Placing plant–soil microbe interactions into natural demographic context

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# Summary

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**Keywords**

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

# Introduction

Plants form interactions with a diverse array of soil microbes, including beneficial mutualists, saprotrophic decomposers, and detrimental pathogens. These interactions are bidirectional, with plants conditioning the soil microbial community and the resulting changes in microbial com- munity composition impacting the performance of plants that later take root in the conditioned soil [(Bever](#_bookmark35) *[et al.](#_bookmark35)*, [1997,](#_bookmark35) [Bever,](#_bookmark33) [2003).](#_bookmark33) The study of plant-soil microbe interactions has its origin in agricultural science [(Huang](#_bookmark90) *[et al.](#_bookmark90)*, [2013,](#_bookmark90) [van der Putten](#_bookmark158) *[et al.](#_bookmark158)*, [2013)](#_bookmark158) and has been popularized in com- munity ecology under the framework of plant–soil feedback (PSF). Since its introduction by [Bever](#_bookmark35) *[et al.](#_bookmark35)* [(1997),](#_bookmark35) studies have extensively discussed how plant–soil microbe interactions influence plant coexistence [(Bever](#_bookmark34) *[et al.](#_bookmark34)*, [2010,](#_bookmark34) [Ke & Miki,](#_bookmark104) [2015).](#_bookmark104) In addition to binary outcomes of coexistence or competitive exclusion, soil microbes also affect relative abundance patterns of plant communities [(Klironomos,](#_bookmark109) [2002,](#_bookmark109) [Mangan](#_bookmark132) *[et al.](#_bookmark132)*, [2010),](#_bookmark132) restoration success [(Wubs](#_bookmark176) *[et al.](#_bookmark176)*, [2016,](#_bookmark176) [Koziol](#_bookmark111) *[et al.](#_bookmark111)*, [2018),](#_bookmark111) exotic plant invasion [(Callaway](#_bookmark41) *[et al.](#_bookmark41)*, [2004,](#_bookmark41) [Suding](#_bookmark167) *[et al.](#_bookmark167)*, [2013),](#_bookmark167) and the biodiversity–productivity relationship [(Kulmatiski](#_bookmark117) *[et al.](#_bookmark117)*, [2012,](#_bookmark117) [Forero](#_bookmark75) *[et al.](#_bookmark75)*, [2021).](#_bookmark75)

To characterize the direction and strength of plant–soil microbe interactions, most studies follow the two-phase experimental design aimed at capturing the two-way interactions between plant and soil microbes [(Bever](#_bookmark35) *[et al.](#_bookmark35)*, [1997).](#_bookmark35) The classic greenhouse experiment consists of a conditioning phase where plants modify the soil microbial community and is immediately followed by a response phase where plants respond to the soil modification [(Bever](#_bookmark34) *[et al.](#_bookmark34)*, [2010,](#_bookmark34) [Brinkman](#_bookmark40) *[et al.](#_bookmark40)*, [2010).](#_bookmark40) Often, there is no explicit statement explaining the rationale behind the temporal duration of the two phases and, understandably, decisions seem to be mostly based on their feasibility [(Chung,](#_bookmark49) [2023;](#_bookmark49) see also Box [1).](#_bookmark16) These necessary simplifications imply certain assumptions when one uses experimental results to predict the long-term consequences of plant–soil microbe interactions (Fig. [1A).](#_bookmark18) In particular, the short duration of both conditioning and response phases (or unknown duration of conditioning in the case of field-collected soil) assumes that microbial effects develop instantaneously and maintain constant strength throughout different plant developmental stages [(Ke](#_bookmark107) *[et al.](#_bookmark107)*, [2021).](#_bookmark107) Moreover, since there is no explicit consideration of the time lag between the conditioning and the response phase (i.e., immediate transplant), extrapolating results assume that recolonization happens immediately or that microbial effects remain as long-lasting legacies

after plant senescence to impact the next generation.

The short-term nature of greenhouse experiments also necessitates researchers measuring a performance proxy for plant population growth [(Ke & Wan,](#_bookmark106) [2022).](#_bookmark106) The most frequently mea- sured proxy is plant biomass, which is then used for calculating theoretically-derived metrics to infer how soil microbes influence plant coexistence. One commonly calculated metric is the pairwise feedback metric that quantifies the frequency-dependent feedback loops generated by plant–soil microbe interactions [(Bever](#_bookmark35) *[et al.](#_bookmark35)*, [1997).](#_bookmark35) A negative pairwise feedback metric implies the scenario where both plants condition their soil microbes in a way that favors heterospecifics over conspecifics, thereby promoting plant coexistence [(Crawford](#_bookmark55) *[et al.](#_bookmark55)*, [2019,](#_bookmark55) [Abbott](#_bookmark23) *[et al.](#_bookmark23)*, [2021).](#_bookmark23) Recently, multi-species extensions of the feedback metric have been proposed [(Eppinga](#_bookmark70) *[et al.](#_bookmark70)*, [2018,](#_bookmark70) [Mack](#_bookmark131) *[et al.](#_bookmark131)*, [2019),](#_bookmark131) as well as metrics that capture the frequency-independent microbial effects by incorporating plant performance in an appropriate reference soil (i.e., microbially-mediated fitness difference *sensu* [Kandlikar](#_bookmark98) *[et al.](#_bookmark98)*, [2019,](#_bookmark98) [Yan](#_bookmark177) *[et al.](#_bookmark177)*, [2022).](#_bookmark177) With their respective underlying assumptions of the plant–soil microbe system, these metrics serve the purpose of extrapolating biomass measurements to predict plant coexistence when soil microbes are the main drivers of plant community dynamics.

While the above simplifications help tremendously to keep experiments tractable, explicit examination of the focal plant–soil system’s temporal and demographic contexts is critical to better predict the influence of soil microbes in their natural context. A growing number of studies have highlighted the importance of the different temporal dimensions of plant–soil microbe interactions [(Kardol](#_bookmark101) *[et al.](#_bookmark101)*, [2013,](#_bookmark101) [Gundale & Kardol,](#_bookmark82) [2021,](#_bookmark82) [Chung,](#_bookmark49) [2023;](#_bookmark49) see also other studies in this review). Within a single plant generation, microbial communities undergo a continuous turnover, and the resulting microbial effects depend on both the duration of plant conditioning and response phases; microbial effects also depend on the time lag and the species identity between consecutive plant generations (Fig. [1B).](#_bookmark18) Moreover, in addition to biomass accumulation, soil microbes can affect other demographic processes across the plant life cycle (e.g., [Dudenhöffer](#_bookmark66) *[et al.](#_bookmark66)*, [2018,](#_bookmark66) [Dostálek](#_bookmark65) *[et al.](#_bookmark65)*, [2022,](#_bookmark65) and other studies in this review). Studies have found that microbial effects on different plant ontogenetic stages may have opposite directions, making it difficult to predict microbe- mediated plant coexistence directly based on measuring seedling biomass performance [(Dostálek](#_bookmark65)

*[et al.](#_bookmark65)*, [2022).](#_bookmark65)

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 above two mechanistic details smoothly to better predict the long-term consequences of plant– soil microbe interactions.

# 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](#_bookmark100) *[et al.](#_bookmark100)*, [2006,](#_bookmark100) [2013,](#_bookmark101) [Bauer](#_bookmark29) *[et al.](#_bookmark29)*, [2015).](#_bookmark29) However, temporal variation also occurs within a shorter time scale, because the conditioned microbial community and plant responsiveness both vary across plant developmental stages (Fig. [1B);](#_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 development of plant–soil microbe interactions and review how microbial effects vary with the duration of soil conditioning (section [II.-1),](#_bookmark4) the time lag between consecutive generations (section [II.-2).plant](#_bookmark4) ontogeny (section [II.-3),](#_bookmark4) and We then discuss how the temporal development of plant-soil microbe interactions over shorter time scale help understand patterns over longer successional time scales (section [II.-4).](#_bookmark4) Note that here we focus on studies that measure plant biomass as their key performance proxy; we discuss other demographic responses in section [III..](#_bookmark10)

## Temporal development during the conditioning phase

Understanding the temporal dimensions of plant–soil microbe interactions begins in the soil con- ditioning phase. Focusing on the shorter time scale within a single plant generation, experimental evidence shows that the relative impact of conspecific- versus heterospecific-conditioned soil on the responding individual varied with the duration of soil conditioning. For example, [Lepinay](#_bookmark123) *[et al.](#_bookmark123)* [(2018)](#_bookmark123) found that heterospecific soil had a more negative impact on aboveground biomass than conspecific soil when soils were only conditioned for two weeks. However, a longer dura- tion of soil conditioning resulted in an opposite relationship: conspecific soil had an increasingly stronger negative impact peaking at six weeks of conditioning whereas heterospecific soils had a less negative effect on aboveground biomass after four to eight weeks of conditioning.

Assumptions that these temporal changes are attributed to microbially-mediated effects are prevalent in the field [(Herrera Paredes & Lebeis,](#_bookmark87) [2016)](#_bookmark87) and are partially supported by evidence showing changes in the microbial community as the conditioning plant ages and matures. Studies have shown compositional shifts in the microbiome as seeds transition to the seedling stage [(Bar-](#_bookmark28) [ret](#_bookmark28) *[et al.](#_bookmark28)*, [2015),](#_bookmark28) as well as continuous shifts in the root-associated microbiome as plants mature [(Hannula](#_bookmark83) *[et al.](#_bookmark83)*, [2019,](#_bookmark83) [Dombrowski](#_bookmark62) *[et al.](#_bookmark62)*, [2016,](#_bookmark62) [Edwards](#_bookmark68) *[et al.](#_bookmark68)*, [2018).](#_bookmark68) Interestingly, with different plant genotypes studies have shown that shifts in the microbiome reflect the progression of de- velopmental stages rather than age alone [(Edwards](#_bookmark68) *[et al.](#_bookmark68)*, [2018;](#_bookmark68) but see [Dombrowski](#_bookmark62) *[et al.](#_bookmark62)*, [2016).](#_bookmark62) However, studies have also shown more complex changes in the root microbiome that depend on the surrounding soil environment [(Igwe](#_bookmark92) *[et al.](#_bookmark92)*, [2021,](#_bookmark92) [Walsh](#_bookmark174) *[et al.](#_bookmark174)*, [2021),](#_bookmark174) or found little difference across plant developmental stages (L[undberg](#_bookmark129) *[et al.](#_bookmark129)*, [2012).](#_bookmark129) Although sometimes there may be little changes in the bacterial community composition over time, plasticity in the functional re- sponses of the microbiome as plants mature was detected using metatranscriptomics. Expression of mRNA associated with nitrogen fixation was found to increase during plant growing phases while antibiotic defense activity increased during bolting and flowering [(Chaparro](#_bookmark45) *[et al.](#_bookmark45)*, [2013).](#_bookmark45) Conversely, functional redundancy among microbes can maintain soil nitrogen and phosphorous cycling activity despite changes in the taxonomy of soil bacterial communities over different plant developmental stages [(Zhao](#_bookmark181) *[et al.](#_bookmark181)*, [2021).](#_bookmark181) Importantly, these changes (or lack thereof) in the soil microbial community have crucial consequences: arresting soil conditioning at different devel-

opmental stages causes the responding plant to encounter microbial communities with different compositions and functions, and thereof results in different microbial effects.

Mechanisms for these observed microbial community responses can be divided into plant- and microbe-centered. Plant-induced controls can result from physiological changes that cause shifts in nutrient allocation during different plant developmental stages [(Zhao](#_bookmark181) *[et al.](#_bookmark181)*, [2021,](#_bookmark181) [Chaparro](#_bookmark45) *[et al.](#_bookmark45)*, [2013).](#_bookmark45) Plants with different life histories may prioritize shoot and root growth differently, therefore recruiting different mutualistic microbial communities at different times according to their different nutritional needs [(Kulmatiski](#_bookmark118) *[et al.](#_bookmark118)*, [2017,](#_bookmark118) [Huberty](#_bookmark91) *[et al.](#_bookmark91)*, [2022).](#_bookmark91) Carbon allocation to flowering and seed production during plant reproduction can reduce carbon exudates in soil that microbes rely on [(Herrera Paredes & Lebeis,](#_bookmark87) [2016).](#_bookmark87) These plant physiological changes can alter soil chemistry [(Lepinay](#_bookmark123) *[et al.](#_bookmark123)*, [2018)](#_bookmark123) and physical properties [(Edwards](#_bookmark68) *[et al.](#_bookmark68)*, [2018)](#_bookmark68) which leads to microbial-centered mechanisms. That is, changes resulting from community assembly processes acting within the microbial community without active plant control (e.g., stochastic drift and competition among microbes; [Herrera Paredes & Lebeis,](#_bookmark87) [2016,](#_bookmark87) [Barret](#_bookmark28) *[et al.](#_bookmark28)*, [2015,](#_bookmark28) [Bittleston](#_bookmark38) *[et al.](#_bookmark38)*, [2021).](#_bookmark38) These changes in microbial community dynamics can impact plant growth and response, inducing further plant-centered microbial changes [(Metcalf](#_bookmark136) *[et al.](#_bookmark136)*, [2019).](#_bookmark136)

The significance of temporal development during the soil conditioning phase is exemplified when one considers plants with different life histories. As the transition of microbial commu- nities aligns with plant developmental stages [(Edwards](#_bookmark68) *[et al.](#_bookmark68)*, [2018),](#_bookmark68) short- and long-lived plants may structure microbial communities at different rates. Therefore, the same duration of soil conditioning, as implemented in experiments, corresponds to different developmental stages and microbial effects [(Kulmatiski](#_bookmark118) *[et al.](#_bookmark118)*, [2017):](#_bookmark118) for short-lived plants (e.g., annuals) a fully matured species-specific microbiome may have been reached, whereas it would require a longer condition- ing time for long-lived perennials. As shown in Box [1,](#_bookmark16) 18% of studies 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 might need more thought. In addition to life history strategies, plants belonging to different functional groups may respond differently to the same temporal turnover in microbial communities. [Ke](#_bookmark107) *[et al.](#_bookmark107)* [(2021)](#_bookmark107) showed that only non-legume plants experienced a microbial effect that aggravated with longer conditioning

time, whereas that experienced by the legume plant remained constant despite temporal changes in the microbial community. The lack of correspondence between compositional shifts in micro- bial community and their impact on plants might indicate functional redundancy within the soil microbial community [(Huberty](#_bookmark91) *[et al.](#_bookmark91)*, [2022).](#_bookmark91) We will return to the logistical challenges when trying to detect this causal relationship in section [II.-5.](#_bookmark4)

## Alterations of microbial effects after plant death

Typical greenhouse experiments grow the responding individual immediately after the condition- ing phase (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 arrival of a succeeding response individual, potentially due to discrete growing seasons or dispersal limitation, thereby leaving the conditioned soil empty for an extended period of time. During this time lag, litter decomposition or stochastic drift may continue to change microbial community, in what we view as an “extension” of the conditioning phase. Experiments following a different duration of time after the death of the conditioning plant showed that negative microbial effects can persist [(Grove](#_bookmark81) *[et al.](#_bookmark81)*, [2015).](#_bookmark81) For example, [Bennett](#_bookmark31) *[et al.](#_bookmark31)* [(2022)](#_bookmark31) showed that shoot biomass of plants grown in soils taken from dead aspens was similar to that when grown in soils collected from live aspen. Conversely, [Esch & Kobe](#_bookmark71) [(2021)](#_bookmark71) showed that the survivorship of transplanted seedlings was lowest soon after the death of the conditioning plant but increased as time since death increased, suggesting that negative microbial effects can fade over time.

The persistence of microbial effects could be due to the continued survival of the microbial community, with functionality being comparable to that of microbes associated with living plants (P[epe](#_bookmark153) *[et al.](#_bookmark153)*, [2018,](#_bookmark153) [Esch](#_bookmark72) *[et al.](#_bookmark72)*, [2021).](#_bookmark72) In short time periods after the aboveground removal of the con- ditioning plant, root systems may remain alive and the rhizosphere microbiome may remain active. Release of nutrients from dead plants can also mirror exudates in live plants, thereby maintaining microbe activity by continuous supply of required resources [(Johansen & Jensen,](#_bookmark96) [1996,](#_bookmark96) [Müller](#_bookmark145) *[et al.](#_bookmark145)*, [2013).](#_bookmark145) 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 & Jones,](#_bookmark122) [2011,](#_bookmark122) [Lloyd,](#_bookmark128) [2021).](#_bookmark128) For example, [Esch](#_bookmark72) *[et al.](#_bookmark72)* [(2021)](#_bookmark72) 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](#_bookmark153) *[et al.](#_bookmark153)* [(2018)](#_bookmark153) showed that arbuscular mycorrhizal fungal continued to remain active and can spread from roots after host shoot removal. 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 still relevant from natural systems.

However, long time periods after the removal of the conditioning plant, the conditioned microbial community can turn over and result in a different impact on the late-arriving respond- ing individual. During this extended period, the litter left behind can introduce microbes from the phyllosphere to the soil (F[anin](#_bookmark73) *[et al.](#_bookmark73)*, [2021),](#_bookmark73) exude chemicals and nutrients that can alter the microbial community [(Veen](#_bookmark171) *[et al.](#_bookmark171)*, [2021),](#_bookmark171) and, in turn, cause the responding individual to encounter different microbial communities [(Veen](#_bookmark170) *[et al.](#_bookmark170)*, [2019,](#_bookmark170) [Grove](#_bookmark81) *[et al.](#_bookmark81)*, [2015).](#_bookmark81) For example, [Minás](#_bookmark141) *[et al.](#_bookmark141)* [(2021)](#_bookmark141) incorporated decay of above- and belowground litter over different time points to show that changes in metabolites exuded by decomposers faded over time, resulting in greater germination and seedling emergence. Finally, over a long enough time without seedling recruitment due to dispersal limitation, drift could decouple microbial community from plant conditioning influence. Therefore, experiments that neglect these continued changes in the microbial community and litter decomposition after plant senescence will fail to replicate the microbial effects experienced by the responding plant in nature. Given all the above mechanisms that shape microbial com- munities during soil conditioning and after plant death, how the conditioning plant died (e.g., logging/herbivory, disease, fire, and disturbance) can change trajectories of microbial communi- ties and subsequent effects beyond seedling survival, with implications on long-term vegetation structure and succession.

## Temporal development during the response phase

Temporal dimensions of plant–soil microbe interactions next include the time-dependent varia- tion during the response phase, i.e., the strength and direction of the microbial effect can change over the lifetime of the responding plant [(Kardol](#_bookmark101) *[et al.](#_bookmark101)*, [2013).](#_bookmark101) This involves sequential harvest- ing of the responding plant at different time intervals and has been the typical focus when past

studies examine the temporal variability of plant–soil feedback [(Gundale & Kardol,](#_bookmark82) [2021).](#_bookmark82) While conspecific-conditioned soils generally impose a stronger negative impact on the responding plant, sequential harvest reveals more nuanced variability in the temporal development: the negative impacts can aggravate or attenuate as the responding individual matures depending on the pres- ence of co-occurring competition [(Dostál,](#_bookmark63) [2021,](#_bookmark63) [Bezemer](#_bookmark36) *[et al.](#_bookmark36)*, [2018)](#_bookmark36) and species origin (i.e., native or invasive; [Hawkes](#_bookmark86) *[et al.](#_bookmark86)*, [2013).](#_bookmark86) This empirical evidence provides a strong impetus to consider the temporal variability in response phases of plant–soil microbial interactions, where harvesting an experiment at different endpoints can alter our understanding of the strength and direction of microbial effects.

The temporal variability in the response plant can be traced to the differential temporal development of microbial legacies as left by earlier soil conditioning. The fungal legacy of the initial conditioning plant persists through the response phase resulting in negative feedback [(Bezemer](#_bookmark36) *[et al.](#_bookmark36)*, [2018),](#_bookmark36) while soil bacterial legacies of the conditioning phase are quickly lost [(Hannula](#_bookmark84) *[et al.](#_bookmark84)*, [2021).](#_bookmark84) As fungi have slower growth rates, they are thought to be more temporally stable and resistant to changes as plant generation turns over [(Allison & Martiny,](#_bookmark24) [2008).](#_bookmark24) In contrast, the high reproduction and evolution rate of bacteria can result in rapid changes in community and function [(Chase](#_bookmark46) *[et al.](#_bookmark46)*, [2021).](#_bookmark46) In the microbial impact on plant response, it may be evolutionarily advantageous for the responding plant to be adapted to the legacies of past microbial conditioning [(Metcalf](#_bookmark136) *[et al.](#_bookmark136)*, [2019).](#_bookmark136) Conversely, as the responding plant matures, they may outgrow the feedback effect of the conditioning phase and exert their own control instead [(Bezemer](#_bookmark36) *[et al.](#_bookmark36)*, [2018),](#_bookmark36) including through the mechanisms discussed in section [II.-1.](#_bookmark4)

While the shifting microbial legacies directly alter the temporal development of the respond- ing plant, it is important to note that interacting elements can negate or enhance the feedback. For example, [Dostálek](#_bookmark65) *[et al.](#_bookmark65)* [(2022)](#_bookmark65) showed that soil conditioning had a strong negative impact on early plant life stages, but competition and drought stress became more significant after one year. Similarly, [Dostál](#_bookmark63) [(2021)](#_bookmark63) found temporal variability being ameliorated by nutrient availability. These studies show that concurrent changes in environmental conditions and resource availability over time can interact with the original soil legacy left by the conditioning plant. Additionally, both studies strongly support that the plant community outcome of these temporal changes can

only be detected when measuring demographic stages and growth rates in addition to biomass [(Dostálek](#_bookmark65) *[et al.](#_bookmark65)*, [2022,](#_bookmark65) [Zhang](#_bookmark180) *[et al.](#_bookmark180)*, [2022),](#_bookmark180) which we elaborate in section [III..](#_bookmark10)

## Multiple generations of soil conditioning

While the above subsections zoom in to focus on changes within one tier of plant-to-plant replace- ment, here we focus on temporal changes that emerge over multiple generations (i.e., multiple tiers of conditioning and response). Based on first principles, [Wubs & Bezemer](#_bookmark175) [(2018)](#_bookmark175) predicted four possible response outcomes of multiple conditioning rounds: the most recent conditioning has the strongest effect, the earliest conditioning has lasting effects, multiple conditioning rounds have ad- ditive effects, or multiple conditioning rounds have interactive effects. Using a unique experiment with two generations of conditioning and one response phase, they found that the most recent conditioning explained the shoot and root biomass of the responding plant, but the interaction between conditioning phases explained the variance in biomass response [(Wubs & Bezemer,](#_bookmark175) [2018).](#_bookmark175) Thus, the potential historical contingency created by unique sequences of conditioning can result in different plant–soil microbe interactions, thereby making it difficult to interpret results without knowledge of earlier soil legacies.

This temporal component is especially important in applied contexts of ecology and has been demonstrated by experiments using soils with conditioning histories spanning multiple genera- tions. In agriculture, successive planting can result in cumulatively negative soil effects, where the persistent monocultures could accumulate pathogens that additively suppress the growth of subsequent generations [(Mazzola,](#_bookmark134) [1999,](#_bookmark134) [Packer & Clay,](#_bookmark152) [2004).](#_bookmark152) A wealth of agricultural literature exists detailing the mechanisms behind observed effects of successive planting and crop rotation [(Huang](#_bookmark90) *[et al.](#_bookmark90)*, [2013,](#_bookmark90) [Mariotte](#_bookmark133) *[et al.](#_bookmark133)*, [2018).](#_bookmark133) In the context of non-native plants, the strengthening of negative feedback over time can prevent the establishment of introduced species [(Diez](#_bookmark61) *[et al.](#_bookmark61)*, [2010,](#_bookmark61) [Dostál,](#_bookmark63) [2021;](#_bookmark63) but see [Day](#_bookmark58) *[et al.](#_bookmark58)*, [2015).](#_bookmark58) However, it is important to note that the biomass impacts of subsequent plant generations may not solely be due to microbe-driven changes, but epigenetic effects where poor plant growth in one generation produces seeds with even poorer growth in the next generation [(De Long](#_bookmark59) *[et al.](#_bookmark59)*, [2021).](#_bookmark59) Additionally, long time scales typically take place in larger spatial scales using field experiments that measure community responses as opposed to biomass

[(De Long](#_bookmark60) *[et al.](#_bookmark60)*, [2019,](#_bookmark60) [Kulmatiski,](#_bookmark116) [2019,](#_bookmark116) [Dostál](#_bookmark64) *[et al.](#_bookmark64)*, [2013),](#_bookmark64) and the ultimate successional out- come depends on population dynamics observed in chronosequences (v[an de Voorde](#_bookmark172) *[et al.](#_bookmark172)*, [2012).](#_bookmark172) This empirical evidence for the importance of the multi-generational temporal dimension justifies the need for measures of plant–soil microbe interactions beyond biomass, and its demographic outcomes which we address in the later section.

## Limitations and future experiments

The lack of experiments that vary the conditioning time, the time lag between removing the conditioning plant and transplanting the responding plant, and the response time limit our un- derstanding of the temporal dynamics of plant–soil microbe interactions. We advocate for more experiments to understand these temporal dimensions, particularly for the dimension and scale that is most relevant for the focal plant–soil system. For instance, in Mediterranean annual plant communities, typical short-term conditioning may suffice due to their short lifespan, but the prac- tice of immediate transplant overlooks the clear seasonality in nature; considering the decay phase may thereby provide a better understanding of how microbes operate in this system. We also rec- ognize logistical challenges for long-lived plants: short-term greenhouse experiments (Box [1)](#_bookmark16) may fail to capture the meaningful conditioning, decomposition, and response temporal effects. While many studies resolved to field-conditioned soil (45% of studies with perennials; Box [1),](#_bookmark16) researchers do not know when a tree has died, how long the time gap between conditioning and response is, and the age of the conditioning or response tree. One way forward is to take advantage of natural experiments by relying on long-term monitoring plots or historical data (e.g., a chronosequence approach such as using aerial photos to track plant age; [Ke](#_bookmark107) *[et al.](#_bookmark107)*, [2021).](#_bookmark107)

Experiments must also be carefully designed to account for confounding temporal factors. While we introduced soil conditioning and plant response as step-wise processes, they happen simultaneously in nature (i.e., the responding plant eventually also shapes the microbial com- munity). Therefore, the observed temporal changes during the response phase in sequential harvesting experiments result from the combination of varying plant responsiveness and the new tier of soil conditioning happening in the pot. We argue that conceptually separating the two steps hints at ways to disentangle the underlying mechanism. For example, planting seedlings of the

same stage in soils with different conditioning lengths controls for variability in plant responsive- ness. Additionally, the developmental stage of a plant is often associated with their age, obscuring whether the mechanism impacting the microbial community is due to top-down plant control or other microbial community assembly processes. [Dombrowski](#_bookmark62) *[et al.](#_bookmark62)* [(2016)](#_bookmark62) resolves this by growing mutants that are only vegetative or flowering, showing that the temporal development of root microbiome with age is robust against flowering phenology. This is particularly important as changes in phenology timing due to shifting climates can destabilize previously cyclical temporal developments.

To understand the temporal dimension of plant–soil microbe interactions, it is also important to exercise discernment in measuring causal relationships between plants and microbes. Existing experiments are often plant-focused and do not record microbial community or activity, thereby assuming that changes can be ascribed to microbiota by relying on negative controls such as steril- ized soils or comparative treatments. As molecular methods become more affordable, indicators of microbial community or activity must also be paired with other measurements of plant responses, including traits like photosynthetic capacity, seed production, etc. (but see [Huberty](#_bookmark91) *[et al.](#_bookmark91)*, [2022](#_bookmark91) on plant metabolome and herbivory response) to pinpoint mechanisms of how microbes affect plants. However, technological limitations may still obscure changes over time. For example, DNA from dead microbes may be detected in sequencing time series and lead to erroneous conclusions [(Carini](#_bookmark43) *[et al.](#_bookmark43)*, [2016).](#_bookmark43) Additionally, plant-associated soil microbes are often characterized by sequencing en- dogenous root-infecting microbes, which may be distinct from that encountered by the responding plant in the surrounding bulk soil. By grounding our understanding of the temporal dimensions of plant–soil microbe interactions in rigorous empirical evidence, we can advance the study of long-term demographic consequences.

# 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 the biomass accumulation of plants. This design corresponds well with the classic feedback model of [Bever](#_bookmark35) *[et al.](#_bookmark35)* [(1997),](#_bookmark35) where microbes control plant species’ intrinsic

growth rates. However, decades of work have shown that soil microbes also influence other key demographic processes across the plant life cycle, sometimes in opposite directions [(Dudenhöffer](#_bookmark66) *[et al.](#_bookmark66)*, [2018).](#_bookmark66) Such 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](#_bookmark65) *[et al.](#_bookmark65)*, [2022).](#_bookmark65) Here, we highlight key studies that provide insights into microbial controls over key plant life demographic processes, with a particular focus on early life stage transitions (Fig. [2).](#_bookmark19) Then in section [IV](#_bookmark14)., we present an outline for integrating the long-term effects of these interactions into demographic models of plant population dynamics.

## Microbial regulation of seed-to-seedling transition

Soil microbes, especially fungi and oomycetes, can have drastic consequences on the early life stages of plants. While these effects can arise from microbial effects on distinct life history processes (seed survival, germination, and early seeding survival; Fig. [2),](#_bookmark19) they are often lumped together given the logistical challenges of separating these effects in field settings. For example, a large body of evidence for microbial effects on the early life stages of plants comes from field studies that track the seed and seedling communities in soil patches that receive a fungicide or control treatment (e.g., [Bagchi](#_bookmark26) *[et al.](#_bookmark26)*, [2014,](#_bookmark26) [Fricke](#_bookmark77) *[et al.](#_bookmark77)*, [2014,](#_bookmark77) [Krishnadas](#_bookmark112) *[et al.](#_bookmark112)*, [2018).](#_bookmark112) Many of these studies are conducted in the context of evaluating microbes as potential drivers of Janzen–Connell effects, patterns that we discuss in more detail in Box [2.](#_bookmark17) Such experiments have generally found that soil microbes have species-specific effects on plant performance, suggesting that the net effects depend on the relative dominance of pathogenic versus mutualistic microbes in the soil, as well as on the degree to which different plant species are defended from pathogens or dependent on mutualists. While studies that evaluate 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.

Soilborne pathogens can cause substantial mortality at the seed stage in nearly all terrestrial ecosystems (e.g., [Meyer](#_bookmark137) *[et al.](#_bookmark137)*, [2007,](#_bookmark137) [Sarmiento](#_bookmark161) *[et al.](#_bookmark161)*, [2017,](#_bookmark161) [Li](#_bookmark125) *[et al.](#_bookmark125)*, [2019,](#_bookmark125) [Kotanen,](#_bookmark110) [2007).](#_bookmark110) One system where the role of fungal seed pathogens in structuring plant species interactions and 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. During their time in the soil seed bank, these seeds are vulnerable to pathogen attack: for example, [Dalling](#_bookmark56) *[et al.](#_bookmark56)* [(1998)](#_bookmark56) found that fungicide treatments reduced seed mortality by 40% in *C. insignis*, a result that was further supported by [Gallery](#_bookmark79) *[et al.](#_bookmark79)* [(2010)’](#_bookmark79)s finding of similar patterns in six additional *Cecropia* species. Moreover, [Dalling](#_bookmark56) *[et al.](#_bookmark56)* [(1998)](#_bookmark56) found that seeds were more susceptible to pathogen attack in soils close to conspecific adults than in soils far from conspecifics, suggesting that fungal-induced seed mortality can leave a signature on the spatial structure of tropical forests. Recent advances have largely focused on coupling classic experimental approaches with modern molecular methods toward understanding longstanding questions about host-specificity and context-dependence of fungal seed pathogens. [Zalamea](#_bookmark178) *[et al.](#_bookmark178)* [(2021)](#_bookmark178) 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 seeds and seed-borne fungi isolated from a group of phylogenetically diverse pioneer tree species, [Sarmiento](#_bookmark161) *[et al.](#_bookmark161)* [(2017)](#_bookmark161) showed that while many fungi are polyphagous (i.e., are able to grow with multiple plant species), their effects on plant 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 microbial effects on seed survival may not be practical in all settings because it requires time-consuming and laborious methods (e.g., tetrazolium staining for testing seed viability; [Sarmiento](#_bookmark161) *[et al.](#_bookmark161)*, [2017),](#_bookmark161) a better understanding of these effects may yield critical insights given that seed limitation can be a critical bottleneck on plant population dynamics [(Harper,](#_bookmark85) [1977,](#_bookmark85) [Clark](#_bookmark51) *[et al.](#_bookmark51)*, [2007),](#_bookmark51) especially in communities dominated by plant species that form persistent seed banks.

In addition to their effects on seed survival, soil microbes can also affect early plant life stages by affecting 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](#_bookmark108) *[et al.](#_bookmark108)*, [2022](#_bookmark108) and [Bottini](#_bookmark39) *[et al.](#_bookmark39)*, [2004)](#_bookmark39) or ethylene (reviewed in [Ravanbakhsh](#_bookmark159) *[et al.](#_bookmark159)*, [2018](#_bookmark159) and [Ishaq,](#_bookmark93) [2017).](#_bookmark93) While studies of how soil microbes regulate germination have historically

focused on managed settings, evidence is now accumulating in ecological settings. In one of the only two-phase experiments that focused on pairwise feedback effects on germination, [Miller](#_bookmark138) *[et al.](#_bookmark138)* [(2019)](#_bookmark138) found species-specific effects of cultivated 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. Soil microbial effects on germination also appear to be dependent on the abiotic context [(David](#_bookmark57) *[et al.](#_bookmark57)*, [2020)](#_bookmark57) and can contribute to the local adaptation of plant populations to environmental stress (P[etipas](#_bookmark155) *[et al.](#_bookmark155)*, [2020).](#_bookmark155) Across a large-scale microcosm experiment, [Eldridge](#_bookmark69) *[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 germination that is not simply explained by shared responses of microbes and seeds to abiotic soil properties. Unlike seed mortality, whose effects on population dynamics are unambiguous (i.e., either an increase or decrease in demographic potential depending on whether microbes decrease or increase seed mortality, respectively), the consequences of altered germination on population dynamics are less straightforward. Delayed germination could hurt population growth if the longer soil residence time results in increased losses to seed pathogens, or if later germination reduces seedlings’ performance due to competition [(Orrock & Christopher,](#_bookmark150) [2010).](#_bookmark150) On the other hand, delayed germination could be beneficial if it allows later germinants to escape severe competition at the seedling stage or avoid abiotic stress [(Leverett](#_bookmark124) *[et al.](#_bookmark124)*, [2018).](#_bookmark124) A first step in enhancing our understanding of this phenomenon would be for two-phase studies, which often transplant germinated seeds into cultivated soils (e.g., [Kandlikar](#_bookmark99) *[et al.](#_bookmark99)*, [2021,](#_bookmark99) [Bauer](#_bookmark29) *[et al.](#_bookmark29)*, [2015,](#_bookmark29) [Oduor](#_bookmark149) *[et al.](#_bookmark149)*, [2022),](#_bookmark149) 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](#_bookmark67) *[et al.](#_bookmark67)*, [2022).](#_bookmark67) This would help clarify how microbial controls over germination relate to the overall role of microbes in regulating plant dynamics [(Dudenhöffer](#_bookmark66) *[et al.](#_bookmark66)*, [2018).](#_bookmark66)

Soil microbes also play a key role in determining the fate of seedlings after germination. The widespread role of mycorrhizal symbioses in promoting seedling establishment and the potential for soilborne pathogens to cause mortality among seedlings has been studied for decades and re- viewed elsewhere [(Horton & van der Heĳden,](#_bookmark88) [2008,](#_bookmark88) [Gilbert,](#_bookmark80) [2002).](#_bookmark80) Recent advances have focused

on elucidating the relative role of harmful and beneficial soil microbes in driving seedling sur- vival and establishment across different environmental contexts, including abiotic conditions (e.g., [Bingham & Simard,](#_bookmark37) [2011)](#_bookmark37) and the relative density of conspecific and heterospecific adults ([Teste](#_bookmark169) *[et al.](#_bookmark169)*, [2017,](#_bookmark169) [Bennett](#_bookmark32) *[et al.](#_bookmark32)*, [2017,](#_bookmark32) [Liang](#_bookmark127) *[et al.](#_bookmark127)*, [2016).](#_bookmark127) While the clearest evidence that soil microbes mediate seedling establishment comes from studies that track the establishment (fate) of seedlings growing in specific microbial contexts, studies that measure the size (biomass) of seedlings may also yield insights into this demographic transition. In particular, microbe-mediated change in plant biomass may provide insights into survival in forest systems, where seedling survival is often size-dependent. Evidence comes from stage-specific CNDD studies showing diminishing CNDD effects as focal individuals increase in size [(Zhu](#_bookmark182) *[et al.](#_bookmark182)*, [2015),](#_bookmark182) as well as data-driven demographic models showing that seedling survival rates remain high once they achieve a certain size threshold [(Chang-Yang](#_bookmark44) *[et al.](#_bookmark44)*, [2021).](#_bookmark44) Therefore, soil microbes that decrease seedling growth rates can manifest in higher mortality among forest seedlings. Interestingly, although microbial controls over seed survival are known to be common in the field, such effects are poorly-studied in the context of plant-soil feedback given the common biomass focus.

## Microbial effects after seedling establishment

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 that focus only on plant biomass. While an exhaustive review of all such effects of soil microbes on plant performance is beyond the scope of this paper, we briefly highlight soil microbial regulation of phenology and susceptibility to herbivores. Examples of microbial regulation of plant phenology are widespread (reviewed in [O’Brien](#_bookmark148) *[et al.](#_bookmark148)*, [2021),](#_bookmark148) and evidence that soil microbes affect the timing of flowering is especially robust [(Lau & Lennon,](#_bookmark120) [2012,](#_bookmark120) [Wagner](#_bookmark173) *[et al.](#_bookmark173)*, [2014,](#_bookmark173) [Fitzpatrick](#_bookmark74) *[et al.](#_bookmark74)*, [2019,](#_bookmark74) [Igwe](#_bookmark92) *[et al.](#_bookmark92)*, [2021).](#_bookmark92) The magnitude of phenology differences generated by microbes (flowering phenology altered by a few days in the examples cited above) can be very meaningful for plant fitness, especially under abiotic stress when earlier flowering can be critical to reproductive success and fitness (reviewed in [Kazan & Lyons,](#_bookmark102) [2016,](#_bookmark102) [O’Brien](#_bookmark148) *[et al.](#_bookmark148)*, [2021).](#_bookmark148) Soil biota can also regulate plant susceptibility to herbivores (e.g., [Howard](#_bookmark89) *[et al.](#_bookmark89)*, [2020,](#_bookmark89) [Kalske](#_bookmark97) *[et al.](#_bookmark97)*, [2022,](#_bookmark97) [Pineda](#_bookmark156) *[et al.](#_bookmark156)*, [2020),](#_bookmark156) with such effects likely arising due to changes in leaf metabolomes or volatile organics induced by microbes [(Kalske](#_bookmark97) *[et al.](#_bookmark97)*,

[2022,](#_bookmark97) [Huberty](#_bookmark91) *[et al.](#_bookmark91)*, [2022).](#_bookmark91) While the consequences of microbial-induced shifts in plant–herbivore interactions on insect fitness and population dynamics are becoming increasingly well-studied (reviewed in [Shikano](#_bookmark163) *[et al.](#_bookmark163)*, [2017),](#_bookmark163) 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 in systems where such effects are known to be important is to pair experiments with system-specific models that propagate their consequences on long-term plant population dynamics.

## Evidence from observational studies

In addition to manipulative experiments, evidence of microbial-mediated demographic transitions also come from field observational studies. Especially for long-lived plants such as forest trees, there is a long history of monitoring individual survival in relation to naturally occurring gradients of conspecific density (e.g., [Comita](#_bookmark52) *[et al.](#_bookmark52)*, [2010,](#_bookmark52) [Swamy](#_bookmark168) *[et al.](#_bookmark168)*, [2011,](#_bookmark168) [Lebrĳa-Trejos](#_bookmark121) *[et al.](#_bookmark121)*, [2016,](#_bookmark121) [Zhu](#_bookmark183) *[et al.](#_bookmark183)*, [2018).](#_bookmark183) Repetitive demographic censuses are often used to test the Janzen–Connell hypothesis [(Janzen,](#_bookmark94) [1970,](#_bookmark94) [Connell,](#_bookmark54) [1971)](#_bookmark54) in the form of conspecific negative density-dependence (CNDD; [Comita & Stump,](#_bookmark53) [2020,](#_bookmark53) [LaManna](#_bookmark119) *[et al.](#_bookmark119)*, [2022,](#_bookmark119) [Song & Corlett,](#_bookmark164) [2022).](#_bookmark164) Increasing evidence from biocide treatments implicates soil-borne pathogens as key drivers of CNDD [(Bell](#_bookmark30) *[et al.](#_bookmark30)*, [2006,](#_bookmark30) [Bagchi](#_bookmark27) *[et al.](#_bookmark27)*, [2010,](#_bookmark27) [2014,](#_bookmark26) [Krishnadas](#_bookmark112) *[et al.](#_bookmark112)*, [2018).](#_bookmark112) Moreover, species’ variation in CNDD strength can be attributed to soil microbes such as the mycorrhizal strategies of trees (e.g., arbuscular mycorrhizal or ectomycorrhizal; [Bennett](#_bookmark32) *[et al.](#_bookmark32)*, [2017,](#_bookmark32) [Liang](#_bookmark126) *[et al.](#_bookmark126)*, [2020).](#_bookmark126) These findings connect the clear demographic outcomes from CNDD studies to their underlying soil microbe-mediated mechanisms (Box [2).](#_bookmark17)

*A paragraph about empirical evidence of CNDD. This paragraph will also mention that there are two types of CNDD focus: (1) seed-to-seedling transition that encompasses many of the early life stage microbial effects mentioned above, and (2) seedling/sapling survival that considers microbial effects on the survival of later life stages.*

# 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. Therefore, when predicting the long-term consequences of soil microbes, we encourage studies to move from biomass-based performance metrics to demographic models that directly incorporate multiple microbial effects (F[reckleton & Lewis,](#_bookmark76) [2006).](#_bookmark76) Our focus on demographic models has the benefit of integrating the temporal and demographic components to generate predictions for multi-species communities, which has been proved difficult in classic models [(Miller](#_bookmark140) *[et al.](#_bookmark140)*, [2022).](#_bookmark140) As the most crucial component differs among plant–soil systems, developing suitable theoretical models and connecting them with empirical data remains a critical research direction. Below, we discuss two potential theoretical frameworks and highlight studies that have parameterized them with either manipulative experiments or observational data.

Patch occupancy models represent a relatively straightforward framework for studying plant–soil microbe interactions (P[acala & Tilman,](#_bookmark151) [1994,](#_bookmark151) [Mouquet](#_bookmark144) *[et al.](#_bookmark144)*, [2002).](#_bookmark144) In this group of models, plants compete for unoccupied sites and the probability of recolonizing a local site de- pends on the microbial legacy left by the previous occupying plant (S[tump & Comita,](#_bookmark166) [2018,](#_bookmark166) [Miller](#_bookmark139) [& Allesina,](#_bookmark139) [2021,](#_bookmark139) [Ke & Levine,](#_bookmark103) [2021).](#_bookmark103) 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,](#_bookmark139) [2021,](#_bookmark139) [Ke & Levine,](#_bookmark103) [2021),](#_bookmark103) 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; [Mack & Bever,](#_bookmark130) [2014,](#_bookmark130) [Bauer](#_bookmark29) *[et al.](#_bookmark29)*, [2015).](#_bookmark29) Detailed formation aside, a common assumption here is that plants only affect the recolonization of each other indirectly via soil microbes, which is similar to [Bever](#_bookmark35) *[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 patch occupancy models with biomass measurements from pot experiments (P[etermann](#_bookmark154) *[et al.](#_bookmark154)*, [2008,](#_bookmark154) [Mangan](#_bookmark132) *[et al.](#_bookmark132)*,

[2010,](#_bookmark132) [Teste](#_bookmark169) *[et al.](#_bookmark169)*, [2017,](#_bookmark169) [Dudenhöffer](#_bookmark67) *[et al.](#_bookmark67)*, [2022).](#_bookmark67) Since most biomass-based metrics only infer how soil microbes influence a pair of plant species, applying a patch occupancy model to experiments that had only measured biomass performance (e.g., by assuming colonization probability scales with the relative biomass performance of different plants in the soil) has the benefit of generating predictions for multi-species communities.

Importantly, the patch occupancy framework can be easily extended to incorporate the tem- poral aspects of plant–soil microbe interactions (Fig [3A).](#_bookmark20) This is because such models can treat different developmental stages of the soil microbial community as distinct states, and the transi- tions between states reflect the conditioning and decay rates of soil microbes. The explicit inclusion of microbial legacies in the form of unoccupied conditioned patches differs from previous feed- back models, which assume tight coupling between plants and microbes via timescale separation [(Eppinga](#_bookmark70) *[et al.](#_bookmark70)*, [2018,](#_bookmark70) [Mack](#_bookmark131) *[et al.](#_bookmark131)*, [2019).](#_bookmark131) [Ke & Levine](#_bookmark103) [(2021)](#_bookmark103) used this approach to show that the stabilization driven by host-specific pathogens depends on how fast conditioned soil regress back to the unconditioned state. In another example, [Ke](#_bookmark107) *[et al.](#_bookmark107)* [(2021)](#_bookmark107) modified a previous model (F[ukami](#_bookmark78) [& 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. The above models directly track the changes of microbial impact on plants through time; such a phe- nomenological approach to modeling plant–soil microbe interactions can be easily parameterized with the type of experiments mentioned in Section [II..](#_bookmark4) Alternatively, [Schroeder](#_bookmark162) *[et al.](#_bookmark162)* [(2020)](#_bookmark162) built a complicated simulation-based model explicitly tracking the population size of pathogens and mu- tualists at each local site, allowing their abundance to vary due to dispersal, microbial competition, and the age of host plant individuals. Such a mechanistic approach allows the temporal devel- opment and decay of microbial effects to emerge naturally in theoretical models but, at the same time, requires detailed knowledge of microbial community dynamics [(Jiang](#_bookmark95) *[et al.](#_bookmark95)*, [2020).](#_bookmark95)

Patch occupancy models can also be parameterized with observational data on demographic transitions, thereby making predictions based on demographic responses other than microbe- mediated biomass performance. For example, when parameterizing the model with seedling recruitment data from repetitive censuses, we are incorporating microbial effects on early life stages (e.g., seed survival, germination, and seedling survival in Fig. [2;](#_bookmark19) [Krishnadas & Stump,](#_bookmark115)

[2021).](#_bookmark115) Moreover, one can go beyond the recolonization process in patch occupancy models and construct more complicated simulation-based models to incorporate microbial effects on multiple demographic processes (F[reckleton & Lewis,](#_bookmark76) [2006).](#_bookmark76) A recent study by [Averill](#_bookmark25) *[et al.](#_bookmark25)* [(2022)](#_bookmark25) fitted statistical models to census data to study how the recruitment, growth, and survival of plants are affected by mycorrhizal feedback. With a demographic simulation, they showed that positive mycorrhizal feedbacks are necessary for maintaining alternative stable states of forests with dif- ferent mycorrhizal strategies. Here, demographic models also provide the opportunity to identify the most critical microbial effect via simulations. For example, [Chu & Adler](#_bookmark48) [(2015)](#_bookmark48) showed that density-dependent feedback loops during the recruitment stage contributed most to plant coexis- tence compared to that during the growth and survival stages, presumably because recruitment data from censuses involved many demographic transitions that are susceptible to soil microbes (F[reckleton & Lewis,](#_bookmark76) [2006,](#_bookmark76) [Krishnadas & Comita,](#_bookmark114) [2019;](#_bookmark114) Fig. [2).](#_bookmark19)

*In addition to models assuming plants interact indirectly via soil microbes, some models assume that plants also interact directly (e.g., competition for resources) and soil microbes act in a manner that changes the density-dependency of plant population growth (Fig [3B).](#_bookmark20) The Lotka–Volterra model in [Bever](#_bookmark35)* [et al.](#_bookmark35) *[(1997)](#_bookmark35) belongs to this category, indicating that it differs fundamentally from [Bever](#_bookmark35)* [et al.](#_bookmark35) *[(1997)](#_bookmark35) despite often being cited as equivalent (see also [Revilla](#_bookmark160)* [et al.](#_bookmark160)*, [2013,](#_bookmark160) [Miller](#_bookmark140)* [et al.](#_bookmark140)*, [2022).](#_bookmark140) For example, microbial effects were incorporated into stage-structured models for grassland communities with a mixture of annual and perennial plants. A series of studies from [Mordecai](#_bookmark142) [(2013)](#_bookmark142) showed how different soil pathogens (i.e., dormant seed versus seedling pathogens) impact the competition between annual and perennial plants.*

# 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 combining short- term greenhouse experiments with theory-derived metrics, the approach from [Bever](#_bookmark35) *[et al.](#_bookmark35)* [(1997)](#_bookmark35) has motivated more than two decades of research to predict the long-term consequences of soil microbes [(Crawford](#_bookmark55) *[et al.](#_bookmark55)*, [2019).](#_bookmark55) 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](#_bookmark98) *[et al.](#_bookmark98)*, [2019,](#_bookmark98) [2021,](#_bookmark99) [Yan](#_bookmark177) *[et al.](#_bookmark177)*, [2022).](#_bookmark177) The simplified temporal perspective of microbial effects and the biomass focus of studies emerge partially due to the assumptions made in past theoretical models. 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,](#_bookmark49) [2023).](#_bookmark49) 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 encourage future studies 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 [3).](#_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](#_bookmark140) *[et al.](#_bookmark140)*, [2022).](#_bookmark140) Second, instead of tracking species’ relative abundance, one can also build demographic models that explicitly track plant population densities, which offer 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,](#_bookmark146) [2016),](#_bookmark146) or those with low propagule pressure such that conditioned soils are not immediately recolonized [(Ke](#_bookmark107) *[et al.](#_bookmark107)*, [2021),](#_bookmark107) 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 [(Mordecai,](#_bookmark143) [2015),](#_bookmark143) 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](#_bookmark154) *[et al.](#_bookmark154)*, [2008,](#_bookmark154) [Mangan](#_bookmark132)

*[et al.](#_bookmark132)*, [2010,](#_bookmark132) [Teste](#_bookmark169) *[et al.](#_bookmark169)*, [2017,](#_bookmark169) [Dudenhöffer](#_bookmark67) *[et al.](#_bookmark67)*, [2022).](#_bookmark67) 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. [2).](#_bookmark19) For instance, [Stump &](#_bookmark166) [Comita](#_bookmark166) [(2018)](#_bookmark166) parameterized their patch occupancy model with CNDD patterns based on 5-year seedling survival [(Comita](#_bookmark52) *[et al.](#_bookmark52)*, [2010),](#_bookmark52) which correspond to microbial effects on the performance and size-based survival of older seedlings. On the other hand, [Krishnadas & Stump](#_bookmark115) [(2021)](#_bookmark115) 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 (see sections [II.](#_bookmark4) and [III.).](#_bookmark10) For instance, repeating the experiment along naturally occurring soil conditioning gradients depicts (i.e., to depict temporal development patterns) and directly planting ungerminated seeds into cultivated soils (i.e., to track multiple early life stage microbial effects). However, some models include processes that cannot be reliably estimated by 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 assumed that soil microbes can modify the density-dependency of plant population growth. Recent studies linking plant–soil microbe interactions and coexistence theory specifically highlight this scenario where soil microbes influence the model’s density-dependent parameters (i.e., competitive coefficients; [Kandlikar](#_bookmark98) *[et al.](#_bookmark98)*, [2019,](#_bookmark98) [Ke & Wan,](#_bookmark105) [2020),](#_bookmark105) which require employing experiments that directly manipulate plant density [(Chung & Rudgers,](#_bookmark50) [2016,](#_bookmark50) [Cardinaux](#_bookmark42) *[et al.](#_bookmark42)*, [2018).](#_bookmark42) 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,](#_bookmark105) [2020)](#_bookmark105) was challenged by the observation that facilitation is common, leading to a revised density gradient design with

greater flexibility [(Ke & Wan,](#_bookmark106) [2022).](#_bookmark106) 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 functional- ity of soil microbial communities [(Jiang](#_bookmark95) *[et al.](#_bookmark95)*, [2020).](#_bookmark95) With a plant-centric 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,](#_bookmark71) [2021,](#_bookmark71) [Ke](#_bookmark107) *[et al.](#_bookmark107)*, [2021,](#_bookmark107) [Hannula](#_bookmark84) *[et al.](#_bookmark84)*, [2021).](#_bookmark84) Finally, there is a need for future developments in the detection of microbial function in empirical studies. Existing sequencing of taxonomic communities may not reliably reflect the function of microbial communities due to their functional plasticities and redundancies. Explicit quantification of microbial activity, such as the abundance of different func- tional groups [(Nguyen](#_bookmark147) *[et al.](#_bookmark147)*, [2016)](#_bookmark147) and measurements of microbial activity 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 short, we conclude that studying the temporal dimension and the multiple demographic 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 knowl- edge gaps can also be important for other ecological processes (e.g., recovery trajectory following disturbance; [Zee & Fukami,](#_bookmark179) [2015).](#_bookmark179) The ultimate important task is to recognize which aspects of the temporal and demographic components are important for the focal plant–soil 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 seedling response phases of experiments included in [Crawford](#_bookmark55) *[et al.](#_bookmark55)* [(2019)](#_bookmark55) and [Yan](#_bookmark177) *[et al.](#_bookmark177)* [(2022),](#_bookmark177) two prominent meta-analysis data sets of plant–soil interactions studies. Since the above two studies focused on the pairwise stabilization metric of [Bever](#_bookmark35) *[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 98 out of 1461 experimental pairs (*≈* 7%; see the upper and right stacked histograms based on the number of experimental pairs). When positioning studies based on their conditioning length (x-axis; field-conditioned soil as a separate category) and response length (y-axis), we see that most studies employed short-term conditioning (mean: 6.6 months; *n* = 58 studies) and a great proportion of studies comparing perennial pairs relied on field-collected soils (48 out of 106 studies; *≈* 45%). 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,](#_bookmark116) [2019)](#_bookmark116) 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, posited half a century ago, serves to link plant con-*

*sumers to distance- and density-dependent mortality of plants [(Janzen,](#_bookmark94) [1970,](#_bookmark94) [Connell,](#_bookmark54) [1971).](#_bookmark54) The main premise is that seeds and seedlings farther from adults have a higher per-capita success of germination and survival because distance helps to escape potential host-specific enemies that aggregate around focal adults. By extension, more abundant species are more likely to encounter their conspecific enemies and individual survival decreases at higher densities.*

*Despite their conceptual concordance, empirical work on J-C effects and plant–soil inter- actions has largely progressed along separate trails. In contrast to PSF greenhouse ex- periments, J-C effects have nearly always been tested using in-situ field experiments and observational data on plant survival and growth. Experiments involve placing seeds and seedlings of selected species near and far from focal conspecific adults, potentially with a factorial density treatment. Combining this with biocides to control for microbes quanti- fies how microbially-mediated survival varies with distance from adult [(Bagchi et al.](#_bookmark27), [2010,](#_bookmark27) [Poulsen et al.](#_bookmark157), [2012),](#_bookmark157) the density of seeds and seedlings [(Krishnadas & Comita,](#_bookmark113) [2018),](#_bookmark113) or their potential interaction (S[tevenson,](#_bookmark165) [2007,](#_bookmark165) [Choo et al.](#_bookmark47), [2017).](#_bookmark47) Biocides can also be used to test density- and distance-dependence in naturally occurring seeds and seedlings [(Bagchi et al.](#_bookmark27), [2010,](#_bookmark27) [2014,](#_bookmark26) [Krishnadas et al.](#_bookmark112), [2018).](#_bookmark112)*

*Field studies of J-C effects, observational and experimental, help connect pot experiments of plant–soil interactions to conspecific density dependence in growth and survival. Census data can show whether biomass outcomes of soil conditioning in the greenhouse reflect density-dependent survival in the field. Even observational studies on density-dependent plant growth could improve demographic predictions from plant-microbe interactions. For instance, how microbes affect the ability of plants to grow from one life stage to the next could be used to parameterize age-stage transitions in projecting population trajectories*

**Box 2 (continued)**

*of plant species. Field experiments (e.g., using biocides) can reveal microbial effects on plant demographic transitions against a backdrop of real-world conditions in which these processes play out.*

*To make J-C studies more comparable with assessments of plant-soil microbe interactions in greenhouse studies, CDD estimated from census observations and/or experiments should be explicitly matched to the strength of feedback experienced by species in pot experiments [(McCarthy-Neumann & Ibáñez,](#_bookmark135) [2013).](#_bookmark135) Surprisingly few studies have done so, perhaps because experiments have logistical constraints of seed and seedling availability and the difficulty of covering a representative set of species in the community, especially in diverse ecosystems. There are also some small but critical considerations of study design to match J-C experiments in the field to greenhouse experiments of plant–soil interactions. Field experiments should place seeds and seedlings near heterospecific trees to assess whether conspecific effects exceed heterospecific effects. Heterospecific treatments would also offer a better indicator of the host-specific impact of microbes, assumed to operate in J-C effects, than distance dependence alone.*

**Figures**

**(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

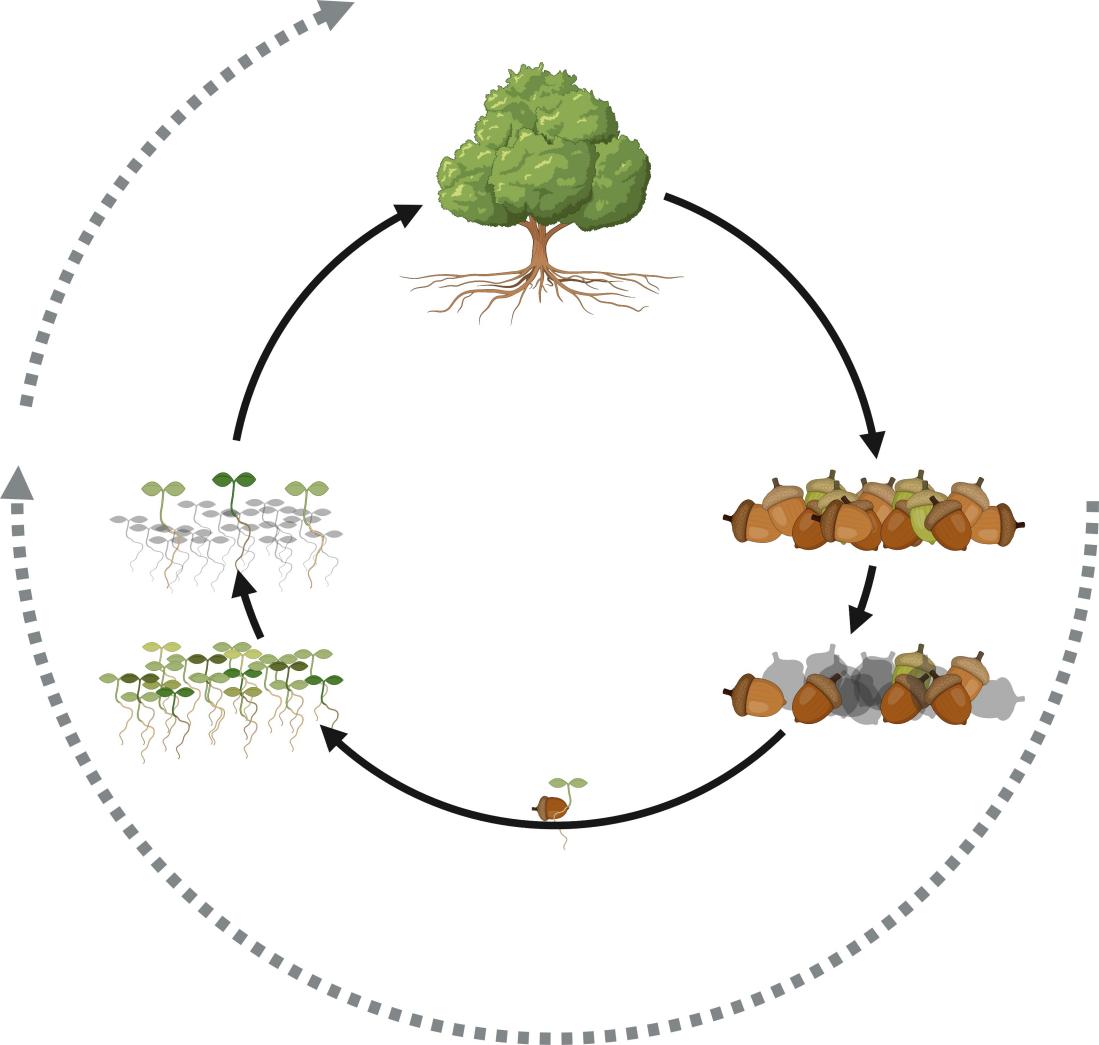
Time

Microbe effect Plant response

Time

Microbe effect Plant response

**Figure 1** 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 condition- ing process, with impacts on plant performance that depend on both the duration of plant conditioning (section [II.-1)](#_bookmark4) and response (section [II.-2).](#_bookmark4) Moreover, microbial communities and their impacts on plant performance may attenuate temporally after the senescence of the previous conditioning individual (section [II.-3)](#_bookmark4) or undergo dif- ferent trajectories depending on the previous rounds of conditioning (section [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 2** 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 CNDD studies; 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

soil seed bank

germination

maximum seed production

number of seeds at time T

seed survival

loss to competition and density-dependent microbial effects

number of seeds at time T+1

**Figure 3** Two proposed modeling frameworks that can incorporate the missing tempo- ral and demographic components of plant–soil microbe interactions. In both panels, demographic processes influenced by soil microbes are highlighted in red. (A) An example from [Ke & Levine](#_bookmark103) [(2021)](#_bookmark103) 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 colonization and death (solid arrows) or the conditioning and decay of microbial ef- fects (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 [Mordecai](#_bookmark143) [(2015),](#_bookmark143) which tracks the density of seeds prior to germination. Here, soil mi- crobes 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

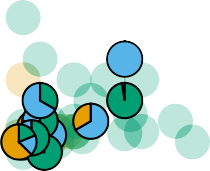
Response length (month)

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](#_bookmark55) *[et al.](#_bookmark55)* [(2019)](#_bookmark55) and [Yan](#_bookmark177) *[et al.](#_bookmark177)* [(2022)](#_bookmark177) data sets. See Box [1](#_bookmark16) for more details.

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**Author Contributions**

All authors conceived the study and wrote the manuscript. P.-J. Ke and S. Ou contributed equally.

**Data Availability**

No new data was presented in this article.

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