

# 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.

**KEY WORDS**

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

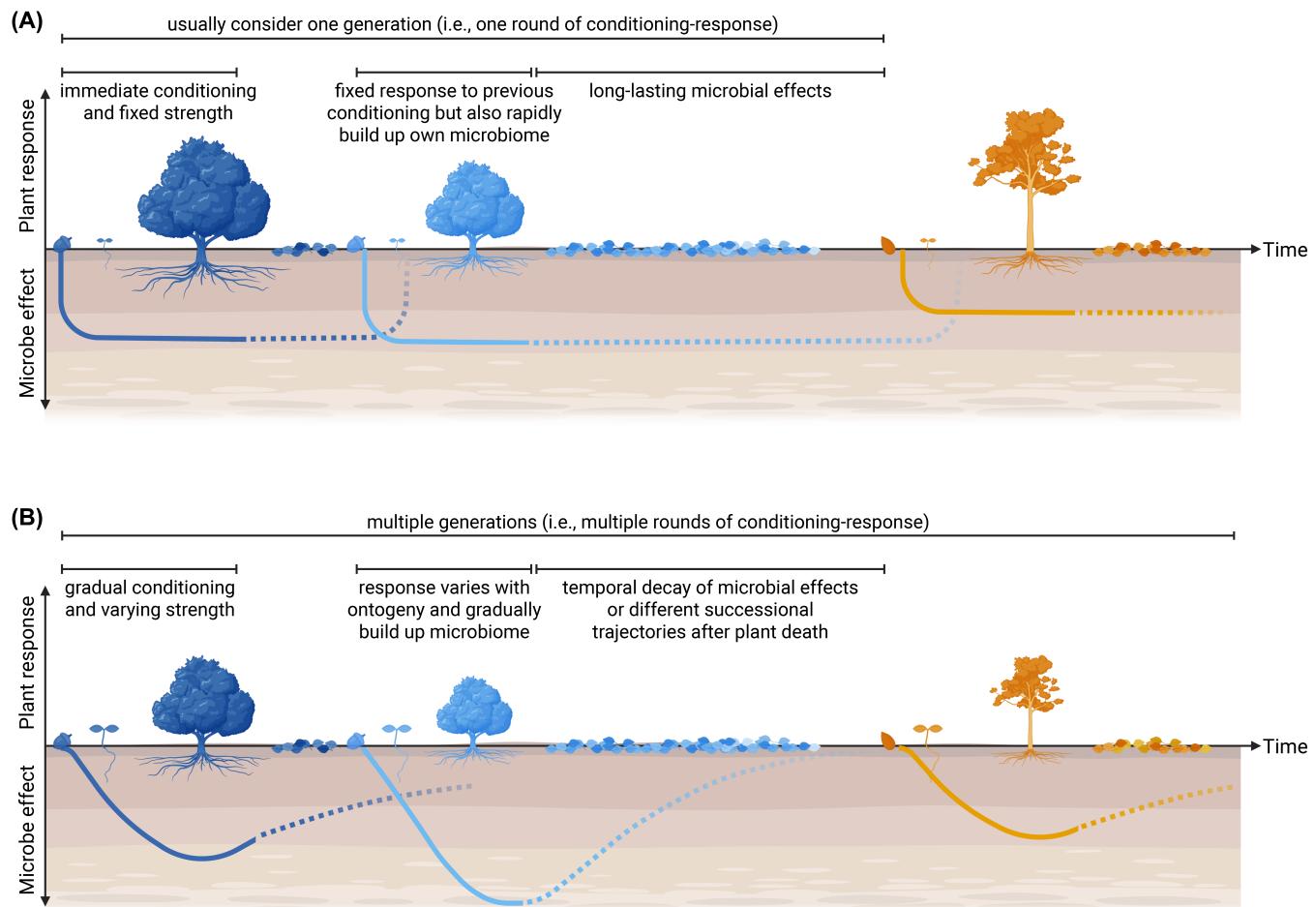
## INTRODUCTION

Plants interact with a diverse array of soil biota that function as herbivores, pathogens, mutualists, and decomposers. In addition to the contributions of soil fauna (ranging from micro- to macrofauna; Ehrenfeld et al., 2005; Kulmatiski et al., 2014; Wilschut & Geisen, 2021), studies have highlighted the importance of plant–soil microbe interactions. These interactions can be bidirectional, with plants altering the composition of the soil microbial community, and the resulting changes in the microbial community impacting subsequent plant performance in the conditioned soil (Bever, 1994, 2003; Bever et al., 1997). 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, 2015; Kandlikar, 2024; Ke & Miki, 2015). 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 (Koziol et al., 2018; Wubs et al., 2016), plant invasion (Callaway et al., 2004; Suding et al., 2013), and the biodiversity–productivity relationship (Forero et al., 2021; Kulmatiski et al., 2012).

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 microbial 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 PSF model (Bever et al., 1997, 2012) and has enabled a strong empirical foundation of PSF research across ecosystems (Crawford et al., 2019a; Yan et al., 2022a). 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 (Chung, 2023; Gundale & Kardol, 2021; Kardol et al., 2013). 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 (Figure 1A). This assumption is at odds with growing evidence that within a single plant generation, microbial communities undergo 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., Bezemer et al., 2018; Hawkes et al., 2013; Lepinay et al., 2018; Figure 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 & 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.



**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 regarding 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 (see *Temporal development during the conditioning and response phases*). Moreover, microbial communities and their impacts on plant performance may diminish with time after the senescence of the previous conditioning individual (see *Alterations of microbial effects after plant death*) or undergo different trajectories depending on the previous rounds of conditioning (mentioned as a future direction in *Implications for experimental design*). Different seedling and tree sizes across the panels indicate varying plant responses (increasing upwards) to soil microbial effects (increasing downwards). Created in BioRender (<https://BioRender.com/a8tl9rj>).

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 & 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., 2019a). 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 good 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 (Dostálek et al., 2022; Dudenhöffer et al., 2018). 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 potential avenues for overcoming them in future empirical and theoretical studies. It is important to note that although we treat the temporal and demographic aspects of plant–microbe interactions separately for analytical clarity, they are intrinsically linked. In nature, temporal shifts in microbial community composition and function can give rise to distinct microbial effects on various demographic processes across plants' life cycles. Conversely, these demographic rates reveal how microbial impacts on plant populations unfold over time and illuminate the temporal dynamics of plant–soil microbe interactions. On the theoretical forefront, 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 logically challenging, we argue that integrating the temporal and demographic details can better predict the outcome of plant–soil microbe interactions in their natural context.

## SIGNIFICANT CONSEQUENCES OF OVERLOOKING THE TEMPORAL AND DEMOGRAPHIC ASPECTS OF PLANT–SOIL MICROBE INTERACTIONS

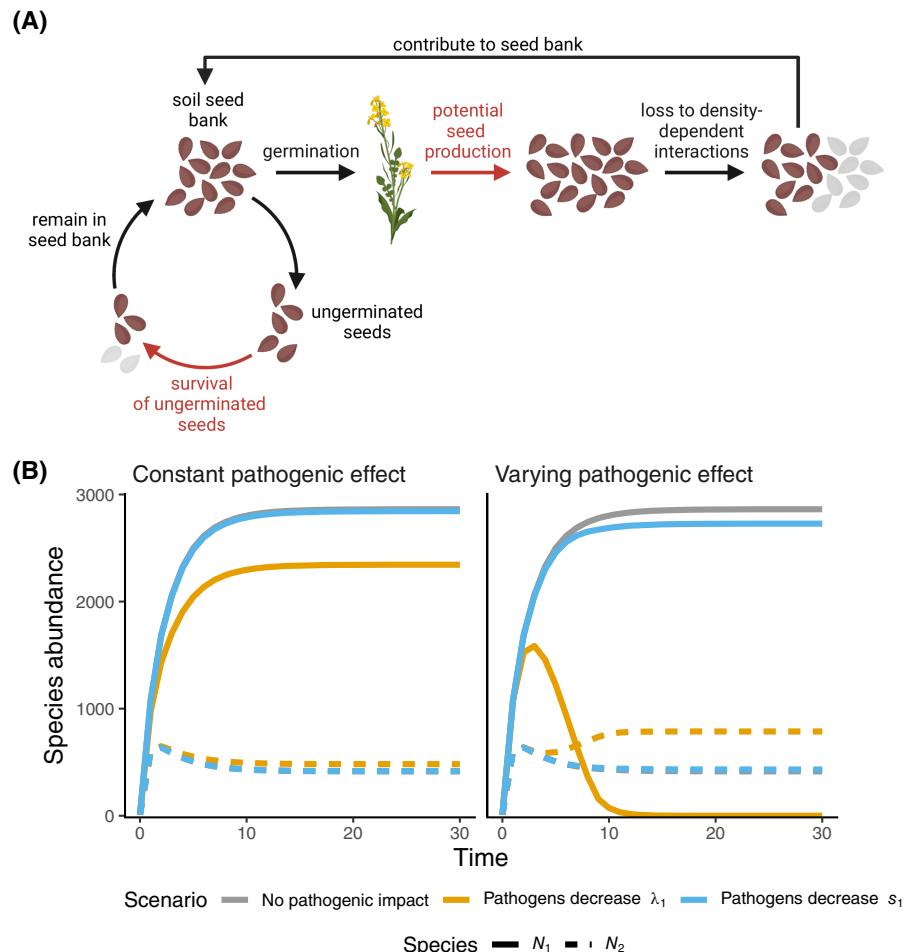
To motivate our thesis that explicitly evaluating the variation in microbial effects across time and across different life stages is important for predicting their consequences in nature, we first present a simple plant demographic model that illustrates the potential consequences of ignoring these temporal dynamics. Specifically, we consider two annual plant species,  $N_1$  and  $N_2$ , with dynamics described by the Beverton–Holt annual plant model:

$$N_{i,t+1} = \underbrace{s_i(1 - g_i)N_{i,t}}_{\text{survival of ungerminated seeds}} + \underbrace{\frac{\lambda_i g_i N_{i,t}}{1 + \alpha_{ii} g_i N_{i,t} + \alpha_{ij} g_j N_{j,t}}}_{\substack{\text{intrinsic fecundity of germinated seeds} \\ \text{effect of neighbors}}},$$

with subscripts  $i$  and  $j$  indicating species 1 and 2, respectively. 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 Figure 2A). The second term represents seed production and density-dependent interactions among germinated seeds, with  $\lambda_i$ ,  $\alpha_{ii}$ , and  $\alpha_{ij}$  representing intrinsic plant fecundity, intraspecific and interspecific competitive impact experienced by  $N_i$ , respectively (rightward arrows in Figure 2A). As opposed to biomass-based metrics, this demographic model provides the opportunity to study microbial effects on five different demographic parameters (i.e.,  $g_i$ ,  $s_i$ ,  $\lambda_i$ ,  $\alpha_{ii}$ , and  $\alpha_{ij}$ ). 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 effect 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 soil microbes on long-term plant community dynamics. This is illustrated in the left panel of Figure 2B, as the gray 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 species 1's intrinsic fecundity ( $\lambda_1$ ) by 10% (orange lines), 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 (Day et al., 2015; Diez et al., 2010). The right panel of Figure 2B depicts the competitive outcomes caused by different microbial effects assuming that the 10% decrease in  $s_1$  and  $\lambda_1$  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  $\lambda_1$  (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



**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. Brown and gray seeds represent viable and dead seeds, respectively. (B) Abundance time series of  $N_1$  (solid line) and  $N_2$  (dashed line) under different microbial effect scenarios: No pathogenic effect (gray), pathogens decrease the seed survival of  $N_1$  ( $s_1$ ; blue), and pathogens decrease the fecundity of  $N_1$  ( $\lambda_1$ ; 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 an 80% decrease after eight generations (i.e., a 10% decrease after every generation). Note that the blue lines often overlap the gray 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  $\alpha_{22} = 0.948$ . Panel (A) created in BioRender (<https://Biorender.com/0kwj3z5>).

realistic concern in nature that is often replaced by the simplifying assumption of a constant microbial effect in greenhouse experiments.

## DISSECTING DIFFERENT TEMPORAL DIMENSIONS OF MICROBIAL EFFECTS

Studies on the temporal patterns of plant–soil microbe interactions have classically focused on their variation

along plant succession, which typically involves plants with different traits or shifts in the external environment (Bauer et al., 2015; Kardol et al., 2006, 2013). 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 (Figure 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; Yin et al., 2023). 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 (see *Temporal development during the conditioning and response phases*), as well as the time lag between consecutive generations (see *Alterations of microbial effects after plant death*). We then discuss how to design experiments that tackle the temporal complexities observed in nature (see *Implications for experimental design*). 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 *Assessing multiple demographic consequences of soil microbes*.

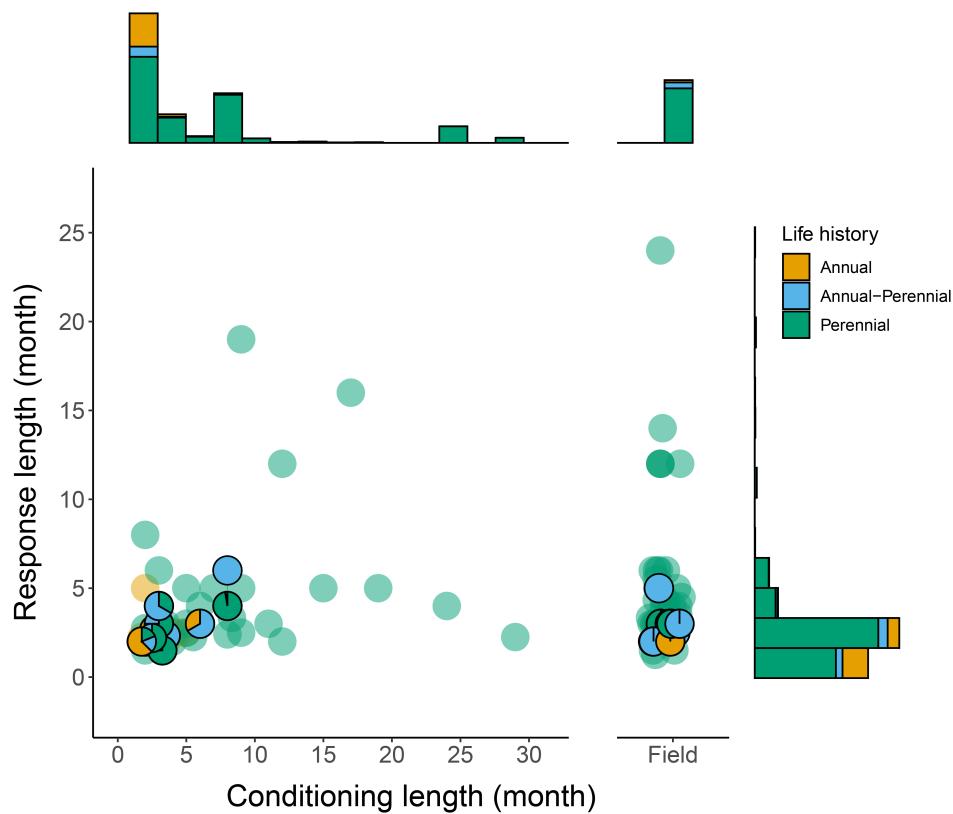
## Temporal development during the conditioning and response phases

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., 2019b; Yan et al., 2022b), we showed that the length of the conditioning and response phases is under a few months in most studies (Figure 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 considering plants with different life histories. For example, 20% of studies (21 out of 106) in Figure 3 evaluated microbially mediated stabilization between plant species pairs comprising 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 (Figure 4A), a few studies have grown plants in soils that were conditioned for different durations (red vertical arrow (i) in Figure 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, Liu et al. (2025) found that *Jacobaea vulgaris* performed worse in conspecific soil than in heterospecific soils, and that this performance difference increased as soil conditioning time extended from 2 to 5 weeks; however, the differences between soil treatments diminished after a longer conditioning duration of 8 weeks. Similarly, while focusing on soil chemical properties, Lepinay et al. (2018) showed that the relative negative impact of conspecific versus heterospecific soils varied with conditioning duration over a span of 2–8 weeks. 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 (Gundale & Kardol, 2021; Kardol et al., 2013; red diagonal arrow (ii) in Figure 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

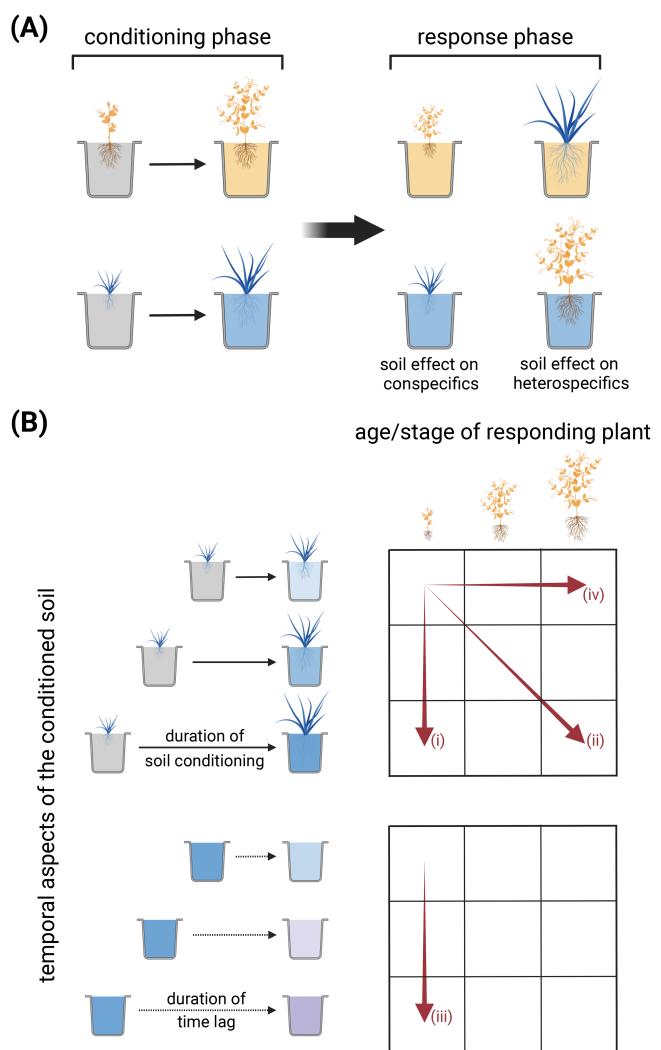


**FIGURE 3** A summary of the experimental duration and life history information of the study species in the Crawford et al. (2019b) and Yan et al. (2022b) datasets. Since the two studies focused on the pairwise plant–soil feedback, we compiled information on plant life history and categorized each pairwise comparison as different “pair types”: Annual (both plants are annuals; orange), perennial (both plants are perennials; green), or annual–perennial (match of an annual vs. a perennial; blue). Fully opaque pie charts represent studies that evaluated plant–soil feedback between annual and perennial plants, with slice colors representing the percentage of different pair types within the study (translucent points are single-color pie charts, representing 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. Data compiled from the publicly available dataset in Crawford et al. (2019b) and Yan et al. (2022b) are available at <https://doi.org/10.5281/zenodo.16566101>.

response phase (Bezemer et al., 2018; Dostál, 2021). For instance, harvesting twice every week for 11 weeks, Bezemer et al. (2018) showed that the negative effect of conspecific-conditioned soil experienced by *J. 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 can occur 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; Zhelnina 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, changes prompted by plants can lead to shifts in microbe–microbe interactions and the processes governing microbial community assembly (Barret et al., 2015; Bittleston et al., 2021; Herrera Paredes & Lebeis, 2016), all of which may trigger further responses in plant physiology via a complex interplay between mechanisms. Even in the absence of detectable shifts in



**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 highlighted 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. Created in BioRender (<https://BioRender.com/yisnt7l>).

soil microbial community composition, ontogenetic changes in plant physiology can drive variable plant responses (Liu et al., 2025). However, as conditioning and response processes operate simultaneously in nature, it is important to note that the same set of mechanisms applies to explain temporal patterns in both phases. For example, strengthening of immunity as plants mature can reduce plant susceptibility to pathogens and alleviate negative microbial effects as the responding individual matures; it can also reduce pathogen abundance as the conditioning phase progresses (Bulgarelli et al., 2013). 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 *Implications for experimental design*.

### Alterations of microbial effects after plant death

One common implicit assumption in PSF studies is that greenhouse-measured microbial effects manifest similarly

on plants neighboring the focal individual as on individuals that arrive and grow in the conditioned soil after the focal plant senesced. 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 Figure 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 1 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 6-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 its corresponding impact on plant coexistence.

Microbial effects could persist after active plant conditioning ceases due to the continued survival and functioning of the conditioned microbial community in the soil (Esch et al., 2021; Hannula et al., 2021; Lennon & Jones, 2011; Pepe et al., 2018). 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. Microbial activity can be maintained 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 & 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 & 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 time, 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; Ou et al., 2024; Veen et al., 2019). 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 suppress pathogens (Augspurger, 1984; Nagendra & Peterson, 2016; Reinhart et al., 2010). Finally, stochastic drift could decouple microbial communities 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.

## 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, for example, 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 setting 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. Second, we encourage modification of the classic two-phase design (Figure 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 Figure 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 variations 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 Figure 3). For example, plant age estimated from historical aerial photos (Ke et al., 2021) and host tree size obtained from forest census (Chen et al., 2019) can be used as a proxy of conditioning time, and chronosequences of abandoned fields or agricultural harvest times can be utilized to study the persistence of microbial effects (Esch & Kobe, 2021; van de Voorde et al., 2012).

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 Figure 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 durations (red vertical arrow (i) in Figure 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 an autoclavable container before transplanting) in soils with identical conditioning duration (red horizontal arrow (iv) in Figure 4B). Moreover, throughout greenhouse experiments, the concurrent application of modern molecular methods can provide critical insights linking microbial changes to variations in plant performance. A recent study by Liu et al. (2025) utilized such an experimental design to illustrate the importance of conditioning and response duration as well as the underlying mechanisms (i.e., changes in plant sensitivity to microbes or soil reconditioning by the responding plant). They found that the soil bacterial community in conspecific and heterospecific soils converged over the course of the response phase, partially explaining why differences in plant performance diminished with longer experimental

duration (see also Steinauer et al., 2023). Finally, 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.

## ASSESSING MULTIPLE DEMOGRAPHIC CONSEQUENCES OF SOIL MICROBES

Most two-phase experiments 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

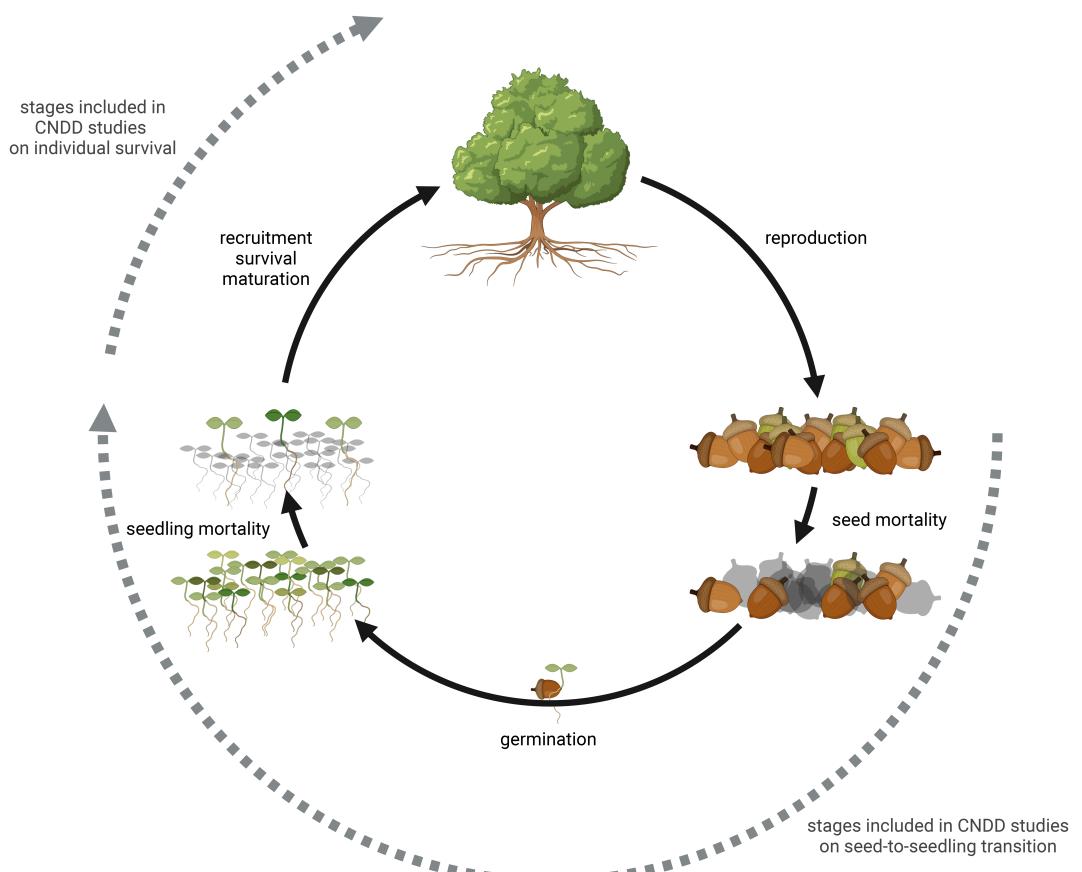
Bever et al. (1997), where microbes regulate the intrinsic growth rate of an exponentially growing plant population. However, soil microbes can also alter other key demographic processes throughout the plant life cycle that are not directly correlated with biomass accumulation (e.g., seed germination 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.

## 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 seedling survival; Figure 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., Bagchi et al., 2014; Bell et al., 2006; Krishnadas et al., 2018, 2020; Song & Corlett, 2022). Many of these studies are conducted to evaluate soil microbes as potential drivers of the Janzen–Connell hypothesis (Connell, 1971; Janzen, 1970) 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 (Figure 5) can enable a nuanced and mechanistic understanding of microbial effects on plant population dynamics (Krishnadas & Comita, 2019).

Soil-borne pathogens can cause substantial mortality at the seed stage across biomes (e.g., Kotanen, 2007; Li et al., 2019; Sarmiento et al., 2017). 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 (Clark et al., 2007; Harper, 1977).

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 Bottini et al., 2004 and Keswani et al., 2022) or ethylene (reviewed in Ishaq, 2017 and Ravanbakhsh et al., 2018). 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



**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 (gray dashed arrows) indicates the life stages included in different studies on conspecific negative density dependence (CNDD). Created in BioRender (<https://Biorender.com/cyus4c6>).

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

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 & 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 & Simard, 2011; Lebrija-Trejos et al., 2023), the relative abundance of conspecific and heterospecific adults (Teste et al., 2017), and the functional groups of mycorrhizal fungi (Bennett et al., 2017; Liang et al., 2016). 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 (Chung et al., 2023; Dudenhofer et al., 2022; Pajares-Murgó et al., 2024).

## 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 that are not captured by experiments focusing only on plant biomass. For example, studies from forest pathology have shown that soil-borne fungi and oomycetes can directly cause adult mortality via root rot diseases, often with long-term impacts on spatial structure and gap dynamics in forest communities (Das et al., 2016; Hansen & Goheen, 2000; Liu et al., 2007; Ruiz Gómez et al., 2019). Experimental studies have also shown that soil microbes can influence the fruit production of herbaceous species (Dostálek et al., 2022), but such direct evidence is notably scarce in natural forest systems. In other cases, soil microbes might have equally important implications for plant population dynamics through less direct pathways. For example, over the past decade, evidence of microbial regulation of flowering phenology across systems has become widespread (Igwe et al., 2021; Lau & Lennon, 2012; Lu et al., 2018; Wagner et al., 2014). 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 & Lyons, 2016 and O'Brien et al., 2021). The soil community can also regulate plant susceptibility to invertebrate herbivores (e.g., Howard et al., 2020; Kalske et al., 2022; Pineda et al., 2020), with such effects likely arising due to soil microbe-induced changes in leaf metabolomes or volatile organics (Huberty et al., 2022; Kalske 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. Further complicating efforts to project microbial consequences across a plant's lifetime is that these effects can be uncorrelated or even contradictory across a plant's lifetime (Dostálek et al., 2022). For example, Dudenhofer et al. (2018) found that conspecific-conditioned soil microbes promote juvenile plant growth but hinder adult growth. Integrating these effects across the plant's lifetime reveals a net negative impact of conspecific soil on plant fitness—a result that would

contradict inferences based on the juvenile stage alone. Thus, variable impacts of soil microbes across plant ontogeny and/or demographic processes could contribute to demographic compensation in plant population dynamics (Villellas et al., 2015). The integration of these microbial effects remains an ongoing challenge, particularly in long-lived plants.

## Implications for experimental design

While incorporating all aforementioned demographic impacts of soil microbes is logically 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 (Chung et al., 2023; Dudenhofer et al., 2022) 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 *Modeling frameworks for incorporating temporal and demographic aspects of plant–soil microbe interactions*). 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. Finally, while the longevity of forest trees precludes direct experimental evidence, one may leverage natural experiments to observe differences in demographic rates across sites with varying disease severity (Cobb et al., 2020).

Compared to greenhouse-based PSF 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 is 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 (Bagchi et al., 2010; Bell et al., 2006; Krishnadas & Comita, 2018; Song & Corlett, 2022). Furthermore, one can add a heterospecific treatment designed to assess heterospecific effects, as well as a reference treatment in randomly located field soil to estimate the frequency-independent microbial impact on survival. These additional treatments allow the interpretation of plant–soil microbe interactions within the framework of modern coexistence theory, which emphasizes that coexistence requires stabilization (niche difference) to be greater than the competitive hierarchy (fitness difference) between species (Kandlikar et al., 2019; Ke & 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 & 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 & 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 can translate 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.

## 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.

### Patch occupancy models

Patch occupancy models represent a relatively straightforward framework for studying plant–soil microbe interactions (Mouquet et al., 2002; Pacala & Tilman, 1994). 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 (Ke & Levine, 2021; Miller & Allesina, 2021; Stump & Comita, 2018). 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., Ke & Levine, 2021; Miller & Allesina, 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; Bauer et al., 2015; Bever et al., 1997; Mack & Bever, 2014). 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 Figure 5; Krishnadas & 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 multispecies communities (e.g., Dudenhofer et al., 2022; Mangan et al., 2010; Teste et al., 2017). Recent theoretical studies have also suggested that patch occupancy models, through competition for limited colonization sites, generate more interpretable frequency-based dynamics for multispecies communities than do direct extensions of the classic pairwise feedback model (Miller et al., 2022).

The patch occupancy framework offers a pathway to effectively incorporate various temporal aspects of plant–soil microbe interactions (see an example in Box 1 and Figure 6). 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

### 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 multispecies patch occupancy model. We considered three different plant–soil microbe states (Figure 6A): 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 & Levine, 2021; Miller & Allesina, 2021):

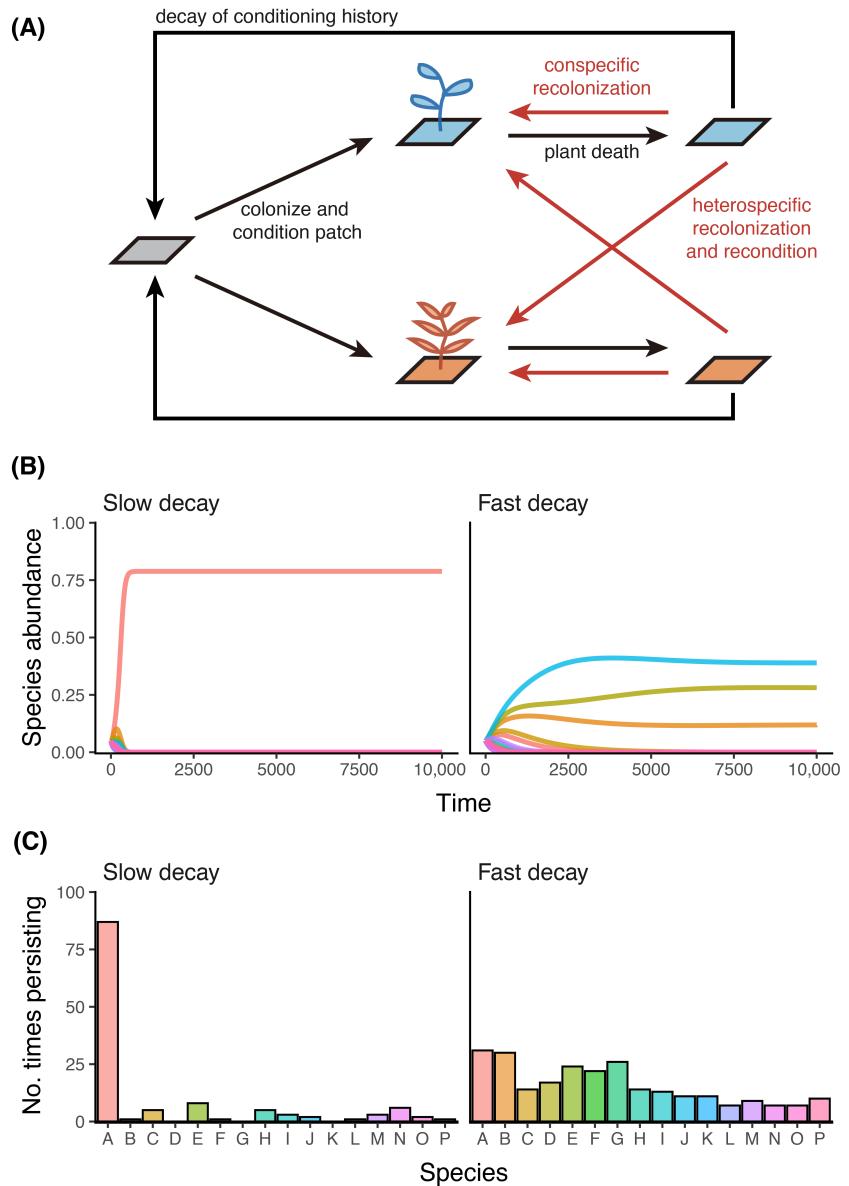
$$\frac{dP_{00}}{dt} = \underbrace{\sum_{i=1}^N d_i P_{0i}}_{\text{decay of conditioning effect in empty patches}} - \underbrace{\sum_{i=1}^N r_i P_{ii} P_{00}}_{\text{plant establishment into empty and unconditioned patches}} \quad (1)$$

$$\frac{dP_{ii}}{dt} = \underbrace{r_i P_{ii} P_{00}}_{\text{plant establishment into empty and unconditioned patches}} + \underbrace{\sum_{j=1}^N r_i \sigma_{ij} P_{ii} P_{0j}}_{\text{plant establishment in empty but conditioned patches}} - \underbrace{\widetilde{m}_i P_{ii}}_{\text{plant mortality}} \quad (2)$$

$$\frac{dP_{0i}}{dt} = \underbrace{\widetilde{m}_i P_{ii}}_{\text{plant mortality}} - \underbrace{d_i P_{0i}}_{\text{decay of conditioning effect in empty patches}} - \underbrace{\sum_{j=1}^N r_j \sigma_{ji} P_{jj} P_{0i}}_{\text{plant establishment in empty but conditioned patches}}. \quad (3)$$

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 Figure 6A). Here, soil microbes affect the ability of plants to recolonize conditioned soils (red arrows in Figure 6A).  $N$  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 ( $\sigma_{ij}$ ) 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 and 0.25. This simulation illustrates how the decay rates of microbial effects determine the overall consequences of soil microbes on plant communities (Figure 6B,C). Specifically, with this parameterization and when microbial effects persist after host death (i.e., low  $d_i$ ; left panels in Figure 6B,C), plant–soil microbe interactions mostly resulted in the dominance of a single species, overwhelming 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 Figure 6B,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.



**FIGURE 6** 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; modified from Ke & Levine, 2021). (B and 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  $i = 1\dots 16$ , and  $P_{0i} = 0.0$ . Seedling illustration created by authors. See Box 1 for additional details.

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 & 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 in microbial impact on plants through time and can thus be

parameterized with the type of experiments mentioned in *Implications for experimental design* of the temporal dimension section. 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).

## 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. Although this approach demands extensive parameterization, it allows for system-specific tailoring and may prove to be especially valuable in demographically complex systems. Demonstrating the power of this approach, a series of studies (Mordecai, 2013a, 2013b, 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 (Figure 2A; see also *Significant consequences of overlooking the temporal and demographic aspects of plant-soil microbe interactions* 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) parameterized 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 those during the growth and survival stages. The authors speculated that this is due to the recruitment stage involving many demographic transitions that are susceptible to soil pathogens (Chu & 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 (Figure 7). 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 multispecies communities. Nonetheless, parameterizing such models for long-lived plants remains a significant ongoing challenge.

While we presented two separate modeling frameworks for incorporating temporal and demographic components, in practice, both approaches are flexible and can be used to answer multiple research questions. For instance, decay dynamics and time-dependent feedback can also be built into a demographically explicit model (e.g., Senthilnathan & D'Andrea, 2023; see also Zou et al., 2024 for a discrete-time model with explicit consideration of the temporal dynamics of soil microbes). Ultimately, the choice depends on the research question and the focal plant-soil system. For example, in systems

## 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:

$$N_a(t+1) = \underbrace{s_a(1-g_a)N_a(t)}_{\text{survival of ungerminated seeds}} + \underbrace{N_a(t)\frac{g_a\lambda_a}{1+\alpha_{ap}A_p(t)+\alpha_{aa}g_aN_a(t)}}_{\text{seed production}} \quad (4)$$

$$N_p(t+1) = \underbrace{s_p(1-g_p)N_p(t)}_{\text{survival of ungerminated seeds}} + \underbrace{A_p(t)\frac{\lambda_p}{1+\alpha_{pp}A_p(t)+\alpha_{pa}g_aN_a(t)}}_{\text{seed production by adult plants}} \quad (5)$$

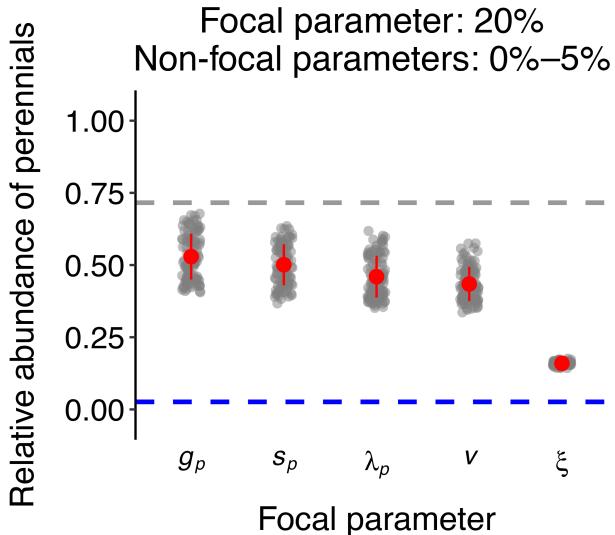
$$A_p(t+1) = \underbrace{A_p(t)\xi}_{\text{survival of existing adults}} + \underbrace{N_p(t)\frac{g_p\nu}{1+\beta_{p,A_p}A_p(t)+\beta_{p,N_p}g_pN_p(t)+\beta_{p,N_a}g_aN_a(t)}}_{\text{maturation of seeds into adult plants}} \quad (6)$$

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 ( $\lambda_i$ ) that is discounted by competition ( $\alpha_{ij}$ ). The perennial plant differs from the annual in that its seed production (second term in Equation 5) depends on the adult stage. The maturation of perennial seeds to adulthood (second term in Equation 6) depends on the survival probability ( $\nu$ ) 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  $\xi$ .

For the perennial plant, there are five demographic parameters that can be affected by soil microbes ( $g_p$ ,  $s_p$ ,  $\lambda_p$ ,  $\nu$ , and  $\xi$ ). As demonstrated in *Significant consequences of overlooking the temporal and demographic aspects of plant-soil microbe interactions*, the first strength of a demographic model is that it can integrate multiple microbial effects. For example, in the case where soil pathogens decreased all parameters of the perennial plant by 20%, the model suggested that it would nearly be outcompeted by the annual plant (i.e., from gray to blue dashed line; Figure 7). By only quantifying the impact of pathogens on the intrinsic fecundity ( $\lambda_p$ ), as is commonly done in studies that grow individual plants in conditioned soils, we would have underestimated 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 competitive outcomes. For example, sensitivity analysis (see Figure 7 legend for details) revealed that, compared to other demographic parameters, the impact of pathogens on adult survival probability ( $\xi$ ) had the strongest impact on the perennial plant population (Figure 7).

affected by wind (Nagendra & Peterson, 2016) or fire disturbances (Senior et al., 2018) that may truncate soil conditioning at different timings, or those where low propagule availability prevents immediate recolonization of conditioned soils, investigating the temporal dimension can yield valuable insights; such analyses can also be performed using individual-based models (Zee & Fukami, 2015). On the other hand, when different soil

microbes are known to impact different phases of the plant life cycle, integrating these microbial effects into a demographic model may be more important. For example, in the pyrogenic Florida scrub ecosystem, David et al. (2019) parameterized an integral projection model (IPM) for the endangered perennial herb *Hypericum cumulicola*, incorporating positive microbial effects on germination estimated via a greenhouse experiment.



**FIGURE 7** 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 ( $\lambda_p$ ), seedling survival rate ( $v$ ) and adult survival rate ( $\xi$ ). The gray 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%–5% (assuming weaker microbial impact). For each focal parameter, we repeated this process in 100 simulations (translucent gray points; red points and error bars represent the means and SDs) and ran each simulation for 200 generations. These simulations reveal that soil pathogens that primarily reduce adult survival ( $\xi$ ) 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 parameters:  $g_p = 0.125$ ,  $s_p = 0.515$ ,  $\lambda_p = 282.127$ ,  $\xi = 0.920$ ,  $v = 0.292$ ; annual plant parameters:  $g_a = 0.168$ ,  $s_a = 0.443$ ,  $\lambda_a = 47.594$ ; competitive reduction of seed production:  $\alpha_{aa} = 0.066$ ,  $\alpha_{ap} = 0.143$ ,  $\alpha_{pp} = 0.018$ ,  $\alpha_{pa} = 0.104$ ; competitive reduction of perennial survival:  $\beta_{p,N_p} = 0.086$ ,  $\beta_{p,A_p} = 0.063$ ,  $\beta_{p,N_a} = 0.002$ .

Their simulations indicated that soil microbes increased the number of post-fire years with positive population growth, particularly in high-elevation and low-nutrient patches. Together, these examples illustrate that system-specific models are key to tailoring predictions to the ecological contexts that shape plant–soil microbe interactions.

## 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., 2019a). 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., 2022a). 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 to 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). 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. Advancing research through the integration of empirical and theoretical approaches not only brings us closer to the long-standing goal of precisely predicting microbial effects in the field but also sharpens our ability to identify the key axes of variation underlying plant–soil microbe interactions.

We have argued that patch occupancy models can be parameterized with either biomass measurements (e.g., Dudenhöffer et al., 2022; Mangan et al., 2010; Teste et al., 2017) or census data (e.g., Stump & Comita, 2018). However, 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 (Figure 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 corresponds 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., Dudenhofer et al., 2022; Teste et al., 2017) 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 new plant demographic models of plant–soil microbe interactions is another frontier of research. Some models require experiments that are similar to the 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. 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 & Wan, 2020; Zou et al., 2024), which require employing experiments that directly manipulate plant density and soil origin (e.g., Cardinaux et al., 2018; Chung & Rudgers, 2016). An empirical–theoretical feedback loop is also central to the design of such theory-driven experiments. For example, Ke and Wan (2020) initially proposed a simplified experimental design based on the premise that plant–plant interactions are exclusively competitive. However, when empiricists implemented the experimental design with low neighbor density, they sometimes found facilitative interactions that rendered our original analytical approach inapplicable (e.g., Wang et al., 2024; Willing et al., 2024). This feedback prompted us to develop a revised density gradient design as a solution with greater flexibility for untangling facilitative or nonlinear microbial effects (Ke & Wan, 2023). Again, the optimal approach depends on feasibility and reflects which research question can provide a fundamental understanding of the focal plant–soil system.

Understanding the temporal dimensions of plant–soil microbe interactions in forest systems remains a difficult challenge. Fortunately, 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 for long-lived plants.

One of the remaining challenges is to move away from a plant-centered viewpoint toward a better understanding of the dynamics and functionality of soil microbial communities (Jiang et al., 2020). Incorporating microbial community assembly processes can help inform which processes need to be prioritized when building mechanistic models of microbial community dynamics (e.g., Schroeder et al., 2020; Zou et al., 2024). 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 & Kobe, 2021; Hannula et al., 2021; Ke et al., 2021). Measuring responses such as mycorrhizal percentage colonization and how they vary over time can also help bridge plant-centric and microbe-centric viewpoints (e.g., Bennett et al., 2023). However, given the functional plasticities and redundancies of microbial communities, improvements in identifying microbial functionality beyond that based on taxonomic information are also needed (see also Carini et al., 2016 for technical challenges related to erroneously detecting DNA from dead microbes in sequencing time series). 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. One outstanding question in the literature is how to predict the seemingly idiosyncratic nature of plant–soil microbe interactions (i.e., its context-dependency; Cheng et al., 2025; De Long et al., 2019). Recognizing that soil conditioning and plant response are temporally varying processes suggests that time itself may serve as a hidden axis of variation: the same environmental shift alters temporal trajectories differently depending on its timing. The temporal dimensions also underscore the significance of phenological mismatches among plants and soil microbes driven by climate change (Rudgers et al., 2020; e.g., late-germinating plants may be more affected by pathogens). As experiments incorporate environmental shifts and employ models to generate predictions (e.g., the impact of drought on plant diversity; Dudenhöffer et al., 2022), embracing the empirical–theoretical feedback loop can further refine the experimental design and enhance our ability to predict responses under real-world settings (e.g., changes in the degree of precipitation variability). 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 the backdrop of real-world conditions in which these interactions unfold.

## AUTHOR CONTRIBUTIONS

Po-Ju Ke, Gaurav S. Kandlikar, and Suzanne Xianran 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.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

Data and the code for simulations (Ke, 2025) are available in Zenodo at <https://doi.org/10.5281/zenodo.16566101>. Data for Figure 3 was sourced from Crawford et al. (2019b) on Figshare at <https://doi.org/10.6084/m9.figshare.7985195.v1> and from Yan et al. (2022b) on Zenodo at <https://doi.org/10.5281/zenodo.6513066>.

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