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

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# Summary

Soil microorganisms can have profound impacts on plant community dynamics and have received increasing attention over the past two decades. Plant-soil microbe interactions are most frequently evaluated in the context of plant–soil feedback, which arises when plants condition and respond to the soil community. Most experiments assume instantaneous and constant microbial effects throughout plant development without a time lag between soil conditioning and plant response. However, growing studies have begun to recognize the importance of time in plant–soil microbe in- teractions. The duration of the conditioning and response phase as well as the timing of interactions at certain plant developmental stages can influence the growth rates and biomass production of responding plants. Moreover, microbial communities may continue to change after the senescence of conditioning plants, thus leading to alterations in the strength and direction of microbial effects on succeeding individuals. Besides plant biomass, which most studies have focused on, soil mi- crobes also govern plant population dynamics via their effects on key demographic processes over the plant life cycle, including seed survival, germination rate and timing, and seedling survival. By incorporating temporal dimensions of plant-soil microbe interactions and plant demographic processes into theoretical models and connecting these models with empirical results, we envisage a better prediction of long-term plant–soil microbe community dynamics in the natural contexts.

**Keywords**

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

# Introduction

Plants interact with a diverse array of soil microbes, including mutualists, decomposers, and pathogens. These interactions are bidirectional, with plants conditioning the soil microbial com- munity and the resulting changes in microbial community composition impacting subsequent plant performance in the conditioned soil [(Bever *et al.*](#_bookmark35), [1997,](#_bookmark35) [Bever,](#_bookmark33) [2003).](#_bookmark33) The study of plant–soil microbe interactions has its origin in agricultural science [(Huang *et al.*](#_bookmark93), [2013,](#_bookmark93) [van der Putten *et al.*](#_bookmark155), [2013)](#_bookmark155) and has been integrated into community ecology under the framework of plant–soil feedback (PSF). Since its introduction by [Bever *et al.*](#_bookmark35)[(1997),](#_bookmark35) studies have extensively discussed how plant–soil microbe interactions influence plant coexistence [(Bever *et al.*](#_bookmark34), [2010,](#_bookmark34) [Ke & Miki,](#_bookmark107) [2015),](#_bookmark107) and the PSF framework has also been used to explore how soil microbes affect relative abundance patterns of plant communities [(Klironomos,](#_bookmark114) [2002,](#_bookmark114) [Mangan *et al.*](#_bookmark135), [2010,](#_bookmark135) [Reinhart *et al.*](#_bookmark157), [2021),](#_bookmark157) restoration success [(Wubs *et al.*](#_bookmark175), [2016,](#_bookmark175) [Koziol *et al.*](#_bookmark116), [2018),](#_bookmark116) plant invasion [(Callaway *et al.*](#_bookmark43), [2004,](#_bookmark43) [Suding *et al.*](#_bookmark165), [2013),](#_bookmark165) and the biodiversity–productivity relationship [(Kulmatiski *et al.*](#_bookmark121), [2012,](#_bookmark121) [Forero *et al.*](#_bookmark76), [2021).](#_bookmark76)

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 plant and soil microbes [(Bever *et al.*](#_bookmark35), [1997).](#_bookmark35) The classic greenhouse experiment consists of a conditioning phase during which plants modify the soil microbial community, and is immediately followed by a response phase during which plants of the same or other species respond to the modified soil community (Fig. [1A;](#_bookmark17) [Bever *et al.*](#_bookmark34), [2010,](#_bookmark34) [Brinkman *et al.*](#_bookmark41), [2010).](#_bookmark41) When conditioning soils from scratch is not feasible, e.g., in the case of long-lived trees whose conditioning effects build up over multiple years, studies can source conditioned soil communities from individuals growing in the field. Although the two-phase design has enabled a strong empirical foundation of PSF research across ecosystems [(Crawford *et al.*](#_bookmark56), [2019),](#_bookmark56) this approach implies a number of assumptions about the nature of plant–soil microbe interactions that fail to comport with our contemporary understanding of their dynamics. In particular, a growing number of studies have highlighted the importance of accounting for different temporal dimensions of plant–soil microbe interactions [(Kardol *et al.*](#_bookmark104), [2013,](#_bookmark104) [Gundale & Kardol,](#_bookmark84) [2021,](#_bookmark84) [Chung,](#_bookmark50) [2023;](#_bookmark50) see also other studies in this review). Such evidence shape 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

performance translate to population-level consequences?). Explicitly considering these unspoken assumptions is thus essential when the goal is to infer the role that soil microbes play in shaping plant communities in nature.

When plant–soil microbe interactions are studied under the two-phase feedback framework, the duration of the two phases is generally short (e.g., a few months) and the same time frame is applied across all species despite potential life history differences between the focal species (e.g., annual vs. perennial plants; Box [1).](#_bookmark14) Alternatively, when conditioned soil is collected from individuals in the field, the age of the conditioning plant is seldom explicitly tracked. Such an approach implicitly assumes that microbial effects develop instantaneously and maintain constant strength throughout different plant developmental stages (Fig. [2A).](#_bookmark18) 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.*](#_bookmark67), [2018,](#_bookmark67) [Gao *et al.*](#_bookmark80), [2019),](#_bookmark80) 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.*](#_bookmark89), [2013,](#_bookmark89) [Bezemer *et al.*](#_bookmark36), [2018,](#_bookmark36) [Lepinay *et al.*](#_bookmark127), [2018;](#_bookmark127) Fig. [2B).](#_bookmark18) Moreover, experiments in which the conditioning phase is immediately followed by the response phase neglect the temporal delays that often happen in nature (e.g., when plant growing seasons are separated by long periods of dormancy). Extrapolating from such results assumes that microbial effects remain as long-lasting legacies after plant senescence to impact the next generation. Therefore, while experimental designs are understandably based on their feasibility, explicit examination of the system’s temporal context is critical to better predict the influence of soil microbes.

The short-term nature of most experiments also necessitates researchers measuring a per- formance proxy for plant population growth [(Ke & Wan,](#_bookmark110) [2022).](#_bookmark110) The most frequently measured proxy is plant biomass, which is then used for calculating theoretically-derived metrics to in- fer how soil microbes influence plant coexistence. The biomass of plants in conspecific- and heterospecific-conditioned soils can be used to calculate the pairwise feedback metric that quanti- fies the frequency-dependent feedback loops generated by plant–soil microbe interactions [(Bever](#_bookmark35) [*et al.*](#_bookmark35), [1997).](#_bookmark35) Negative frequency-dependence arises when both plants condition their soil microbes in a way that favors heterospecifics over conspecifics, thereby promoting plant coexistence (de- picted in Fig. [1A;](#_bookmark17) [Crawford *et al.*](#_bookmark56), [2019,](#_bookmark56) [Abbott *et al.*](#_bookmark23), [2021).](#_bookmark23) Recently, multi-species extensions of

the feedback metric have been proposed [(Eppinga *et al.*](#_bookmark71), [2018,](#_bookmark71) [Mack *et al.*](#_bookmark134), [2019),](#_bookmark134) as well as metrics that capture the frequency-independent microbial effects [(Kandlikar *et al.*](#_bookmark101), [2019,](#_bookmark101) [2021,](#_bookmark102) [Yan *et al.*](#_bookmark176), [2022).](#_bookmark176) In the context of the classic PSF model, where soil microbes are the main driver of plant community dynamics and do so by changing plants’ intrinsic growth rates [(Bever *et al.*](#_bookmark35), [1997),](#_bookmark35) these metrics are well suited to extrapolate from biomass measurements to predict plant coexistence. However, soil microbes can also affect other demographic processes across the plant life cycle (e.g., changing survival rates or the nature of density-dependent interactions; [Chung & Rudgers,](#_bookmark51) [2016),](#_bookmark51) potentially with opposing effects at different plant ontogenetic stages [(Dudenhöffer *et al.*](#_bookmark65), [2018,](#_bookmark65) [Dostálek *et al.*](#_bookmark64), [2022).](#_bookmark64) Integrating these different impacts, instead of making predictions based on any one life stage, is another challenge when predicting the long-term demographic consequences of soil microbes.

Here, we discuss why the aforementioned temporal and demographic aspects represent two critical knowledge gaps when one studies the role of soil microbes in a natural context. We humbly recognize that a complete review of the plant–soil microbe interaction literature is too ambitious and therefore not our goal. Instead, we aim to highlight evidence of the two missing components, discuss their relevance when extrapolating experimental results, and outline future avenues to incorporate them. In particular, we advocate for a shift from using biomass-based performance indices to parameterizing plant demographic models with microbial effects, which can integrate the temporal and demographic details smoothly to better predict the outcome of plant–soil microbe interactions in their natural context.

# 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.*](#_bookmark103), [2006,](#_bookmark103) [2013,](#_bookmark104) [Bauer *et al.*](#_bookmark28), [2015).](#_bookmark28) However, temporal variation also occurs within shorter time scales because the conditioned microbial community and plant physiological response both vary over time (Fig. [2B).](#_bookmark18) The strength of plant–soil microbe interactions thereby depends on the timing of interactions. Recognizing this type of temporal

variation directly influences the experimental design and how we interpret experimental results. In this section, we zoom in on the temporal dimensions of plant–soil microbe interactions and review how microbial effects vary with the duration of soil conditioning (subsection [II.1),](#_bookmark4) the time lag between consecutive generations (subsection [II.2),](#_bookmark4) and the ontogeny of responding plants (subsection [II.3).](#_bookmark4) We then discuss how to improve current experimental designs to tackle the temporal complexities observed in nature (subsection [II.4).](#_bookmark4) Note that for this section we focus on studies that measure plant biomass as their key performance proxy; we will discuss other demographic responses in section [III.](#_bookmark9)

## Temporal development during the conditioning phase

Understanding the temporal dimensions begin by examining the soil conditioning phase. By growing seedlings in soils with different duration of soil conditioning (red vertical arrow (i) in Fig. [1B),](#_bookmark17) studies have shown that the relative impact of conspecific- and heterospecific-conditioned soil on the responding individual can vary with the degree of soil conditioning. For example, [Lepinay *et al.*](#_bookmark127)[(2018)](#_bookmark127) found that heterospecific soil had a more negative impact on aboveground biomass of *Rorippa austriaca* than its conspecific soil when soils were only conditioned for two weeks. However, a longer duration of soil conditioning resulted in an 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 addition to changes in the physical and chemical soil properties [(Ehrenfeld *et al.*](#_bookmark68), [2005),](#_bookmark68) studies often attribute these temporal changes to soil microbes. Studies have shown continuous shifts in the root-associated microbiome as plants mature or enter different developmental stages [(Dombrowski](#_bookmark61) [*et al.*](#_bookmark61), [2016,](#_bookmark61) [Edwards *et al.*](#_bookmark67), [2018,](#_bookmark67) [Hannula *et al.*](#_bookmark85), [2019;](#_bookmark85) but see [Lundberg *et al.*](#_bookmark132), [2012).](#_bookmark132) In addition to taxonomic composition, the functionality of the microbial community can also change over time. For example, metatranscriptomics revealed that the expression of mRNA associated with nitrogen fixation increased during plant growing phases while antibiotic defense activity increased during bolting and flowering [(Chaparro *et al.*](#_bookmark47), [2013).](#_bookmark47) Importantly, these changes (or lack thereof) in the soil microbial community have crucial consequences on the results obtained from two-phase experiments: arresting soil conditioning at different time points causes the responding plant to

encounter microbial communities with different compositions and functions, thereby experiencing different plant–soil microbe interactions.

Current literature discussing mechanisms of microbial community assembly has distin- guished between plant- and microbe-centered mechanisms, although we note that both forces often act simultaneously. Plant-centered mechanisms often result from physiological changes in nutrient allocation or root exudation during different plant developmental stages [(Chaparro *et al.*](#_bookmark47), [2013,](#_bookmark47) [Zhalnina *et al.*](#_bookmark179), [2018,](#_bookmark179) [Zhao *et al.*](#_bookmark181), [2021).](#_bookmark181) For example, plants with different life histories may prioritize shoot and root growth differently, therefore recruiting different mutualistic microbial communities at different times according to their nutritional needs [(Kulmatiski *et al.*](#_bookmark122), [2017,](#_bookmark122) [Hu-](#_bookmark94) [berty *et al.*](#_bookmark94), [2022).](#_bookmark94) In addition to shifts in resource allocation, strengthening in immunity against pathogens as plants mature can also affect the structure of soil microbial communities [(Bulgarelli](#_bookmark42) [*et al.*](#_bookmark42), [2013).](#_bookmark42) On the other hand, microbial-centered mechanisms focus on microbe–microbe interac- tions such as competition and facilitation, as well as other processes affecting microbial community assemblies such as stochastic drift and evolutionary response [(Barret *et al.*](#_bookmark27), [2015,](#_bookmark27) [Herrera Paredes](#_bookmark90) [& Lebeis,](#_bookmark90) [2016,](#_bookmark90) [Bittleston *et al.*](#_bookmark39), [2021).](#_bookmark39) Importantly, these mechanisms underlying changes in the microbial community are interconnected: changes in microbial interactions often occur due to plant-induced changes in soil chemistry [(Lepinay *et al.*](#_bookmark127), [2018)](#_bookmark127) and physical properties [(Edwards](#_bookmark67) [*et al.*](#_bookmark67), [2018),](#_bookmark67) and outcomes of microbial interactions can trigger plant physiological responses.

The significance of temporal development during the soil conditioning phase is exemplified when one considers plants with different life histories. Short- and long-lived plants may structure microbial communities at different rates and the same duration of soil conditioning, as imple- mented in experiments, may correspond to different developmental stages and microbial effects [(Kulmatiski *et al.*](#_bookmark122), [2017):](#_bookmark122) for short-lived annual plants a fully matured species-specific microbiome may have been reached, whereas it would require a longer conditioning time for long-lived peren- nials. As shown in Box [1,](#_bookmark14) 19 out of 106 studies (18%) have included annual–perennial pairs in their experiment while implementing the same (usually short) conditioning time; how to interpret the results in the context of the focal system’s natural history thereby becomes a critical issue. In addition to life history strategies, plants belonging to different functional groups may respond dif- ferently to the same temporal turnover in microbial communities. In [Ke *et al.*](#_bookmark111)[(2021),](#_bookmark111) the microbial

effect experienced by their focal legume species *Lupinus arboreus* remained constant despite tem- poral changes in the microbial community, potentially indicating functional redundancy within the soil microbial community [(Birnbaum *et al.*](#_bookmark38), [2018,](#_bookmark38) [Huberty *et al.*](#_bookmark94), [2022).](#_bookmark94) We will return to the logistical challenges when trying to detect this causal relationship in section [V.](#_bookmark13)

## Alterations of microbial effects after plant death

After soil conditioning, greenhouse experiments typically grow the responding individual imme- diately (i.e., immediate transplant). This neglects the fact that in nature there may be a temporal lag between the senescence of the conditioning individual and the growth of the next responding individual, potentially due to discrete growing seasons or dispersal limitation. During this lag phase when the conditioned soil is left empty for an extended period of time, processes such as litter decomposition, abiotic filtering, and stochastic drift may continue to change the microbial community. Studies growing seedlings in soils collected from dead individuals (red vertical arrow

(ii) in Fig. [1B)](#_bookmark17) suggests that such lags can have distinct effects across different ecosystems. For example, [Bennett *et al.*](#_bookmark31)[(2022)](#_bookmark31) showed that microbial communities from soils collected under dead and live adult *Populus tremuloides* trees had similar effects on conspecific seedlings. Conversely, [Esch & Kobe](#_bookmark72) [(2021)](#_bookmark72) showed that, while soils collected from live *Prunus serotina* caused lower sur- vival of conspecific seedlings, the negative effect faded away within one year after tree removal. Below, we discuss the mechanisms that could either maintain or alter microbial effects when a temporal lag exists between consecutive generations.

The persistence of microbial effects after active plant conditioning ceases could be due to the continued survival of the conditioned microbial community in the soil, with functionality being comparable to that of microbes associated with living plants (P[epe *et al.*](#_bookmark152), [2018,](#_bookmark152) [Esch *et al.*](#_bookmark73), [2021).](#_bookmark73) 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 & Jensen,](#_bookmark99) [1996,](#_bookmark99) [Müller *et al.*](#_bookmark147), [2013).](#_bookmark147) For example, [Esch *et al.*](#_bookmark73)[(2021)](#_bookmark73) found the persisting pathogenic oomycetes taken from dead tree stumps still negatively affect seedling survival to an extent similar to oomycetes detected from live trees. Similarly, [Pepe *et al.*](#_bookmark152)[(2018)](#_bookmark152) showed that arbuscular mycorrhizal fungi remain active and can spread from roots after

host shoot removal. Additionally, microbial dormancy 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](#_bookmark126) [& Jones,](#_bookmark126) [2011,](#_bookmark126) [Shade *et al.*](#_bookmark161), [2012,](#_bookmark161) [Lloyd,](#_bookmark131) [2021).](#_bookmark131) 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 conditioning effect to change after plant senescence, such that subsequent responding individuals encounter a soil microbial community different from that obtained in an immediate transplant scenario. The process of litter decomposition can introduce microbes from the phyllosphere to the soil (F[anin *et al.*](#_bookmark74), [2021,](#_bookmark74) [Minás *et al.*](#_bookmark142), [2021),](#_bookmark142) exude chemicals and nutrients that can alter the microbial community [(Veen *et al.*](#_bookmark171), [2021),](#_bookmark171) and, in turn, cause the responding individual to encounter different microbial communities [(Grove *et al.*](#_bookmark83), [2015,](#_bookmark83) [Veen *et al.*](#_bookmark170), [2019).](#_bookmark170) Additionally, different causes of plant death (e.g., herbivory, fire, and disturbance) are often associated with different changes in abiotic factors, thereby altering 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,](#_bookmark24) [1984,](#_bookmark24) [Reinhart](#_bookmark158) [*et al.*](#_bookmark158), [2010,](#_bookmark158) [Nagendra & Peterson,](#_bookmark148) [2016).](#_bookmark148) Finally, 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 will fail to replicate the microbial effects experienced by the responding plant in nature.

## Temporal development during the response phase

The final temporal dimension of plant–soil microbe interactions involves the duration of the re- sponse phase, i.e., how the strength and direction of the microbial effect can change over the lifetime of the responding plant [(Kardol *et al.*](#_bookmark104), [2013).](#_bookmark104) Studying such dynamics has been the typ- ical focus when past studies examine the temporal development of plant–soil feedback [(Gundale](#_bookmark84) [& Kardol,](#_bookmark84) [2021).](#_bookmark84) By sequentially harvesting plant individuals at different time intervals (red diagonal arrow (iii) in Fig. [1B),](#_bookmark17) studies have found that the relative impact of conspecific- and heterospecific-conditioned soil varied as the responding plant matures (e.g., [Dudenhöffer *et al.*](#_bookmark65), [2018,](#_bookmark65) [Dostálek *et al.*](#_bookmark64), [2022).](#_bookmark64) Moreover, the specific temporal pattern depends on nutrient availability

[(Dostál,](#_bookmark62) [2021),](#_bookmark62) the origin of the responding species (i.e., native or invasive; [Hawkes *et al.*](#_bookmark89), [2013),](#_bookmark89) and whether individuals face co-occurring competitors [(Dostál,](#_bookmark62) [2021,](#_bookmark62) [Bezemer *et al.*](#_bookmark36), [2018).](#_bookmark36) This empirical evidence provides a strong impetus to consider the temporal variability in the response phase since harvesting an experiment at different endpoints can alter our understanding of the microbial effect.

While studies distinguish between conditioning and response phases in their experimental designs, it is important to note that the two processes operate simultaneously in nature and represent two sides of the same coin. Therefore, the plant- and microbe-centered mechanisms that drive changes in the soil microbial community during the conditioning phase also apply to explain patterns in the response phase. For example, strengthening of immunity as plants mature indicates reduced pathogen abundance at the end of the conditioning phase [(Bulgarelli *et al.*](#_bookmark42), [2013)l;](#_bookmark42) the same ecological process reduces plant susceptibility to pathogens and results in alleviated negative microbial effect 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. Moreover, since the two processes act simultaneously, responding individuals will also impose their own conditioning impact and the extent of which can depend on plant and microbial functional group [(Hannula *et al.*](#_bookmark86), [2021).](#_bookmark86) We will elaborate on necessary experiments that can tease apart different temporal dimensions in the next subsection.

## Future experiments

While the current lack of empirical information limits our understanding of the temporal dimen- sions of plant–soil microbe interactions, we see a path forward. We encourage studies to explicitly contextualize the temporal aspects of the experiment relative to the temporal dynamics of the focal plant–soil system in nature (Fig. [1B).](#_bookmark17) For instance, in Mediterranean annual plant communities, a short-term conditioning phase typical of previous studies (Box [1)](#_bookmark14) may suffice due to their short lifespan, but the practice of immediately following the conditioning phase with a subsequent response phase overlooks the clear seasonality in nature [(Kandlikar *et al.*](#_bookmark102), [2021).](#_bookmark102) In such sys- tems, incorporating a decay phase during which the conditioned soils are exposed to a prolonged

drought with no vegetative growth, thereby mirroring the characteristics of the system, may pro- vide a better understanding of how soil microbes shape community dynamics (red vertical arrow

(ii) in Fig. [1B).](#_bookmark17) Moreover, researchers can build on natural experiments, long-term monitoring plots, or 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 plant–soil microbe interactions in long-lived plants, which often source field-conditioned soils for greenhouse experiments (47 out of 106 studies; Box [1).](#_bookmark14) For example, [Ke *et al.*](#_bookmark111)[(2021)](#_bookmark111) used historical aerial photos to track plant age and employed a chronosequence approach to study how plant–soil microbe interactions vary with the duration of soil conditioning. Other examples include using host tree size as a proxy of conditioning time [(Dinnage *et al.*](#_bookmark60), [2019,](#_bookmark60) [Chen *et al.*](#_bookmark48), [2019),](#_bookmark48) and utilizing chronosequences of abandoned fields or agricultural harvest times to study the persistence of microbial effects (v[an de Voorde *et al.*](#_bookmark172), [2012,](#_bookmark172) [Esch & Kobe,](#_bookmark72) [2021).](#_bookmark72)

One can also design experiments that isolate a particular facet of temporal variability, poten- tially disentangling the mechanisms behind observed temporal patterns. Current studies on the temporal development of microbial effects typically employ sequential harvesting (e.g., [Hawkes](#_bookmark89) [*et al.*](#_bookmark89), [2013,](#_bookmark89) [Bezemer *et al.*](#_bookmark36), [2018).](#_bookmark36) Since soil conditioning and plant response in fact unfold simulta- neously in nature [(Chung,](#_bookmark50) [2023),](#_bookmark50) the observed temporal changes in microbial effects result from the combination of varying plant physiological responses and the new tier of soil conditioning hap- pening in the pot (red diagonal arrow (iii) in Fig. [1B).](#_bookmark17) In this case, an experiment where seedlings of the same age were planted in soils with different conditioning duration can isolate the temporal development during the conditioning phase (red vertical arrow (i) in Fig. [1B).](#_bookmark17) Alternatively, plant- ing seedlings of different ages (kept in a relatively sterilized environment such as a Magenta box before transplanting) in soils with identical conditioning duration can isolate the effects caused by changing plant physiology (red horizontal arrow (iv) in Fig. [1B).](#_bookmark17) Additionally, mutants or cul- tivars with different developmental rates can also be used to further separate the effects of plant developmental stage (e.g., vegetative growth or flowering) and age *per se* [(Dombrowski *et al.*](#_bookmark61), [2016).](#_bookmark61) While the above scenarios are deliberately created, these experiments serve the purpose to provide a mechanistic understanding underlying the observed temporal patterns.

While we have focused on changes happening over the course of plant-to-plant replacement,

future studies should also study temporal changes that develop over multiple generations (i.e., multiple tiers of conditioning and response). In agriculture, a wealth of literature exists detailing the microbial underpinning of soil sickness following successive planting [(Huang *et al.*](#_bookmark93), [2013,](#_bookmark93) [Mariotte *et al.*](#_bookmark136), [2018).](#_bookmark136) In the ecological context, studies on non-native plants have documented the strengthening of negative microbial effects over time since introduction [(Diez *et al.*](#_bookmark59), [2010,](#_bookmark59) [Dostál](#_bookmark63) [*et al.*](#_bookmark63), [2013;](#_bookmark63) but see [Day *et al.*](#_bookmark58), [2015).](#_bookmark58) While this temporal dimension 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 & Bezemer](#_bookmark174) [(2018)](#_bookmark174) demonstrated the interactive effects arising from multiple rounds of soil conditioning. We look forward to future work expanding upon [Wubs & Bezemer](#_bookmark174) [(2018)](#_bookmark174) to study how the unique sequences of soil conditioning can result in different plant–soil microbe interactions.

So far, we have mostly highlighted studies that measure plant biomass as the key response variable. Even with this single performance proxy, the aforementioned temporal considerations have already complicated the overarching goal of predicting the long-term consequences of plant– soil microbe interactions in nature. However, as the responding individual matures, in addition to varying biomass responses it also involves different demographic processes that might be suscep- tible to soil microbes. Indeed, multiple studies have shown that other demographic processes are also influenced by the soil conditioning history, and final plant fitness cannot be easily predicted by only measuring a single demographic response [(Dudenhöffer *et al.*](#_bookmark65), [2018,](#_bookmark65) [Dostálek *et al.*](#_bookmark64), [2022,](#_bookmark64) [Zhang *et al.*](#_bookmark180), [2022).](#_bookmark180) This demographic facet of plant–soil microbial interactions is tightly inter- connected with the temporal dimensions and represents another missing component, which we elaborate on in section [III.](#_bookmark9)

# Assessing multiple demographic consequences of soil microbes

Most two-phased studies of plant–soil microbe interactions are designed to evaluate how different soil microbial contexts influence plant biomass performance. Experimentally, the implicit assump-

tion is that individual biomass at the end of the experiment integrates all impacts of the microbial community, and that biomass is a good indicator of plant fitness at the population level. This design corresponds well with the classic feedback model of [Bever *et al.*](#_bookmark35)[(1997),](#_bookmark35) where microbes control plant species’ intrinsic growth rates. However, such an assumption may not hold for real plant communities because soil microbes can alter not only biomass performance but also other key demographic processes across the plant life cycle, often in opposite directions [(Dudenhöffer](#_bookmark65) [*et al.*](#_bookmark65), [2018).](#_bookmark65) These effects are not directly captured by studies that only focus on biomass, and integrating these different impacts to predict the long-term consequences of soil microbes on plant dynamics remains a gap [(Dostálek *et al.*](#_bookmark64), [2022).](#_bookmark64) Here, we highlight key studies that provide insights into microbial control over other 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 seeding survival; Fig. [3),](#_bookmark19) they are often grouped together given the logistical challenges of separating these effects in field settings. For example, for long-lived plants such as forest trees, repetitive demographic censuses are often used to monitor seed-to-seedling transition (e.g., [Harms](#_bookmark87) [*et al.*](#_bookmark87), [2000,](#_bookmark87) [Swamy *et al.*](#_bookmark166), [2011).](#_bookmark166) A large body of evidence for microbial effects on plant early life stages comes from field studies finding that fungicide applications altered patterns of seed and seedling demography (e.g., [Bell *et al.*](#_bookmark30), [2006,](#_bookmark30) [Bagchi *et al.*](#_bookmark25), [2014,](#_bookmark25) [Fricke *et al.*](#_bookmark77), [2014,](#_bookmark77) [Krishnadas *et al.*](#_bookmark117), [2018).](#_bookmark117) Many of these studies are conducted in the context of evaluating microbes as potential drivers of conspecific negative density-dependence (CNDD; [Comita & Stump,](#_bookmark54) [2020,](#_bookmark54) [LaManna](#_bookmark123) [*et al.*](#_bookmark123), [2022,](#_bookmark123) [Song & Corlett,](#_bookmark163) [2022),](#_bookmark163) a demographic signature of the Janzen–Connell hypothesis [(Janzen,](#_bookmark97) [1970,](#_bookmark97) [Connell,](#_bookmark55) [1971;](#_bookmark55) see also Box [2).](#_bookmark15) While evaluating the integrative microbial effect across multiple early life stages can yield critical insights, studies that isolate microbial effects on specific underlying demographic transitions, i.e., seed survival, seed germination, and early seedling performance, are necessary for building a mechanistic understanding of microbial effects on plant population dynamics.

Soil-borne pathogens can cause substantial mortality at the seed stage in nearly all terrestrial ecosystems (e.g., [Meyer *et al.*](#_bookmark138), [2007,](#_bookmark138) [Kotanen,](#_bookmark115) [2007,](#_bookmark115) [Sarmiento *et al.*](#_bookmark159), [2017,](#_bookmark159) [Li *et al.*](#_bookmark129), [2019).](#_bookmark129) One system where the role of fungal seed pathogens in structuring plant community dynamics 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: for example, [Dalling *et al.*](#_bookmark57)[(1998)](#_bookmark57) found that fungicide treatments substantially reduced seed mortality in *C. insignis* and another pioneer species (see also [Gallery *et al.*](#_bookmark79), [2010).](#_bookmark79) Moreover, [Dalling](#_bookmark57) [*et al.*](#_bookmark57)[(1998)](#_bookmark57) found that seeds were more susceptible to pathogen attack in soils close to conspecific adults than in soils far from conspecifics. Recent advances have largely focused on employing molecular methods toward understanding longstanding questions about pathogen host-specificity. [Zalamea *et al.*](#_bookmark177)[(2021)](#_bookmark177) 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 diverse group of pioneer tree species, [Sarmiento *et al.*](#_bookmark159)[(2017)](#_bookmark159) 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 have highlighted soilborne fungal seed pathogens as key microbial players in the dynamics of pioneer trees in tropical forests. While quantifying seed survival requires laborious methods (e.g., tetrazolium staining for testing seed viability; [Sarmiento *et al.*](#_bookmark159), [2017),](#_bookmark159) a better understanding of these effects is critical given that seed limitation can be a bottleneck on plant population dynamics [(Harper,](#_bookmark88) [1977,](#_bookmark88) [Clark *et al.*](#_bookmark52), [2007),](#_bookmark52) especially in communities dominated by plant species that form persistent seed banks.

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.*](#_bookmark113), [2022](#_bookmark113) and [Bottini *et al.*](#_bookmark40), [2004)](#_bookmark40) or ethylene (reviewed in [Ravanbakhsh *et al.*](#_bookmark156), [2018](#_bookmark156) and [Ishaq,](#_bookmark96) [2017).](#_bookmark96) While studies of how soil microbes regulate germination have historically focused on managed settings, evidence is now accumulating in ecological settings. In the only two-phase experiment that focused on pairwise feedback effects on germination, [Miller](#_bookmark139) [*et al.*](#_bookmark139)[(2019)](#_bookmark139) found species-specific effects of conditioned microbes on germination. Specifically, the

legume species *Desmodium illinoense* achieved lower germination rates in conspecific-conditioned soils as compared to that in both sterilized and four out of six heterospecific-conditioned soils. Across a large-scale microcosm experiment, [Eldridge *et al.*](#_bookmark69)[(2021)](#_bookmark69) 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 simply explained by their shared responses to abiotic soil properties. Even when overall rates of germination are unaffected by soil microbes, they can alter the phenology of germination [(Keeler &](#_bookmark112) [Rafferty,](#_bookmark112) [2022),](#_bookmark112) which could either hurt (e.g., if later germination reduces seedlings’ performance due to competition; [Orrock & Christopher,](#_bookmark150) [2010)](#_bookmark150) or benefit (e.g., if later germinants escape severe competition at the seedling stage or avoid abiotic stress; [Leverett *et al.*](#_bookmark128), [2018)](#_bookmark128) population growth. A first step in enhancing our understanding of this phenomenon would be for two-phase studies, which often transplant germinated seeds into cultivated soils, to alter their design when possible to directly plant ungerminated seeds into cultivated soils and report germination rates along with biomass performance of germinated seedlings (e.g., [Dudenhöffer *et al.*](#_bookmark66), [2022).](#_bookmark66) This would help clarify how microbial controls over germination relate to the overall role of microbes in regulating plant dynamics [(Dudenhöffer *et al.*](#_bookmark65), [2018).](#_bookmark65)

Soil microbes also play a key role in determining the fate of seedlings after germination. The widespread role of mycorrhizal symbioses in promoting seedling survival and the potential for soilborne pathogens to cause mortality among seedlings has been studied for decades and reviewed elsewhere (e.g., [Horton & van der Heĳden,](#_bookmark91) [2008,](#_bookmark91) [Gilbert,](#_bookmark81) [2002).](#_bookmark81) 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,](#_bookmark37) [2011),](#_bookmark37) the relative density of conspecific and heterospecific adults ([Teste](#_bookmark167) [*et al.*](#_bookmark167), [2017),](#_bookmark167) and the functional groups of mycorrhizal fungi [(Liang *et al.*](#_bookmark130), [2016,](#_bookmark130) [Bennett *et al.*](#_bookmark32), [2017).](#_bookmark32) 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.*](#_bookmark53), [2010).](#_bookmark53) Although microbial controls over seed survival are known to be common in the field, such effects are poorly studied in the context of greenhouse experiments given their

common biomass focus. However, for some systems such as forest trees, individual survival can be size-dependent, and therefore measuring microbe-mediated changes in plant biomass may provide insights into this demographic transition. Evidence comes from data-driven demographic models showing that seedling survival rates remain high once they achieve a certain size threshold [(Chang-Yang *et al.*](#_bookmark46), [2021).](#_bookmark46) Therefore, soil microbes that decrease seedling growth rates can manifest in higher mortality among forest seedlings, thereby having a clear demographic consequence on plant populations.

## 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 paper, 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 & Lennon,](#_bookmark124) [2012,](#_bookmark124) [Wagner *et al.*](#_bookmark173), [2014,](#_bookmark173) [Fitzpatrick *et al.*](#_bookmark75), [2019,](#_bookmark75) [Igwe *et al.*](#_bookmark95), [2021).](#_bookmark95) While the consequences of such phenological shifts at the population level are seldom quantified, the few-day differences reported in these studies can have drastic consequences for plant fitness, especially under abiotic stress when earlier flowering can be critical to reproductive success and fitness (reviewed in [Kazan & Lyons,](#_bookmark105) [2016,](#_bookmark105) [O’Brien *et al.*](#_bookmark149), [2021).](#_bookmark149) The soil community can also regulate plant susceptibility to herbivores (e.g., [Howard *et al.*](#_bookmark92), [2020,](#_bookmark92) [Pineda](#_bookmark154) [*et al.*](#_bookmark154), [2020,](#_bookmark154) [Kalske *et al.*](#_bookmark100), [2022),](#_bookmark100) with such effects likely arising due to changes in leaf metabolomes or volatile organics induced by soil microbes [(Kalske *et al.*](#_bookmark100), [2022,](#_bookmark100) [Huberty *et al.*](#_bookmark94), [2022).](#_bookmark94) While the consequences of microbial-induced shifts in plant–herbivore interactions on insect and population dynamics are becoming increasingly well-studied (reviewed in [Shikano *et al.*](#_bookmark162), [2017),](#_bookmark162) their impacts on plant population dynamics are less so. We do not see a universal path for integrating all such microbial effects into mathematical models or experiments, but an ideal way forward is to pair experiments with system-specific models that propagate their consequences on long-term plant population dynamics.

# Incorporating plant–soil microbe interactions into ecological mod- els

As reviewed in the above sections, the strength and direction of plant–soil microbe interactions vary along different temporal axes and can influence various demographic processes. While empirical studies are essential for growing our understanding of the nature of these aspects, predicting their long-term consequences requires an integration of data with models of plant population dynamics. Therefore, we encourage studies to move from biomass-based performance metrics to demographic models that directly incorporate microbial effects. Developing suitable theoretical models for the focal plant–soil system and connecting them with empirical data remains a critical 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 represent a relatively straightforward framework for studying plant–soil microbe interactions (P[acala & Tilman,](#_bookmark151) [1994,](#_bookmark151) [Mouquet *et al.*](#_bookmark146), [2002).](#_bookmark146) In this group of models, plants compete for unoccupied sites (patches) and the probability that a particular plant establishes in a local site depends on the microbial legacy of the site (S[tump & Comita,](#_bookmark164) [2018,](#_bookmark164) [Miller](#_bookmark140) [& Allesina,](#_bookmark140) [2021,](#_bookmark140) [Ke & Levine,](#_bookmark106) [2021).](#_bookmark106) 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 & Allesina,](#_bookmark140) [2021,](#_bookmark140) [Ke & Levine,](#_bookmark106) [2021),](#_bookmark106) 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.*](#_bookmark35), [1997,](#_bookmark35) [Mack & Bever,](#_bookmark133) [2014,](#_bookmark133) [Bauer *et al.*](#_bookmark28), [2015).](#_bookmark28) Detailed formation aside, a common assumption to such models is that plants only affect the colonization of each other indirectly via soil microbes, which is similar to [Bever *et al.*](#_bookmark35)[(1997)](#_bookmark35) where plants grow exponentially with an intrinsic growth rate affected by soil microbes. This assumption aligns well with two-phase experiments growing a single individual in soils with different conditioning histories, thereby allowing one to parameterize such models with biomass measurements from pot experiments (e.g., by assuming colonization probability scales with the relative biomass performance of different plants in the

soil). 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., [Petermann *et al.*](#_bookmark153), [2008,](#_bookmark153) [Mangan *et al.*](#_bookmark135), [2010,](#_bookmark135) [Teste *et al.*](#_bookmark167), [2017,](#_bookmark167) [Dudenhöffer *et al.*](#_bookmark66), [2022).](#_bookmark66) Finally, patch occupancy models can also be parameterized with re- cruitment data from repetitive censuses, thereby incorporating microbial effects on early life stages (e.g., seed survival, germination, and seedling survival in Fig. [3;](#_bookmark19) [Krishnadas & Stump,](#_bookmark119) [2021).](#_bookmark119)

The patch occupancy framework offers a pathway to effectively incorporate various temporal aspects of plant–soil microbe interactions (Fig [4A).](#_bookmark20) This is because such models can treat different developmental stages of the soil microbial community as distinct states, and 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 differs from previous feedback models, which usually assume tight coupling between plants and microbes via timescale separation [(Eppinga *et al.*](#_bookmark71), [2018,](#_bookmark71) [Mack *et al.*](#_bookmark134), [2019).](#_bookmark134) For example, [Ke *et al.*](#_bookmark111)[(2021)](#_bookmark111) modified a previous model (F[ukami & Nakajima,](#_bookmark78) [2013)](#_bookmark78) by making microbial effects vary with the duration of soil conditioning and showed that the pattern of which influences the transient trajectory of community assembly. In another example, [Ke & Levine](#_bookmark106) [(2021)](#_bookmark106) 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, thereby these models can be parameterized with the type of experiments mentioned in section [II.4.](#_bookmark4) 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.*](#_bookmark160), [2020).](#_bookmark160) However, such models are harder to parameterize with empirical data since detailed knowledge of microbial traits and population regulating processes is required [(Jiang *et al.*](#_bookmark98), [2020).](#_bookmark98)

In contrast to patch occupancy models, which usually assume microbes only impact the col- onization process, other studies have formulated models that directly consider microbial impacts on multiple plant demographic processes. While relatively few studies have applied the demo- graphically explicit approach to study plant–soil microbe interactions (perhaps due to the extensive amount of work required to obtain all parameters), it may be particularly useful for demographi-

cally complex systems. Demonstrating the power of this approach, a series of studies [(Mordecai,](#_bookmark143) [2013a,b,](#_bookmark144) [2015,](#_bookmark145) **?**) integrated models and empirical observations to investigate how pathogens affect competition between native perennials and invasive annual grasses. The plant demography com- ponent of these models begins 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. [4B;](#_bookmark20) see also Box [3).](#_bookmark16) The authors then incor- porate 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,](#_bookmark143) [2013a).](#_bookmark143) With a plant competition experiment and experimental manipulations of pathogen densities, [Mordecai](#_bookmark144) [(2013b)](#_bookmark144) parameterize 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](#_bookmark145) [(2015)](#_bookmark145) demonstrated 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.*](#_bookmark168)[(2019)](#_bookmark168) combined field observa- tions 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 allows one to identify the most critical one via simulations. For instance, in the annual–perennial plant model in [Uricchio *et al.*](#_bookmark168)[(2019),](#_bookmark168) foliar pathogens had little impact but seed pathogens can have a more significant effect on neutral 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.*](#_bookmark108), [2015,](#_bookmark108) [Schroeder *et al.*](#_bookmark160), [2020)](#_bookmark160) 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

also provide insights for future studies and guide more targeted experiments. With an integral projection model parameterized with long-term demographic data, [Chu & Adler](#_bookmark49) [(2015)](#_bookmark49) showed that density-dependent feedback loops during the recruitment stage contributed most to plant coexistence compared to that during the growth and survival stages (see also [Ellner *et al.*](#_bookmark70), [2019).](#_bookmark70) The authors speculate this is due to the recruitment stage involving many demographic transitions that are susceptible to soil pathogens. In Box [3,](#_bookmark16) with an annual plant model incorporating microbial effects as qualitative switches in parameter values, we also demonstrated how sensitivity analysis can help identify the relative importance of different microbial effects. In conclusion, we believe that 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.

# Moving forward with an empirical-theoretical feedback loop

Since its introduction to community ecology, the field 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.*](#_bookmark35)[(1997)](#_bookmark35) has motivated more than two decades of research to predict the long-term consequences of soil microbes [(Crawford *et al.*](#_bookmark56), [2019).](#_bookmark56) 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.*](#_bookmark101), [2019,](#_bookmark101) [2021,](#_bookmark102) [Yan *et al.*](#_bookmark176), [2022).](#_bookmark176) 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 is sufficient to capture the population dynamic consequences of soil microbes. While such abstractions made models generalizable, increasing evidence has proved the relevance of the two knowledge gaps when predicting the role of soil microbes in natural communities [(Chung,](#_bookmark50) [2023).](#_bookmark50) Depending on the plant community, some temporal aspects or demographic responses may be more critical than others and, therefore, should be explicitly considered. 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 identified two paths moving forward (Fig [4).](#_bookmark20) 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, each with a different impact on future plant recolonization. This framework also echoes recent theoretical studies suggesting that competition for limited colonization sites generates more interpretable frequency- based dynamics for multi-species communities [(Miller *et al.*](#_bookmark141), [2022).](#_bookmark141) 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 multiple microbial effects. 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 & Peterson,](#_bookmark148) [2016),](#_bookmark148) or those with low propagule pressure such that conditioned soils are not immediately recolonized, investigating the temporal dimension can provide great insights into the role of soil microbes in nature. 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 model may be of more importance.

With assumptions that resemble the ecological processes underlying common experimental setup, patch occupancy models can be parameterized with either common biomass measurements from two-phase experiments or census data from CNDD studies (P[etermann *et al.*](#_bookmark153), [2008,](#_bookmark153) [Mangan](#_bookmark135) [*et al.*](#_bookmark135), [2010,](#_bookmark135) [Teste *et al.*](#_bookmark167), [2017,](#_bookmark167) [Dudenhöffer *et al.*](#_bookmark66), [2022).](#_bookmark66) However, we caution that the model itself is agnostic to the details of plant–soil microbe interactions and will encompass different microbial effects depending on the empirical data used for parameterization (Fig. [3).](#_bookmark19) For instance, [Stump &](#_bookmark164) [Comita](#_bookmark164) [(2018)](#_bookmark164) parameterized their patch occupancy model with CNDD patterns based on 5-year seedling survival [(Comita *et al.*](#_bookmark53), [2010),](#_bookmark53) which correspond to microbial effects on the performance and size-dependent survival of older seedlings. On the other hand, [Krishnadas & Stump](#_bookmark119) [(2021)](#_bookmark119) parameterized a similar model with CNDD patterns based on seed-to-seedling transition, thereby representing microbial effects on earlier life stages. Moreover, using different data to parameterize

the model implies different assumptions on how microbial effects operate. In particular, using biomass measurements from single-individual pot experiments implies that soil microbes affect density-independent parameters of plant population growth, whereas using CNDD patterns from observational data might imply that soil microbes act on density-dependent parameters.

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 variation in the duration of soil conditioning; to track multiple early life stage microbial effects one can just directly plant ungerminated seeds into cultivated soils (see sections [II.](#_bookmark4) and [III.).](#_bookmark9) However, some microbial effects cannot be reliably estimated by classic two-phased experiments with a single-growing plant individual. For example, in demographic models that allow direct plant–plant interactions (e.g., an annual plant model or a Lotka–Volterra model), it is often as- sumed that soil microbes can modify the density-dependency of plant population growth (e.g., competitive coefficients *αij* in Box [3).](#_bookmark16) Recent studies linking plant–soil microbe interactions and coexistence theory specifically highlight this scenario where soil microbes influence the model’s density-dependent parameters [(Kandlikar *et al.*](#_bookmark101), [2019,](#_bookmark101) [Ke & Wan,](#_bookmark109) [2020),](#_bookmark109) which require employ- ing experiments that directly manipulate plant density and soil origin [(Chung & Rudgers,](#_bookmark51) [2016,](#_bookmark51) [Cardinaux *et al.*](#_bookmark44), [2018).](#_bookmark44) An empirical–theoretical feedback loop is also central to the design of such theory-driven experiments, e.g., a proposed design based on the premise that plant–plant interactions are competitive [(Ke & Wan,](#_bookmark109) [2020)](#_bookmark109) was challenged by the observation that facilitation is common, leading to a revised density gradient design with greater flexibility [(Ke & Wan,](#_bookmark110) [2022).](#_bookmark110) Again, the optimal approach depends on feasibility and which research question can provide a critical understanding of the focal plant–soil system.

One of the remaining challenges is a better understanding of the dynamics and functionality of soil microbial communities [(Jiang *et al.*](#_bookmark98), [2020).](#_bookmark98) With a plant-centered viewpoint, 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 as- sembly processes, as outlined in section [II.,](#_bookmark4) can help inform which processes need to be prioritized

when building mechanistic models of microbial community dynamics. Moreover, experiments that establish the causal relationship between measured microbial dynamics and plant demo- graphic 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 [(Esch & Kobe,](#_bookmark72) [2021,](#_bookmark72) [Ke *et al.*](#_bookmark111), [2021,](#_bookmark111) [Hannula *et al.*](#_bookmark86), [2021).](#_bookmark86) However, some technical challenges remain when detecting the dynamics of the microbial community. For example, DNA from dead microbes may still be detected in sequencing time series [(Carini *et al.*](#_bookmark45), [2016),](#_bookmark45) which can lead to erroneous conclusions about how conditioning time, time lags, or other temporal considerations affect plant–soil microbe interactions. Given that taxonomic information may not reliably reflect the function of microbial communities due to their functional plasticities and redundancies, there is also a need for future developments in the detection of microbial functionality. Explicit quantification of microbial activ- ity, such as measurements through multi-omics or metabolite outputs, can allow better modeling of microbial dynamics. Future studies taking a microbe-centered perspective 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 demo- graphic consequences of plant–soil microbe interactions provides a better understanding of their role in the natural context. In addition to the maintenance of plant coexistence and diversity, the two knowledge gaps can also be important for other ecological processes (e.g., recovery trajectory following disturbance and gap dynamics; [Zee & Fukami,](#_bookmark178) [2015).](#_bookmark178) 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 provide an avenue to predict the long-term consequences of plant–soil microbe interactions against a backdrop of real-world conditions in which these interactions play out.

**Boxes**

**Box 1: Quantitative summary of the temporal aspects of PSF experiments**

We compiled information on the length of soil conditioning and response phases of experiments included in [Crawford *et al.*](#_bookmark56)[(2019)](#_bookmark56) and [Yan *et al.*](#_bookmark176)[(2022),](#_bookmark176) two prominent meta-analysis data sets of plant–soil feedback studies. Since the above two studies focused on the pairwise stabilization metric of [Bever *et al.*](#_bookmark35)[(1997),](#_bookmark35) we compiled information on plant life history and categorized each pairwise comparison as either annual (both plants are annuals; orange), perennial (both plants are perennials; green), or annual-perennial (mismatch of an annual versus a perennial; blue). While the majority of the plant pairs were perennials, 19 out of 106 studies (*≈* 18%) included annual–perennial pairs that compared microbe-mediated performance change of annuals to that of perennials (see the central panel where each pie chart represents a study and the color proportions indicate the percentage of different “pair types” within the study). However, this comprises only 107 out of 1519 experimental pairs (*≈* 7%; see the upper and right stacked histograms based on the number of experimental pairs). When positioning studies based on the duration of their conditioning (x-axis; field-conditioned soil as a separate category) and response phase (y-axis), we see that most studies employed short-term conditioning (mean: 6.5 months, after excluding studies with field-conditioned soils; *n* = 59 studies) and a great proportion of studies comparing perennial pairs relied on field-collected soils (47 out of 106 studies;

*≈* 44%). On average, the length of the response phase (mean: 4.5 months; *n* = 106 studies) is shorter than that of the conditioning phase. Note that one study with a conditioning length of 48 months and a response length of 32 months [(Kulmatiski,](#_bookmark120) [2019)](#_bookmark120) was excluded from the figure to improve visualization (see supplementary data).

[*Box Figure 1 about here*]

**Box 2: Linking soil microbes to Janzen–Connell patterns in plant demographic transitions**

The Janzen–Connell (J–C) hypothesis states that seeds and seedlings farther from adults have

higher per-capita survival because distance helps to escape potential host-specific enemies that aggregate around focal adults [(Janzen,](#_bookmark97) [1970,](#_bookmark97) [Connell,](#_bookmark55) [1971).](#_bookmark55) Biocide experiments have implicated soil microbes as key drivers of J–C effects in seed and seedling mortality [(Bell](#_bookmark30) [*et al.*](#_bookmark30), [2006,](#_bookmark30) [Bagchi *et al.*](#_bookmark26), [2010,](#_bookmark26) [Song & Corlett,](#_bookmark163) [2022,](#_bookmark163) [Krishnadas & Comita,](#_bookmark118) [2018).](#_bookmark118) While greenhouse experiments of plant–soil microbe interactions estimate microbial effects on plant biomass, J–C studies (using in-situ field experiments and observational data) usually estimate conspecific effects on survival [(Comita *et al.*](#_bookmark53), [2010,](#_bookmark53) [Swamy *et al.*](#_bookmark166), [2011,](#_bookmark166) [Lebrĳa-Trejos](#_bookmark125) [*et al.*](#_bookmark125), [2016,](#_bookmark125) [Zhu *et al.*](#_bookmark182), [2018).](#_bookmark182) Surprisingly, few studies integrate insights from these two types of assessments [(Klironomos,](#_bookmark114) [2002,](#_bookmark114) [Beckman *et al.*](#_bookmark29), [2022).](#_bookmark29)

To make J–C studies more comparable with greenhouse studies of plant–soil microbe inter- actions, density dependence in demographic transitions estimated from census observations and/or experiments should be explicitly matched to the strength of microbial effects cal- culated as biomass responses in pot experiments [(McCarthy-Neumann & Ibáñez,](#_bookmark137) [2013).](#_bookmark137) Microbial effects on biomass-dependent growth from one life stage to the next can help parameterize age-stage transitions to project population trajectories of plant species.

Some considerations of study design can help to further match J–C studies to pot experi- ments. Laying seeds and seedlings at both conspecific and heterospecific trees in a factorial design will provide the theoretical metrics to assess the potential for coexistence, as done in greenhouse experiments implicit in J–C effects (**?**), especially when combined with bio- cides. Adding a reference treatment allows estimates of microbial impacts on frequency- independent survival [(Kandlikar *et al.*](#_bookmark101), [2019).](#_bookmark101) Finally, field studies reveal microbial effects on plant demographic transitions relative to abiotic conditions that affect survival, which can improve the parameterization of models to assess plant community dynamics.

**Box 3: Detecting the most critical microbial effect with a demographic model** Here, we demonstrate how a demographic model may help integrate multiple microbial effects and identify the most critical one. We consider two annual plant species, *N*1 and *N*2, with dynamics described by the classic Beverton–Holt annual plant model (see also Fig. [4B):](#_bookmark20)

*Ni*,*t*+1

= *si*

(1 *− gi*) *N*

*i*,*t*

+ *λigiNi*,*t* . 1 + *αiigiNi*,*t* + *αij gj Nj*,*t*

The first term represents the survival of ungerminated seeds, with *gi* and *si* representing seed germination and survival rate, respectively (circular loop in Fig. [4B).](#_bookmark20) The second term represents seed production and density-dependent interactions among germinated seeds, with *λi*, *αii* and *αij* representing plant fecundity, intraspecific and interspecific competitive impact experienced by *Ni*, respectively (rightward arrows in Fig. [4B).](#_bookmark20)

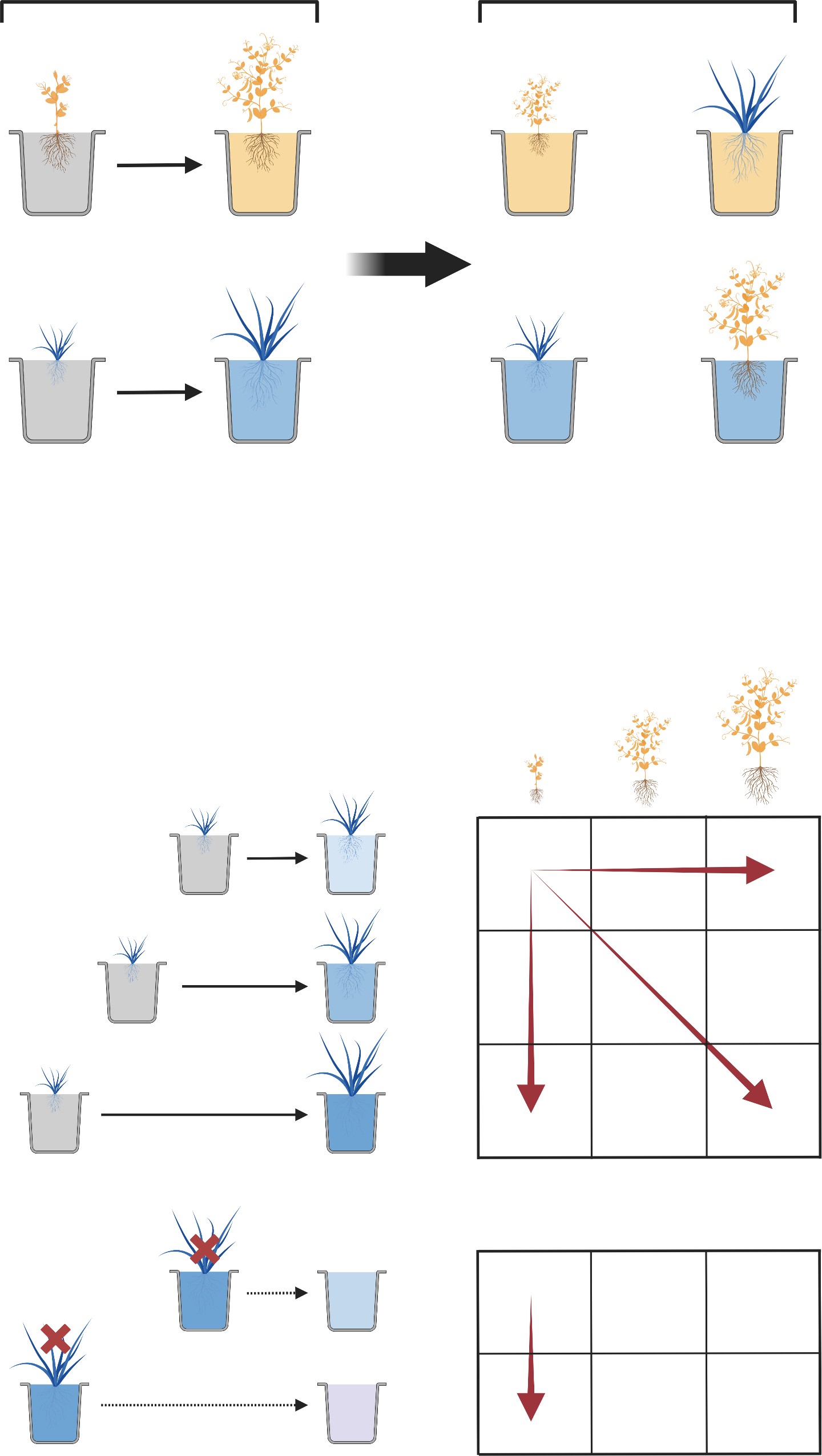
For each plant species, there are in total five demographic parameters that can be affected by soil microbes; researchers can design experiments to quantify each of them (e.g., by comparing the demographic process either in conditioned or sterilized soil). We consider the case where the inferior species (i.e., *N*2, with a low relative abundance indicated by the grey dashed line) is affected by soil microbes. The first strength of a demographic model, as supposed to biomass-based metrics, is that it can integrate multiple microbial effects. For example, if all parameters of *N*2 increased by 40% due to the presence of soil microbes, the model suggests that the relative abundance of *N*2 will nearly double (i.e., from grey to blue dashed line). 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 microbe-mediated increase in plant fecundity had the largest positive im- pact on *N*2 population, whereas the impact of microbes on seed survival had a minor impact.

[*Box Figure 2 about here*]

**(A)**

**(B)**

conditioning phase response phase



soil effect on conspecifics

soil effect on heterospecifics

age/stage of responding plant

(iv)

duration of

soil conditioning

(i)

(iii)

duration of

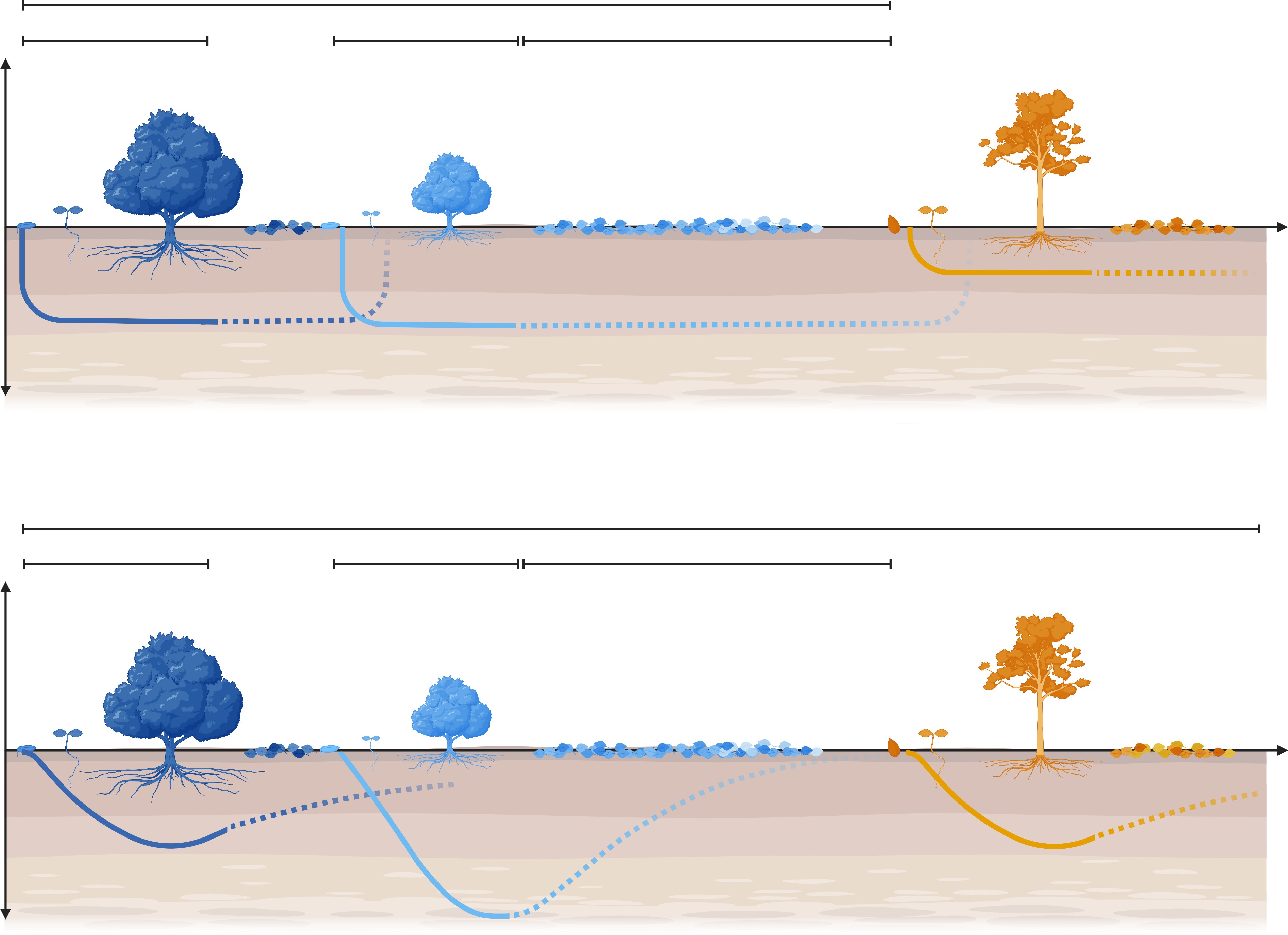
time lag

(ii)

**Figure 1** Experiments for studying plant–soil microbe interactions. (A) The clas- sic 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 a negative frequency-dependent feedback where conditioned soils favor the perfor- mance of heterospecifics over conspecifics. (B) Experimental designs that aim to study the various temporal dimensions: (i) isolating changes in the soil microbial commu- nity by varying the duration of soil conditioning, (ii) isolating the decay process by incorporating a time lag after soil conditioning, (iii) sequential harvesting with both conditioning effect and plant age advancing simultaneously, and (iv) isolating changes in plant physiology by transplanting individuals of different age in the same condi- tioned soil.

temporal aspects of the conditioned soil

**(A)** usually consider one generation (i.e., one round of conditioning-response)



immediate conditioning and fixed strength

fixed response to previous conditioning but also rapidly build up own microbiome

long-lasting microbial effects

**(B)**

multiple generations (i.e., multiple rounds of conditioning-response)

gradual conditioning and varying strength

response varies with temporal decay of microbial effects or ontogeny and gradually different successional trajectories after

build up microbiome plant death

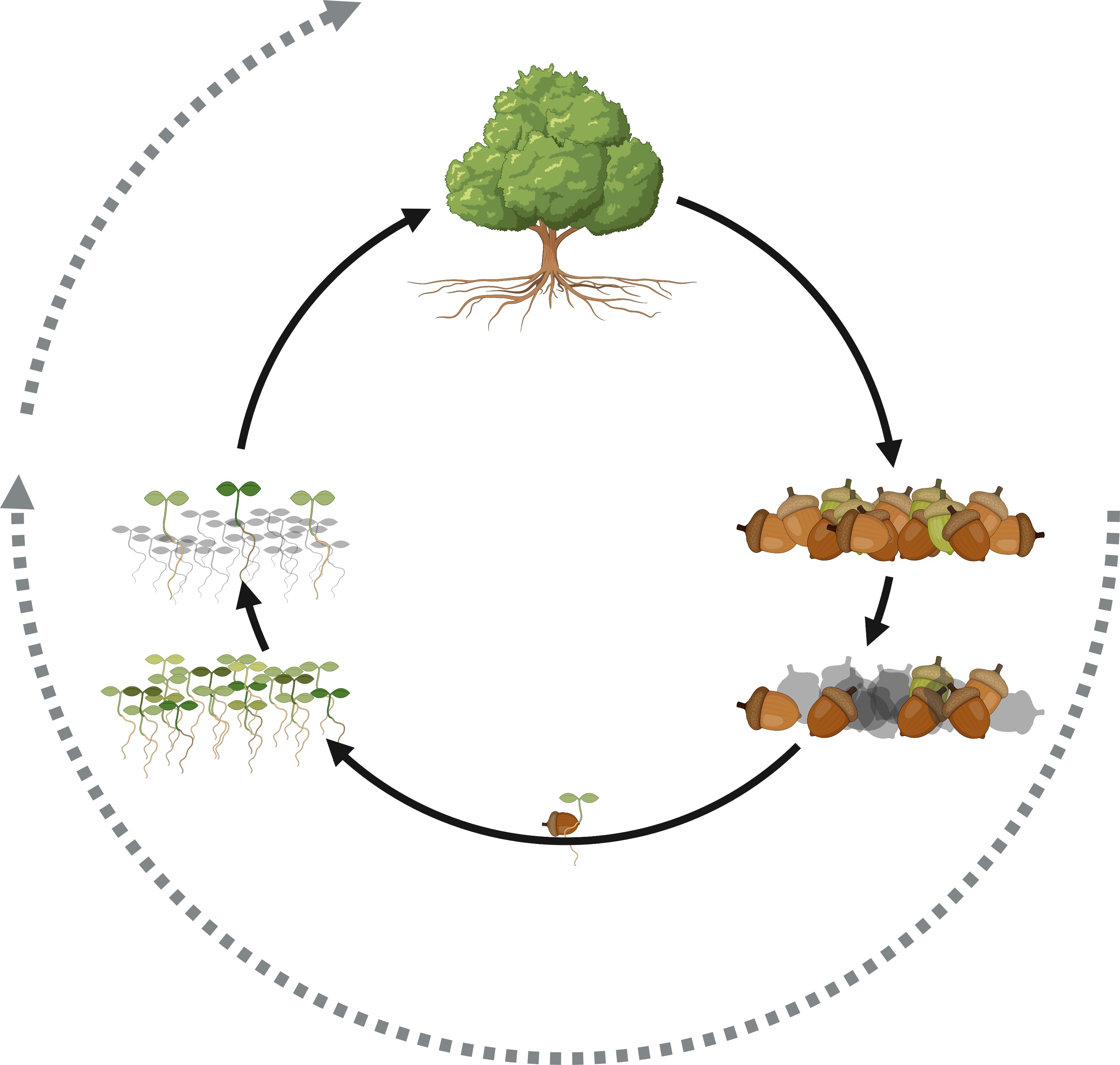
Time

Microbe effect Plant response

Time

Microbe effect Plant response

**Figure 2** Temporal dimensions of plant–soil microbe interactions throughout the re- peated 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 instantaneously, with resulting microbial effects that maintain 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 (subsection [II.1)](#_bookmark4) and response (subsection [II.2).](#_bookmark4) Moreover, microbial com- munities and their impacts on plant performance may attenuate temporally after the senescence of the previous conditioning individual (subsection [II.3)](#_bookmark4) or undergo dif- ferent trajectories depending on the previous rounds of conditioning (mentioned as a future direction in subsection [II.4).](#_bookmark4)

Stages included in CNDD studies

on individual survival

Recruitment Survival Maturation

Seedling mortality

Reproduction

Seed mortality

Germination

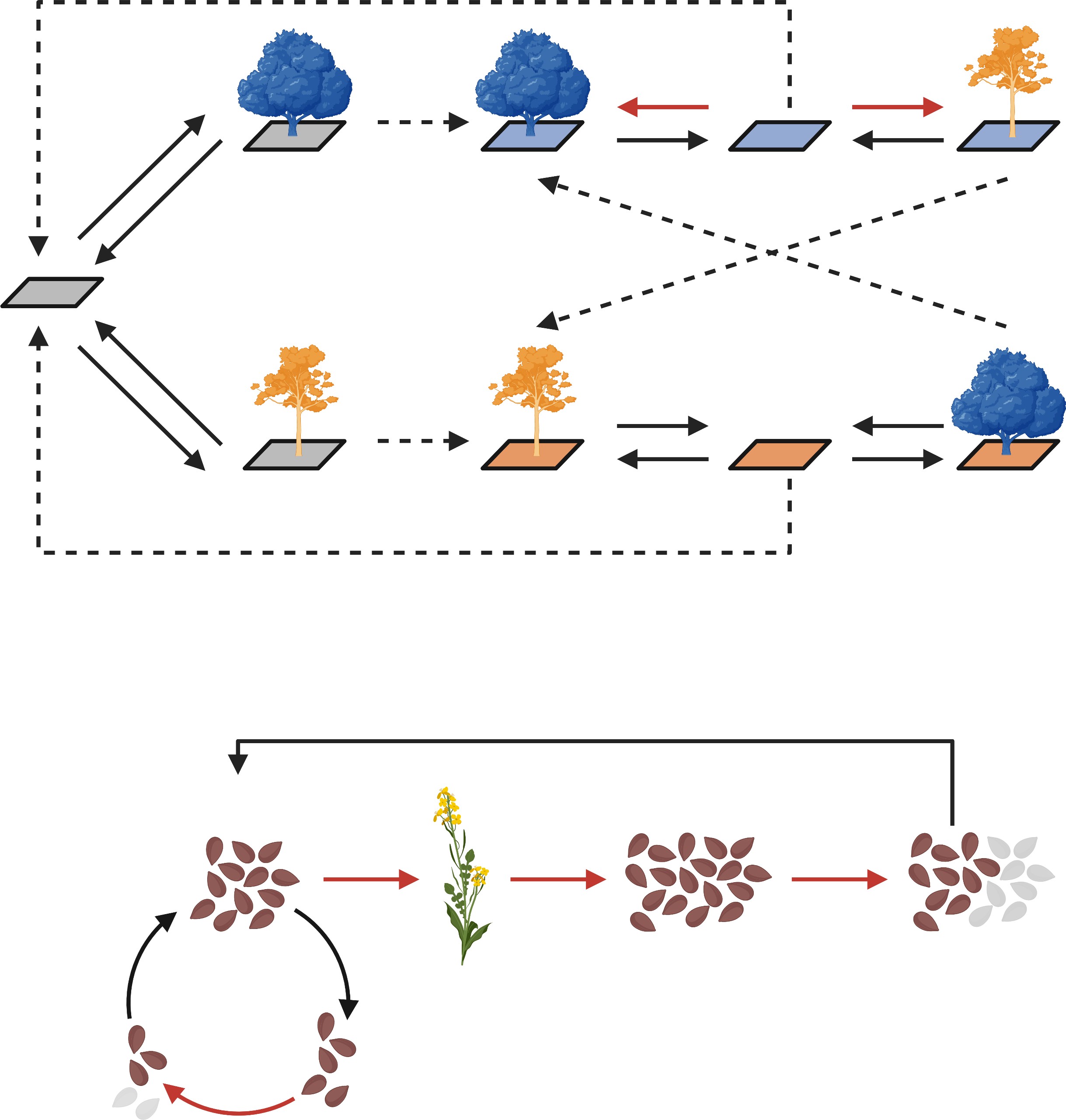
Stages included in CNDD studies on seed-to-seedling transition

**Figure 3** 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 evi- dence on seed mortality, germination, and early seedling survival. The outer circle (grey dashed arrows) indicates the life stages included in different studies on conspe- cific negative density dependence (CNDD). Operationally, CNDD studies may include multiple demographic processes due to the logistical challenges of repetitive censuses.

**(A)**

decay of conditioning history

**(B)**



colonize unconditioned patch

conspecific recolonization

heterospecific recolonization

soil

conditioning plant death plant death

plant death

over-writing previous soil history

contribute to seed bank

soil seed bank

germination

potential seed production

loss to density- dependent interactions

remain in seed bank

ungerminated seeds

survival

of ungerminated seeds

**Figure 4** Two modeling frameworks that can incorporate the missing temporal and demographic components of plant–soil microbe interactions. In both panels, demo- graphic processes influenced by soil microbes are highlighted in red. (A) An example from [Ke & Levine](#_bookmark106) [(2021)](#_bookmark106) demonstrating how the temporal decay of microbial effects can be studied with a patch occupancy model. The model tracks the frequency of different plant-soil microbe states (here depicted as various combinations of plants and soil) and the transitions among them. State transitions may occur due to plant col- onization and death (solid arrows) or the conditioning and decay of microbial effects (dashed arrows). In this example, soil microbes affect the ability of plants to recolonize conditioned soils. (B) An example demonstrating how microbial effects on multiple demographic processes can be incorporated in the annual plant model in **?** (see also [Godoy & Levine,](#_bookmark82) [2014),](#_bookmark82) which tracks the density of seeds prior to germination. Here, soil microbes influence the seed survival in the soil seed bank, the germination rate of seeds, the fecundity of germinated plants, and the density-dependency of plant population growth.

25 Life history



Annual Annual−Perennial

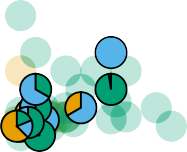
Response length (month)

20 Perennial

15



10

5  



0

0 5 10 15 20 25 30 Field

#### Conditioning length (month)

**Box Figure 1** A summary of the experimental duration and life history information of the study species in the [Crawford *et al.*](#_bookmark56)[(2019)](#_bookmark56) and [Yan *et al.*](#_bookmark176)[(2022)](#_bookmark176) data sets. See text in Box [1](#_bookmark14) for more details.

Focal parameter: +40%

Non−focal parameters: ±5%

0.4



Relative abundance of N2

0.3

0.2

0.1

0.0

2 *g*2 *s*2 22 21

Focal parameter

**Box Figure 2** Detecting the most critical microbial effect for a system described by the Beverton–Holt annual plant model. Here, soil microbes can impact five demographic parameters of *N*2: intrinsic fecundity (*λ*2), seed germination rate (*g*2), seed survival rate (*s*2), the intraspecific (*α*22) and interspecific (*α*21) competitive impact experienced by *N*2. To identify which microbial effect had the largest impact, we performed the following sensitivity analysis: the value of each focal parameter was increased by 40% (assuming microbes mainly impact this focal demographic process) while the other non-focal parameters were randomly perturbed by *±*5% (assuming weaker microbial impact); this process was repeated 100 times for each focal parameter. Each grey point represents a random simulation (100 time steps) for the focal parameter (red points and error bars represent the means and standard deviations). The grey dashed line represents the original relative abundance of *N*2 and the blue dashed line represents its relative abundance when soil microbes increased all parameters by 40%. Parameters with a point cloud deviating further away from the grey dashed line have a stronger impact. Parameters are obtained from the species pair *Festuca microstachys* (our *N*1) versus *Hordeum murinum* (our *N*2) in [Van Dyke *et al.*](#_bookmark169)[(2022).](#_bookmark169) See text in Box [3](#_bookmark16) for more details.

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**Author Contributions**

P.-J. Ke, S. Ou, and G.S. Kandlikar conceived the study and wrote the majority of the first draft. All authors contributed to finalizing the content and writing. P.-J. Ke and S. Ou contributed equally.

**Data Availability**

The dataset and code used to generate figures in Box 1 and Box 3 will be made available on Dryad upon publication.

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