the duration of soil conditioning, the life stage of responding plants, and the time delay between consecutive colonizing plants. Current CNDD studies often calculate size-weighted abundance when estimating conspecific densities, thereby implicitly considering soil conditioning time by linking plant size to microbial effects. Additionally, microbial communities associated with plants of different ages can be sequenced to examine the relationship between pathogen accumulation and species' CNDD strength (Chen et al., 2019). Long-term observational data should also allow us to test whether conspecific effects change with the age/stage of the responding focal individual (Bagchi et al., 2014, Zhu et al., 2015, 2018). For instance, Zhu et al. (2015) showed that the CNDD effects attenuated as individuals mature from seedlings to adults. Finally, a recent study also pioneered the inclusion of dead tree individuals into the abundance calculation (i.e., the effects of decay; Magee et al., 2024). Insights from such CNDD studies can be used to parameterize patch occupancy models with corresponding temporal aspects, offering new insights by integrating the two overlooked components.

One of the remaining challenges is to move away from a plant-centered viewpoint towards a better understanding of the dynamics and functionality of soil microbial communities (Jiang et al., 2020). Theoretical models often assume simplified microbial dynamics (e.g., separation of timescales) or treat soil microbes as a qualitative modifier of plant parameters. Incorporating microbial community assembly processes, as outlined in section II, can help inform which processes need to be prioritized when building mechanistic models of microbial community dynamics (e.g.,

Schroeder et al., 2020, see also Zou et al., 2024 for a discrete-time model with explicit consideration of the temporal dynamics of soil microbes). Empirically, experiments that establish the causal relationship between measured microbial dynamics and plant demographic responses can help feed theory with realistically parameterized temporal patterns. To this end, a starting point is to simultaneously measure shifts in both plant response and microbial community composition within studies that vary the temporal components (e.g., Esch and Kobe, 2021, Ke et al., 2021, Hannula et al., 2021, but see Carini et al., 2016 for technical challenges related to erroneously detecting DNA from dead microbes in sequencing time series). Moreover, given the functional plasticities and redundancies of microbial communities, improvements in identifying microbial functionality beyond that based on taxonomic information are also needed. Explicit quantification of microbial activity, such as measurements through multi-omics outputs, can allow for better modeling of functional microbial dynamics. Future studies balancing both the plant and microbe perspectives can further facilitate the empirical–theoretical feedback loop when studying the two missing components of plant–soil microbe interactions.

In summary, we conclude that studying the temporal dimension and the multiple demographic consequences of plant–soil microbe interactions provides a better understanding of their natural context. In addition to the maintenance of plant diversity, the two knowledge gaps can also be important for other ecological processes (e.g., recovery following disturbance and gap dynamics). The temporal dimensions highlighted here also underline the significance of phenological mismatch among plants and soil microbes driven by climate change (Rudgers et al., 2020; e.g., late-germinating plants may be more vulnerable to pathogens). Recognizing that soil conditioning and plant response are temporally varying processes also provides insights into the context-dependency of plant-soil microbe interactions: shifts in the abiotic environment can occur throughout a plant's lifetime, and the timing of these shifts can alter the temporal trajectory differently. Ultimately, knowledge of the system's natural history should guide researchers to recognize which aspects of the temporal and demographic components are important for the focal system and the research question. With the most critical aspect being identified, we believe that parameterizing new demographic models provides an avenue to predict the long-term consequences of plant–soil microbe interactions against a backdrop of real-world conditions in which

these interactions unfold.

Boxes

Box 1: Implementing a patch occupancy model to study the temporal decay of microbial effects

Here, we demonstrate how the temporal decay of microbial effects can be studied with a multi-species patch occupancy model. We considered three different plant–soil microbe states (Box Fig. 1A): unconditioned soil (P_{00}), soils colonized and conditioned by plant i (P_{ii}), and uncolonized soils with a microbial legacy (P_{0i}). The transition among these different states can be described as follows (see also Ke and Levine, 2021 and Miller and Allesina, 2021):

$$\frac{dP_{00}}{dt} = \overbrace{\sum_{i=1}^{N} d_i P_{0i}}^{\text{decay of conditioning effect in empty patches}} - \overbrace{\sum_{i=1}^{N} r_i P_{ii} P_{00}}^{\text{plant establishment into empty and unconditioned patches}} \tag{1}$$

$$\frac{dP_{ii}}{dt} = \overbrace{r_i P_{ii} P_{00}}^{\text{plant establishment into empty and unconditioned patches}} + \overbrace{\sum_{j=1}^{N} r_i \sigma_{ij} P_{ii} P_{0j}}^{\text{plant establishment in empty but conditioned patches}} - \overbrace{m_i P_{ii}}^{\text{plant mortality}} \tag{2}$$

$$\frac{dP_{0i}}{dt} = \overbrace{m_i P_{ii}}^{\text{plant mortality}} - \overbrace{d_i P_{0i}}^{\text{decay of conditioning effect in empty patches}} - \overbrace{\sum_{j=1}^{N} r_j \sigma_{ji} P_{jj} P_{0i}}^{\text{plant establishment in empty but conditioned patches}}. \tag{3}$$

Specifically, state transitions occur due to plant colonization/soil conditioning (r_i), plant mortality (m_i), and the decay of microbial effects (d_i, black arrows in Box Fig. 1A). Here, soil microbes affect the ability of plants to recolonize conditioned soils (red arrows in Box Fig. 1A). N represents the total number of species within the community.

To illustrate the consequences of variable decay rates of microbial effects, we simulated the microbial effects (σ_{ij}) for 16 plant species with data from Teste et al., 2017, which measured soil microbial effects on plant biomass accumulation. We randomly drew species' fecundity (r_i) from a uniform distribution between 0.2 to 0.25. This simulation illustrates how the decay rates of microbial effects determine the overall consequences of soil microbes on plant communities (Box Fig. **??**B & C). Specifically, with this parameterization and when microbial effects persist after host death (i.e., low d_i; left panels in Box Fig. 1B & C), plant–soil microbe interactions mostly result in the dominance of a single species, overwhelming

Box 1 (continued)

species' variation in fecundity. However, if the conditioned microbial effect decayed rapidly after the death of host plants (i.e., high d_i; right panels in Box Fig. 1B & C), variation in species' fecundity allowed higher diversity in each simulation and more equal persistence probability across species. Therefore, predicting the consequences of plant–soil microbe interactions in nature also requires quantifying the decay rate of greenhouse-measured microbial effects.

Box 2: Implementing a demographic model to detect the most critical microbial effect

Here, we demonstrate how situating microbial effects within a demographic model of plant population dynamics can help integrate multiple microbial effects and identify the most critical one. We modified the model from Uricchio et al. (2019) to describe the competition between an annual plant (N_a) and a perennial plant with two stages, denoted as N_p and A_p for its seed and adult abundance, respectively:

$$N_a(t+1) = \overbrace{s_a\left(1-g_a\right)N_a(t)}^{\substack{\text{survival of}\\ \text{ungerminated seeds}}} + \overbrace{N_a(t)\frac{g_a\lambda_a}{1+\alpha_{ap}A_p(t)+\alpha_{aa}g_aN_a(t)}}^{\text{seed production}} \tag{1}$$

$$N_p(t+1) = \overbrace{s_p\left(1-g_p\right)N_p(t)}^{\substack{\text{survival of}\\ \text{ungerminated seeds}}} + \overbrace{A_p(t)\frac{\lambda_p}{1+\alpha_{pp}A_p(t)+\alpha_{pa}g_aN_a(t)}}^{\text{seed production by adult plants}} \tag{2}$$

$$A_p(t+1) = \overbrace{A_p(t)\xi}^{\substack{\text{survival of}\\ \text{existing adults}}} + \overbrace{N_p(t)\frac{g_pv}{1+\beta_{p,A_p}A_p(t)+\beta_{p,N_p}g_pN_p(t)+\beta_{p,N_a}g_aN_a(t)}}^{\text{maturation of seeds into adult plants}} \tag{3}$$

The seed dynamics of both life history types are similar to that in the Beverton–Holt model, with a seed bank term influenced by germination (g_i, $i = a$ or p) and survival (s_i) as well as a seed production term (λ_i) that is discounted by competition (α_{ij}). The perennial plant differs from the annual in that its seed production (second term in equation 2) depends on the adult stage. The maturation of perennial seeds to adulthood (second term in equation 3) depends on the survival probability (v) and competition ($\beta_{p,j}$, $j = A_p$, N_p, and N_a) from individuals of all stages. Finally, perennial adults suffer mortality in a competition-independent manner such that the proportion surviving after each year is ξ.

For the perennial plant, there are five demographic parameters that can be affected by soil microbes (g_p, s_p, λ_p, v, and ξ). As demonstrated in section II., the first strength of a demographic model is that it can integrate multiple microbial effects. For example, if soil pathogens decreased all parameters of the perennial plant by 20%, the model suggests that it would nearly be outcompeted by the annual plant (i.e., from grey to blue dashed line). By only quantifying the impact of pathogens on the intrinsic fecundity (λ_p), as is commonly done in studies that grow individual plants in conditioned soils, we would have underestimated

Box 2 (continued)

the impacts of soil microbes in this system. The second strength of a demographic model is that it helps identify the most critical microbial effect. For example, sensitivity analysis (see Box figure legend for details) revealed that, compared to other demographic parameters, the impact of pathogens on adult survival probability (ξ) had the strongest impact on the perennial plant population.

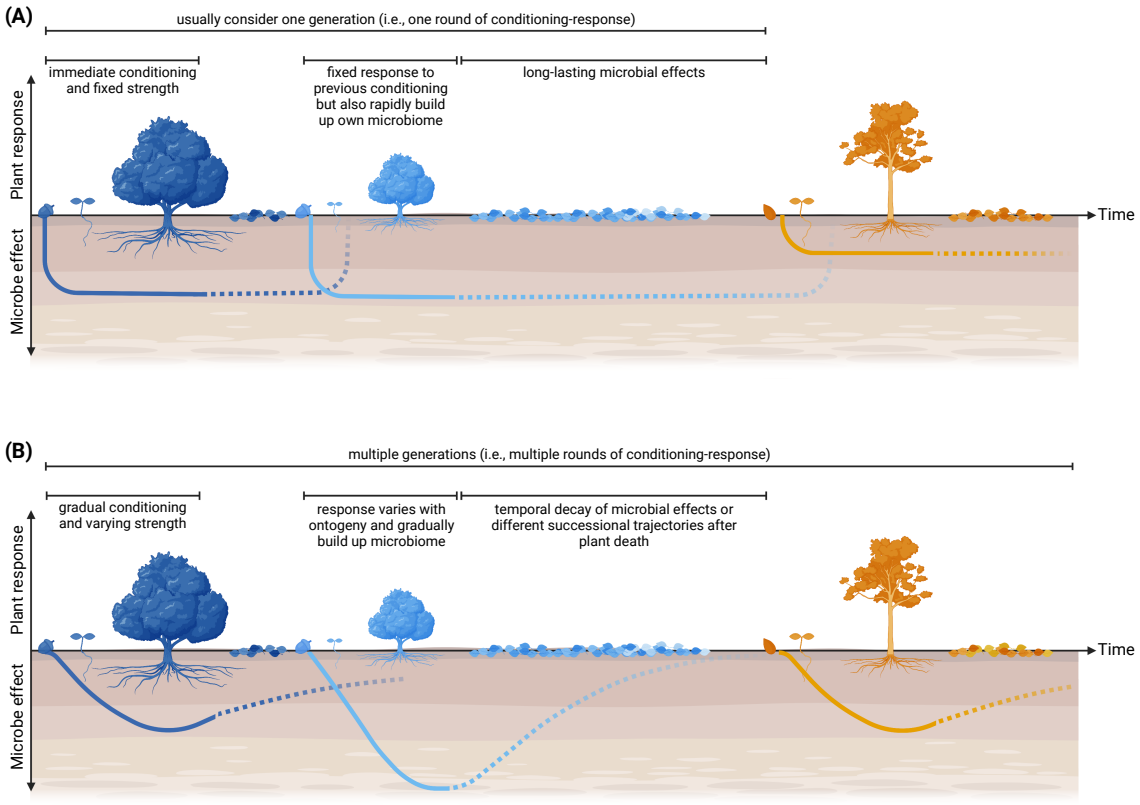


Figure 1 Temporal dimensions of plant–soil microbe interactions throughout the repeated process of plant establishment, growth, death, and recolonization by another individual. (A) The common assumptions of plant–soil microbe interactions implied by the design of classic experiments: microbial communities develop relatively quickly, with resulting microbial effects that are constant throughout different plant life stages and remain as long-lasting legacies after plant senescence to impact the next generation. (B) The dynamic plant–soil microbe interaction perspective highlighted in our review: microbial communities change continuously throughout the conditioning process, with impacts on plant performance that depend on both the duration of plant conditioning and response (subsection III.1). Moreover, microbial communities and their impacts on plant performance may diminish with time after the senescence of the previous conditioning individual (subsection III.2) or undergo different trajectories depending on the previous rounds of conditioning (mentioned as a future direction in subsection III.3).

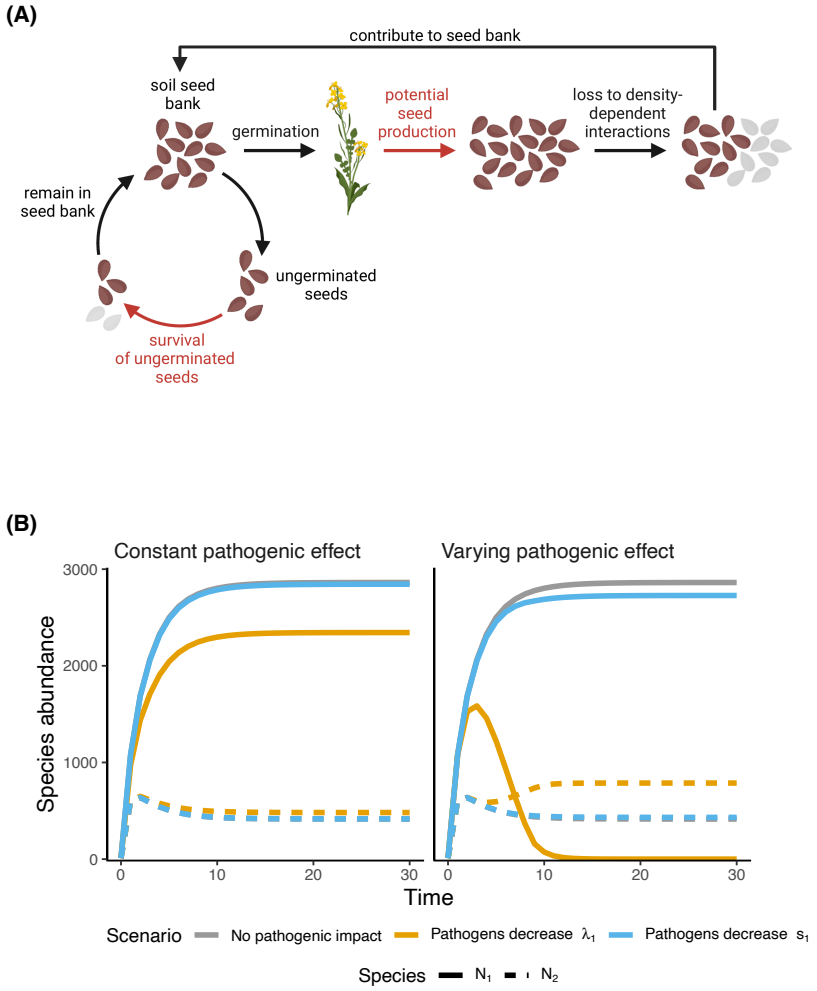


Figure 2 An example demonstrating how incorporating the temporal and demographic aspects of plant–soil microbe interactions can generate different competitive outcomes in the annual plant model. (A) A graphical representation of the Beverton–Holt annual plant model, which tracks the density of seeds prior to germination. Demographic processes influenced by soil microbes in this simulation are highlighted in red, including seed survival and the fecundity of germinated plants. (B) Abundance time series of N_1 (solid line) and N_2 (dashed line) under different microbial effect scenarios: no pathogenic effect (grey), pathogens decrease the seed survival of N_1 (s_1; blue), and pathogens decrease the fecundity of N_1 (λ_1; orange). The left panel assumes a 10% decrease in N_1's demographic parameters, whereas the right panel assumes that the initial 10% decrease after one generation aggravates to a 80% decrease after eight generations (i.e., 10% decrease after every generation). Note that the blue lines often overlap the grey lines due to the minor impact of s_1. Parameters are obtained from the species pair *Festuca microstachys* (N_1) versus *Hordeum murinum* (N_2) in Van Dyke et al. (2022): $g_1 = 0.752$, $g_2 = 0.667$, $s_1 = 0.134$, $s_2 = 0.045$, $\lambda_1 = 2129.950$, $\lambda_2 = 736.667$, $\alpha_{11} = 0.588$, $\alpha_{12} = 1.411$, $\alpha_{21} = 0.109$, and $\alpha_{22} = 0.948$.

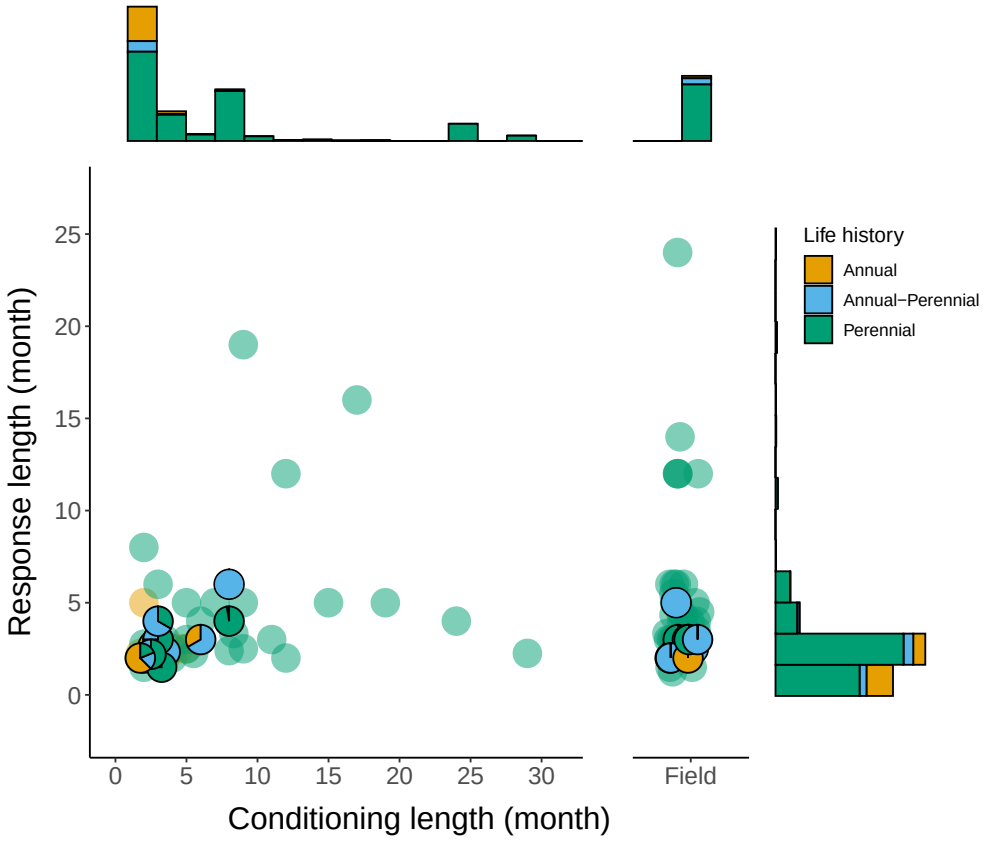


Figure 3 A summary of the experimental duration and life history information of the study species in the Crawford et al. (2019) and Yan et al. (2022) data sets. Since the two studies focused on the pairwise plant–soil feedback, we compiled information on plant life history and categorized each pairwise comparison as different "pair types": annual (both plants are annuals; orange), perennial (both plants are perennials; green), or annual–perennial (match of an annual versus a perennial; blue). Highlighted points represent studies that evaluated plant–soil feedback between annual and perennial plants, with each pie chart representing the percentage of different pair types within the study (translucent points indicate studies that included only annual or only perennial species). The position of each pie chart indicates the duration of a study's conditioning (x-axis; field-conditioned soil as a separate category) and response phase (y-axis). The upper and right stacked histograms depict the same information but are based on the number of experimental pairs across all studies. Note that one study with a conditioning length of 48 months and a response length of 32 months (Kulmatiski, 2019) was excluded from the figure to improve visualization (see supplementary data).

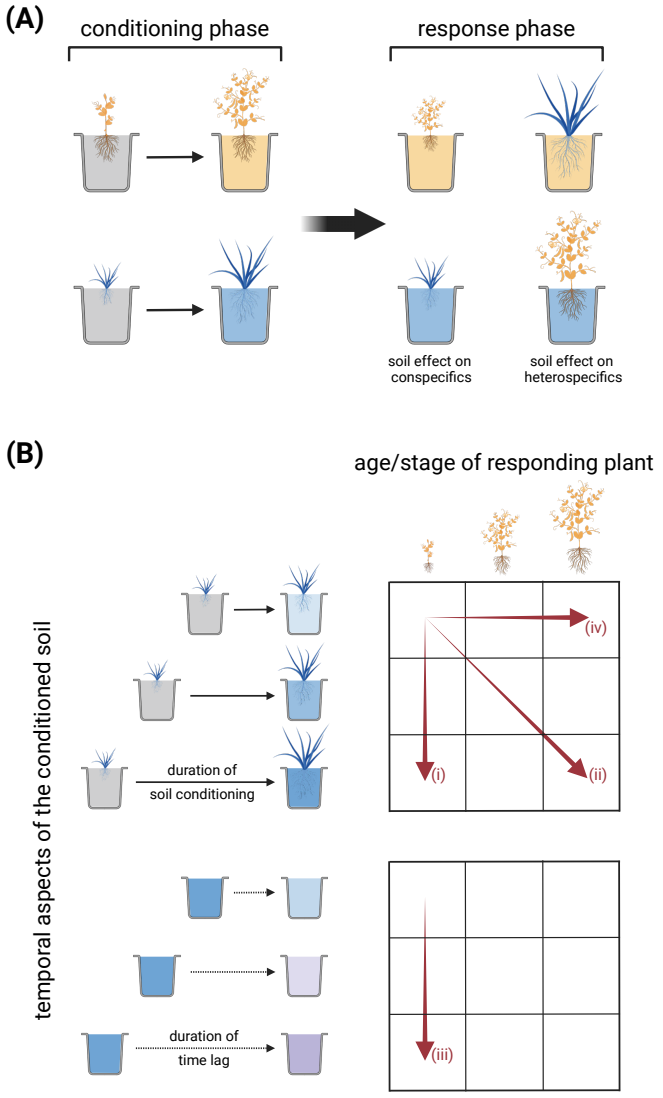


Figure 4 Experiments for studying plant–soil microbe interactions. (A) The classic two-phase experimental design, consisting of a conditioning phase during which plants modify the soil microbial community and a response phase during which plants respond to the soil modification. Depicted here in the response phase is the case of negative frequency-dependent feedback where conditioned soils favor the performance of heterospecifics over conspecifics. (B) Proposed experimental designs to study the various temporal dimensions in the main text (measuring the orange plant's performance in soils conditioned by the blue plant as an example): (i) isolating changes in the soil microbial community by varying the duration of soil conditioning, (ii) sequential harvesting with both conditioning effect and plant age advancing simultaneously, (iii) isolating the decay process by incorporating a time lag after soil conditioning, and (iv) isolating changes in plant physiology by transplanting individuals of different age in the same conditioned soil.

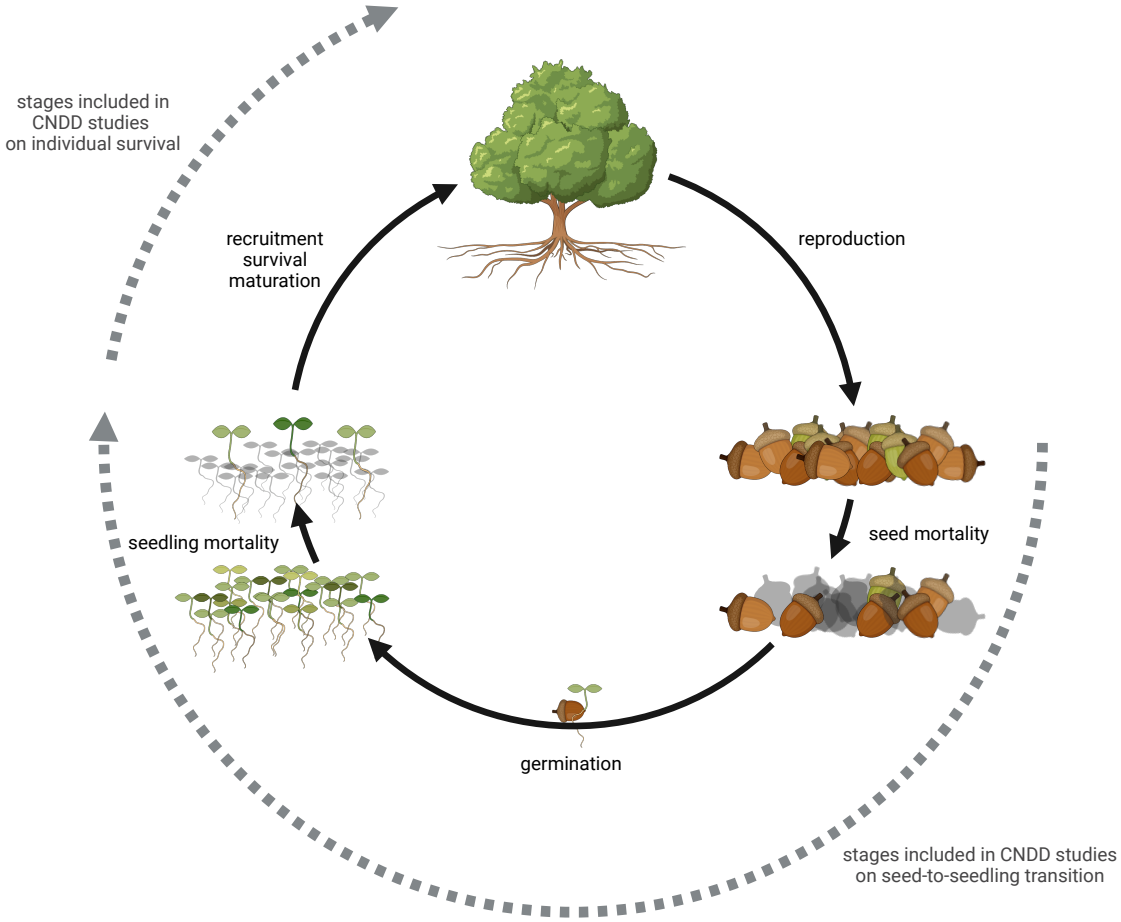
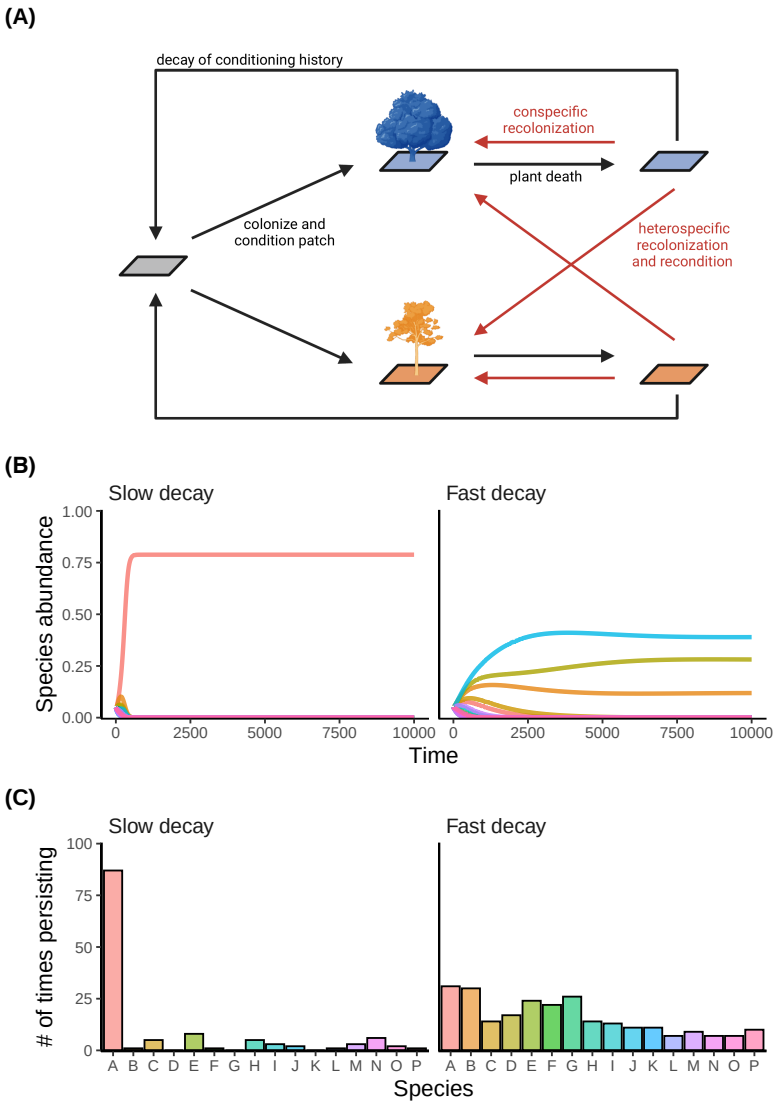
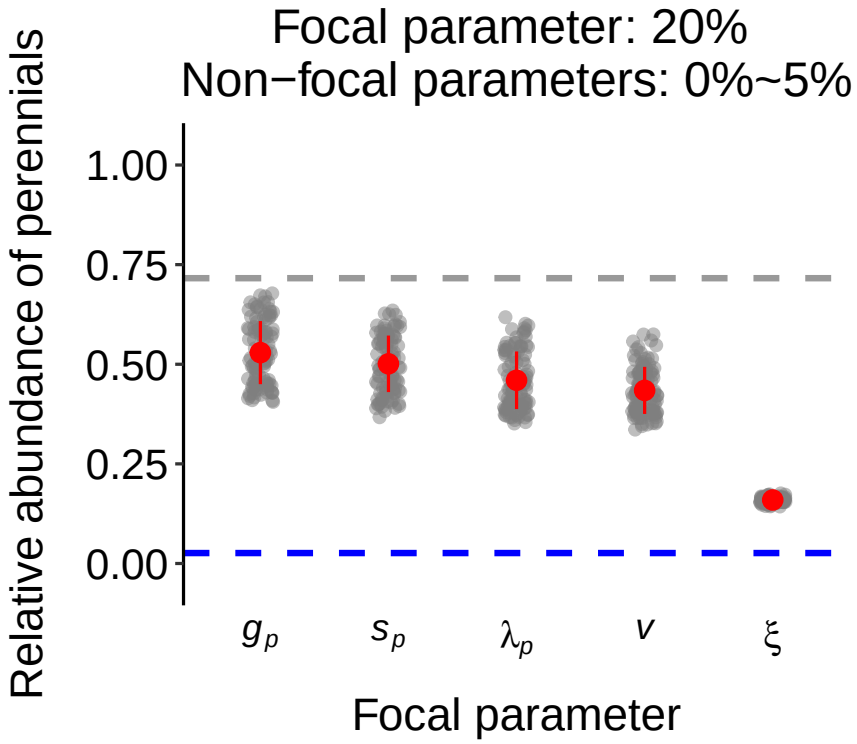


Figure 5 Conceptual diagram depicting multiple demographic consequences of soil microbes, with a particular focus on early plant life stages following most empirical studies. The inner circle (black arrows) indicates the distinct demographic processes that can be affected by soil microbes; in the main text, we highlight empirical evidence on seed mortality, germination, and early seedling survival. The outer circle (grey dashed arrows) indicates the life stages included in different studies on conspecific negative density dependence (CNDD).



Box Figure 1 An example demonstrating how the temporal decay of microbial effects can be studied with a patch occupancy model. (A) Transitions among different plant-soil microbe states occur due to plant colonization/conditioning, plant death, and the decay of microbial effects. Here, soil microbes affect the ability of plants to recolonize conditioned soil (red arrows). (B & C) Diversity of the plant community when microbial effects decay slowly ($d_i = 0.01$; left panels) or rapidly ($d_i = 0.99$; right panels). We simulated the dynamics of 16 plant species (depicted with different colors and letters). We ran 100 simulations; each time we randomly generated a new fecundity value for each species (i.e., $r_i \sim U\,(0.2, 0.25)$) while fixing the microbial effect parameters based on data from Teste et al. (2017). Panel (B) shows a representative time series of the relative abundance of different plant species (frequencies of empty patches are omitted). Panel (C) shows the number of times (out of 100 simulations) the focal species (x-axis; different species labeled with different capitalized letters) persisted in the final community. Mortality (m_i) is set to 0.05 for all plants and initial conditions are: $P_{00} = 0.2$, $P_{ii} = 0.05$ for $i = 1 \ldots 16$, and $P_{0i} = 0.0$. See Box 1 for additional details.



Box Figure 2 Detecting the most critical microbial effect within an annual–perennial plant competition model (modified from Uricchio et al., 2019). Here, soil microbes can impact five demographic parameters of the perennial plant: seed germination rate (g_p), seed survival rate (s_p), intrinsic fecundity (λ_p), seedling survival rate (v) and adult survival rate (ξ). The grey dashed line represents the relative abundance of the perennial plant in the absence of any pathogenic effects from the microbes (i.e., unperturbed baseline parameters), while the dashed blue line shows the perennial's relative abundance when the pathogen simultaneously causes a 20% reduction in all five parameters. To evaluate the demographic consequences of microbes primarily impacting one demographic process, we sequentially decreased the value of each parameter by 20%, while the other four non-focal parameters were randomly decreased by 0% to 5% (assuming weaker microbial impact). For each focal parameter, we repeated this process in 100 simulations (translucent grey points; red points and error bars represent the means and standard deviations) and ran each simulation for 200 generations. These simulations reveal that soil pathogens that primarily reduce adult survival (ξ) have substantially stronger demographic consequences than pathogens that primarily affect other demographic processes. See Box 2 for model description. The baseline parameters are obtained from the species pair *Elymus glaucus* (our perennial) versus *Bromus diandrus* (our annual) in Uricchio et al. (2019) – perennial plant parameter: $g_p = 0.125$, $s_p = 0.515$, $\lambda_p = 282.127$, $\xi = 0.920$, $v = 0.292$; annual plant parameters: $g_a = 0.168$, $s_a = 0.443$, $\lambda_a = 47.594$; competition reduction on seed production: $\alpha_{aa} = 0.066$, $\alpha_{ap} = 0.143$, $\alpha_{pp} = 0.018$, $\alpha_{pa} = 0.104$; competition reduction on perennial survival: $\beta_{p,N_p} = 0.086$, $\beta_{p,A_p} = 0.063$, $\beta_{p,N_a} = 0.002$.

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Author Contributions

P.-J. Ke, G.S. Kandlikar, and S.X. Ou conceived the study and took the lead in writing the first draft. All authors contributed critically to developing the ideas and finalizing the manuscript.

Data Availability

The dataset used in Figure 3 and code used to generate model simulations are available on GitHub (https://github.com/pojuke/DemographicReviewPSF) and will be made available on Zenodo with a DOI upon publication. Figures 1, 2A, 5, and Box Figure 1A are created with BioRender.com.

References

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

Bagchi, R., R. E. Gallery, S. Gripenberg, S. J. Gurr, L. Narayan, C. E. Addis, R. P. Freckleton, and O. T. Lewis, 2014. Pathogens and insect herbivores drive rainforest plant diversity and composition. *Nature* **506**:85–88.

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

Barret, M., M. Briand, S. Bonneau, A. Préveaux, S. Valière, O. Bouchez, G. Hunault, P. Simoneau, and M. A. Jacquesa, 2015. Emergence shapes the structure of the seed microbiota. *Applied and Environmental Microbiology* **81**:1257–1266.

Bauer, J. T., K. M. L. Mack, and J. D. Bever, 2015. Plant–soil feedbacks as drivers of succession: evidence from remnant and restored tallgrass prairies. *Ecosphere* **6**:art158.

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

Bennett, J. A., J. Franklin, and J. Karst, 2023. Plant-soil feedbacks persist following tree death, reducing survival and growth of populus tremuloides seedlings. *Plant and Soil* **485**:103–115.

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

Bever, J. D., 1994. Feeback between plants and their soil communities in an old field community. *Ecology* **75**:1965–1977.

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 & 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.

Bezemer, T. M., J. Jing, J. M. T. Bakx-Schotman, and E.-J. Bijleveld, 2018. Plant competition alters the temporal dynamics of plant–soil feedbacks. *Journal of Ecology* **106**:2287–2300.

Bingham, M. A. and S. W. Simard, 2011. Do mycorrhizal network benefits to survival and growth of interior douglas-fir seedlings increase with soil moisture stress? *Ecology and Evolution* **1**:306–316.

Bittleston, L. S., Z. B. Freedman, J. R. Bernardin, J. J. Grothjan, E. B. Young, S. Record, B. Baiser, and S. M. Gray, 2021. Exploring microbiome functional dynamics through space and time with trait-based theory. *mSystems* **6**:10–1128.

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.

Bottini, R., F. Cassán, and P. Piccoli, 2004. Gibberellin production by bacteria and its involvement in plant growth promotion and yield increase. *Applied Microbiology and Biotechnology* **65**:497–503.

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.

Bulgarelli, D., K. Schlaeppi, S. Spaepen, E. V. L. Van Themaat, and P. Schulze-Lefert, 2013. Structure and functions of the bacterial microbiota of plants. *Annual Review of Plant Biology* **64**:807–838.

Callaway, R. M., G. C. Thelen, A. Rodriguez, and W. E. Holben, 2004. Soil biota and exotic plant invasion. *Nature* **427**:731–733.

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

Carini, P., P. J. Marsden, J. W. Leff, E. E. Morgan, M. S. Strickland, and N. Fierer, 2016. Relic DNA is abundant in soil and obscures estimates of soil microbial diversity. *Nature Microbiology* **2**:1–6.

Chang-Yang, C.-H., J. Needham, C.-L. Lu, C.-F. Hsieh, I.-F. Sun, and S. M. McMahon, 2021. Closing the life cycle of forest trees: The difficult dynamics of seedling-to-sapling transitions in a subtropical rainforest. *Journal of Ecology* **109**:2705–2716.

Chaparro, J. M., D. V. Badri, and J. M. Vivanco, 2013. Rhizosphere microbiome assemblage is affected by plant development. *The ISME Journal* **8**:790–803.

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.

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., 2023. The temporal and spatial dimensions of plant–soil feedbacks. *New Phytologist* **237**:2012–2019.

Chung, Y. A., T. A. Monaco, J. B. Taylor, and P. B. Adler, 2023. Do plant–soil feedbacks promote coexistence in a sagebrush steppe? *Ecology* **104**:e4056.

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.

Clark, C., J. Poulsen, D. Levey, and C. Osenberg, 2007. Are plant populations seed limited? A critique and meta-analysis of seed addition experiments. *The American Naturalist* **170**:128–142.

Comita, L. S., H. C. Muller-Landau, S. Aguilar, and S. P. Hubbell, 2010. Asymmetric density dependence shapes species abundances in a tropical tree community. *Science* **329**:330–332.

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

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

Dalling, J. W., M. Swaine, and N. C. Garwood, 1998. Dispersal patterns and seed bank dynamics of pioneer trees in moist tropical forest. *Ecology* **79**:564–578.

Das, A. J., N. L. Stephenson, and K. P. Davis, 2016. Why do trees die? characterizing the drivers of background tree mortality. *Ecology* **97**:2616–2627.

David, A. S., P. F. Quintana-Ascencio, E. S. Menges, K. B. Thapa-Magar, M. E. Afkhami, and C. A. Searcy, 2019. Soil microbiomes underlie population persistence of an endangered plant species. *The American Naturalist* **194**:488–494.

Day, N. J., K. E. Dunfield, and P. M. Antunes, 2015. Temporal dynamics of plant–soil feedback and root-associated fungal communities over 100 years of invasion by a non-native plant. *Journal of Ecology* **103**:1557–1569.

Diez, J. M., I. Dickie, G. Edwards, P. E. Hulme, J. J. Sullivan, and R. P. Duncan, 2010. Negative soil feedbacks accumulate over time for non-native plant species. *Ecology Letters* **13**:803–809.

Dombrowski, N., K. Schlaeppi, M. T. Agler, S. Hacquard, E. Kemen, R. Garrido-Oter, J. Wunder, G. Coupland, and P. Schulze-Lefert, 2016. Root microbiota dynamics of perennial *Arabis alpina* are dependent on soil residence time but independent of flowering time. *The ISME Journal* **11**:43–55.

Dostál, P., 2021. The temporal development of plant-soil feedback is contingent on competition and nutrient availability contexts. *Oecologia* **196**:185–194.

Dostál, P., J. Müllerová, P. Pyšek, J. Pergl, and T. Klinerová, 2013. The impact of an invasive plant changes over time. *Ecology Letters* **16**:1277–1284.

Dostálek, T., J. Knappová, and Z. Münzbergová, 2022. The role of plant–soil feedback in long-term species coexistence cannot be predicted from its effects on plant performance. *Annals of Botany* **130**:535–546.

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.

Dudenhöffer, J.-H., N. C. Luecke, and K. M. Crawford, 2022. Changes in precipitation patterns can destabilize plant species coexistence via changes in plant–soil feedback. *Nature Ecology & Evolution* **6**:546–554.

Edwards, J. A., C. M. Santos-Medellín, Z. S. Liechty, B. Nguyen, E. Lurie, S. Eason, G. Phillips, and V. Sundaresan, 2018. Compositional shifts in root-associated bacterial and archaeal microbiota track the plant life cycle in field-grown rice. *PLOS Biology* **16**:e2003862.

Eldridge, D. J., S. K. Travers, J. Val, J. Ding, J.-T. Wang, B. K. Singh, and M. Delgado-Baquerizo, 2021. Experimental evidence of strong relationships between soil microbial communities and plant germination. *Journal of Ecology* **109**:2488–2498.

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

Esch, C. M. and R. K. Kobe, 2021. Short-lived legacies of *Prunus serotina* plant–soil feedbacks. *Oecologia* **196**:529–538.

Esch, C. M., C. M. Medina-Mora, R. K. Kobe, and M. L. Sakalidis, 2021. Oomycetes associated with *Prunus serotina* persist in soil after tree harvest. *Fungal Ecology* **53**:101094.

Fanin, N., D. Lin, G. T. Freschet, A. D. Keiser, L. Augusto, D. A. Wardle, and G. F. Veen, 2021. Home-field advantage of litter decomposition: from the phyllosphere to the soil. *New Phytologist* **231**:1353–1358.

Forero, L. E., A. Kulmatiski, J. Grenzer, and J. M. Norton, 2021. Plant-soil feedbacks help explain biodiversity-productivity relationships. *Communications Biology* **4**:789.

881 Fukami, T. and M. Nakajima, 2013. Complex plant–soil interactions enhance plant species diversity
882 by delaying community convergence. *Journal of Ecology* **101**:316–324.

883 Gallery, R. E., D. J. Moore, and J. W. Dalling, 2010. Interspecific variation in susceptibility to
884 fungal pathogens in seeds of 10 tree species in the neotropical genus *Cecropia*. *Journal of Ecology*
885 **98**:147–155.

886 Gao, C., L. Montoya, L. Xu, M. Madera, J. Hollingsworth, E. Purdom, R. B. Hutmacher, J. A.
887 Dahlberg, D. Coleman-Derr, P. G. Lemaux, et al., 2019. Strong succession in arbuscular mycor-
888 rhizal fungal communities. *The ISME journal* **13**:214–226.

889 Gilbert, G. S., 2002. Evolutionary ecology of plant diseases in natural ecosystems. *Annual Review*
890 *of Phytopathology* **40**:13–43.

891 Grove, S., I. M. Parker, and K. A. Haubensak, 2015. Persistence of a soil legacy following removal
892 of a nitrogen-fixing invader. *Biological Invasions* **17**:2621–2631.

893 Gundale, M. J. and P. Kardol, 2021. Multi-dimensionality as a path forward in plant-soil feedback
894 research. *Journal of Ecology* **109**:3446–3465.

895 Hannula, S. E., R. Heinen, M. Huberty, K. Steinauer, J. R. De Long, R. Jongen, and T. M. Bezemer,
896 2021. Persistence of plant-mediated microbial soil legacy effects in soil and inside roots. *Nature*
897 *Communications* **12**:5686.

898 Hannula, S. E., A. M. Kielak, K. Steinauer, M. Huberty, R. Jongen, J. R. De Long, R. Heinen, and
899 T. M. Bezemer, 2019. Time after time: temporal variation in the effects of grass and forb species
900 on soil bacterial and fungal communities. *MBio* **10**:10–1128.

901 Harms, K. E., S. J. Wright, O. Calderón, A. Hernandez, and E. A. Herre, 2000. Pervasive density-
902 dependent recruitment enhances seedling diversity in a tropical forest. *Nature* **404**:493–495.

903 Harper, J. L., 1977. Population biology of plants. Academic Press.

904 Hawkes, C. V., S. N. Kivlin, J. Du, and V. T. Eviner, 2013. The temporal development and additivity
905 of plant-soil feedback in perennial grasses. *Plant and Soil* **369**:141–150.

Herrera Paredes, S. and S. L. Lebeis, 2016. Giving back to the community: microbial mechanisms of plant–soil interactions. *Functional Ecology* **30**:1043–1052.

Horton, T. and M. van der Heijden, 2008. The role of symbioses in seedling establishment and survival. *Seedling Ecology and Evolution* pages 189–214.

Howard, M. M., J. Kao-Kniffin, and A. Kessler, 2020. Shifts in plant–microbe interactions over community succession and their effects on plant resistance to herbivores. *New Phytologist* **226**:1144–1157.

Huang, L.-F., L.-X. Song, X.-J. Xia, W.-H. Mao, K. Shi, Y.-H. Zhou, and J.-Q. Yu, 2013. Plant-soil feedbacks and soil sickness: from mechanisms to application in agriculture. *Journal of Chemical Ecology* **39**:232–242.

Huberty, M., K. Steinauer, R. Heinen, R. Jongen, S. E. Hannula, Y. H. Choi, and T. M. Bezemer, 2022. Temporal changes in plant–soil feedback effects on microbial networks, leaf metabolomics and plant–insect interactions. *Journal of Ecology* **110**:1328–1343.

Igwe, A. N., B. Quasem, N. Liu, and R. L. Vannette, 2021. Plant phenology influences rhizosphere microbial community and is accelerated by serpentine microorganisms in Plantago erecta. *FEMS Microbiology Ecology* **97**:85.

Ishaq, S. L., 2017. Plant-microbial interactions in agriculture and the use of farming systems to improve diversity and productivity. *AIMS Microbiology* **3**:335.

Janzen, D. H., 1970. Herbivores and the number of tree species in tropical forests. *The 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. *The American Naturalist* **195**:591–602.

Johansen, A. and E. S. Jensen, 1996. Transfer of N and P from intact or decomposing roots of pea to barley interconnected by an arbuscular mycorrhizal fungus. *Soil Biology and Biochemistry* **28**:73–81.

Kalske, A., J. D. Blande, and S. Ramula, 2022. Soil microbiota explain differences in herbivore resistance between native and invasive populations of a perennial herb. *Journal of Ecology* **110**:2649–2660.

Kandlikar, G. S., 2024. Quantifying soil microbial effects on plant species coexistence: A conceptual synthesis. *American Journal of Botany* **111**:e16316.

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.

Kandlikar, G. S., X. Yan, J. M. Levine, and N. J. Kraft, 2021. Soil microbes generate stronger fitness differences than stabilization among california annual plants. *The American Naturalist* **197**:E30–E39.

Kardol, P., M. T. Bezemer, and W. H. van der Putten, 2006. Temporal variation in plant–soil feedback controls succession. *Ecology Letters* **9**:1080–1088.

Kardol, P., G. B. De Deyn, E. Laliberté, P. Mariotte, and C. V. Hawkes, 2013. Biotic plant–soil feedbacks across temporal scales. *Journal of Ecology* **101**:309–315.

Kazan, K. and R. Lyons, 2016. The link between flowering time and stress tolerance. *Journal of Experimental Botany* **67**:47–60.

Ke, P.-J. and J. M. Levine, 2021. The temporal dimension of plant–soil microbe interactions: mechanisms promoting feedback between generations. *The American Naturalist* **198**:E80–E94.

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

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

Ke, P.-J. and J. Wan, 2023. A general approach for quantifying microbial effects on plant competition. *Plant and Soil* **485**:57–70.

Ke, P.-J., P. C. Zee, and T. Fukami, 2021. Dynamic plant–soil microbe interactions: the neglected effect of soil conditioning time. *New Phytologist* **231**:1546–1558.

Keeler, A. M. and N. E. Rafferty, 2022. Legume germination is delayed in dry soils and in sterile soils devoid of microbial mutualists: Species-specific implications for upward range expansions. *Ecology and Evolution* **12**:e9186.

Keswani, C., S. P. Singh, C. García-Estrada, S. Mezaache-Aichour, T. R. Glare, R. Borriss, V. D. Rajput, T. M. Minkina, A. Ortiz, and E. Sansinenea, 2022. Biosynthesis and beneficial effects of microbial gibberellins on crops for sustainable agriculture. *Journal of Applied Microbiology* **132**:1597–1615.

Kotanen, P. M., 2007. Effects of fungal seed pathogens under conspecific and heterospecific trees in a temperate forest. *Botany* **85**:918–925.

Koziol, L., P. A. Schultz, G. L. House, J. T. Bauer, E. L. Middleton, and J. D. Bever, 2018. The plant microbiome and native plant restoration: the example of native mycorrhizal fungi. *BioScience* **68**:996–1006.

Krishnadas, M., R. Bagchi, S. Sridhara, and L. S. Comita, 2018. Weaker plant-enemy interactions decrease tree seedling diversity with edge-effects in a fragmented tropical forest. *Nature Communications* **9**:1–7.

Krishnadas, M. and L. S. Comita, 2018. Influence of soil pathogens on early regeneration success of tropical trees varies between forest edge and interior. *Oecologia* **186**:259–268.

Krishnadas, M. and S. M. Stump, 2021. Dispersal limitation and weaker stabilizing mechanisms mediate loss of diversity with edge effects in forest fragments. *Journal of Ecology* **109**:2137–2151.

Kulmatiski, A., 2019. Plant-soil feedbacks predict native but not non-native plant community composition: a 7-year common-garden experiment. *Frontiers in Ecology and Evolution* **7**:326.

Kulmatiski, A., K. H. Beard, and J. Heavilin, 2012. Plant–soil feedbacks provide an additional explanation for diversity–productivity relationships. *Proceedings of the Royal Society B: Biological Sciences* **279**:3020–3026.

Kulmatiski, A., K. H. Beard, J. M. Norton, J. E. Heavilin, L. E. Forero, and J. Grenzer, 2017. Live long and prosper: plant–soil feedback, lifespan, and landscape abundance covary. *Ecology* **98**:3063–3073.

Lau, J. A. and J. T. Lennon, 2012. Rapid responses of soil microorganisms improve plant fitness in novel environments. *Proceedings of the National Academy of Sciences* **109**:14058–14062.

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

Lepinay, C., Z. Vondráková, T. Dostálek, and Z. Münzbergová, 2018. Duration of the conditioning phase affects the results of plant–soil feedback experiments via soil chemical properties. *Oecologia* **186**:459–470.

Leverett, L. D., G. F. Schieder IV, and K. Donohue, 2018. The fitness benefits of germinating later than neighbors. *American Journal of Botany* **105**:20–30.

Li, Y. M., J. P. Shaffer, B. Hall, and H. Ko, 2019. Soil-borne fungi influence seed germination and mortality, with implications for coexistence of desert winter annual plants. *PLoS One* **14**:e0224417.

Liang, M., X. Liu, G. S. Gilbert, Y. Zheng, S. Luo, F. Huang, and S. Yu, 2016. Adult trees cause density-dependent mortality in conspecific seedlings by regulating the frequency of pathogenic soil fungi. *Ecology Letters* **19**:1448–1456.

Liu, X., K. Steinauer, K. van der Veen-van Wijk, and T. M. Bezemer, 2024. Zooming in on the temporal dimensions of plant–soil feedback: Plant sensitivity and microbial dynamics. *Journal of Ecology* .

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.

Mack, K. M., M. B. Eppinga, and J. D. Bever, 2019. Plant-soil feedbacks promote coexistence and resilience in multi-species communities. *PLoS One* **14**:e0211572.

Magee, L. J., J. A. LaManna, A. T. Wolf, R. W. Howe, Y. Lu, D. Valle, D. J. Smith, R. Bagchi, D. Bauman, and D. J. Johnson, 2024. The unexpected influence of legacy conspecific density dependence. *Ecology Letters* **27**:e14449.

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.

Miller, E. C., G. G. Perron, and C. D. Collins, 2019. Plant-driven changes in soil microbial communities influence seed germination through negative feedbacks. *Ecology and Evolution* **9**:9298–9311.

Miller, Z. R. and S. Allesina, 2021. Metapopulations with habitat modification. *Proceedings of the National Academy of Sciences* **118**:e2109896118.

Miller, Z. R., P. Lechón-Alonso, and S. Allesina, 2022. No robust multispecies coexistence in a canonical model of plant–soil feedbacks. *Ecology Letters* **25**:1690–1698.

Minás, A., P. A. García-Parisi, H. Chludil, and M. Omacini, 2021. Endophytes shape the legacy left by the above- and below-ground litter of the host affecting the establishment of a legume. *Functional Ecology* **35**:2870–2881.

Mordecai, E. A., 2013a. Consequences of pathogen spillover for cheatgrass-invaded grasslands: coexistence, competitive exclusion, or priority effects. *The American Naturalist* **181**:737–747.

Mordecai, E. A., 2013b. Despite spillover, a shared pathogen promotes native plant persistence in a cheatgrass-invaded grassland. *Ecology* **94**:2744–2753.

Mordecai, E. A., 2015. Pathogen impacts on plant diversity in variable environments. *Oikos* **124**:414–420.

Mouquet, N., J. L. Moore, and M. Loreau, 2002. Plant species richness and community productivity: why the mechanism that promotes coexistence matters. *Ecology Letters* **5**:56–65.

Müller, A., E. George, and E. Gabriel-Neumann, 2013. The symbiotic recapture of nitrogen from dead mycorrhizal and non-mycorrhizal roots of tomato plants. *Plant and Soil* **364**:341–355.

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.

Neytcheva, M. S. and L. W. Aarssen, 2008. More plant biomass results in more offspring production in annuals, or does it? *Oikos* **117**:1298–1307.

O'Brien, A. M., N. A. Ginnan, M. Rebolleda-Gómez, and M. R. Wagner, 2021. Microbial effects on plant phenology and fitness. *American Journal of Botany* **108**:1824–1837.

Orrock, J. L. and C. C. Christopher, 2010. Density of intraspecific competitors determines the occurrence and benefits of accelerated germination. *American Journal of Botany* **97**:694–699.

Ou, S. X., G. S. Kandlikar, M. L. Warren, and P.-J. Ke, 2024. Realistic time-lags and litter dynamics alter predictions of plant–soil feedback across generations. *bioRxiv* pages 2024–01.

Pacala, S. W. and D. Tilman, 1994. Limiting similarity in mechanistic and spatial models of plant competition in heterogeneous environments. *The American Naturalist* **143**:222–257.

Pajares-Murgó, M., J. L. Garrido, A. J. Perea, Á. López-García, J. M. Bastida, J. Prieto-Rubio, S. Lendínez, C. Azcón-Aguilar, and J. M. Alcántara, 2024. Intransitivity in plant–soil feedbacks is rare but is associated with multispecies coexistence. *Ecology Letters* **27**:e14408.

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

Pepe, A., M. Giovannetti, and C. Sbrana, 2018. Lifespan and functionality of mycorrhizal fungal mycelium are uncoupled from host plant lifespan. *Scientific Reports* **8**:10235.

Pineda, A., I. Kaplan, S. E. Hannula, W. Ghanem, and T. M. Bezemer, 2020. Conditioning the soil microbiome through plant–soil feedbacks suppresses an aboveground insect pest. *New Phytologist* **226**:595–608.

Ravanbakhsh, M., R. Sasidharan, L. A. Voesenek, G. A. Kowalchuk, and A. Jousset, 2018. Microbial modulation of plant ethylene signaling: ecological and evolutionary consequences. *Microbiome* **6**:1–10.

Reinhart, K. O., J. T. Bauer, S. McCarthy-Neumann, A. S. MacDougall, J. L. Hierro, M. C. Chiuffo, S. A. Mangan, J. Heinze, J. Bergmann, J. Joshi, et al., 2021. Globally, plant-soil feedbacks are weak predictors of plant abundance. *Ecology and Evolution* **11**:1756–1768.

Reinhart, K. O., A. A. Royo, S. A. Kageyama, and K. Clay, 2010. Canopy gaps decrease microbial densities and disease risk for a shade-intolerant tree species. *Acta Oecologica* **36**:530–536.

Rudgers, J. A., M. E. Afkhami, L. Bell-Dereske, Y. A. Chung, K. M. Crawford, S. N. Kivlin, M. A. Mann, and M. A. Nuñez, 2020. Climate disruption of plant-microbe interactions. *Annual Review of Ecology, Evolution, and Systematics* **51**:561–586.

Sarmiento, C., P.-C. Zalamea, J. W. Dalling, A. S. Davis, S. M. Stump, J. M. U'Ren, and A. E. Arnold, 2017. Soilborne fungi have host affinity and host-specific effects on seed germination and survival in a lowland tropical forest. *Proceedings of the National Academy of Sciences USA* **114**:11458–11463.

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.

Senthilnathan, A. and R. D'Andrea, 2023. Niche theory for positive plant-soil feedbacks. *Ecology* **104**:e3993.

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

Shemesh, H., T. D. Bruns, K. G. Peay, P. G. Kennedy, and N. H. Nguyen, 2023. Changing balance between dormancy and mortality determines the trajectory of ectomycorrhizal fungal spore longevity over a 15-yr burial experiment. *New Phytologist* **238**:11–15.

Shikano, I., C. Rosa, C.-W. Tan, and G. W. Felton, 2017. Tritrophic interactions: microbe-mediated plant effects on insect herbivores. *Annual Review of Phytopathology* **55**:313–331.

Song, X. and R. T. Corlett, 2022. Do natural enemies mediate conspecific negative distance-and density-dependence of trees? a meta-analysis of exclusion experiments. *Oikos* **2022**:e08509.

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.

Suding, K. N., W. Stanley Harpole, T. Fukami, A. Kulmatiski, A. S. MacDougall, C. Stein, and W. H. van der Putten, 2013. Consequences of plant–soil feedbacks in invasion. *Journal of Ecology* **101**:298–308.

Swamy, V., J. Terborgh, K. G. Dexter, B. D. Best, P. Alvarez, and F. Cornejo, 2011. Are all seeds equal? spatially explicit comparisons of seed fall and sapling recruitment in a tropical forest. *Ecology Letters* **14**:195–201.

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.

Uricchio, L. H., S. C. Daws, E. R. Spear, and E. A. Mordecai, 2019. Priority effects and nonhierarchical competition shape species composition in a complex grassland community. *The American Naturalist* **193**:213–226.

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, J. N. Klironomos, A. Kulmatiski, J. A. Schweitzer, K. N. Suding, T. F. J. van der Voorde, and D. A. Wardle, 2013. Plant–soil feedbacks : the past, the present and future challenges. *Journal of Ecology* **101**:265–276.

Van Dyke, M. N., J. M. Levine, and N. J. Kraft, 2022. Small rainfall changes drive substantial changes in plant coexistence. *Nature* **611**:507–511.

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.

Veen, G. F., F. C. ten Hooven, C. Weser, and S. E. Hannula, 2021. Steering the soil microbiome by repeated litter addition. *Journal of Ecology* **109**:2499–2513.

Wagner, M. R., D. S. Lundberg, D. Coleman-Derr, S. G. Tringe, J. L. Dangl, and T. Mitchell-Olds, 2014. Natural soil microbes alter flowering phenology and the intensity of selection on flowering time in a wild arabidopsis relative. *Ecology Letters* **17**:717–726.

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, M. Bosch, and T. M. Bezemer, 2016. Soil inoculation steers restoration of terrestrial ecosystems. *Nature Plants* **2**:16107.

Yan, X., J. M. Levine, and G. S. Kandlikar, 2022. A quantitative synthesis of soil microbial effects on plant species coexistence. *Proceedings of the National Academy of Sciences* **119**:e2122088119.

Younginger, B. S., D. Sirová, M. B. Cruzan, and D. J. Ballhorn, 2017. Is biomass a reliable estimate of plant fitness? *Applications in plant sciences* **5**:1600094.

Zalamea, P.-C., C. Sarmiento, A. E. Arnold, A. S. Davis, A. Ferrer, and J. W. Dalling, 2021. Closely related tree species support distinct communities of seed-associated fungi in a lowland tropical forest. *Journal of Ecology* **109**:1858–1872.

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

Zhalnina, K., K. B. Louie, Z. Hao, N. Mansoori, U. N. Da Rocha, S. Shi, H. Cho, U. Karaoz, D. Loqué, B. P. Bowen, et al., 2018. Dynamic root exudate chemistry and microbial substrate preferences drive patterns in rhizosphere microbial community assembly. *Nature Microbiology* **3**:470–480.

Zhu, Y., L. S. Comita, S. P. Hubbell, and K. Ma, 2015. Conspecific and phylogenetic density-dependent survival differs across life stages in a tropical forest. *Journal of Ecology* **103**:957–966.

Zhu, Y., S. Queenborough, R. Condit, S. Hubbell, K. Ma, and L. Comita, 2018. Density-dependent survival varies with species life-history strategy in a tropical forest. *Ecology Letters* **21**:506–515.

Zou, H.-X., X. Yan, and V. H. Rudolf, 2024. Time-dependent interaction modification generated from plant–soil feedback. *Ecology Letters* **27**:e14432.