

WILEY

ECOLOGICAL MONOGRAPHS

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

Journal:	<i>Ecological Monographs</i>
Manuscript ID	ECM24-0207.R1
Wiley - Manuscript type:	Concepts & Synthesis
Date Submitted by the Author:	n/a
Complete List of Authors:	Ke, Po-Ju; National Taiwan University, Institute of Ecology and Evolutionary Biology Kandlikar, Gaurav; Louisiana State University and A&M College, Department of Biological Sciences; Ou, Suzanne; Stanford University, Department of Biology Hsu, Gen-Chang; National Taiwan University, Institute of Ecology and Evolutionary Biology; Cornell University, Department of Entomology Wan, Joe; National Taiwan University, Institute of Ecology and Evolutionary Biology; ETH Zürich, Institute of Integrative Biology, Department of Environmental Systems Science Krishnadas, Meghna; Tata Institute of Fundamental Research National Centre for Biological Sciences; CSIR - Centre for Cellular and Molecular Biology; Academy of Scientific and Innovative Research, CSIR-Human Resource Development Center
Substantive Area:	Demography/Life History < Population Dynamics and Life History < Population Ecology < Substantive Area, Patch Dynamics < Community Ecology < Substantive Area, Plant/Fungal/Microbial Interactions < Species Interactions < Community Ecology < Substantive Area, Experimental Design and Analysis < Statistics and Modeling < Theory < Substantive Area, Modeling (general) < Statistics and Modeling < Theory < Substantive Area
Organism:	
Habitat:	
Geographic Area:	
Key words/phrases:	conspecific negative density dependence, demographic models, Janzen-Connell hypothesis, microbial community, patch occupancy model, plant-soil feedback
Abstract:	Soil microorganisms can have profound impacts on plant community dynamics and have received increasing attention in the context of plant-soil feedback. The effects of soil microbes on plant community dynamics are classically evaluated with a two-phase experimental design that consists of a conditioning phase, during which plants modify the soil microbial community, and a response phase, during which the biomass

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

SCHOLARONE™
Manuscripts

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

Po-Ju Ke^{1,†}, Gaurav S. Kandlikar², Suzanne Xianran Ou³, Gen-Chang Hsu^{1,4}, Joe Wan^{1,5}, and Meghna Krishnadas^{6,7,8}

¹Institute of Ecology and Evolutionary Biology, National Taiwan University, Taipei, Taiwan

²Department of Biological Sciences, Louisiana State University, Baton Rouge, LA 70803, USA

³Department of Biology, Stanford University, Stanford, California 94305, USA

⁴Department of Entomology, Cornell University, Ithaca, New York, NY 14853, USA

⁵Institute of Integrative Biology, Department of Environmental Systems Science, ETH Zürich,
8092 Zürich, Switzerland

⁶TIFR National Centre for Biological Sciences, GKVK Campus, Bellary Road, Bengaluru India

⁷Laboratory for Conservation of Endangered Species, Centre for Cellular and Molecular Biology,
Hyderabad, Telangana, India

⁸Academy of Scientific and Innovative Research, CSIR-Human Resource Development Centre,
Ghaziabad, Utter Pradesh, India

April 12, 2025

Total word count for main body of text: 11115

Number of color figures: 7

Number of Boxes: 2

Open research statement: The dataset used in Figure 3 are from publicly available datasets of two publications: Figshare Repository for Crawford et al. (2019a) (DOI: 10.6084/m9.figshare.7985195.v1; cited as Crawford et al., 2019b) and Zenodo for Yan et al. (2022a) (DOI: 10.5281/zenodo.6513066; cited as Yan et al., 2022b). The R-scripts for simulations and data compiled for Figure 3 are available on GitHub (<https://github.com/pojuke/DemographicReviewPSF>) and will be made available on Zenodo upon publication.

† Correspondence author: pojuke@ntu.edu.tw; +886-33662467

1 Abstract

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

19 Keywords

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

22 I. Introduction

23 Plants interact with a diverse array of soil biota that function as herbivores, pathogens, mutu-
24 alists, and decomposers. In addition to the contributions of soil fauna (ranging from micro- to
25 macrofauna; Ehrenfeld et al., 2005, Kulmatiski et al., 2014, Wilschut and Geisen, 2021), studies
26 have highlighted the importance of plant–soil microbe interactions. These interactions can be bidi-
27 rectional, with plants altering the composition of the soil microbial community, and the resulting
28 changes in microbial community impacting subsequent plant performance in the conditioned soil
29 (Bever, 1994, Bever et al., 1997, Bever, 2003). The study of plant–soil microbe interactions has its
30 origin in agricultural science (Huang et al., 2013, van der Putten et al., 2013) and has been integrated
31 into community ecology under the framework of plant–soil feedback (PSF). Since its introduction
32 by Bever et al. (1997), studies have extensively discussed how plant–soil microbe interactions in-
33 fluence plant coexistence (Bever et al., 2010, Ke and Miki, 2015, Bever et al., 2015, Kandlikar, 2024).
34 The PSF framework has also been used to explore how soil microbes affect patterns in the relative
35 abundance of plant communities (Mangan et al., 2010, Reinhart et al., 2021), restoration success
36 (Wubs et al., 2016, Koziol et al., 2018), plant invasion (Callaway et al., 2004, Suding et al., 2013), and
37 the biodiversity–productivity relationship (Kulmatiski et al., 2012, Forero et al., 2021).

38 To characterize the direction and strength of plant–soil microbe interactions, most studies
39 follow a two-phase experimental design aimed at capturing the two-way interactions between
40 plants and soil microbes (Bever et al., 1997). The classic greenhouse experiment consists of a
41 “conditioning” phase during which plants modify the soil microbial community, directly followed
42 by a “response” phase during which plants of the same or other species respond to the conditioned
43 soil microbial community (Bever et al., 2010, Brinkman et al., 2010). This distinct two-phase design
44 elegantly captures the necessary information for parameterizing the key terms in the classic plant–
45 soil feedback model (Bever et al., 1997, 2012) and has enabled a strong empirical foundation of
46 PSF research across ecosystems (Crawford et al., 2019a, Yan et al., 2022a). However, this approach
47 implies a number of assumptions about the nature of plant–soil microbe interactions that do not
48 align with our contemporary understanding of their dynamics. In particular, a growing number
49 of studies have highlighted the importance of accounting for different temporal and demographic
50 dimensions of plant–soil microbe interactions (Kardol et al., 2013, Gundale and Kardol, 2021,

51 Chung, 2023). Such evidence should reshape both the design of experiments (e.g., how long
52 should the conditioning phase last?) and the interpretation of their results (e.g., how do microbial
53 effects on early-life stage plant performance translate to population-level consequences?). In this
54 paper, we focus on two key assumptions: first, the temporal assumption that microbial effects
55 develop quickly during the conditioning phase and maintain constant strength over time; and
56 second, the demographic assumption that plant biomass performance during the response phase
57 reflects microbial impact on plant population growth.

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

77 The short-term nature of most experiments also constrains researchers to focus on a sin-
78 gle plant demographic response that presumably reflects the most critical impact of the mi-
79 crobial community (Ke and Wan, 2023). The most frequently measured performance proxy is

80 plant biomass, which is then used to calculate theoretically derived metrics to infer how soil
81 microbes influence plant coexistence. For instance, the biomass of plants in conspecific- and
82 heterospecific-conditioned soils can be used to calculate the pairwise feedback metric that quanti-
83 fies the frequency-dependent feedback loops generated by plant–soil microbe interactions (Bever
84 et al., 1997). Negative frequency-dependence arises when both plants condition their soil mi-
85 crobes in a way that favors heterospecifics over conspecifics, thereby promoting plant coexistence
86 (Crawford et al., 2019a). In the context of the classic PSF model, where soil microbes drive plant
87 community dynamics by changing plants' intrinsic growth rates (Bever et al., 1997), these metrics
88 operate under the assumption that plant biomass performance is a good proxy for plant popu-
89 lation growth. However, soil microbes can also affect other demographic processes across the
90 plant life cycle that are not captured simply by measuring plant biomass (e.g., changing seed
91 and seedling survival rates or the nature of density-dependence among plants), potentially with
92 opposing effects at different plant ontogenetic stages that lead to different coexistence predictions
93 (Dudenhöffer et al., 2018, Dostálek et al., 2022). Integrating these different impacts, instead of
94 making predictions based on microbial effects on any one life stage, is another challenge when
95 predicting the long-term demographic consequences of soil microbes.

96 Here, we discuss the two critical assumptions regarding temporal and demographic aspects
97 of plant–soil microbe interactions in nature. We aim to highlight the relevance of these assumptions
98 when extrapolating greenhouse results, and outline potential avenues for overcoming them in
99 future empirical and theoretical studies. It is important to note that although we treat the temporal
100 and demographic aspects of plant–microbe interactions separately for analytical clarity, they are
101 intrinsically linked. In nature, temporal shifts in microbial community composition and function
102 can give rise to distinct microbial effects on various demographic processes across plants' life
103 cycles. Conversely, these demographic rates reveal how microbial impacts on plant populations
104 unfold over time and illuminate the temporal dynamics of plant–soil microbe interactions. On
105 the theoretical forefront, we advocate for a shift from using biomass-based performance indices
106 to parameterizing patch occupancy models and plant demographic models with microbial effects.
107 While these biologically important complications make experiments more logically challenging,
108 we argue that integrating the temporal and demographic details can better predict the outcome of

¹⁰⁹ plant–soil microbe interactions in their natural context.

¹¹⁰ II. Significant consequences of overlooking the temporal and demo- ¹¹¹ graphic aspects of plant–soil microbe interactions

¹¹² To motivate our thesis that explicitly evaluating the variation in microbial effects across time and
¹¹³ across different life stages is important for predicting their consequences in nature, we first present
¹¹⁴ a simple plant demographic model that illustrates the potential consequences of ignoring these
¹¹⁵ temporal dynamics. Specifically, we consider two annual plant species, N_1 and N_2 , with dynamics
described by the Beverton–Holt annual plant model:

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

¹¹⁶ with subscripts i and j indicating species 1 or 2. The first term represents the survival of ungerminated seeds, with g_i and s_i representing seed germination and survival rate, respectively (circular loop in Fig. 2A). The second term represents seed production and density-dependent interactions among germinated seeds, with λ_i , α_{ii} and α_{ij} representing intrinsic plant fecundity, intraspecific and interspecific competitive impact experienced by N_i , respectively (rightward arrows in Fig. 2A). As opposed to biomass-based metrics, this demographic model provides the opportunity to study microbial effects on five different demographic parameters (i.e., g_i , s_i , λ_i , α_{ii} , and α_{ij}). For short-term greenhouse studies comparing these demographic processes in conditioned versus sterilized soil, this model offers a way to predict the long-term effect of soil microbes on plant competitive outcomes.

¹²⁶ As a case study, consider a scenario in which pathogenic microbes operate by harming one of these demographic processes for a given species. If a short-term greenhouse study were to suggest that the primary effect of the soil pathogen is to reduce species 1's seed survival (s_1) by 10% while leaving s_2 unaffected, the model would predict negligible impacts of soil microbes on long-term plant community dynamics. This is illustrated in the left panel of Fig. 2B, as the grey lines

131 (indicating species abundance under no pathogenic impact) and blue lines (indicating a pathogenic
132 impact on species 1's seed survival) almost overlap completely. If instead the greenhouse study
133 were to find that the pathogen decreases species 1's intrinsic fecundity (λ_1) by 10%, the model
134 predicts substantially lower population sizes for species 1 in the long-term ($\approx 18\%$ reduction in
135 equilibrium abundance). This exercise highlights the importance of understanding where in the
136 plant demographic cycle microbial effects arise, an aspect of plant–soil microbe interactions that
137 is often overlooked when assuming a single performance measurement can predict demographic
138 outcomes.

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

150 III. Dissecting different temporal dimensions of microbial effects

151 Studies on the temporal patterns of plant–soil microbe interactions have classically focused on their
152 variation along plant succession, which typically involves plants with different traits or shifts in
153 the external environment (Kardol et al., 2006, 2013, Bauer et al., 2015). However, temporal variation
154 in plant–microbe interactions also occurs across shorter time scales because the conditioned soil
155 microbial community and plant response both vary over time (Fig. 1B). Recognizing that plant–soil
156 microbe interactions are not constant through time directly influences the experimental design and
157 how we interpret experimental results. Moreover, this temporal variability may be a key mecha-

158 nism behind the effects of phenological mismatch between plants and soil microbes (Peay, 2018,
159 Rudgers et al., 2020, Yin et al., 2023). In this section, we review evidence of temporal variability and
160 discuss mechanisms by which the impact of microbial communities on plant biomass performance
161 varies with the duration of the conditioning and response phases (subsection III.1), as well as
162 the time lag between consecutive generations (subsection III.2). We then discuss how to design
163 experiments that tackle the temporal complexities observed in nature (subsection III.3). Note that
164 for this section, we focus on studies that measure plant biomass as the key performance proxy; we
165 will discuss other demographic responses in section IV.

166 III.1 Temporal development during the conditioning and response phases

167 As the strength and direction of plant–soil microbe interactions depend on the timing of interac-
168 tions, the duration of the conditioning and response phases influences the greenhouse-measured
169 interaction strength. By compiling information on the experimental duration of studies included
170 in two prominent meta-analyses (Crawford et al., 2019b, Yan et al., 2022b), we showed that the
171 length of the conditioning and response phases is under a few months in most studies (Fig. 3).
172 The median conditioning length is 3.5 months ($n = 59$ studies, after excluding 47 studies with
173 field-collected soils) while that of the response phase is 3 months ($n = 106$ studies). Extrapolating
174 from these experiments to predict the long-term consequences of soil microbes is based on the
175 assumption that the relative impact of conspecific- and heterospecific-conditioned soils remains
176 constant throughout plant development. The significance of overlooking the temporal develop-
177 ment of plant–soil microbe interactions is exemplified when considering plants with different life
178 histories. For example, 20% of studies (21 out of 106) in Fig. 3 evaluated microbially mediated
179 stabilization between plant species pairs comprising one annual and one perennial species while
180 implementing the same (usually short) experimental duration. This overlooks the potential for
181 short- and long-lived plants to condition microbial communities at different rates, such that the
182 same duration of soil conditioning may correspond to different developmental stages and micro-
183 bial effects (Kulmatiski et al., 2017): the species-specific microbiome of a short-lived annual plant
184 may be fully conditioned by the end of an experiment, whereas that of a long-lived perennial may
185 require a longer conditioning time. Similarly, a short response phase may capture the full physi-

186 ological response of an annual plant, while that of a perennial may vary with its ontogeny. This
187 mismatch in temporal development patterns highlights the challenge of interpreting experimental
188 results in the context of the focal system's natural history.

189 Compared to the classic two-phase design with a single fixed duration of soil conditioning
190 (Fig. 4A), a few studies have grown plants in soils that were conditioned for different durations
191 (red vertical arrow (i) in Fig. 4B). Studies have shown that the relative impact of conspecific- and
192 heterospecific-conditioned soil on the responding individual can vary with the duration of soil
193 conditioning. For example, Liu et al. (2025) found that *Jacobaea vulgaris* performed worse in con-
194 specific soil than in heterospecific soils, and that this performance difference increased as soil
195 conditioning time extended from two to five weeks; however, the differences between soil treat-
196 ments diminished after a longer conditioning duration of eight weeks. Similarly, while focusing
197 on soil chemical properties, Lepinay et al. (2018) showed that the relative negative impact of con-
198 specific versus heterospecific soils varied with conditioning duration over a span of two to eight
199 weeks. In a more natural setting, Ke et al. (2021) studied how the microbial impact varied with soil
200 conditioning length by transplanting seedlings into field-conditioned soil collected under plant
201 individuals of different ages. They found that the soil microbial community underwent continuous
202 successional dynamics over the span of 20 years and three out of four species experienced negative
203 microbial effects that intensified with longer conditioning time. Importantly, these results have
204 crucial implications on the design of two-phase experiments: arresting soil conditioning at differ-
205 ent time points causes the responding plant to encounter microbial communities with different
206 compositions and functions, thereby giving rise to different plant–soil microbe interactions.

207 Previous experimental studies on the temporal dynamics of plant–soil microbe interactions
208 have largely focused on the development of microbial effects across the lifespan of the responding
209 individual, which is typically achieved by harvesting responding plants at various time intervals
210 (Kardol et al., 2013, Gundale and Kardol, 2021; red diagonal arrow (ii) in Fig. 4B). For example,
211 by sequentially harvesting seedlings at four time points spanning 19 months, Hawkes et al. (2013)
212 showed that the microbial effect experienced by native plants became more negative through time,
213 whereas the development patterns for invasive plants were more variable. Recent studies have
214 also highlighted that other factors can modify the temporal pattern of microbial effects during

215 the response phase (Dostál, 2021, Bezemer et al., 2018). For instance, harvesting twice every week
216 for 11 weeks, Bezemer et al. (2018) showed that the negative effect of conspecific-conditioned soil
217 experienced by *Jacobaea vulgaris* attenuated as plants became older; however, when grown together
218 with a heterospecific competitor, the negative effect instead aggravated over time (but see Dostál,
219 2021 for a nonlinear pattern for three harvests spanning 13 months). Together, this empirical
220 evidence provides a strong impetus to consider temporal variability in the response phase since
221 harvesting an experiment at different endpoints can alter our understanding of the microbial
222 effect.

223 The temporal development of plant–soil microbe interaction can occur due to shifts in the
224 composition and/or functionality of microbial communities as plants mature or enter different de-
225 velopmental stages (Chaparro et al., 2013, Dombrowski et al., 2016, Edwards et al., 2018, Hannula
226 et al., 2019). Mechanisms underlying these shifts in soil microbial communities include physio-
227 logical changes in nutrient allocation or root exudation across plant ontogenetic stages (Chaparro
228 et al., 2013, Zhelnina et al., 2018), as well as an increase in immunity and antibiotic defense against
229 pathogens as plants mature (Bulgarelli et al., 2013, Chaparro et al., 2013). Furthermore, changes
230 prompted by plants can lead to shifts in microbe–microbe interactions and the processes governing
231 microbial community assembly (Barret et al., 2015, Herrera Paredes and Lebeis, 2016, Bittleston
232 et al., 2021), all of which may trigger further responses in plant physiology via a complex interplay
233 between mechanisms. Even in the absence of detectable shifts in soil microbial community com-
234 position, ontogenetic changes in plant physiology can drive variable plant responses (Liu et al.,
235 2025). However, as conditioning and response processes operate simultaneously in nature, it is
236 important to note that the same set of mechanisms applies to explain temporal patterns in both
237 phases. For example, strengthening of immunity as plants mature can reduce plant susceptibility
238 to pathogens and alleviate negative microbial effects as the responding individual matures; it can
239 also reduce pathogen abundance as the conditioning phase progresses (Bulgarelli et al., 2013).
240 Similarly, mechanisms that reduce the abundance of beneficial microbes after soil conditioning
241 (e.g., mature plants becoming less reliant on mutualistic partners) also act upon the responding
242 individual to diminish the observed positive microbial effect. We will elaborate on necessary
243 experiments to tease apart different temporal dimensions and mechanisms in the subsection III.3.

244

245 III.2 Alterations of microbial effects after plant death

246 One common implicit assumption in plant–soil feedback studies is that greenhouse-measured
247 microbial effects manifest similarly on plants neighboring the focal individuals as on individuals
248 that arrive and grow in the conditioned soil after the focal plant senesced. However, whether
249 microbial effects carry over through time and how long they persist remains an understudied
250 temporal aspect of plant–soil microbe interactions. This question is especially important for
251 systems with discrete growing seasons or dispersal limitation, where a temporal lag exists between
252 the senescence of one plant (the conditioning individual) and the growth of another (responding)
253 individual. This introduces a lag phase during which the conditioned soil is left unoccupied for
254 an extended period of time; processes such as litter decomposition, abiotic filtering, and stochastic
255 drift may restructure the microbial community during such lags. Studies growing seedlings in
256 soils collected from dead individuals (red vertical arrow (iii) in Fig. 4B) suggest that such lags
257 can have distinct effects across different systems. For example, Esch and Kobe (2021) showed that
258 the negative effects of soil from live *Prunus serotina* on the survival of conspecific seedlings faded
259 away within one year after tree removal. Conversely, Bennett et al. (2023) showed that microbial
260 communities from soils collected under dead and live adult *Populus tremuloides* trees had similar
261 effects on conspecific seedlings. As an alternative to collecting soil from naturally occurring
262 dead individuals, Ou et al. (2024) modified the two-phase experiment to include a six-month
263 delay between the conditioning and response phase; their results suggest that the seasonal lag
264 in Mediterranean annual plant systems changes the microbial community and its corresponding
265 impact on plant coexistence.

266 Microbial effects could persist after active plant conditioning ceases due to the continued
267 survival and functioning of the conditioned microbial community in the soil (Lennon and Jones,
268 2011, Pepe et al., 2018, Esch et al., 2021, Hannula et al., 2021). For example, Esch et al. (2021) found
269 that the persisting pathogenic oomycetes collected from live versus dead tree stumps have similar
270 negative effects on conspecific seedling survival. Similarly, Pepe et al. (2018) showed that arbuscular
271 mycorrhizal fungi remain active and can spread from roots after host shoot removal. Microbial

272 activity can be maintained if root systems remain active after the removal of aboveground tissues
273 or if the release of nutrients from dead belowground tissues mirrors exudates from living plants
274 (Johansen and Jensen, 1996, Müller et al., 2013). Additionally, trophic flexibility (e.g., saprotrophic
275 ability of certain pathogens; Bonanomi et al., 2010) and dormancy of soil microbes can allow the
276 microbial communities to persist after the death of their host, enabling microbes to wait for the
277 arrival of a new host (Lennon and Jones, 2011, Shade et al., 2012, Shemesh et al., 2023). In these
278 cases, the succeeding (response) individual will experience a similar microbial effect despite the
279 temporal lag in arrival timing, and predictions from immediate transplant experiments are relevant
280 to natural systems.

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

295 III.3 Implications for experimental design

296 While an increasing number of studies have recognized the temporal dimensions of plant–soil
297 microbe interactions, synthesizing the factors contributing to this variability, e.g., the life history of
298 plants and functional groups of microbes involved, requires more targeted studies. Here, we rec-
299 ommend a path forward for understanding these context dependencies. First, the temporal setting

300 of the experiment should guide our interpretation of the results. For instance, in Mediterranean
301 plant communities where the growing season only lasts a few months, traditional experiments in
302 which a short-term conditioning phase is immediately followed by the response phase may ade-
303 quately reflect potential microbial effects on concurrently growing neighbors that unfold within
304 one growing season. However, such a design may not be adequate to project microbial effects
305 on population dynamics across years because it overlooks the temporal lag associated with the
306 clear seasonality of plant growth in nature. Second, we encourage modification of the classic
307 two-phase design (Fig. 4A) to reflect the temporal aspects of a focal plant–soil system in nature.
308 For Mediterranean annual plant communities, mirroring the temporal dynamics of the natural
309 system by incorporating a decay phase during which the conditioned soils are exposed to a pro-
310 longed drought with no vegetative growth (red vertical arrow (iii) in Fig. 4B) may provide a better
311 understanding of how soil microbes shape plant community dynamics across years (Ou et al.,
312 2024). Moreover, researchers can build on long-term monitoring plots and historical information
313 to account for variations in conditioning duration, host plant age, or time since host tree death.
314 This approach may be especially applicable in studies that focus on long-lived plants, which often
315 source field-conditioned soils for greenhouse experiments (44%; 47 out of 106 studies in Fig. 3).
316 For example, plant age estimated from historical aerial photos (Ke et al., 2021) and host tree size
317 obtained from forest census (Chen et al., 2019) can be used as a proxy of conditioning time, and
318 chronosequences of abandoned fields or agricultural harvest times can be utilized to study the
319 persistence of microbial effects (van de Voorde et al., 2012, Esch and Kobe, 2021).

320 One can also design experiments that isolate a particular facet of temporal variability to help
321 disentangle the mechanisms behind observed temporal patterns. Current studies on the temporal
322 development of microbial effects typically employ sequential harvesting, where the observed
323 temporal changes result from the combination of varying plant physiological responses and any
324 changes to the soil community that are due to the effects of the responding plant itself (red diagonal
325 arrow (ii) in Fig. 4B). To isolate the effects associated with changing soil microbial communities
326 during soil conditioning, studies could plant seedlings of the same age in soils with different
327 conditioning durations (red vertical arrow (i) in Fig. 4B). Alternatively, if the goal is to isolate the
328 effects caused by changing plant physiology, an experiment could instead grow plants of different

329 ages/sizes (kept in a relatively sterilized environment such as an autoclavable container before
330 transplanting) in soils with identical conditioning duration (red horizontal arrow (iv) in Fig. 4B).
331 Moreover, throughout greenhouse experiments, the concurrent application of modern molecular
332 methods can provide critical insights linking microbial changes to variations in plant performance.
333 A recent study by Liu et al. (2025) utilized such an experimental design to illustrate the importance
334 of conditioning and response duration as well as the underlying mechanisms (i.e., changes in
335 plant sensitivity to microbes or soil re-conditioning by the responding plant). They found that
336 the soil bacterial community in conspecific and heterospecific soils converged over the course of
337 the response phase, partially explaining why differences in plant performance diminished with
338 longer experimental duration (see also Steinauer et al., 2023). Finally, mutants or cultivars with
339 different developmental rates can also be used to separate the effects of plant developmental stage
340 (e.g., vegetative growth or flowering) and age *per se* (Dombrowski et al., 2016). While the above
341 scenarios are deliberately artificial, such experiments can provide important mechanistic insights
342 into the observed temporal patterns of plant–soil microbe interactions.

343 While we have focused on changes happening over the course of a single plant-to-plant
344 replacement, these dynamics are closely related to other temporal patterns. One direction of re-
345 search is how microbial effects build up over generations through multiple rounds of conditioning
346 and response. A wealth of literature has explored the microbial changes underpinning reduced
347 crop yield following repeated planting (i.e., soil sickness; reviewed in Huang et al., 2013) and the
348 strengthening of conspecific microbial effects experienced by non-native plants after their intro-
349 duction (Diez et al., 2010, Dostál et al., 2013; but see Day et al., 2015). The temporal scale of these
350 studies typically spans hundreds of years. While this temporal pattern has been demonstrated
351 by experiments using soils with conditioning histories that span multiple generations, few studies
352 have generalized the traditional focus of single species to multiple species. In a unique greenhouse
353 experiment consisting of two rounds of soil conditioning by different combinations of six plant
354 species, Wubs and Bezemer (2018) demonstrated the complicated patterns arising from multiple
355 rounds of soil conditioning. Future work can expand upon Wubs and Bezemer (2018) to study
356 how the unique sequences of soil conditioning result in different plant–soil microbe interactions.
357 Another tightly interconnected aspect is the demographic facet of plant–soil microbial interactions:

358 as the responding individual matures, soil microbes can influence various demographic processes
359 in addition to varying biomass responses. We elaborate on this in the next section.

360 IV. Assessing multiple demographic consequences of soil microbes

361 Most two-phase experiments of plant–soil microbe interactions are designed to evaluate how
362 different soil microbial contexts influence plant biomass performance. Experimentally, the implicit
363 assumption is that individual biomass at the end of the experiment integrates all critical impacts
364 of the microbial community and that variation in individual biomass growth is predictive of
365 variation in population growth rates. This assumption corresponds well with the classic feedback
366 model of Bever et al. (1997), where microbes regulate the intrinsic growth rate of an exponentially
367 growing plant population. However, soil microbes can also alter other key demographic processes
368 throughout the plant life cycle that are not directly correlated with biomass accumulation (e.g.,
369 seed germination and pollinator visitation in Dudenhöffer et al., 2018). Dostálek et al. (2022)
370 demonstrated that it can be difficult to predict plant coexistence by using the microbial effect
371 measured at a single life stage—while biomass performance suggests self-limitation of both *Bromus*
372 *erectus* and *Inula salicina*, including microbial effects on seed germination and fruit production
373 suggests that both species in fact benefited from self-conditioned soil. Here, we highlight key
374 studies that provide insights into microbial control over non-biomass plant demographic processes,
375 with a particular focus on early life stage transitions.

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

377 Soil microbes can have drastic consequences on the early life stages of plants. While these effects
378 can arise from microbial effects on distinct life history processes (i.e., seed survival, germination,
379 and early seedling survival; Fig. 5), empirical studies often group them together given the logistical
380 challenges of separating these effects in field settings. For example, when studying long-lived
381 plants such as forest trees, repeated demographic censuses are often used to monitor seed-to-
382 seedling transitions (e.g., Harms et al., 2000, Swamy et al., 2011). A large body of evidence
383 for microbial effects on plant early life stages comes from field studies finding that fungicide

384 applications alter patterns of seed and seedling demography (e.g., Bell et al., 2006, Bagchi et al.,
385 Krishnadas et al., 2018, 2020, Song and Corlett, 2022). Many of these studies are conducted
386 to evaluate soil microbes as potential drivers of the Janzen–Connell hypothesis (Janzen, 1970,
387 Connell, 1971) and conspecific negative density-dependence (CNDD). These hypotheses suggest
388 that the aggregation of host-specific enemies around adult plants reduces the survival probability
389 of seedlings that disperse close to adults and under high conspecific densities. While evaluating the
390 compound microbial effect across multiple early life stages can yield important insights, studies
391 that isolate microbial effects on specific underlying demographic transitions (Fig. 5) can enable
392 a nuanced and mechanistic understanding of microbial effects on plant population dynamics
393 (Krishnadas and Comita, 2019).

394 Soil-borne pathogens can cause substantial mortality at the seed stage across biomes (e.g.,
395 Kotanen, 2007, Sarmiento et al., 2017, Li et al., 2019). One system where the impact of fungal seed
396 pathogens has been systematically dissected is that of pioneer tree species in neotropical forests,
397 especially those in the genus *Cecropia*. As pioneer species whose seeds need to germinate quickly
398 in response to new gap openings, these species produce seeds that can persist in the soil until the
399 formation of nearby gaps. These seeds are vulnerable to pathogen attack during their time in the
400 soil seed bank, and as a result, fungicide treatments can nearly double their survival and emergence
401 (Dalling et al., 1998, Gallery et al., 2010). Moreover, Dalling et al. (1998) found that seeds were more
402 susceptible to pathogen attack in soils close to conspecific adults than in soils far from conspecifics,
403 implicating soil pathogens as potential drivers of Janzen–Connell dynamics. Furthermore, recent
404 advances have employed molecular methods toward understanding longstanding questions about
405 pathogen host specificity. Zalamea et al. (2021) found that seeds of closely related *Cecropia* species
406 harbor vastly distinct fungal communities, with species identity explaining substantially more
407 variation than the seeds' location or their viability. Working with a more diverse group of pioneer
408 tree species, Sarmiento et al. (2017) showed that while many fungi can grow on seeds of multiple
409 plant species, their effects on seed mortality are highly species-specific. Together, this series of
410 studies has highlighted soil-borne fungal seed pathogens as key microbial players in the dynamics
411 of pioneer trees in tropical forests. While quantifying microbial effects on seed survival requires
412 laborious methods (e.g., tetrazolium staining for testing seed viability; Sarmiento et al., 2017), a

413 better understanding of these effects is critical given that seed limitation can be a bottleneck on
414 plant population dynamics (Harper, 1977, Clark et al., 2007).

415 Soil microbes can also affect the rates and timing of germination. Such regulation primarily
416 arises due to the production and/or metabolism of key germination-related phytohormones like
417 gibberellins (reviewed in Keswani et al., 2022 and Bottini et al., 2004) or ethylene (reviewed in
418 Ravanbakhsh et al., 2018 and Ishaq, 2017). While studies of how soil microbes regulate germination
419 have historically focused on managed settings, evidence that microbes also affect germination in
420 natural settings is now accumulating. In one of the few two-phase experiments focused on pairwise
421 feedback effects on germination, Miller et al. (2019) found species-specific effects of conditioned
422 microbes on germination. Specifically, the legume *Desmodium illinoense* achieved lower germination
423 rates in conspecific-conditioned soils than in sterilized or heterospecific-conditioned soils, while
424 germination of *Bromus inermis* and *Solidago canadensis* was unaffected by soil microbes. Across
425 a large-scale microcosm experiment, Eldridge et al. (2021) found that soil bacterial and fungal
426 communities help explain substantial variation in patterns of seed germination across nine plant
427 species, suggesting a relationship between soil microbes and plant germination that is not explained
428 simply by their shared responses to abiotic soil properties. Even when soil microbes do not affect
429 overall rates of germination, they can alter the phenology of germination (Keeler and Rafferty,
430 2022) which could either harm (e.g., if later germination reduces seedlings' performance due to
431 competition; Orrock and Christopher, 2010) or benefit population growth (e.g., if later germinating
432 seedlings escape severe competition or avoid abiotic stress; Leverett et al., 2018).

433 Finally, soil microbes also play a key role in determining the survival of seedlings after
434 germination. The widespread role of mycorrhizal symbioses in promoting seedling survival and
435 the potential for soil-borne pathogens to cause mortality among seedlings have been studied for
436 decades and reviewed elsewhere (e.g., Gilbert, 2002, Horton and van der Heijden, 2008). Recent
437 advances have focused on elucidating the relative role of harmful and beneficial soil microbes
438 in driving seedling survival and establishment across different environmental contexts, including
439 abiotic conditions (Bingham and Simard, 2011, Lebrija-Trejos et al., 2023), the relative abundance of
440 conspecific and heterospecific adults (Teste et al., 2017), and the functional groups of mycorrhizal
441 fungi (Liang et al., 2016, Bennett et al., 2017). In addition to studies that directly track the fate of

442 newly germinated seedlings in specific microbial contexts, studies that monitor the fate of older
443 plant individuals also often speculate soil microbes as the underlying mechanism (e.g., CNDD
444 studies on the survival of larger individuals; Comita et al., 2010). While, in comparison, the
445 effect of soil microbes on seedling survival has rarely been the target variable in biomass-focused
446 greenhouse experiments, recent studies have also started to quantify the contribution of this
447 demographic process to microbe-mediated coexistence (Dudenhöffer et al., 2022, Chung et al.,
448 2023, Pajares-Murgó et al., 2024).

449 IV.2 Microbial effects beyond early life stages

450 As seedlings establish and grow into reproductive adults, the soil microbial community continues
451 to affect their performance in various ways that are not captured by experiments focusing only on
452 plant biomass. For example, studies from forest pathology have shown that soilborne fungi and
453 oomycetes can directly cause adult mortality via root rot diseases, often with long-term impacts
454 on spatial structure and gap dynamics in forest communities (Hansen and Goheen, 2000, Liu et al.,
455 2007, Das et al., 2016, Ruiz Gómez et al., 2019). Experimental studies have also shown that soil
456 microbes can influence the fruit production of herbaceous species (Dostálek et al., 2022), but such
457 direct evidence is notably scarce in natural forest systems. In other cases, soil microbes might have
458 equally important implications for plant population dynamics through less direct pathways. For
459 example, over the past decade, evidence of microbial regulation of flowering phenology across
460 systems has become widespread (Lau and Lennon, 2012, Wagner et al., 2014, Igwe et al., 2021,
461 Lu et al., 2018). Although the consequences of such phenological shifts at the population level
462 are seldom quantified, the few-day differences reported in these studies could in principle have
463 drastic consequences for plant fitness, especially under abiotic stress when earlier flowering can
464 be crucial to reproductive success and fitness (reviewed in Kazan and Lyons, 2016, O'Brien et al.,
465 2021). The soil community can also regulate plant susceptibility to invertebrate herbivores (e.g.,
466 Howard et al., 2020, Pineda et al., 2020, Kalske et al., 2022), with such effects likely arising due to
467 soil microbe-induced changes in leaf metabolomes or volatile organics (Kalske et al., 2022, Huberty
468 et al., 2022). The consequences of microbe-mediated shifts in plant–herbivore interactions on insect
469 population dynamics are becoming increasingly well-studied (reviewed in Shikano et al., 2017),

470 but whether these changes affect plant population dynamics is less well established. Further
471 complicating efforts to project microbial consequences across a plant's lifetime are that these
472 effects can be uncorrelated or even contradictory across a plant's lifetime (Dostálek et al., 2022).
473 For example, Dudenhofer et al. (2018) found that conspecific-conditioned soil microbes promote
474 juvenile plant growth but hinder adult growth. Integrating these effects across the plant's lifetime
475 reveals a net negative impact of conspecific soil in plant fitness — a result that would contradict
476 inferences based on the juvenile stage alone. Thus, variable impacts of soil microbes across plant
477 ontogeny and/or demographic processes could contribute to demographic compensation in plant
478 population dynamics (Villellas et al., 2015). The integration of these microbial effects remains an
479 ongoing challenge, particularly in long-lived plants.

480 IV.3 Implications for experimental design

481 While incorporating all aforementioned demographic impacts of soil microbes is logically chal-
482 lenging, we also see a path forward. Current experimental studies of plant–microbe interactions
483 often transplant pre-germinated seeds into conditioned soils, thereby neglecting the impact of soil
484 microbes on seed survival and germination. Accordingly, a first step in enhancing our under-
485 standing of this phenomenon is for two-phase studies to plant ungerminated seeds and report
486 germination rates along with the biomass performance and survival rates of germinated plants.
487 Studies can employ statistical approaches (Dudenhofer et al., 2022, Chung et al., 2023) or other
488 population demographic models (David et al., 2019, Dostálek et al., 2022) to integrate the impact
489 of microbes on multiple early-stage transitions (see also section V.). Moreover, for short-lived
490 plants, one can aim to follow the entire plant life cycle. For example, Dostálek et al. (2022) doc-
491 umented seedling establishment and biomass dynamics for two growing seasons, and recorded
492 final fruit production of plants in different soil microbial backgrounds. While such an experiment
493 is more challenging, the matrix population model parameterized by Dostálek et al. (2022), where
494 soil microbes modulate transition probabilities across states, enables a more nuanced estimate of
495 microbial impact compared to solely relying on biomass-based metrics. Finally, while the longevity
496 of forest trees precludes direct experimental evidence, one may leverage natural experiments to
497 observe differences in demographic rates across sites with varying disease severity (Cobb et al.,

498 2020).

499 Compared to greenhouse-based plant–soil feedback studies that focus on biomass perfor-
500 mance, CNDD studies using field census data are arguably more directly linked to population
501 growth due to their emphasis on individual survival. However, observational CNDD studies can
502 be limited as it is challenging to attribute demographic patterns to soil microbes, and the impact
503 of heterospecifics, which are necessary to infer coexistence outcomes, is sometimes overlooked.
504 We propose that controlled experiments could complement census data for more mechanistic in-
505 sights. For example, field-based biocide experiments have been used to identify soil microbes
506 as key drivers of Janzen–Connell effects in seed and seedling mortality (Bell et al., 2006, Bagchi
507 et al., 2010, Song and Corlett, 2022, Krishnadas and Comita, 2018). Furthermore, one can add a
508 heterospecific treatment designed to assess heterospecific effects, as well as a reference treatment
509 in randomly located field soil to estimate the frequency-independent microbial impact on survival.
510 These additional treatments allow the interpretation of plant–soil microbe interactions with the
511 framework of modern coexistence theory, which emphasizes that coexistence requires stabiliza-
512 tion (niche difference) to be greater than the competitive hierarchy (fitness difference) between
513 species (Kandlikar et al., 2019, Ke and Wan, 2020). Greenhouse experiments can also be adapted
514 to capture the density-dependent microbial effects implicit in CNDD studies. To this end, one can
515 use field-conditioned soil from locations with varying adult densities or perform a pot experiment
516 with varying seedling densities (Ke and Wan, 2023). These modifications in study design can help
517 bridge the gap between microbial impacts inferred from experiments and field census data.

518 Finally, we argue that researchers should identify the demographic process that acts as a
519 bottleneck for plant population growth in the focal system and prioritize studying the microbial
520 impact on that specific demographic process. For example, in communities dominated by species
521 with persistent seed banks, the microbial effect on seed survival may be particularly important.
522 In systems where plant germination is highly constrained by soil-borne pathogens, germination
523 success in soils with different conditioning histories should be measured. We also recognize
524 that in some plant communities, individual biomass growth indeed correlates well with critical
525 demographic processes. For annual plants, individual biomass at the time of peak flowering may
526 reflect fecundity (Neytcheva and Aarssen, 2008, Younginger et al., 2017). For forest trees, since

527 seedling survival beneath the forest canopy is often size-dependent (Chang-Yang et al., 2021),
528 microbial effects that reduce seedling biomass can translate to higher mortality and thus have a
529 clear demographic consequence on plant populations. However, while individual biomass can
530 serve as a proxy for population growth in these particular systems, it is crucial to recognize that
531 the underlying demographic process enabling this interpretation varies among systems.

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

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

544 **V.1 Patch occupancy models**

545 Patch occupancy models represent a relatively straightforward framework for studying plant–soil
546 microbe interactions (Pacala and Tilman, 1994, Mouquet et al., 2002). In this group of models,
547 plants compete for unoccupied sites (patches) and the probability that a particular plant species
548 establishes in a local site depends on the site’s microbial legacy (Stump and Comita, 2018, Miller and
549 Allesina, 2021, Ke and Levine, 2021). Such models can either be spatially implicit, which assumes
550 that the landscape can be divided into an infinite number of patches and tracks the proportion of
551 different plant–soil microbe states (e.g., Miller and Allesina, 2021, Ke and Levine, 2021), or spa-
552 tially explicit, which considers a fixed-size arena and allows one to consider spatial proximity when

modeling microbial impact (e.g., the diffusion of microbial effects from live individuals nearby; Bever et al., 1997, Mack and Bever, 2014, Bauer et al., 2015). Detailed formulation aside, a common assumption in such models is that plants only indirectly influence each other by modifying soil microbial legacies. This assumption aligns well with two-phase experiments that grow individual plants in soils with different conditioning histories, and as such, patch occupancy models can be readily parameterized with biomass measurements from pot experiments (e.g., by assuming establishment probability scales with the relative biomass performance). Alternatively, patch occupancy models can also be parameterized with recruitment data from repeated censuses, thereby incorporating microbial effects on multiple early life stages (e.g., seed survival, germination, and seedling survival in Fig. 5; Krishnadas and Stump, 2021). Due to this connection with empirical data, patch occupancy models are commonly used in the PSF literature when studies wish to extrapolate predictions based on pairwise biomass-based metrics to multi-species communities (e.g., Mangan et al., 2010, Teste et al., 2017, Dudenhöffer et al., 2022). Recent theoretical studies have also suggested that patch occupancy models, through competition for limited colonization sites, generate more interpretable frequency-based dynamics for multi-species communities than do direct extensions of the classic pairwise feedback model (Miller et al., 2022).

The patch occupancy framework offers a pathway to effectively incorporate various temporal aspects of plant–soil microbe interactions (see an example in Box 1 and Fig. 6). This is because such models can treat different developmental stages of the soil microbial community as distinct states so that the transitions between states reflect the conditioning and decay rates of soil microbes. The explicit inclusion of microbial legacies in the form of an unoccupied but conditioned patch state differs from previous feedback models, which usually assume tight coupling between plants and microbes (Eppinga et al., 2018, Mack et al., 2019). For example, Ke et al. (2021) modified a previous model (Fukami and Nakajima, 2013) by making microbial effects vary with the duration of soil conditioning, which in turn influences the transient trajectory of community assembly. In another example, Ke and Levine (2021) used a spatially implicit model to show that the strength of stabilization driven by host-specific pathogens depends on how quickly the conditioning effects of plants erode. The above models directly track the changes of microbial impact on plants through time, and can thus be parameterized with the type of experiments mentioned in subsection III.3.

582 Alternatively, one can build simulation-based models that explicitly track the population size of
583 microbes at each local site, allowing the temporal development and decay of microbial effects to
584 emerge naturally (Schroeder et al., 2020). However, such models are harder to parameterize with
585 empirical data since they require detailed knowledge of microbial traits and population dynamics
586 (Jiang et al., 2020).

587 **V.2 Models incorporating multiple demographic processes**

588 In contrast to patch occupancy models, which usually assume that microbes only impact the
589 establishment process, one can also formulate models that directly consider distinct microbial
590 impacts on distinct plant demographic processes. Although this approach demands extensive
591 parameterization, it allows for system-specific tailoring and may prove to be especially valuable in
592 demographically complex systems. Demonstrating the power of this approach, a series of studies
593 (Mordecai, 2013a,b, 2015, Uricchio et al., 2019) integrated models and empirical observations
594 to investigate how pathogens affect competition between native perennials and invasive annual
595 grasses. The plant demography components of these models begin with an approach often used
596 for annual plants: they track the yearly population of each species' seeds, which persist in the soil
597 seed bank from previous years or are produced by reproductive-stage individuals, and capture the
598 effect of plant competition through density-dependent decreases in seed production (Fig. 2A; see
599 also section II. and Box 2). The authors then incorporated perennial demography by additionally
600 tracking the number of adult perennials, reflecting successful seed germination and recruitment,
601 as well as adult survival from the previous year. This model structure can flexibly incorporate
602 the effect of microbes by allowing them to modify various demographic transitions; in particular,
603 the authors focused on a soil-borne pathogen that reduces seed persistence and germination
604 (Mordecai, 2013a). With a plant competition experiment and manipulations of pathogen densities,
605 Mordecai (2013b) parameterized a model with density-dependent microbial effects and concluded
606 that pathogen spillover promotes the persistence of perennial bunchgrasses. Subsequent work
607 further demonstrated the adaptability of this framework: Mordecai (2015) showed that the plant
608 life stage attacked by pathogens (i.e., seedlings or dormant seeds) and environmental variation
609 jointly determined the coexistence of competing annual plants. In another application, Uricchio
610 et al. (2019) parameterized an even more realistic model, considering multiple annual and perennial

611 species and incorporating two additional microbial effects (i.e., the impacts of foliar pathogens on
612 seedling survival and adult perennial fecundity).

613 In addition to integrating multiple microbial effects, a demographically explicit model can
614 help identify the most critical microbial effect via simulations. For instance, in the annual–perennial
615 plant model in Uricchio et al. (2019), foliar pathogens have little impact but seed pathogens can
616 have a more significant effect on perennial competitors in the system. Such a sensitivity analysis
617 is particularly useful when models include many mechanistic parameters for microbial dynamics
618 (e.g., Ke et al., 2015, Schroeder et al., 2020) and represents another reason why isolating microbial
619 effects on specific demographic transitions can be enlightening. Even for models that do not
620 explicitly incorporate microbial dynamics, identifying the bottleneck for population growth can
621 provide insights for future studies and guide more targeted experiments. Using an integral
622 projection model parameterized with long-term demographic data, Chu and Adler (2015) showed
623 that feedback loops during the recruitment stage contributed most to plant coexistence compared
624 to those during the growth and survival stages. The authors speculated that this is due to the
625 recruitment stage involving many demographic transitions that are susceptible to soil pathogens
626 (Chu and Adler, 2015). In Box 2, with an annual–perennial plant model incorporating microbial
627 effects as qualitative switches in parameter values, we also demonstrate how sensitivity analysis can
628 help identify the relative importance of different microbial effects on the perennial plant (Fig. 7).
629 In sum, formulating demographic models not only allows smooth integration of the temporal
630 and demographic dimensions of plant–soil microbe interactions but also provides an opportunity
631 to explore their consequences in multi-species communities. Nonetheless, parameterizing such
632 models for long-lived plants remains a significant ongoing challenge.

633 While we presented two separate modeling frameworks for incorporating temporal and
634 demographic components, in practice, both approaches are flexible and can be used to answer
635 multiple research questions. For instance, decay dynamics and time-dependent feedback can also
636 be built into a demographically explicit model (e.g., (Senthilnathan and D'Andrea, 2023); see also
637 Zou et al., 2024 for a discrete-time model with explicit consideration of the temporal dynamics of
638 soil microbes). Ultimately, the choice depends on the research question and the focal plant–soil
639 system. For example, in systems affected by wind (Nagendra and Peterson, 2016) or fire distur-

bances (Senior et al., 2018) that may truncate soil conditioning at different timings, or those where low propagule availability prevents immediate recolonization of conditioned soils, investigating the temporal dimension can yield valuable insights; such analyses can also be performed using individual-based models (Zee and Fukami, 2015). On the other hand, when different soil microbes are known to impact different phases of the plant life cycle, integrating these microbial effects into a demographic model may be more important. For example, in the pyrogenic Florida scrub ecosystem, David et al. (2019) parameterized an integral projection model (IPM) for the endangered perennial herb *Hypericum cumulicola*, incorporating positive microbial effects on germination estimated via a greenhouse experiment. Their simulations indicated that soil microbes increased the number of post-fire years with positive population growth, particularly in high-elevation and low-nutrient patches. Together, these examples illustrate that system-specific models are key to tailoring predictions to the ecological contexts that shape plant–soil microbe interactions.

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

Since its introduction to community ecology, the study of plant–soil microbe interactions has long been shaped by a tight link between empirical and theoretical approaches. By showing how empirically tractable greenhouse experiments can yield data to calculate theory-derived metrics, the approach from Bever et al. (1997) has motivated more than two decades of research to predict the long-term consequences of soil microbes (Crawford et al., 2019a). To date, new studies continue to follow this integration, proposing new theories to capture different impacts of soil microbes as well as new experimental designs to quantify them (e.g., Kandlikar et al., 2019, 2021, Yan et al., 2022a). Two key assumptions of this approach are that plant-soil microbe interactions follow a simplified temporal trajectory and that measuring microbial impact on plant biomass captures the population dynamic consequences of soil microbes. While such abstractions have helped make models generalizable, growing evidence has proven the relevance of the two knowledge gaps when predicting the role of soil microbes in natural communities (Chung, 2023). As such, we see tremendous value in future efforts that aim to (1) develop theoretical models that can explicitly

incorporate the temporal and demographic components of plant–soil microbe interactions, and (2) parameterize such models with corresponding observational data or experiments aimed at quantifying these past-missing components. Advancing research through the integration of empirical and theoretical approaches not only brings us closer to the long-standing goal of precisely predicting microbial effects in the field but also sharpens our ability to identify the key axes of variation underlying plant–soil microbe interactions.

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

Designing new experiments that provide the necessary information to parameterize new plant demographic models of plant–soil microbe interactions is another frontier of research. Some models require experiments that are similar to the current two-phase experiments. For instance, to depict temporal development patterns, one can repeat an experiment along naturally occurring variations in the duration of soil conditioning. However, some microbial effects cannot be reliably estimated by classic two-phase experiments with a single-growing plant individual. For example,

696 if microbes are expected to affect not only plant intrinsic growth rate but also the nature of
697 density dependence among plants, then estimating microbial effects requires additional treatments
698 beyond the classic two-phase design. Recent studies linking plant–soil microbe interactions and
699 coexistence theory specifically highlight this scenario where soil microbes influence the model’s
700 density dependence parameters (Kandlikar et al., 2019, Ke and Wan, 2020, Zou et al., 2024),
701 which require employing experiments that directly manipulate plant density and soil origin (e.g.,
702 Chung and Rudgers, 2016, Cardinaux et al., 2018). An empirical–theoretical feedback loop is also
703 central to the design of such theory-driven experiments. For example, Ke and Wan (2020) initially
704 proposed a simplified experimental design based on the premise that plant–plant interactions are
705 exclusively competitive. However, when empiricists implemented the experimental design with
706 low neighbor density, they sometimes found facilitative interactions that rendered our original
707 analytical approach inapplicable (e.g., Wang et al., 2024, Willing et al., 2024). This feedback
708 prompted us to develop a revised density gradient design as a solution with greater flexibility
709 for untangling facilitative or nonlinear microbial effects (Ke and Wan, 2023). Again, the optimal
710 approach depends on feasibility and reflects which research question can provide a fundamental
711 understanding of the focal plant–soil system.

712 Understanding the temporal dimensions of plant–soil microbe interactions in forest systems
713 remains a difficult challenge. Fortunately, recent census-based CNDD studies have introduced a
714 promising approach to investigate how microbe-mediated plant demography interacts with the
715 three temporal aspects, namely, the duration of soil conditioning, the life stage of responding plants,
716 and the time delay between consecutive colonizing plants. Current CNDD studies often calculate
717 size-weighted abundance when estimating conspecific densities, thereby implicitly considering soil
718 conditioning time by linking plant size to microbial effects. Additionally, microbial communities
719 associated with plants of different ages can be sequenced to examine the relationship between
720 pathogen accumulation and species’ CNDD strength (Chen et al., 2019). Long-term observational
721 data should also allow us to test whether conspecific effects change with the age/stage of the
722 responding focal individual (Bagchi et al., 2014, Zhu et al., 2015, 2018). For instance, Zhu et al.
723 (2015) showed that the CNDD effects attenuated as individuals mature from seedlings to adults.
724 Finally, a recent study also pioneered the inclusion of dead tree individuals into the abundance

725 calculation (i.e., the effects of decay; Magee et al., 2024). Insights from such CNDD studies can be
726 used to parameterize patch occupancy models with corresponding temporal aspects, offering new
727 insights by integrating the two overlooked components for long-lived plants.

728 One of the remaining challenges is to move away from a plant-centered viewpoint towards a
729 better understanding of the dynamics and functionality of soil microbial communities (Jiang et al.,
730 2020). Incorporating microbial community assembly processes can help inform which processes
731 need to be prioritized when building mechanistic models of microbial community dynamics
732 (e.g., Schroeder et al., 2020, Zou et al., 2024). Empirically, experiments that establish the causal
733 relationship between measured microbial dynamics and plant demographic responses can help
734 feed theory with realistically parameterized temporal patterns. To this end, a starting point is
735 to simultaneously measure shifts in both plant response and microbial community composition
736 within studies that vary the temporal components (e.g., Esch and Kobe, 2021, Ke et al., 2021,
737 Hannula et al., 2021). Measuring responses such as mycorrhizal percentage colonization and how
738 they vary over time can also help bridge plant-centric and microbe-centric viewpoints (e.g., Bennett
739 et al., 2023). However, given the functional plasticities and redundancies of microbial communities,
740 improvements in identifying microbial functionality beyond that based on taxonomic information
741 are also needed (see also Carini et al., 2016 for technical challenges related to erroneously detecting
742 DNA from dead microbes in sequencing time series). Explicit quantification of microbial activity,
743 such as measurements through multi-omics outputs, can allow for better modeling of functional
744 microbial dynamics. Future studies balancing both the plant and microbe perspectives can further
745 facilitate the empirical–theoretical feedback loop when studying the two missing components of
746 plant–soil microbe interactions.

747 In summary, we conclude that studying the temporal dimension and the multiple demo-
748 graphic consequences of plant–soil microbe interactions provides a better understanding of their
749 natural context. One outstanding question in the literature is how to predict the seemingly id-
750 iosyncratic nature of plant–soil microbe interactions (i.e., its context-dependency; De Long et al.,
751 2019, Cheng et al., 2024). Recognizing that soil conditioning and plant response are temporally
752 varying processes suggests that time itself may serve as a hidden axis of variation: the same en-
753 vironmental shift alters temporal trajectories differently depending on its timing. The temporal

dimensions also underscore the significance of phenological mismatches among plants and soil microbes driven by climate change (Rudgers et al., 2020; e.g., late-germinating plants may be more affected by pathogens). As experiments incorporate environmental shifts and employ models to generate predictions (e.g., the impact of drought on plant diversity; Dudenhöffer et al., 2022), embracing the empirical–theoretical feedback loop can further refine the experimental design and enhance our ability to predict responses under real-world settings (e.g., changes in the degree of precipitation variability). Ultimately, knowledge of the system’s natural history should guide researchers to recognize which aspects of the temporal and demographic components are important for the focal system and the research question. With the most critical aspect being identified, we believe that parameterizing new demographic models provides an avenue to predict the long-term consequences of plant–soil microbe interactions against the backdrop of real-world conditions in which these interactions unfold.

766 Boxes

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

Here, we demonstrate how the temporal decay of microbial effects can be studied with a multi-species patch occupancy model. We considered three different plant–soil microbe states (Fig. 6A): unconditioned soil (P_{00}), soils colonized and conditioned by plant i (P_{ii}), and uncolonized soils with a microbial legacy (P_{0i}). The transition among these different states can be described as follows (see also Ke and Levine, 2021 and Miller and Allesina, 2021):

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

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

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

Specifically, state transitions occur due to plant colonization/soil conditioning (r_i), plant mortality (m_i), and the decay of microbial effects (d_i , black arrows in Fig. 6A). Here, soil microbes affect the ability of plants to recolonize conditioned soils (red arrows in Fig. 6A). N represents the total number of species within the community.

To illustrate the consequences of variable decay rates of microbial effects, we simulated the microbial effects (σ_{ij}) for 16 plant species with data from Teste et al., 2017, which measured soil microbial effects on plant biomass accumulation. We randomly drew species' fecundity (r_i) from a uniform distribution between 0.2 to 0.25. This simulation illustrates how the decay rates of microbial effects determine the overall consequences of soil microbes on plant communities (Fig. 6B & C). Specifically, with this parameterization and when microbial effects persist after host death (i.e., low d_i ; left panels in Fig. 6B & C), plant–soil microbe interactions mostly resulted in the dominance of a single species, overwhelming species'

Box 1 (continued)

variation in fecundity. However, if the conditioned microbial effect decayed rapidly after the death of host plants (i.e., high d_i ; right panels in Fig. 6B & C), variation in species' fecundity allowed higher diversity in each simulation and more equal persistence probability across species. Therefore, predicting the consequences of plant–soil microbe interactions in nature also requires quantifying the decay rate of greenhouse-measured microbial effects.

768

For Review Only

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

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

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

$$N_p(t+1) = \underbrace{s_p(1-g_p)N_p(t)}_{\text{survival of ungerminated seeds}} + \underbrace{A_p(t)\frac{\lambda_p}{1+\alpha_{pp}A_p(t)+\alpha_{pa}g_aN_a(t)}}_{\text{seed production by adult plants}} \quad (2)$$

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

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

For the perennial plant, there are five demographic parameters that can be affected by soil microbes (g_p , s_p , λ_p , v , and ξ). As demonstrated in section II., the first strength of a demographic model is that it can integrate multiple microbial effects. For example, in the case where soil pathogens decreased all parameters of the perennial plant by 20%, the model suggested that it would nearly be outcompeted by the annual plant (i.e., from grey to blue dashed line; Fig. 7). By only quantifying the impact of pathogens on the intrinsic fecundity (λ_p), as is commonly done in studies that grow individual plants in conditioned

Box 2 (continued)

soils, we would have underestimated the impacts of soil microbes in this system. The second strength of a demographic model is that it helps identify the most critical microbial effect for competitive outcomes. For example, sensitivity analysis (see Fig. 7 legend for details) revealed that, compared to other demographic parameters, the impact of pathogens on adult survival probability (ξ) had the strongest impact on the perennial plant population (Fig. 7).

771

For Review Only

772 Figure legends

773 **Figure 1.** Temporal dimensions of plant–soil microbe interactions throughout the repeated
774 process of plant establishment, growth, death, and recolonization by another individual. (A) The
775 common assumptions regarding plant–soil microbe interactions implied by the design of classic
776 experiments: microbial communities develop relatively quickly, with resulting microbial effects
777 that are constant throughout different plant life stages and remain as long-lasting legacies after
778 plant senescence to impact the next generation. (B) The dynamic plant–soil microbe interaction
779 perspective highlighted in our review: microbial communities change continuously throughout the
780 conditioning process, with impacts on plant performance that depend on both the duration of plant
781 conditioning and response (subsection III.1). Moreover, microbial communities and their impacts
782 on plant performance may diminish with time after the senescence of the previous conditioning
783 individual (subsection III.2) or undergo different trajectories depending on the previous rounds of
784 conditioning (mentioned as a future direction in subsection III.3). Different seedling and tree sizes
785 across the panels indicate varying plant responses (increasing upwards) to soil microbial effects
786 (increasing downwards). Created in BioRender (<https://BioRender.com/a8tl9rj>).

787 **Figure 2.** An example demonstrating how incorporating the temporal and demographic aspects
788 of plant–soil microbe interactions can generate different competitive outcomes in the annual plant
789 model. (A) A graphical representation of the Beverton–Holt annual plant model, which tracks the
790 density of seeds prior to germination. Demographic processes influenced by soil microbes in this
791 simulation are highlighted in red, including seed survival and the fecundity of germinated plants.
792 Brown and grey seeds represent viable and dead seeds, respectively. (B) Abundance time series of
793 N_1 (solid line) and N_2 (dashed line) under different microbial effect scenarios: no pathogenic effect
794 (grey), pathogens decrease the seed survival of N_1 (s_1 ; blue), and pathogens decrease the fecundity
795 of N_1 (λ_1 ; orange). The left panel assumes a 10% decrease in N_1 's demographic parameters, whereas
796 the right panel assumes that the initial 10% decrease after one generation aggravates to an 80%
797 decrease after eight generations (i.e., a 10% decrease after every generation). Note that the blue lines
798 often overlap the grey lines due to the minor impact of s_1 . Parameters are obtained from the species
799 pair *Festuca microstachys* (N_1) versus *Hordeum murinum* (N_2) in Van Dyke et al. (2022): $g_1 = 0.752$,
800 $g_2 = 0.667$, $s_1 = 0.134$, $s_2 = 0.045$, $\lambda_1 = 2129.950$, $\lambda_2 = 736.667$, $\alpha_{11} = 0.588$, $\alpha_{12} = 1.411$,
801 $\alpha_{21} = 0.109$, and $\alpha_{22} = 0.948$. Panel (A) created in BioRender (<https://BioRender.com/0kwj3z5>).

802

803 **Figure 3.** A summary of the experimental duration and life history information of the study species
804 in the Crawford et al. (2019b) and Yan et al. (2022b) data sets. Since the two studies focused on the
805 pairwise plant–soil feedback, we compiled information on plant life history and categorized each
806 pairwise comparison as different “pair types”: annual (both plants are annuals; orange), perennial
807 (both plants are perennials; green), or annual–perennial (match of an annual versus a perennial;
808 blue). Fully opaque pie charts represent studies that evaluated plant–soil feedback between annual
809 and perennial plants, with slice colors representing the percentage of different pair types within
810 the study (translucent points are single-color pie charts, representing studies that included only
811 annual or only perennial species). The position of each pie chart indicates the duration of a study’s
812 conditioning (x-axis; field-conditioned soil as a separate category) and response phase (y-axis). The
813 upper and right stacked histograms depict the same information but are based on the number of
814 experimental pairs across all studies. Note that one study with a conditioning length of 48 months
815 and a response length of 32 months (Kulmatiski, 2019) was excluded from the figure to improve
816 visualization. Data compiled from the publicly available dataset in Crawford et al. (2019b) and
817 Yan et al. (2022b) are available at <https://github.com/pojuke/DemographicReviewPSF>.

818 **Figure 4.** Experiments for studying plant–soil microbe interactions. (A) The classic two-phase
819 experimental design, consisting of a conditioning phase during which plants modify the soil mi-
820 crobial community and a response phase during which plants respond to the soil modification.
821 Depicted here in the response phase is the case of negative frequency-dependent feedback where
822 conditioned soils favor the performance of heterospecifics over conspecifics. (B) Proposed experi-
823 mental designs to study the various temporal dimensions in the main text (measuring the orange
824 plant’s performance in soils conditioned by the blue plant as an example): (i) isolating changes
825 in the soil microbial community by varying the duration of soil conditioning, (ii) sequential har-
826 vesting with both conditioning effect and plant age advancing simultaneously, (iii) isolating the
827 decay process by incorporating a time lag after soil conditioning, and (iv) isolating changes in plant
828 physiology by transplanting individuals of different age in the same conditioned soil. Created in
829 BioRender (<https://BioRender.com/yisnt7l>).

830 **Figure 5.** Conceptual diagram depicting multiple demographic consequences of soil microbes,
831 with a particular focus on early plant life stages following most empirical studies. The inner

832 circle (black arrows) indicates the distinct demographic processes that can be affected by soil
833 microbes; in the main text, we highlight empirical evidence on seed mortality, germination, and
834 early seedling survival. The outer circle (grey dashed arrows) indicates the life stages included
835 in different studies on conspecific negative density dependence (CNDD). Created in BioRender
836 (<https://BioRender.com/cyus4c6>).

837 **Figure 6.** An example demonstrating how the temporal decay of microbial effects can be studied
838 with a patch occupancy model. (A) Transitions among different plant-soil microbe states occur
839 due to plant colonization/conditioning, plant death, and the decay of microbial effects. Here, soil
840 microbes affect the ability of plants to recolonize conditioned soil (red arrows). (B & C) Diversity
841 of the plant community when microbial effects decay slowly ($d_i = 0.01$; left panels) or rapidly
842 ($d_i = 0.99$; right panels). We simulated the dynamics of 16 plant species (depicted with different
843 colors and letters). We ran 100 simulations; each time we randomly generated a new fecundity
844 value for each species (i.e., $r_i \sim U(0.2, 0.25)$) while fixing the microbial effect parameters based on
845 data from Teste et al. (2017). Panel (B) shows a representative time series of the relative abundance
846 of different plant species (frequencies of empty patches are omitted). Panel (C) shows the number
847 of times (out of 100 simulations) the focal species (x-axis; different species labeled with different
848 capitalized letters) persisted in the final community. Mortality (m_i) is set to 0.05 for all plants and
849 initial conditions are: $P_{00} = 0.2$, $P_{ii} = 0.05$ for $i = 1 \dots 16$, and $P_{0i} = 0.0$. See Box 1 for additional
850 details.

851 **Figure 7.** Detecting the most critical microbial effect within an annual-perennial plant competi-
852 tion model (modified from Uricchio et al., 2019). Here, soil microbes can impact five demographic
853 parameters of the perennial plant: seed germination rate (g_p), seed survival rate (s_p), intrinsic
854 fecundity (λ_p), seedling survival rate (v) and adult survival rate (ξ). The grey dashed line rep-
855 resents the relative abundance of the perennial plant in the absence of any pathogenic effects
856 from the microbes (i.e., unperturbed baseline parameters), while the dashed blue line shows the
857 perennial's relative abundance when the pathogen simultaneously causes a 20% reduction in all
858 five parameters. To evaluate the demographic consequences of microbes primarily impacting one
859 demographic process, we sequentially decreased the value of each parameter by 20%, while the
860 other four non-focal parameters were randomly decreased by 0% to 5% (assuming weaker micro-
861 bial impact). For each focal parameter, we repeated this process in 100 simulations (translucent

grey points; red points and error bars represent the means and standard deviations) and ran each simulation for 200 generations. These simulations reveal that soil pathogens that primarily reduce adult survival (ξ) have substantially stronger demographic consequences than pathogens that primarily affect other demographic processes. See Box 2 for model description. The baseline parameters are obtained from the species pair *Elymus glaucus* (our perennial) versus *Bromus diandrus* (our annual) in Uricchio et al. (2019) – perennial plant parameters: $g_p = 0.125$, $s_p = 0.515$, $\lambda_p = 282.127$, $\xi = 0.920$, $v = 0.292$; annual plant parameters: $g_a = 0.168$, $s_a = 0.443$, $\lambda_a = 47.594$; competitive reduction of seed production: $\alpha_{aa} = 0.066$, $\alpha_{ap} = 0.143$, $\alpha_{pp} = 0.018$, $\alpha_{pa} = 0.104$; competitive reduction of perennial survival: $\beta_{p,N_p} = 0.086$, $\beta_{p,A_p} = 0.063$, $\beta_{p,N_a} = 0.002$.

For Review Only

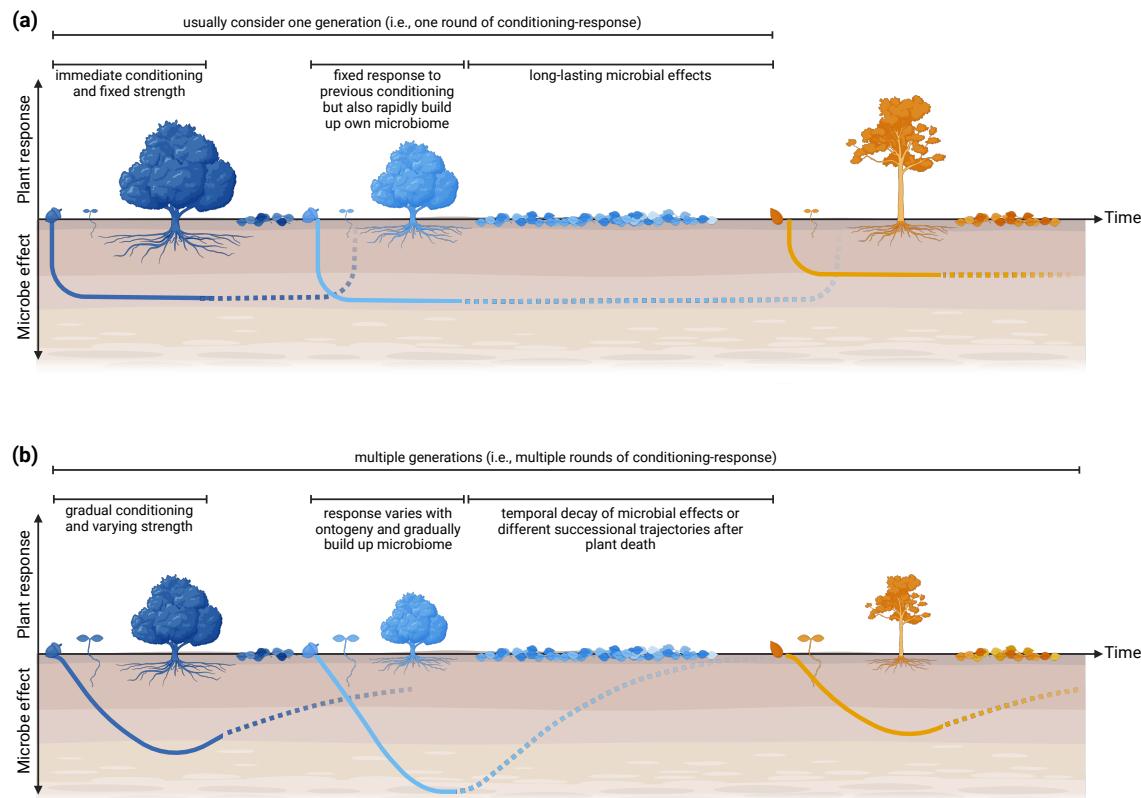


Figure 1 Temporal dimensions of plant–soil microbe interactions throughout the repeated process of plant establishment, growth, death, and recolonization by another individual. (A) The common assumptions regarding plant–soil microbe interactions implied by the design of classic experiments: microbial communities develop relatively quickly, with resulting microbial effects that are constant throughout different plant life stages and remain as long-lasting legacies after plant senescence to impact the next generation. (B) The dynamic plant–soil microbe interaction perspective highlighted in our review: microbial communities change continuously throughout the conditioning process, with impacts on plant performance that depend on both the duration of plant conditioning and response (subsection III.1). Moreover, microbial communities and their impacts on plant performance may diminish with time after the senescence of the previous conditioning individual (subsection III.2) or undergo different trajectories depending on the previous rounds of conditioning (mentioned as a future direction in subsection III.3). Different seedling and tree sizes across the panels indicate varying plant responses (increasing upwards) to soil microbial effects (increasing downwards). Created in BioRender (<https://BioRender.com/a8tl9rj>).

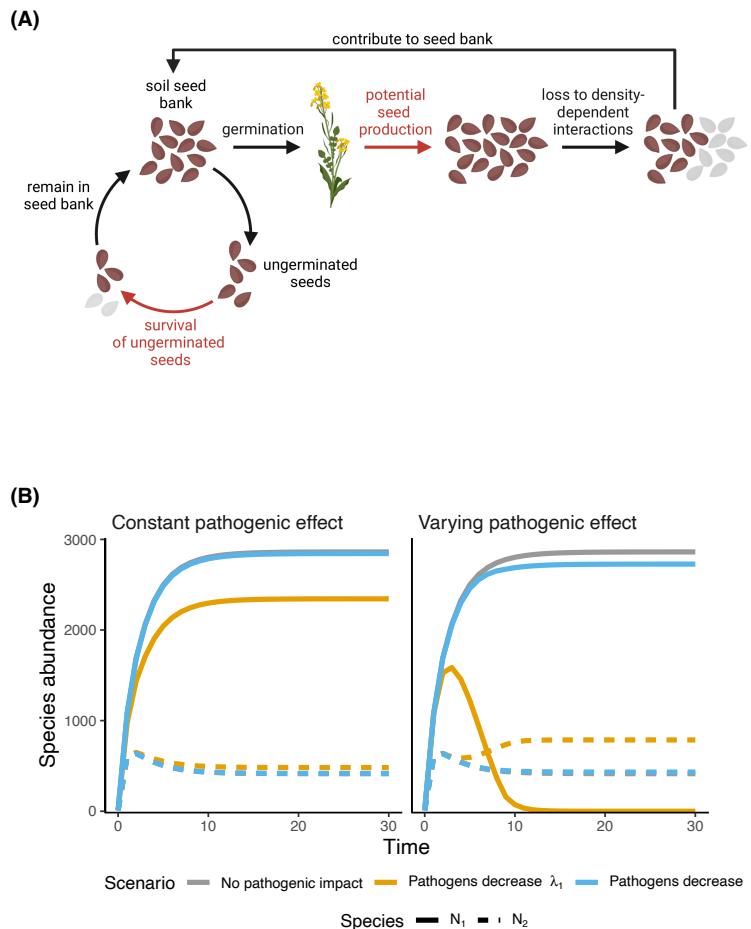


Figure 2 An example demonstrating how incorporating the temporal and demographic aspects of plant–soil microbe interactions can generate different competitive outcomes in the annual plant model. (A) A graphical representation of the Beverton–Holt annual plant model, which tracks the density of seeds prior to germination. Demographic processes influenced by soil microbes in this simulation are highlighted in red, including seed survival and the fecundity of germinated plants. Brown and grey seeds represent viable and dead seeds, respectively. (B) Abundance time series of N_1 (solid line) and N_2 (dashed line) under different microbial effect scenarios: no pathogenic effect (grey), pathogens decrease the seed survival of N_1 (s_1 ; blue), and pathogens decrease the fecundity of N_1 (λ_1 ; orange). The left panel assumes a 10% decrease in N_1 's demographic parameters, whereas the right panel assumes that the initial 10% decrease after one generation aggravates to an 80% decrease after eight generations (i.e., a 10% decrease after every generation). Note that the blue lines often overlap the grey lines due to the minor impact of s_1 . Parameters are obtained from the species pair *Festuca microstachys* (N_1) versus *Hordeum murinum* (N_2) in Van Dyke et al. (2022): $g_1 = 0.752$, $g_2 = 0.667$, $s_1 = 0.134$, $s_2 = 0.045$, $\lambda_1 = 2129.950$, $\lambda_2 = 736.667$, $\alpha_{11} = 0.588$, $\alpha_{12} = 1.411$, $\alpha_{21} = 0.109$, and $\alpha_{22} = 0.948$. Panel (A) created in BioRender (<https://BioRender.com/0kwj3z5>).

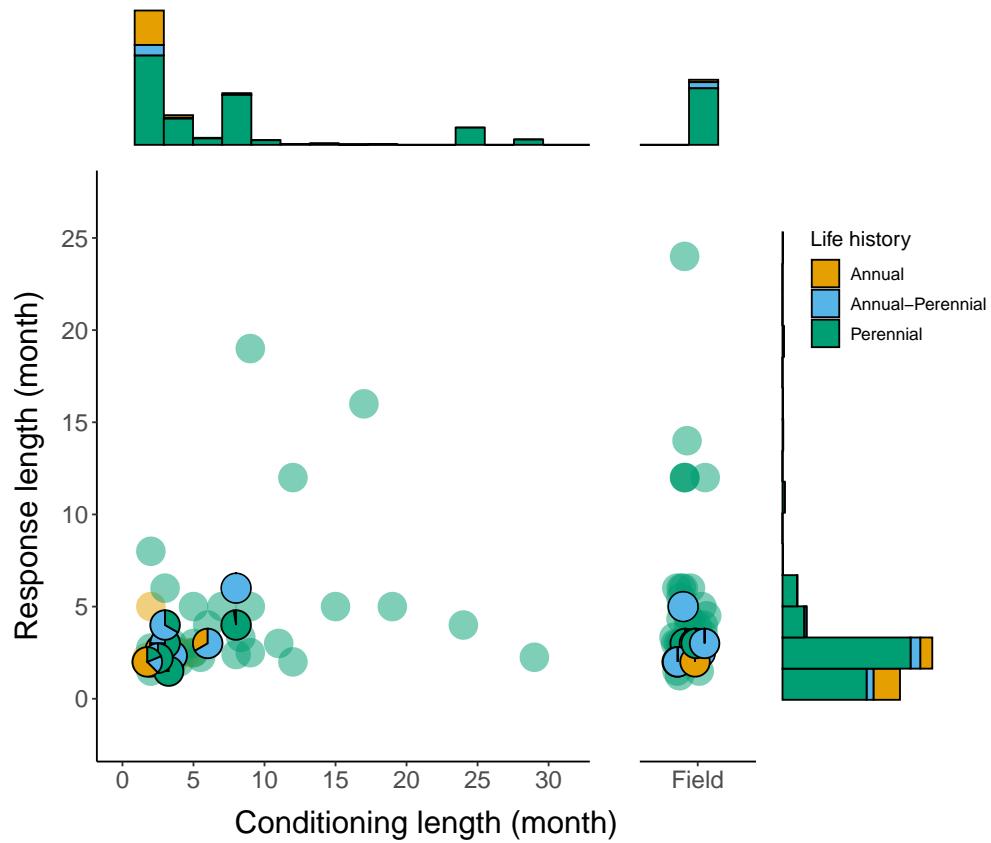


Figure 3 A summary of the experimental duration and life history information of the study species in the Crawford et al. (2019b) and Yan et al. (2022b) data sets. Since the two studies focused on the pairwise plant–soil feedback, we compiled information on plant life history and categorized each pairwise comparison as different “pair types”: annual (both plants are annuals; orange), perennial (both plants are perennials; green), or annual–perennial (match of an annual versus a perennial; blue). Fully opaque pie charts represent studies that evaluated plant–soil feedback between annual and perennial plants, with slice colors representing the percentage of different pair types within the study (translucent points are single-color pie charts, representing studies that included only annual or only perennial species). The position of each pie chart indicates the duration of a study’s conditioning (x-axis; field-conditioned soil as a separate category) and response phase (y-axis). The upper and right stacked histograms depict the same information but are based on the number of experimental pairs across all studies. Note that one study with a conditioning length of 48 months and a response length of 32 months (Kulmatiski, 2019) was excluded from the figure to improve visualization. Data compiled from the publicly available dataset in Crawford et al. (2019b) and Yan et al. (2022b) are available at <https://github.com/pojuke/DemographicReviewPSF>.

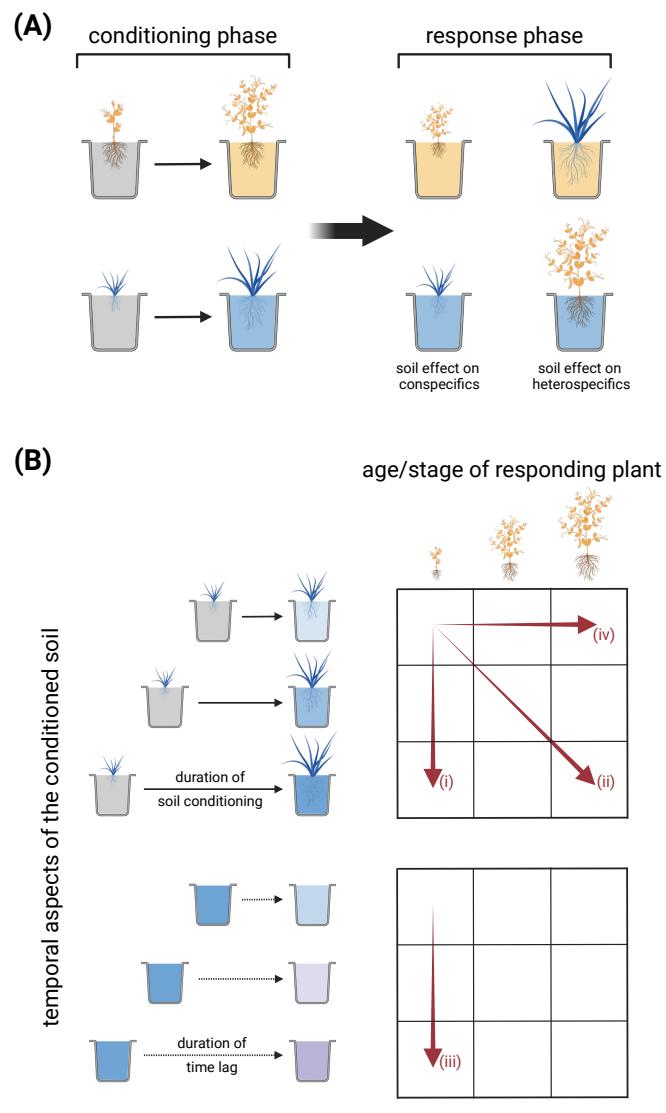


Figure 4 Experiments for studying plant–soil microbe interactions. (A) The classic two-phase experimental design, consisting of a conditioning phase during which plants modify the soil microbial community and a response phase during which plants respond to the soil modification. Depicted here in the response phase is the case of negative frequency-dependent feedback where conditioned soils favor the performance of heterospecifics over conspecifics. (B) Proposed experimental designs to study the various temporal dimensions in the main text (measuring the orange plant’s performance in soils conditioned by the blue plant as an example): (i) isolating changes in the soil microbial community by varying the duration of soil conditioning, (ii) sequential harvesting with both conditioning effect and plant age advancing simultaneously, (iii) isolating the decay process by incorporating a time lag after soil conditioning, and (iv) isolating changes in plant physiology by transplanting individuals of different age in the same conditioned soil. Created in BioRender (<https://BioRender.com/yisnt7l>).

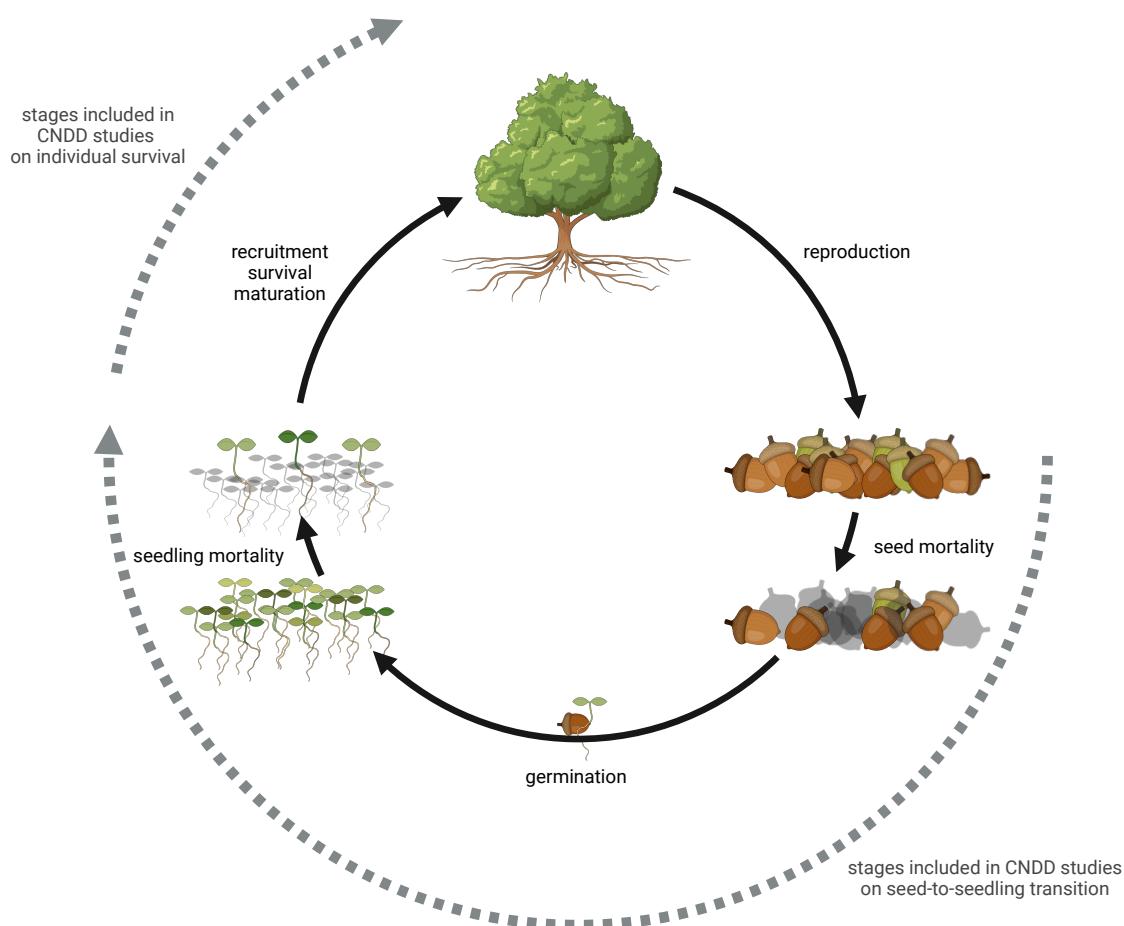


Figure 5 Conceptual diagram depicting multiple demographic consequences of soil microbes, with a particular focus on early plant life stages following most empirical studies. The inner circle (black arrows) indicates the distinct demographic processes that can be affected by soil microbes; in the main text, we highlight empirical evidence on seed mortality, germination, and early seedling survival. The outer circle (grey dashed arrows) indicates the life stages included in different studies on conspecific negative density dependence (CNDD). Created in BioRender (<https://BioRender.com/cyus4c6>).

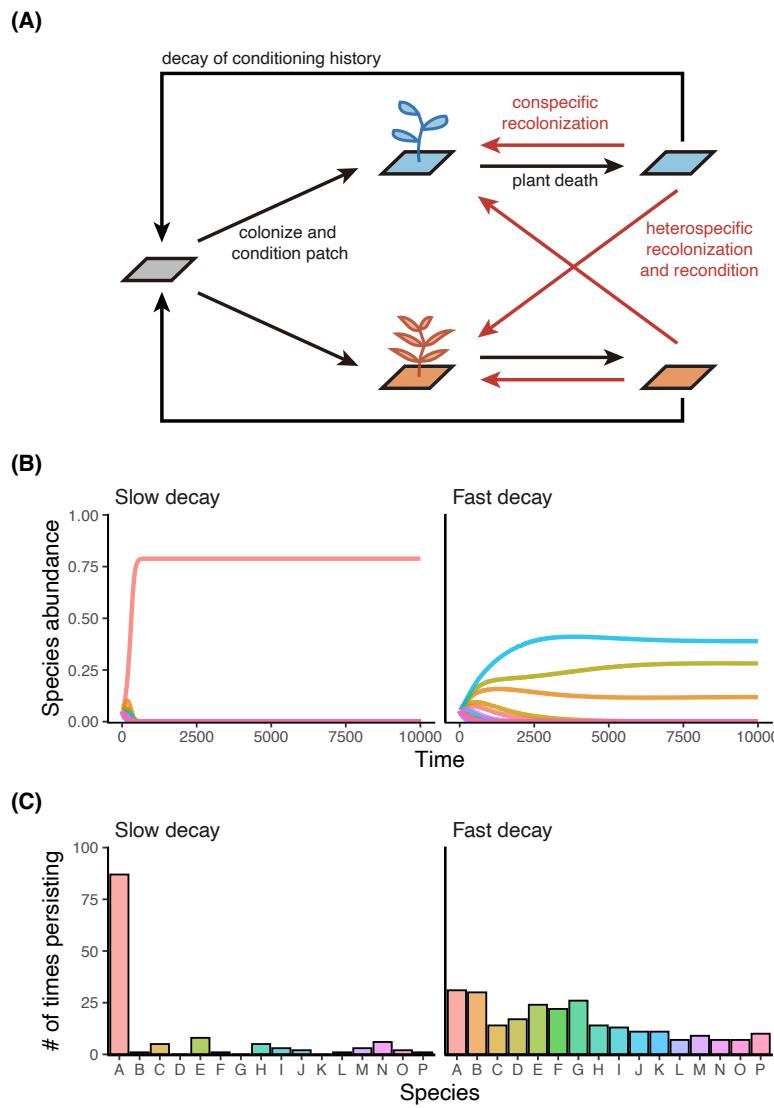


Figure 6 An example demonstrating how the temporal decay of microbial effects can be studied with a patch occupancy model. (A) Transitions among different plant-soil microbe states occur due to plant colonization/conditioning, plant death, and the decay of microbial effects. Here, soil microbes affect the ability of plants to recolonize conditioned soil (red arrows; modified from Ke and Levine, 2021). (B & C) Diversity of the plant community when microbial effects decay slowly ($d_i = 0.01$; left panels) or rapidly ($d_i = 0.99$; right panels). We simulated the dynamics of 16 plant species (depicted with different colors and letters). We ran 100 simulations; each time we randomly generated a new fecundity value for each species (i.e., $r_i \sim U(0.2, 0.25)$) while fixing the microbial effect parameters based on data from Teste et al. (2017). Panel (B) shows a representative time series of the relative abundance of different plant species (frequencies of empty patches are omitted). Panel (C) shows the number of times (out of 100 simulations) the focal species (x-axis; different species labeled with different capitalized letters) persisted in the final community. Mortality (m_i) is set to 0.05 for all plants and initial conditions are: $P_{00} = 0.2$, $P_{ii} = 0.05$ for $i = 1 \dots 16$, and $P_{0i} = 0.0$. See Box 1 for additional details.

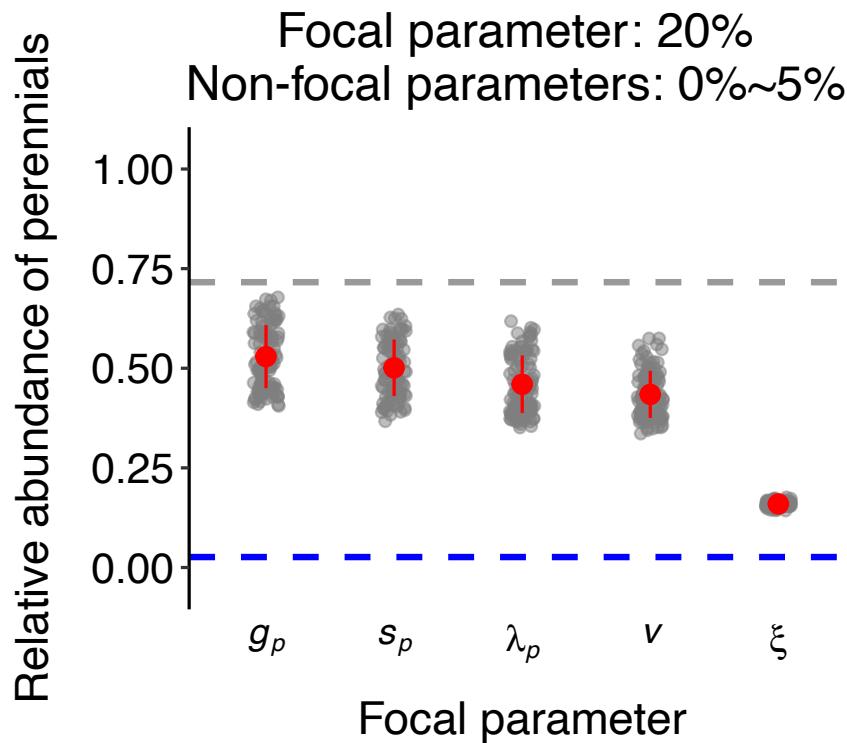


Figure 7 Detecting the most critical microbial effect within an annual–perennial plant competition model (modified from Uricchio et al., 2019). Here, soil microbes can impact five demographic parameters of the perennial plant: seed germination rate (g_p), seed survival rate (s_p), intrinsic fecundity (λ_p), seedling survival rate (v) and adult survival rate (ξ). The grey dashed line represents the relative abundance of the perennial plant in the absence of any pathogenic effects from the microbes (i.e., unperturbed baseline parameters), while the dashed blue line shows the perennial’s relative abundance when the pathogen simultaneously causes a 20% reduction in all five parameters. To evaluate the demographic consequences of microbes primarily impacting one demographic process, we sequentially decreased the value of each parameter by 20%, while the other four non-focal parameters were randomly decreased by 0% to 5% (assuming weaker microbial impact). For each focal parameter, we repeated this process in 100 simulations (translucent grey points; red points and error bars represent the means and standard deviations) and ran each simulation for 200 generations. These simulations reveal that soil pathogens that primarily reduce adult survival (ξ) have substantially stronger demographic consequences than pathogens that primarily affect other demographic processes. See Box 2 for model description. The baseline parameters are obtained from the species pair *Elymus glaucus* (our perennial) versus *Bromus diandrus* (our annual) in Uricchio et al. (2019) – perennial plant parameters: $g_p = 0.125$, $s_p = 0.515$, $\lambda_p = 282.127$, $\xi = 0.920$, $v = 0.292$; annual plant parameters: $g_a = 0.168$, $s_a = 0.443$, $\lambda_a = 47.594$; competitive reduction of seed production: $\alpha_{aa} = 0.066$, $\alpha_{ap} = 0.143$, $\alpha_{pp} = 0.018$, $\alpha_{pa} = 0.104$; competitive reduction of perennial survival: $\beta_{p,N_p} = 0.086$, $\beta_{p,A_p} = 0.063$, $\beta_{p,N_a} = 0.002$.

871 Acknowledgments

872 We thank Xinyi Yan for contributing to the dataset used for Figure 3 and for insightful comments
873 that improved the manuscript. We thank Lawrence Uricchio and Erin Mordecai for help with the
874 model and parameter estimates used in Figure 7. We thank Hengxing Zou, Chia-Hao Chang-Yang,
875 Y. Anny Chung, Ching-Lin Huang, Yu-Pei Tseng, Yi Sun, and Shuo Wei for their discussions.
876 P.-J. Ke and J.W. are funded by the Taiwan Ministry of Education Yushan Fellow Program (MOE-
877 110-YSFAG-0003-001-P1) and the Taiwan Ministry of Science and Technology (MOST 111-2621-B-
878 002-001-MY3 and NSTC 113-2811-B-002-118). J.W. is also supported by NTU postdoctoral grant
879 112L4000-1. G.S. Kandlikar, M. Krishnadas, and P.-J. Ke acknowledge support from sDiv, the
880 Synthesis Centre of iDiv (DFG FZT 118, 202548816).

881 Author Contributions

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

884 References

- 885 Augspurger, C. K., 1984. Seedling survival of tropical tree species: interactions of dispersal
886 distance, light-gaps, and pathogens. *Ecology* **65**:1705–1712.
- 887 Bagchi, R., R. E. Gallery, S. Gripenberg, S. J. Gurr, L. Narayan, C. E. Addis, R. P. Freckleton, and O. T.
888 Lewis, 2014. Pathogens and insect herbivores drive rainforest plant diversity and composition.
889 *Nature* **506**:85–88.
- 890 Bagchi, R., T. Swinfield, R. E. Gallery, O. T. Lewis, S. Gripenberg, L. Narayan, and R. P. Freckle-
891 ton, 2010. Testing the Janzen-Connell mechanism: pathogens cause overcompensating density
892 dependence in a tropical tree. *Ecology Letters* **13**:1262–1269.
- 893 Barret, M., M. Briand, S. Bonneau, A. Préveaux, S. Valière, O. Bouchez, G. Hunault, P. Simoneau,
894 and M. A. Jacques, 2015. Emergence shapes the structure of the seed microbiota. *Applied and*
895 *Environmental Microbiology* **81**:1257–1266.
- 896 Bauer, J. T., K. M. L. Mack, and J. D. Bever, 2015. Plant-soil feedbacks as drivers of succession:
897 evidence from remnant and restored tallgrass prairies. *Ecosphere* **6**:art158.
- 898 Bell, T., R. P. Freckleton, and O. T. Lewis, 2006. Plant pathogens drive density-dependent seedling
899 mortality in a tropical tree. *Ecology Letters* **9**:569–574.
- 900 Bennett, J. A., J. Franklin, and J. Karst, 2023. Plant-soil feedbacks persist following tree death,
901 reducing survival and growth of *populus tremuloides* seedlings. *Plant and Soil* **485**:103–115.
- 902 Bennett, J. A., H. Maherli, K. O. Reinhart, Y. Lekberg, M. M. Hart, and J. Klironomos, 2017. Plant-
903 soil feedbacks and mycorrhizal type influence temperate forest population dynamics. *Science*
904 **355**:181–184.
- 905 Bever, J. D., 1994. Feedback between plants and their soil communities in an old field community.
906 *Ecology* **75**:1965–1977.
- 907 Bever, J. D., 2003. Soil community feedback and the coexistence of competitors: conceptual
908 frameworks and empirical tests. *New Phytologist* **157**:465–473.

- 909 Bever, J. D., I. A. Dickie, E. Facelli, J. M. Facelli, J. Klironomos, M. Moora, M. C. Rillig, W. D.
910 Stock, M. Tibbett, and M. Zobel, 2010. Rooting theories of plant community ecology in microbial
911 interactions. *Trends in Ecology & Evolution* **25**:468–478.
- 912 Bever, J. D., S. A. Mangan, and H. M. Alexander, 2015. Maintenance of plant species diversity by
913 pathogens. *Annual Review of Ecology, Evolution, and Systematics* **46**:305–325.
- 914 Bever, J. D., T. G. Platt, and E. R. Morton, 2012. Microbial population and community dynamics on
915 plant roots and their feedbacks on plant communities. *Annual Review of Microbiology* **66**:265–283.
- 916 Bever, J. D., K. M. Westover, and J. Antonovics, 1997. Incorporating the soil community into plant
917 population dynamics: The utility of the feedback approach. *Journal of Ecology* **85**:561–573.
- 918 Bezemer, T. M., J. Jing, J. M. T. Bakx-Schotman, and E.-J. Bijleveld, 2018. Plant competition alters
919 the temporal dynamics of plant–soil feedbacks. *Journal of Ecology* **106**:2287–2300.
- 920 Bingham, M. A. and S. W. Simard, 2011. Do mycorrhizal network benefits to survival and growth of
921 interior douglas-fir seedlings increase with soil moisture stress? *Ecology and Evolution* **1**:306–316.
- 922 Bittleston, L. S., Z. B. Freedman, J. R. Bernardin, J. J. Grothjan, E. B. Young, S. Record, B. Baiser,
923 and S. M. Gray, 2021. Exploring microbiome functional dynamics through space and time with
924 trait-based theory. *mSystems* **6**:10–1128.
- 925 Bonanomi, G., V. Antignani, M. Capodilupo, and F. Scala, 2010. Identifying the characteristics of
926 organic soil amendments that suppress soilborne plant diseases. *Soil Biology and Biochemistry*
927 **42**:136–144.
- 928 Bottini, R., F. Cassán, and P. Piccoli, 2004. Gibberellin production by bacteria and its involvement
929 in plant growth promotion and yield increase. *Applied Microbiology and Biotechnology* **65**:497–503.
- 930 Brinkman, E. P., W. H. van der Putten, E.-j. Bakker, and K. J. F. Verhoeven, 2010. Plant–soil feedback:
931 experimental approaches, statistical analyses and ecological interpretations. *Journal of Ecology*
932 **98**:1063–1073.
- 933 Bulgarelli, D., K. Schlaepi, S. Spaepen, E. V. L. Van Themaat, and P. Schulze-Lefert, 2013. Structure
934 and functions of the bacterial microbiota of plants. *Annual Review of Plant Biology* **64**:807–838.

- 935 Callaway, R. M., G. C. Thelen, A. Rodriguez, and W. E. Holben, 2004. Soil biota and exotic plant
936 invasion. *Nature* **427**:731–733.
- 937 Cardinaux, A., S. P. Hart, and J. M. Alexander, 2018. Do soil biota influence the outcome of novel
938 interactions between plant competitors? *Journal of Ecology* **106**:1853–1863.
- 939 Carini, P., P. J. Marsden, J. W. Leff, E. E. Morgan, M. S. Strickland, and N. Fierer, 2016. Relic DNA
940 is abundant in soil and obscures estimates of soil microbial diversity. *Nature Microbiology* **2**:1–6.
- 941 Chang-Yang, C.-H., J. Needham, C.-L. Lu, C.-F. Hsieh, I.-F. Sun, and S. M. McMahon, 2021. Clos-
942 ing the life cycle of forest trees: The difficult dynamics of seedling-to-sapling transitions in a
943 subtropical rainforest. *Journal of Ecology* **109**:2705–2716.
- 944 Chaparro, J. M., D. V. Badri, and J. M. Vivanco, 2013. Rhizosphere microbiome assemblage is
945 affected by plant development. *The ISME Journal* **8**:790–803.
- 946 Chen, L., N. G. Swenson, N. Ji, X. Mi, H. Ren, L. Guo, and K. Ma, 2019. Differential soil fungus
947 accumulation and density dependence of trees in a subtropical forest. *Science* **366**:124–128.
- 948 Cheng, C., M. J. Gundale, B. Li, and J. Wu, 2024. Deciphering the drivers of plant-soil feedbacks
949 and their context-dependence: A meta-analysis. *Plant and Soil* pages 1–15.
- 950 Chu, C. and P. B. Adler, 2015. Large niche differences emerge at the recruitment stage to stabilize
951 grassland coexistence. *Ecological Monographs* **85**:373–392.
- 952 Chung, Y. A., 2023. The temporal and spatial dimensions of plant–soil feedbacks. *New Phytologist*
953 **237**:2012–2019.
- 954 Chung, Y. A., T. A. Monaco, J. B. Taylor, and P. B. Adler, 2023. Do plant–soil feedbacks promote
955 coexistence in a sagebrush steppe? *Ecology* **104**:e4056.
- 956 Chung, Y. A. and J. A. Rudgers, 2016. Plant–soil feedbacks promote negative frequency dependence
957 in the coexistence of two aridland grasses. *Proceedings of the Royal Society B* **283**:20160608.
- 958 Clark, C., J. Poulsen, D. Levey, and C. Osenberg, 2007. Are plant populations seed limited? A
959 critique and meta-analysis of seed addition experiments. *The American Naturalist* **170**:128–142.

- 960 Cobb, R. C., S. E. Haas, N. Kruskamp, W. W. Dillon, T. J. Swiecki, D. M. Rizzo, S. J. Frankel, and
961 R. K. Meentemeyer, 2020. The magnitude of regional-scale tree mortality caused by the invasive
962 pathogen *Phytophthora ramorum*. *Earth's Future* **8**:e2020EF001500.
- 963 Comita, L. S., H. C. Muller-Landau, S. Aguilar, and S. P. Hubbell, 2010. Asymmetric density
964 dependence shapes species abundances in a tropical tree community. *Science* **329**:330–332.
- 965 Connell, J., 1971. On the role of natural enemies in preventing competitive exclusion in some
966 marine animals and in rain forest trees. In P. Den Boer and G. Gradwell, editors, *Dynamics of
967 Populations*, pages 298–312. Centre for Agricultural Publishing and Documentation, Wageningen,
968 The Netherlands.
- 969 Crawford, K. M., J. T. Bauer, L. S. Comita, M. B. Eppinga, D. J. Johnson, S. A. Mangan, S. A.
970 Queenborough, A. E. Strand, K. N. Suding, J. Umbanhowar, et al., 2019a. When and where
971 plant-soil feedback may promote plant coexistence: a meta-analysis. *Ecology Letters* **22**:1274–
972 1284.
- 973 Crawford, K. M., J. T. Bauer, L. S. Comita, M. B. Eppinga, D. J. Johnson, S. A. Mangan, S. A.
974 Queenborough, A. E. Strand, K. N. Suding, J. Umbanhowar, et al., 2019b. When and where
975 plant-soil feedback may promote plant coexistence: a meta-analysis: raw data and citations for
976 the meta-analysis. *Figshare Repository*: <https://doi.org/10.6084/m9.figshare.7985195.v1>.
- 977 Dalling, J. W., M. Swaine, and N. C. Garwood, 1998. Dispersal patterns and seed bank dynamics
978 of pioneer trees in moist tropical forest. *Ecology* **79**:564–578.
- 979 Das, A. J., N. L. Stephenson, and K. P. Davis, 2016. Why do trees die? characterizing the drivers of
980 background tree mortality. *Ecology* **97**:2616–2627.
- 981 David, A. S., P. F. Quintana-Ascencio, E. S. Menges, K. B. Thapa-Magar, M. E. Afkhami, and C. A.
982 Searcy, 2019. Soil microbiomes underlie population persistence of an endangered plant species.
983 *The American Naturalist* **194**:488–494.
- 984 Day, N. J., K. E. Dunfield, and P. M. Antunes, 2015. Temporal dynamics of plant–soil feedback and
985 root-associated fungal communities over 100 years of invasion by a non-native plant. *Journal of
986 Ecology* **103**:1557–1569.

- 987 De Long, J. R., E. L. Fry, G. Veen, and P. Kardol, 2019. Why are plant–soil feedbacks so unpredictable,
988 and what to do about it? *Functional Ecology* **33**:118–128.
- 989 Diez, J. M., I. Dickie, G. Edwards, P. E. Hulme, J. J. Sullivan, and R. P. Duncan, 2010. Negative soil
990 feedbacks accumulate over time for non-native plant species. *Ecology Letters* **13**:803–809.
- 991 Dombrowski, N., K. Schlaeppi, M. T. Agler, S. Hacquard, E. Kemen, R. Garrido-Oter, J. Wunder,
992 G. Coupland, and P. Schulze-Lefert, 2016. Root microbiota dynamics of perennial *Arabis alpina*
993 are dependent on soil residence time but independent of flowering time. *The ISME Journal*
994 **11**:43–55.
- 995 Dostál, P., 2021. The temporal development of plant-soil feedback is contingent on competition
996 and nutrient availability contexts. *Oecologia* **196**:185–194.
- 997 Dostál, P., J. Müllerová, P. Pyšek, J. Pergl, and T. Klinarová, 2013. The impact of an invasive plant
998 changes over time. *Ecology Letters* **16**:1277–1284.
- 999 Dostálek, T., J. Knappová, and Z. Münzbergová, 2022. The role of plant–soil feedback in long-term
1000 species coexistence cannot be predicted from its effects on plant performance. *Annals of Botany*
1001 **130**:535–546.
- 1002 Dudenhöffer, J.-H., A. Ebeling, A.-M. Klein, and C. Wagg, 2018. Beyond biomass: Soil feedbacks
1003 are transient over plant life stages and alter fitness. *Journal of Ecology* **106**:230–241.
- 1004 Dudenhöffer, J.-H., N. C. Luecke, and K. M. Crawford, 2022. Changes in precipitation patterns
1005 can destabilize plant species coexistence via changes in plant–soil feedback. *Nature Ecology &*
1006 *Evolution* **6**:546–554.
- 1007 Edwards, J. A., C. M. Santos-Medellín, Z. S. Liechty, B. Nguyen, E. Lurie, S. Eason, G. Phillips, and
1008 V. Sundaresan, 2018. Compositional shifts in root-associated bacterial and archaeal microbiota
1009 track the plant life cycle in field-grown rice. *PLOS Biology* **16**:e2003862.
- 1010 Ehrenfeld, J. G., B. Ravit, and K. Elgersma, 2005. Feedback in the plant-soil system. *Annual Review*
1011 *of Environment and Resources* **30**:75–115.

- 1012 Eldridge, D. J., S. K. Travers, J. Val, J. Ding, J.-T. Wang, B. K. Singh, and M. Delgado-Baquerizo,
1013 2021. Experimental evidence of strong relationships between soil microbial communities and
1014 plant germination. *Journal of Ecology* **109**:2488–2498.
- 1015 Eppinga, M. B., M. Baudena, D. J. Johnson, J. Jiang, K. M. L. Mack, A. E. Strand, and J. D. Bever,
1016 2018. Frequency-dependent feedback constrains plant community coexistence. *Nature Ecology
& Evolution* **2**:1403–1407.
- 1018 Esch, C. M. and R. K. Kobe, 2021. Short-lived legacies of *Prunus serotina* plant–soil feedbacks.
1019 *Oecologia* **196**:529–538.
- 1020 Esch, C. M., C. M. Medina-Mora, R. K. Kobe, and M. L. Sakalidis, 2021. Oomycetes associated with
1021 *Prunus serotina* persist in soil after tree harvest. *Fungal Ecology* **53**:101094.
- 1022 Fanin, N., D. Lin, G. T. Freschet, A. D. Keiser, L. Augusto, D. A. Wardle, and G. F. Veen, 2021.
1023 Home-field advantage of litter decomposition: from the phyllosphere to the soil. *New Phytologist*
1024 **231**:1353–1358.
- 1025 Forero, L. E., A. Kulmatiski, J. Grenzer, and J. M. Norton, 2021. Plant-soil feedbacks help explain
1026 biodiversity-productivity relationships. *Communications Biology* **4**:789.
- 1027 Fukami, T. and M. Nakajima, 2013. Complex plant–soil interactions enhance plant species diversity
1028 by delaying community convergence. *Journal of Ecology* **101**:316–324.
- 1029 Gallery, R. E., D. J. Moore, and J. W. Dalling, 2010. Interspecific variation in susceptibility to
1030 fungal pathogens in seeds of 10 tree species in the neotropical genus *Cecropia*. *Journal of Ecology*
1031 **98**:147–155.
- 1032 Gao, C., L. Montoya, L. Xu, M. Madera, J. Hollingsworth, E. Purdom, R. B. Hutmacher, J. A.
1033 Dahlberg, D. Coleman-Derr, P. G. Lemieux, et al., 2019. Strong succession in arbuscular mycor-
1034 rhizal fungal communities. *The ISME journal* **13**:214–226.
- 1035 Gilbert, G. S., 2002. Evolutionary ecology of plant diseases in natural ecosystems. *Annual Review
of Phytopathology* **40**:13–43.

- 1037 Grove, S., I. M. Parker, and K. A. Haubensak, 2015. Persistence of a soil legacy following removal
1038 of a nitrogen-fixing invader. *Biological Invasions* **17**:2621–2631.
- 1039 Gundale, M. J. and P. Kardol, 2021. Multi-dimensionality as a path forward in plant-soil feedback
1040 research. *Journal of Ecology* **109**:3446–3465.
- 1041 Hannula, S. E., R. Heinen, M. Huberty, K. Steinauer, J. R. De Long, R. Jongen, and T. M. Bezemer,
1042 2021. Persistence of plant-mediated microbial soil legacy effects in soil and inside roots. *Nature
1043 Communications* **12**:5686.
- 1044 Hannula, S. E., A. M. Kielak, K. Steinauer, M. Huberty, R. Jongen, J. R. De Long, R. Heinen, and
1045 T. M. Bezemer, 2019. Time after time: temporal variation in the effects of grass and forb species
1046 on soil bacterial and fungal communities. *MBio* **10**:10–1128.
- 1047 Hansen, E. M. and E. M. Goheen, 2000. *Phellinus weiri* and other native root pathogens as determi-
1048 nants of forest structure and process in western north america. *Annual review of phytopathology*
1049 **38**:515–539.
- 1050 Harms, K. E., S. J. Wright, O. Calderón, A. Hernandez, and E. A. Herre, 2000. Pervasive density-
1051 dependent recruitment enhances seedling diversity in a tropical forest. *Nature* **404**:493–495.
- 1052 Harper, J. L., 1977. Population biology of plants. Academic Press.
- 1053 Hawkes, C. V., S. N. Kivlin, J. Du, and V. T. Eviner, 2013. The temporal development and additivity
1054 of plant-soil feedback in perennial grasses. *Plant and Soil* **369**:141–150.
- 1055 Herrera Paredes, S. and S. L. Lebeis, 2016. Giving back to the community: microbial mechanisms
1056 of plant–soil interactions. *Functional Ecology* **30**:1043–1052.
- 1057 Horton, T. and M. van der Heijden, 2008. The role of symbioses in seedling establishment and
1058 survival. *Seedling Ecology and Evolution* pages 189–214.
- 1059 Howard, M. M., J. Kao-Kniffin, and A. Kessler, 2020. Shifts in plant–microbe interactions over com-
1060 munity succession and their effects on plant resistance to herbivores. *New Phytologist* **226**:1144–
1061 1157.

- 1062 Huang, L.-F., L.-X. Song, X.-J. Xia, W.-H. Mao, K. Shi, Y.-H. Zhou, and J.-Q. Yu, 2013. Plant-soil
1063 feedbacks and soil sickness: from mechanisms to application in agriculture. *Journal of Chemical*
1064 *Ecology* **39**:232–242.
- 1065 Huberty, M., K. Steinauer, R. Heinen, R. Jongen, S. E. Hannula, Y. H. Choi, and T. M. Bezemer,
1066 2022. Temporal changes in plant–soil feedback effects on microbial networks, leaf metabolomics
1067 and plant–insect interactions. *Journal of Ecology* **110**:1328–1343.
- 1068 Igwe, A. N., B. Quasem, N. Liu, and R. L. Vannette, 2021. Plant phenology influences rhizosphere
1069 microbial community and is accelerated by serpentine microorganisms in *plantago erecta*. *FEMS*
1070 *Microbiology Ecology* **97**:85.
- 1071 Ishaq, S. L., 2017. Plant-microbial interactions in agriculture and the use of farming systems to
1072 improve diversity and productivity. *AIMS Microbiology* **3**:335.
- 1073 Janzen, D. H., 1970. Herbivores and the number of tree species in tropical forests. *The American*
1074 *Naturalist* **104**:501–528.
- 1075 Jiang, J., K. C. Abbott, M. Baudena, M. B. Eppinga, J. A. Umbanhowar, and J. D. Bever, 2020.
1076 Pathogens and mutualists as joint drivers of host species coexistence and turnover: implications
1077 for plant competition and succession. *The American Naturalist* **195**:591–602.
- 1078 Johansen, A. and E. S. Jensen, 1996. Transfer of N and P from intact or decomposing roots of
1079 pea to barley interconnected by an arbuscular mycorrhizal fungus. *Soil Biology and Biochemistry*
1080 **28**:73–81.
- 1081 Kalske, A., J. D. Blande, and S. Ramula, 2022. Soil microbiota explain differences in herbivore
1082 resistance between native and invasive populations of a perennial herb. *Journal of Ecology*
1083 **110**:2649–2660.
- 1084 Kandlikar, G. S., 2024. Quantifying soil microbial effects on plant species coexistence: A conceptual
1085 synthesis. *American Journal of Botany* **111**:e16316.
- 1086 Kandlikar, G. S., C. A. Johnson, X. Yan, N. J. Kraft, and J. M. Levine, 2019. Winning and losing with
1087 microbes: how microbially mediated fitness differences influence plant diversity. *Ecology Letters*
1088 **22**:1178–1191.

- 1089 Kandlikar, G. S., X. Yan, J. M. Levine, and N. J. Kraft, 2021. Soil microbes generate stronger
1090 fitness differences than stabilization among California annual plants. *The American Naturalist*
1091 **197**:E30–E39.
- 1092 Kardol, P., M. T. Bezemer, and W. H. van der Putten, 2006. Temporal variation in plant–soil feedback
1093 controls succession. *Ecology Letters* **9**:1080–1088.
- 1094 Kardol, P., G. B. De Deyn, E. Laliberté, P. Mariotte, and C. V. Hawkes, 2013. Biotic plant–soil
1095 feedbacks across temporal scales. *Journal of Ecology* **101**:309–315.
- 1096 Kazan, K. and R. Lyons, 2016. The link between flowering time and stress tolerance. *Journal of*
1097 *Experimental Botany* **67**:47–60.
- 1098 Ke, P.-J. and J. M. Levine, 2021. The temporal dimension of plant–soil microbe interactions:
1099 mechanisms promoting feedback between generations. *The American Naturalist* **198**:E80–E94.
- 1100 Ke, P.-J. and T. Miki, 2015. Incorporating the soil environment and microbial community into plant
1101 competition theory. *Frontiers in Microbiology* **6**:1066.
- 1102 Ke, P.-J., T. Miki, and T. Ding, 2015. The soil microbial community predicts the importance of plant
1103 traits in plant–soil feedback. *New Phytologist* **206**:329–341.
- 1104 Ke, P.-J. and J. Wan, 2020. Effects of soil microbes on plant competition: a perspective from modern
1105 coexistence theory. *Ecological Monographs* **90**:e01391.
- 1106 Ke, P.-J. and J. Wan, 2023. A general approach for quantifying microbial effects on plant competition.
1107 *Plant and Soil* **485**:57–70.
- 1108 Ke, P.-J., P. C. Zee, and T. Fukami, 2021. Dynamic plant–soil microbe interactions: the neglected
1109 effect of soil conditioning time. *New Phytologist* **231**:1546–1558.
- 1110 Keeler, A. M. and N. E. Rafferty, 2022. Legume germination is delayed in dry soils and in sterile
1111 soils devoid of microbial mutualists: Species-specific implications for upward range expansions.
1112 *Ecology and Evolution* **12**:e9186.
- 1113 Keswani, C., S. P. Singh, C. García-Estrada, S. Mezaache-Aichour, T. R. Glare, R. Borriss, V. D.
1114 Rajput, T. M. Minkina, A. Ortiz, and E. Sansinenea, 2022. Biosynthesis and beneficial effects

- 1115 of microbial gibberellins on crops for sustainable agriculture. *Journal of Applied Microbiology*
1116 **132**:1597–1615.
- 1117 Kotanen, P. M., 2007. Effects of fungal seed pathogens under conspecific and heterospecific trees
1118 in a temperate forest. *Botany* **85**:918–925.
- 1119 Koziol, L., P. A. Schultz, G. L. House, J. T. Bauer, E. L. Middleton, and J. D. Bever, 2018. The plant
1120 microbiome and native plant restoration: the example of native mycorrhizal fungi. *BioScience*
1121 **68**:996–1006.
- 1122 Krishnadas, M., K. Agarwal, and L. S. Comita, 2020. Edge effects alter the role of fungi and insects
1123 in mediating functional composition and diversity of seedling recruits in a fragmented tropical
1124 forest. *Annals of Botany* **126**:1181–1191.
- 1125 Krishnadas, M., R. Bagchi, S. Sridhara, and L. S. Comita, 2018. Weaker plant-enemy interac-
1126 tions decrease tree seedling diversity with edge-effects in a fragmented tropical forest. *Nature*
1127 *Communications* **9**:1–7.
- 1128 Krishnadas, M. and L. S. Comita, 2018. Influence of soil pathogens on early regeneration success
1129 of tropical trees varies between forest edge and interior. *Oecologia* **186**:259–268.
- 1130 Krishnadas, M. and L. S. Comita, 2019. Edge effects on seedling diversity are mediated by impacts
1131 of fungi and insects on seedling recruitment but not survival. *Frontiers in Forests and Global*
1132 *Change* **2**:76.
- 1133 Krishnadas, M. and S. M. Stump, 2021. Dispersal limitation and weaker stabilizing mechanisms
1134 mediate loss of diversity with edge effects in forest fragments. *Journal of Ecology* **109**:2137–2151.
- 1135 Kulmatiski, A., 2019. Plant-soil feedbacks predict native but not non-native plant community
1136 composition: a 7-year common-garden experiment. *Frontiers in Ecology and Evolution* **7**:326.
- 1137 Kulmatiski, A., A. Anderson-Smith, K. H. Beard, S. Doucette-Riise, M. Mazzacavallo, N. E. Nolan,
1138 R. A. Ramirez, and J. R. Stevens, 2014. Most soil trophic guilds increase plant growth: a meta-
1139 analytical review. *Oikos* **123**:1409–1419.

- 1140 Kulmatiski, A., K. H. Beard, and J. Heavilin, 2012. Plant–soil feedbacks provide an additional
1141 explanation for diversity–productivity relationships. *Proceedings of the Royal Society B: Biological
1142 Sciences* **279**:3020–3026.
- 1143 Kulmatiski, A., K. H. Beard, J. M. Norton, J. E. Heavilin, L. E. Forero, and J. Grenzer, 2017. Live
1144 long and prosper: plant–soil feedback, lifespan, and landscape abundance covary. *Ecology*
1145 **98**:3063–3073.
- 1146 Lau, J. A. and J. T. Lennon, 2012. Rapid responses of soil microorganisms improve plant fitness in
1147 novel environments. *Proceedings of the National Academy of Sciences* **109**:14058–14062.
- 1148 Lebrija-Trejos, E., A. Hernández, and S. J. Wright, 2023. Effects of moisture and density-dependent
1149 interactions on tropical tree diversity. *Nature* **615**:100–104.
- 1150 Lennon, J. T. and S. E. Jones, 2011. Microbial seed banks: the ecological and evolutionary implica-
1151 tions of dormancy. *Nature Reviews Microbiology* **9**:119–130.
- 1152 Lepinay, C., Z. Vondráková, T. Dostálek, and Z. Münzbergová, 2018. Duration of the conditioning
1153 phase affects the results of plant–soil feedback experiments via soil chemical properties. *Oecologia*
1154 **186**:459–470.
- 1155 Leverett, L. D., G. F. Schieder IV, and K. Donohue, 2018. The fitness benefits of germinating later
1156 than neighbors. *American Journal of Botany* **105**:20–30.
- 1157 Li, Y. M., J. P. Shaffer, B. Hall, and H. Ko, 2019. Soil-borne fungi influence seed germination and
1158 mortality, with implications for coexistence of desert winter annual plants. *PLoS One* **14**:e0224417.
- 1159 Liang, M., X. Liu, G. S. Gilbert, Y. Zheng, S. Luo, F. Huang, and S. Yu, 2016. Adult trees cause
1160 density-dependent mortality in conspecific seedlings by regulating the frequency of pathogenic
1161 soil fungi. *Ecology Letters* **19**:1448–1456.
- 1162 Liu, D., M. Kelly, P. Gong, and Q. Guo, 2007. Characterizing spatial–temporal tree mortality
1163 patterns associated with a new forest disease. *Forest Ecology and Management* **253**:220–231.
- 1164 Liu, X., K. Steinauer, K. van der Veen-van Wijk, and T. M. Bezemer, 2025. Zooming in on the

- 1165 temporal dimensions of plant–soil feedback: Plant sensitivity and microbial dynamics. *Journal*
1166 *of Ecology* **113**:39–52.
- 1167 Lu, T., M. Ke, M. Lavoie, Y. Jin, X. Fan, Z. Zhang, Z. Fu, L. Sun, M. Gillings, J. Peñuelas, et al., 2018.
1168 Rhizosphere microorganisms can influence the timing of plant flowering. *Microbiome* **6**:1–12.
- 1169 Mack, K. M. and J. D. Bever, 2014. Coexistence and relative abundance in plant communities are
1170 determined by feedbacks when the scale of feedback and dispersal is local. *Journal of Ecology*
1171 **102**:1195–1201.
- 1172 Mack, K. M., M. B. Eppinga, and J. D. Bever, 2019. Plant-soil feedbacks promote coexistence and
1173 resilience in multi-species communities. *PLoS One* **14**:e0211572.
- 1174 Magee, L. J., J. A. LaManna, A. T. Wolf, R. W. Howe, Y. Lu, D. Valle, D. J. Smith, R. Bagchi,
1175 D. Bauman, and D. J. Johnson, 2024. The unexpected influence of legacy conspecific density
1176 dependence. *Ecology Letters* **27**:e14449.
- 1177 Mangan, S. A., S. A. Schnitzer, E. A. Herre, K. M. L. Mack, M. C. Valencia, E. I. Sanchez, and J. D.
1178 Bever, 2010. Negative plant–soil feedback predicts tree-species relative abundance in a tropical
1179 forest. *Nature* **466**:752–755.
- 1180 Miller, E. C., G. G. Perron, and C. D. Collins, 2019. Plant-driven changes in soil microbial communi-
1181 ties influence seed germination through negative feedbacks. *Ecology and Evolution* **9**:9298–9311.
- 1182 Miller, Z. R. and S. Allesina, 2021. Metapopulations with habitat modification. *Proceedings of the*
1183 *National Academy of Sciences* **118**:e2109896118.
- 1184 Miller, Z. R., P. Lechón-Alonso, and S. Allesina, 2022. No robust multispecies coexistence in a
1185 canonical model of plant–soil feedbacks. *Ecology Letters* **25**:1690–1698.
- 1186 Minás, A., P. A. García-Parisi, H. Chludil, and M. Omacini, 2021. Endophytes shape the legacy
1187 left by the above- and below-ground litter of the host affecting the establishment of a legume.
1188 *Functional Ecology* **35**:2870–2881.
- 1189 Mordecai, E. A., 2013a. Consequences of pathogen spillover for cheatgrass-invaded grasslands:
1190 coexistence, competitive exclusion, or priority effects. *The American Naturalist* **181**:737–747.

- 1191 Mordecai, E. A., 2013b. Despite spillover, a shared pathogen promotes native plant persistence in
1192 a cheatgrass-invaded grassland. *Ecology* **94**:2744–2753.
- 1193 Mordecai, E. A., 2015. Pathogen impacts on plant diversity in variable environments. *Oikos*
1194 **124**:414–420.
- 1195 Mouquet, N., J. L. Moore, and M. Loreau, 2002. Plant species richness and community productivity:
1196 why the mechanism that promotes coexistence matters. *Ecology Letters* **5**:56–65.
- 1197 Müller, A., E. George, and E. Gabriel-Neumann, 2013. The symbiotic recapture of nitrogen from
1198 dead mycorrhizal and non-mycorrhizal roots of tomato plants. *Plant and Soil* **364**:341–355.
- 1199 Nagendra, U. J. and C. J. Peterson, 2016. Plant-soil feedbacks differ in intact and tornado-damaged
1200 areas of the southern Appalachian mountains, USA. *Plant and Soil* **402**:103–116.
- 1201 Neytcheva, M. S. and L. W. Aarssen, 2008. More plant biomass results in more offspring production
1202 in annuals, or does it? *Oikos* **117**:1298–1307.
- 1203 O'Brien, A. M., N. A. Ginnan, M. Rebollo-Gómez, and M. R. Wagner, 2021. Microbial effects on
1204 plant phenology and fitness. *American Journal of Botany* **108**:1824–1837.
- 1205 Orrock, J. L. and C. C. Christopher, 2010. Density of intraspecific competitors determines the
1206 occurrence and benefits of accelerated germination. *American Journal of Botany* **97**:694–699.
- 1207 Ou, S. X., G. S. Kandlikar, M. L. Warren, and P.-J. Ke, 2024. Realistic time-lags and litter dynamics
1208 alter predictions of plant-soil feedback across generations. *bioRxiv* pages 2024–01.
- 1209 Pacala, S. W. and D. Tilman, 1994. Limiting similarity in mechanistic and spatial models of plant
1210 competition in heterogeneous environments. *The American Naturalist* **143**:222–257.
- 1211 Pajares-Murgó, M., J. L. Garrido, A. J. Perea, Á. López-García, J. M. Bastida, J. Prieto-Rubio,
1212 S. Lendínez, C. Azcón-Aguilar, and J. M. Alcántara, 2024. Intransitivity in plant-soil feedbacks
1213 is rare but is associated with multispecies coexistence. *Ecology Letters* **27**:e14408.
- 1214 Peay, K. G., 2018. Timing of mutualist arrival has a greater effect on *Pinus muricata* seedling growth
1215 than interspecific competition. *Journal of Ecology* **106**:514–523.

- 1216 Pepe, A., M. Giovannetti, and C. Sbrana, 2018. Lifespan and functionality of mycorrhizal fungal
1217 mycelium are uncoupled from host plant lifespan. *Scientific Reports* **8**:10235.
- 1218 Pineda, A., I. Kaplan, S. E. Hannula, W. Ghanem, and T. M. Bezemer, 2020. Conditioning the
1219 soil microbiome through plant–soil feedbacks suppresses an aboveground insect pest. *New
1220 Phytologist* **226**:595–608.
- 1221 Ravanbakhsh, M., R. Sasidharan, L. A. Voesenek, G. A. Kowalchuk, and A. Jousset, 2018. Microbial
1222 modulation of plant ethylene signaling: ecological and evolutionary consequences. *Microbiome*
1223 **6**:1–10.
- 1224 Reinhart, K. O., J. T. Bauer, S. McCarthy-Neumann, A. S. MacDougall, J. L. Hierro, M. C. Chiuffo,
1225 S. A. Mangan, J. Heinze, J. Bergmann, J. Joshi, et al., 2021. Globally, plant-soil feedbacks are
1226 weak predictors of plant abundance. *Ecology and Evolution* **11**:1756–1768.
- 1227 Reinhart, K. O., A. A. Royo, S. A. Kageyama, and K. Clay, 2010. Canopy gaps decrease microbial
1228 densities and disease risk for a shade-intolerant tree species. *Acta Oecologica* **36**:530–536.
- 1229 Rudgers, J. A., M. E. Afkhami, L. Bell-Dereske, Y. A. Chung, K. M. Crawford, S. N. Kivlin, M. A.
1230 Mann, and M. A. Nuñez, 2020. Climate disruption of plant-microbe interactions. *Annual Review
1231 of Ecology, Evolution, and Systematics* **51**:561–586.
- 1232 Ruiz Gómez, F. J., R. M. Navarro-Cerrillo, A. Pérez-de Luque, W. Oßwald, A. Vannini, and
1233 C. Morales-Rodríguez, 2019. Assessment of functional and structural changes of soil fungal
1234 and oomycete communities in holm oak declined dehesas through metabarcoding analysis.
1235 *Scientific reports* **9**:5315.
- 1236 Sarmiento, C., P.-C. Zalamea, J. W. Dalling, A. S. Davis, S. M. Stump, J. M. U'Ren, and A. E.
1237 Arnold, 2017. Soilborne fungi have host affinity and host-specific effects on seed germination
1238 and survival in a lowland tropical forest. *Proceedings of the National Academy of Sciences USA*
1239 **114**:11458–11463.
- 1240 Schroeder, J. W., A. Dobson, S. A. Mangan, D. F. Petticord, and E. A. Herre, 2020. Mutualist and
1241 pathogen traits interact to affect plant community structure in a spatially explicit model. *Nature
1242 Communications* **11**:2204.

- 1243 Senior, J. K., J. M. O'Reilly-Wapstra, J. A. Schweitzer, J. K. Bailey, and B. M. Potts, 2018. Forest fire
1244 may disrupt plant–microbial feedbacks. *Plant Ecology* **219**:497–504.
- 1245 Senthilnathan, A. and R. D'Andrea, 2023. Niche theory for positive plant-soil feedbacks. *Ecology*
1246 **104**:e3993.
- 1247 Shade, A., H. Peter, S. D. Allison, D. Baho, M. Berga, H. Bürgmann, D. H. Huber, S. Langenheder,
1248 J. T. Lennon, J. B. Martiny, et al., 2012. Fundamentals of microbial community resistance and
1249 resilience. *Frontiers in Microbiology* **3**:417.
- 1250 Shemesh, H., T. D. Bruns, K. G. Peay, P. G. Kennedy, and N. H. Nguyen, 2023. Changing balance
1251 between dormancy and mortality determines the trajectory of ectomycorrhizal fungal spore
1252 longevity over a 15-yr burial experiment. *New Phytologist* **238**:11–15.
- 1253 Shikano, I., C. Rosa, C.-W. Tan, and G. W. Felton, 2017. Tritrophic interactions: microbe-mediated
1254 plant effects on insect herbivores. *Annual Review of Phytopathology* **55**:313–331.
- 1255 Song, X. and R. T. Corlett, 2022. Do natural enemies mediate conspecific negative distance-and
1256 density-dependence of trees? a meta-analysis of exclusion experiments. *Oikos* **2022**:e08509.
- 1257 Steinauer, K., M. P. Thakur, S. Emilia Hannula, A. Weinhold, H. Uthe, N. M. van Dam, and T. Mar-
1258 tijn Bezemer, 2023. Root exudates and rhizosphere microbiomes jointly determine temporal
1259 shifts in plant-soil feedbacks. *Plant, cell & environment* **46**:1885–1899.
- 1260 Stump, S. M. and L. S. Comita, 2018. Interspecific variation in conspecific negative density depen-
1261 dence can make species less likely to coexist. *Ecology Letters* **21**:1541–1551.
- 1262 Suding, K. N., W. Stanley Harpole, T. Fukami, A. Kulmatiski, A. S. MacDougall, C. Stein, and
1263 W. H. van der Putten, 2013. Consequences of plant–soil feedbacks in invasion. *Journal of Ecology*
1264 **101**:298–308.
- 1265 Swamy, V., J. Terborgh, K. G. Dexter, B. D. Best, P. Alvarez, and F. Cornejo, 2011. Are all seeds
1266 equal? spatially explicit comparisons of seed fall and sapling recruitment in a tropical forest.
1267 *Ecology Letters* **14**:195–201.

- 1268 Teste, F. P., P. Kardol, B. L. Turner, D. A. Wardle, G. Zemunik, M. Renton, and E. Laliberté, 2017.
1269 Plant–soil feedback and the maintenance of diversity in Mediterranean-climate shrublands.
1270 *Science* **355**:173–176.
- 1271 Uricchio, L. H., S. C. Daws, E. R. Spear, and E. A. Mordecai, 2019. Priority effects and nonhierar-
1272 chical competition shape species composition in a complex grassland community. *The American*
1273 *Naturalist* **193**:213–226.
- 1274 van de Voorde, T. F., W. H. van der Putten, and T. M. Bezemer, 2012. The importance of plant–soil
1275 interactions, soil nutrients, and plant life history traits for the temporal dynamics of jacobaea
1276 vulgaris in a chronosequence of old-fields. *Oikos* **121**:1251–1262.
- 1277 van der Putten, W. H., R. D. Bardgett, J. D. Bever, T. M. Bezemer, B. B. Casper, T. Fukami, P. Kardol,
1278 J. N. Klironomos, A. Kulmatiski, J. A. Schweitzer, K. N. Suding, T. F. J. van der Voorde, and
1279 D. A. Wardle, 2013. Plant–soil feedbacks : the past, the present and future challenges. *Journal of*
1280 *Ecology* **101**:265–276.
- 1281 Van Dyke, M. N., J. M. Levine, and N. J. Kraft, 2022. Small rainfall changes drive substantial
1282 changes in plant coexistence. *Nature* **611**:507–511.
- 1283 Veen, C., E. Fry, F. ten Hooven, P. Kardol, E. Morriën, and J. R. De Long, 2019. The role of plant
1284 litter in driving plant-soil feedbacks. *Frontiers in Environmental Science* **7**:168.
- 1285 Veen, G. F., F. C. ten Hooven, C. Weser, and S. E. Hannula, 2021. Steering the soil microbiome by
1286 repeated litter addition. *Journal of Ecology* **109**:2499–2513.
- 1287 Villegas, J., D. F. Doak, M. B. García, and W. F. Morris, 2015. Demographic compensation among
1288 populations: what is it, how does it arise and what are its implications? *Ecology Letters* **18**:1139–
1289 1152.
- 1290 Wagner, M. R., D. S. Lundberg, D. Coleman-Derr, S. G. Tringe, J. L. Dangl, and T. Mitchell-Olds,
1291 2014. Natural soil microbes alter flowering phenology and the intensity of selection on flowering
1292 time in a wild arabidopsis relative. *Ecology Letters* **17**:717–726.

- 1293 Wang, W., H. Wu, T. Wu, Z. Luo, W. Lin, H. Liu, J. Xiao, W. Luo, Y. Li, Y. Wang, et al., 2024.
1294 Soil microbial influences over coexistence potential in multispecies plant communities in a
1295 subtropical forest. *Ecology* **105**:e4415.
- 1296 Willing, C. E., J. Wan, J. J. Yeam, A. M. Cessna, and K. G. Peay, 2024. Arbuscular mycorrhizal
1297 fungi equalize differences in plant fitness and facilitate plant species coexistence through niche
1298 differentiation. *Nature Ecology & Evolution* **8**:2058–2071.
- 1299 Wilschut, R. A. and S. Geisen, 2021. Nematodes as drivers of plant performance in natural systems.
1300 *Trends in Plant Science* **26**:237–247.
- 1301 Wubs, E. R. J. and T. M. Bezemer, 2018. Temporal carry-over effects in sequential plant–soil
1302 feedbacks. *Oikos* **127**:220–229.
- 1303 Wubs, E. R. J., W. H. van der Putten, M. Bosch, and T. M. Bezemer, 2016. Soil inoculation steers
1304 restoration of terrestrial ecosystems. *Nature Plants* **2**:16107.
- 1305 Yan, X., J. M. Levine, and G. S. Kandlikar, 2022a. A quantitative synthesis of soil microbial effects
1306 on plant species coexistence. *Proceedings of the National Academy of Sciences* **119**:e2122088119.
- 1307 Yan, X., J. M. Levine, and G. S. Kandlikar, 2022b. A quantitative synthesis of soil microbial effects
1308 on plant species coexistence: code and data. *Zenodo*: <https://doi.org/10.5281/zenodo.6513066>.
- 1309 Yin, R., W. Qin, X. Wang, D. Xie, H. Wang, H. Zhao, Z. Zhang, J.-S. He, M. Schädler, P. Kardol,
1310 et al., 2023. Experimental warming causes mismatches in alpine plant-microbe-fauna phenology.
1311 *Nature Communications* **14**:2159.
- 1312 Younginger, B. S., D. Sirová, M. B. Cruzan, and D. J. Ballhorn, 2017. Is biomass a reliable estimate
1313 of plant fitness? *Applications in plant sciences* **5**:1600094.
- 1314 Zalamea, P.-C., C. Sarmiento, A. E. Arnold, A. S. Davis, A. Ferrer, and J. W. Dalling, 2021. Closely
1315 related tree species support distinct communities of seed-associated fungi in a lowland tropical
1316 forest. *Journal of Ecology* **109**:1858–1872.
- 1317 Zee, P. C. and T. Fukami, 2015. Complex organism–environment feedbacks buffer species diversity
1318 against habitat fragmentation. *Ecography* **38**:370–379.

- 1319 Zhelnina, K., K. B. Louie, Z. Hao, N. Mansoori, U. N. Da Rocha, S. Shi, H. Cho, U. Karaoz, D. Loqué,
1320 B. P. Bowen, et al., 2018. Dynamic root exudate chemistry and microbial substrate preferences
1321 drive patterns in rhizosphere microbial community assembly. *Nature Microbiology* **3**:470–480.
- 1322 Zhu, Y., L. S. Comita, S. P. Hubbell, and K. Ma, 2015. Conspecific and phylogenetic density-
1323 dependent survival differs across life stages in a tropical forest. *Journal of Ecology* **103**:957–966.
- 1324 Zhu, Y., S. Queenborough, R. Condit, S. Hubbell, K. Ma, and L. Comita, 2018. Density-dependent
1325 survival varies with species life-history strategy in a tropical forest. *Ecology Letters* **21**:506–515.
- 1326 Zou, H.-X., X. Yan, and V. H. Rudolf, 2024. Time-dependent interaction modification generated
1327 from plant–soil feedback. *Ecology Letters* **27**:e14432.

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

Po-Ju Ke^{1,†}, Gaurav S. Kandlikar², Suzanne Xianran Ou³, Gen-Chang Hsu^{1,4}, Joe Wan^{1,5}, and Meghna Krishnadas^{6,7,8}

¹Institute of Ecology and Evolutionary Biology, National Taiwan University, Taipei, Taiwan

²Department of Biological Sciences, Louisiana State University, Baton Rouge, LA 70803, USA

³Department of Biology, Stanford University, Stanford, California 94305, USA

⁴Department of Entomology, Cornell University, Ithaca, New York, NY 14853, USA

⁵Institute of Integrative Biology, Department of Environmental Systems Science, ETH Zürich,
8092 Zürich, Switzerland

⁶TIFR National Centre for Biological Sciences, GKVK Campus, Bellary Road, Bengaluru India

⁷Laboratory for Conservation of Endangered Species, Centre for Cellular and Molecular Biology,
Hyderabad, Telangana, India

⁸Academy of Scientific and Innovative Research, CSIR-Human Resource Development Centre,
Ghaziabad, Utter Pradesh, India

April 12, 2025

Total word count for main body of text: 980711115

Number of color figures: 7

Number of Boxes: 2

ORCID information [Open research statement](#): Po-Ju Ke: 0000-0002-8371-7984 Gaurav S. Kandlikar: 0000-0003-3043-6780 Suzanne Xianran Ou: 0000-0002-8542-4149 Gen-Chang Hsu: 0000-0002-6607-4382 Joe Wan: 0000-0001-5950-2353 Meghna Krishnadas: 0000-0003-2231-9787 The dataset used in Figure 3 are from publicly available datasets of two publications: Figshare Repository for Crawford et al. (2019a) ([DOI: 10.6084/m9.figshare.7985195.v1](#); cited as Crawford et al., 2019b) and Zenodo for Yan et al. (2022a) ([DOI: 10.5281/zenodo.6513066](#); cited as Yan et al., 2022b). The R-scripts for simulations and data

† Correspondence author: pojuke@ntu.edu.tw; +886-33662467

compiled for Figure 3 are available on GitHub (<https://github.com/pojuke/DemographicReviewPSF>) and will be made available on Zenodo upon publication.

For Review Only

1 Abstract

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

19 Keywords

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

22 I. Introduction

23 Plants interact with a diverse array of soil ~~microbes, including mutualists, decomposers, and~~
24 ~~pathogens~~biota that function as herbivores, pathogens, mutualists, and decomposers. In addition
25 to the contributions of soil fauna (ranging from micro- to macrofauna; Ehrenfeld et al., 2005, Kulmatiski et al., 2014
26), studies have highlighted the importance of plant–soil microbe interactions. These interactions
27 can be bidirectional, with plants altering the composition of the soil microbial community, and
28 the resulting changes in microbial community impacting subsequent plant performance in the
29 conditioned soil (Bever, 1994, Bever et al., 1997, Bever, 2003). The study of plant–soil microbe
30 interactions has its origin in agricultural science (Huang et al., 2013, van der Putten et al., 2013) and
31 has been integrated into community ecology under the framework of plant–soil feedback (PSF).
32 Since its introduction by Bever et al. (1997), studies have extensively discussed how plant–soil
33 microbe interactions influence plant coexistence (Bever et al., 2010, Ke and Miki, 2015, Bever et al.,
34 2015, Kandlikar, 2024). The PSF framework has also been used to explore how soil microbes affect
35 patterns in the relative abundance of plant communities (Mangan et al., 2010, Reinhart et al., 2021),
36 restoration success (Wubs et al., 2016, Koziol et al., 2018), plant invasion (Callaway et al., 2004,
37 Suding et al., 2013), and the biodiversity–productivity relationship (Kulmatiski et al., 2012, Forero
38 et al., 2021).

39 To characterize the direction and strength of plant–soil microbe interactions, most studies
40 follow a two-phase experimental design aimed at capturing the two-way interactions between
41 plants and soil microbes (Bever et al., 1997). The classic greenhouse experiment consists of a
42 “conditioning” phase during which plants modify the soil microbial community, directly followed
43 by a “response” phase during which plants of the same or other species respond to the conditioned
44 soil microbial community (Bever et al., 2010, Brinkman et al., 2010). This distinct two-phase design
45 elegantly captures the necessary information for parameterizing the key terms in the classic plant–
46 soil feedback model (Bever et al., 1997, 2012) and has enabled a strong empirical foundation of
47 PSF research across ecosystems (Crawford et al., 2019a, Yan et al., 2022a). However, this approach
48 implies a number of assumptions about the nature of plant–soil microbe interactions that do not
49 align with our contemporary understanding of their dynamics. In particular, a growing number
50 of studies have highlighted the importance of accounting for different temporal and demographic

51 dimensions of plant–soil microbe interactions (Kardol et al., 2013, Gundale and Kardol, 2021,
52 Chung, 2023). Such evidence should reshape both the design of experiments (e.g., how long
53 should the conditioning phase last?) and the interpretation of their results (e.g., how do microbial
54 effects on early-life stage plant performance translate to population-level consequences?). In this
55 paper, we focus on two key assumptions: first, the temporal assumption that microbial effects
56 develop quickly during the conditioning phase and maintain constant strength over time; and
57 second, the demographic assumption that plant biomass performance during the response phase
58 reflects microbial impact on plant population growth.

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

78 The short-term nature of most experiments also constrains researchers to focus on a sin-
79 gle plant demographic response that presumably reflects the most critical impact of the mi-

crobial community (Ke and Wan, 2023). The most frequently measured performance proxy is plant biomass, which is then used to calculate theoretically derived metrics to infer how soil microbes influence plant coexistence. For instance, the biomass of plants in conspecific- and heterospecific-conditioned soils can be used to calculate the pairwise feedback metric that quantifies the frequency-dependent feedback loops generated by plant–soil microbe interactions (Bever et al., 1997). Negative frequency-dependence arises when both plants condition their soil microbes in a way that favors heterospecifics over conspecifics, thereby promoting plant coexistence (Crawford et al., 2019a). In the context of the classic PSF model, where soil microbes drive plant community dynamics by changing plants' intrinsic growth rates (Bever et al., 1997), these metrics operate under the assumption that plant biomass performance is a good proxy for plant population growth. However, soil microbes can also affect other demographic processes across the plant life cycle that are not captured simply by measuring plant biomass (e.g., changing seed and seedling survival rates or the nature of density-dependence among plants), potentially with opposing effects at different plant ontogenetic stages that lead to different coexistence predictions (Dudenhöffer et al., 2018, Dostálek et al., 2022). Integrating these different impacts, instead of making predictions based on microbial effects on any one life stage, is another challenge when predicting the long-term demographic consequences of soil microbes.

Here, we discuss the two critical assumptions regarding temporal and demographic aspects of plant–soil microbe interactions in nature. We aim to highlight the relevance of these assumptions when extrapolating greenhouse results, and outline potential avenues for overcoming them in future empirical and theoretical avenues to incorporate them. ~~In particular, studies. It is important to note that although we treat the temporal and demographic aspects of plant–microbe interactions separately for analytical clarity, they are intrinsically linked. In nature, temporal shifts in microbial community composition and function can give rise to distinct microbial effects on various demographic processes across plants' life cycles. Conversely, these demographic rates reveal how microbial impacts on plant populations unfold over time and illuminate the temporal dynamics of plant–soil microbe interactions. On the theoretical forefront,~~ we advocate for a shift from using biomass-based performance indices to parameterizing patch occupancy models and plant demographic models with microbial effects. While these biologically important complica-

¹⁰⁹ tions make experiments more logically challenging, we argue that integrating the temporal and
¹¹⁰ demographic details can better predict the outcome of plant–soil microbe interactions in their
¹¹¹ natural context.

¹¹² II. Significant consequences of overlooking the temporal and demo- ¹¹³ graphic aspects of plant–soil microbe interactions

¹¹⁴ To motivate our thesis that explicitly evaluating the variation in microbial effects across time and
¹¹⁵ across different life stages is important for predicting their consequences in nature, we first present
¹¹⁶ a simple plant demographic model that illustrates the potential consequences of ignoring these
¹¹⁷ temporal dynamics. Specifically, we consider two annual plant species, N_1 and N_2 , with dynamics
described by the Beverton–Holt annual plant model:

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

¹¹⁸ with subscripts i and j indicating species 1 or 2. The first term represents the survival of ungermi-
¹¹⁹ nated seeds, with g_i and s_i representing seed germination and survival rate, respectively (circular
¹²⁰ loop in Fig. 2A). The second term represents seed production and density-dependent interactions
¹²¹ among germinated seeds, with λ_i , α_{ii} and α_{ij} representing intrinsic plant fecundity, intraspecific
¹²² and interspecific competitive impact experienced by N_i , respectively (rightward arrows in Fig. 2A).
¹²³ As opposed to biomass-based metrics, this demographic model provides the opportunity to study
¹²⁴ microbial effects on five different demographic parameters (i.e., g_i , s_i , λ_i , α_{ii} , and α_{ij}). For short-
¹²⁵ term greenhouse studies comparing these demographic processes in conditioned versus sterilized
¹²⁶ soil, this model offers a way to predict the long-term effect of soil microbes on plant competitive
¹²⁷ outcomes.

¹²⁸ As a case study, consider a scenario in which pathogenic microbes operate by harming one of
¹²⁹ these demographic processes for a given species. If a short-term greenhouse study were to suggest
¹³⁰ that the primary **effect** of the soil pathogen is to reduce species 1's seed survival (s_1) by 10%

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

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

152 III. Dissecting different temporal dimensions of microbial effects

153 Studies on the temporal patterns of plant–soil microbe interactions have classically focused on
154 its variation along plant succession, which typically involves plants with different traits or
155 shifts in the external environment (Kardol et al., 2006, 2013, Bauer et al., 2015). However, tem-
156 poral variation in plant–microbe interactions also occurs across shorter time scales because the
157 conditioned soil microbial community and plant response both vary over time (Fig. 1B). Recog-

nizing that plant–soil microbe interactions are not constant through time directly influences the experimental design and how we interpret experimental results. Moreover, this temporal variability may be a key mechanism behind the effects of phenological mismatch between plants and soil microbes (Peay, 2018, Rudgers et al., 2020) (Peay, 2018, Rudgers et al., 2020, Yin et al., 2023). In this section, we review evidence of temporal variability and discuss mechanisms by which the impact of microbial communities on plant biomass performance varies with the duration of the conditioning and response phases (subsection III.1), as well as the time lag between consecutive generations (subsection III.2). We then discuss how to design experiments that tackle the temporal complexities observed in nature (subsection III.3). Note that for this section, we focus on studies that measure plant biomass as the key performance proxy; we will discuss other demographic responses in section IV.

III.1 Temporal development during the conditioning and response phases

As the strength and direction of plant–soil microbe interactions depend on the timing of interactions, the duration of the conditioning and response phases influences the greenhouse-measured interaction strength. By compiling information on the experimental duration of studies included in two prominent meta-analyses (Crawford et al., 2019a, Yan et al., 2022a) (Crawford et al., 2019b, Yan et al., 2022b), we showed that the length of the conditioning and response phases are short is under a few months in most studies (Fig. 3). The median conditioning length is 3.5 months ($n = 59$ studies, after excluding 47 studies with field-collected soils) while that of the response phase is 3 months ($n = 106$ studies). Extrapolating from these experiments to predict the long-term consequences of soil microbes is based on the assumption that the relative impact of conspecific- and heterospecific-conditioned soils remains constant throughout plant development. The significance of overlooking the temporal development of plant–soil microbe interactions is exemplified when one considers considering plants with different life histories. For example, 20% of studies (21 out of 106) in Fig. 3 evaluated microbially mediated stabilization between plant species pairs comprised of comprising one annual and one perennial species while implementing the same (usually short) experimental duration. This overlooks the potential for short- and long-lived plants to condition microbial communities at different rates, such that the same duration of soil conditioning may correspond to

186 different developmental stages and microbial effects (Kulmatiski et al., 2017): the species-specific
187 microbiome of a short-lived annual plant may be fully conditioned by the end of an experiment,
188 whereas that of a long-lived perennial may require a longer conditioning time. Similarly, a short
189 response phase may capture the full physiological response of an annual plant, while that of a
190 perennial may vary with its ontogeny. This mismatch in temporal development patterns high-
191 lights the challenge of interpreting experimental results in the context of the focal system's natural
192 history.

193 Compared to the classic two-phase design with a single fixed duration of soil conditioning
194 (Fig. 4A), a few studies have grown plants in soils that were conditioned for different ~~duration~~
195 durations (red vertical arrow (i) in Fig. 4B). Studies have shown that the relative impact of
196 conspecific- and heterospecific-conditioned soil on the responding individual can vary with
197 the duration of soil conditioning. For example, ~~Lepinay et al. (2018) found that after a brief~~
198 ~~conditioning period of two weeks, heterospecific soil had a more negative impact on *Rorippa*~~
199 ~~austriaca~~ performance than its conspecific soil. However, a longer duration ~~Liu et al. (2025)~~
200 found that *Jacobaea vulgaris* performed worse in conspecific soil than in heterospecific soils, and
201 that this performance difference increased as soil conditioning time extended from two to five
202 weeks; however, the differences between soil treatments diminished after a longer conditioning
203 duration of eight weeks. Similarly, while focusing on soil chemical properties, Lepinay et al. (2018)
204 showed that the relative negative impact of soil conditioning resulted in the opposite relationship:
205 ~~conspecific soil had an increasingly stronger negative impact peaking at six weeks of conditioning,~~
206 ~~whereas the negative effect of heterospecific soils diminished after four~~ conspecific versus heterospecific
207 soils varied with conditioning duration over a span of two to eight weeks of conditioning. In a more
208 natural setting, Ke et al. (2021) studied how the microbial impact varied with soil conditioning
209 length by transplanting seedlings into field-conditioned soil collected under plant individuals of
210 different ages. They found that the soil microbial community underwent continuous successional
211 dynamics over the span of 20 years and three out of four species experienced negative microbial
212 effects that intensified with longer conditioning time. Importantly, these results have crucial impli-
213 cations on the design of two-phase experiments: arresting soil conditioning at different time points
214 causes the responding plant to encounter microbial communities with different compositions and

215 functions, thereby giving rise to different plant–soil microbe interactions.

216 Previous experimental studies on the temporal dynamics of plant–soil microbe interactions
217 have largely focused on the development of microbial effects across the lifespan of the responding
218 individual, which is typically achieved by harvesting responding plants at various time intervals
219 (Kardol et al., 2013, Gundale and Kardol, 2021; red diagonal arrow (ii) in Fig. 4B). For example,
220 by sequentially harvesting seedlings at four time points spanning 19 months, Hawkes et al. (2013)
221 showed that the microbial effect experienced by native plants became more negative through time,
222 whereas the development patterns for invasive plants were more variable. Recent studies have
223 also highlighted that other factors can modify the temporal pattern of microbial effects during
224 the response phase (Dostál, 2021, Bezemer et al., 2018). For instance, harvesting twice every week
225 for 11 weeks, Bezemer et al. (2018) showed that the negative effect of conspecific-conditioned soil
226 experienced by *Jacobaea vulgaris* attenuated as plants became older; however, when grown together
227 with a heterospecific competitor, the negative effect instead aggravated over time (but see Dostál,
228 2021 for a nonlinear pattern for three harvests spanning 13 months). Together, this empirical
229 evidence provides a strong impetus to consider temporal variability in the response phase since
230 harvesting an experiment at different endpoints can alter our understanding of the microbial
231 effect.

232 The temporal development of plant–soil microbe interaction ~~likely occurs~~ can occur due to
233 shifts in the composition and/or functionality of microbial communities as plants mature or enter
234 different developmental stages (Chaparro et al., 2013, Dombrowski et al., 2016, Edwards et al.,
235 2018, Hannula et al., 2019). Mechanisms underlying these shifts in soil microbial communities
236 include physiological changes in nutrient allocation or root exudation across plant ontogenetic
237 stages (Chaparro et al., 2013, Zhelnina et al., 2018), as well as an increase in immunity and an-
238 tibiotic defense against pathogens as plants mature (Bulgarelli et al., 2013, Chaparro et al., 2013).
239 ~~Furthermore, alterations~~ Furthermore, changes prompted by plants can lead to shifts in microbe–
240 microbe interactions and the processes governing microbial community assembly (Barret et al.,
241 2015, Herrera Paredes and Lebeis, 2016, Bittleston et al., 2021), all of which may trigger further
242 responses in plant physiology via a complex interplay between mechanisms. ~~Importantly,~~ Even
243 in the absence of detectable shifts in soil microbial community composition, ontogenetic changes

244 in plant physiology can drive variable plant responses (Liu et al., 2025). However, as conditioning
245 and response processes operate simultaneously in nature, it is important to note that the same set
246 of mechanisms applies to explain temporal patterns in both phases. For example, strength-
247 ening of immunity as plants mature can reduce pathogen abundance as the conditioning phase
248 progresses (Bulgarelli et al., 2013); it can also reduce plant susceptibility to pathogens and allevi-
249 ate negative microbial effects experienced by the plant as the responding individual matures; it
250 can also reduce pathogen abundance as the conditioning phase progresses (Bulgarelli et al., 2013)
251 . Similarly, mechanisms that reduce the abundance of beneficial microbes after soil conditioning
252 (e.g., mature plants becoming less reliant on mutualistic partners) also act upon the responding
253 individual to diminish the observed positive microbial effect. We will elaborate on necessary
254 experiments to tease apart different temporal dimensions and mechanisms in the subsection III.3.

255

256 III.2 Alterations of microbial effects after plant death

257 One common implicit assumption in plant–soil feedback studies is that greenhouse-measured
258 microbial effects manifest similarly on plants neighboring the focal individuals as on individuals
259 that arrive and grow in the conditioned soil after the focal plant senesced. However, whether
260 microbial effects carry over through time and how long they persist remains an understudied
261 temporal aspect of plant–soil microbe interactions. This question is especially important for
262 systems with discrete growing seasons or dispersal limitation, where a temporal lag exists between
263 the senescence of one plant (the conditioning individual) and the growth of another (responding)
264 individual. This introduces a lag phase during which the conditioned soil is left unoccupied for
265 an extended period of time; processes such as litter decomposition, abiotic filtering, and stochastic
266 drift may restructure the microbial community during such lags. Studies growing seedlings in
267 soils collected from dead individuals (red vertical arrow (iii) in Fig. 4B) suggest that such lags
268 can have distinct effects across different systems. For example, Esch and Kobe (2021) showed that
269 the negative effects of soil from live *Prunus serotina* on the survival of conspecific seedlings faded
270 away within one year after tree removal. Conversely, Bennett et al. (2023) showed that microbial
271 communities from soils collected under dead and live adult *Populus tremuloides* trees had similar

272 effects on conspecific seedlings. As an alternative to collecting soil from naturally occurring
273 dead individuals, Ou et al. (2024) modified the two-phase experiment to include a six-month
274 delay between the conditioning and response phase; their results suggest that the seasonal lag in
275 Mediterranean annual plant systems changes the microbial community and ~~their its~~ corresponding
276 impact on plant coexistence. ~~Below, we discuss the mechanisms that could either maintain or alter~~
277 ~~microbial effects when a temporal lag exists between consecutive generations.~~

278 Microbial effects could persist after active plant conditioning ceases due to the continued
279 survival and functioning of the conditioned microbial community in the soil (Lennon and Jones,
280 2011, Pepe et al., 2018, Esch et al., 2021, Hannula et al., 2021). For example, Esch et al. (2021)
281 found that the persisting pathogenic oomycetes collected from live versus dead tree stumps have
282 similar negative effects on conspecific seedling survival. Similarly, Pepe et al. (2018) showed that
283 arbuscular mycorrhizal fungi remain active and can spread from roots after host shoot removal. ~~The~~
284 ~~maintenance of microbial activity can occur~~ Microbial activity can be maintained if root systems
285 remain active after the removal of aboveground tissues or if the release of nutrients from dead
286 belowground tissues mirrors exudates from living plants (Johansen and Jensen, 1996, Müller et al.,
287 2013). Additionally, trophic flexibility (e.g., saprotrophic ability of certain pathogens; Bonanomi
288 et al., 2010) and dormancy of soil microbes can allow the microbial communities to persist after
289 the death of their host, enabling microbes to wait for the arrival of a new host (Lennon and Jones,
290 2011, Shade et al., 2012, Shemesh et al., 2023). In these cases, the succeeding (response) individual
291 will experience a similar microbial effect despite the temporal lag in arrival timing, and predictions
292 from immediate transplant experiments are relevant to natural systems.

293 However, various processes can cause the microbial community to change after plants stop
294 actively conditioning the soil, such that subsequent responding individuals encounter a different
295 soil microbial community than that obtained in an immediate transplant scenario (Grove et al., 2015,
296 Veen et al., 2019, Ou et al., 2024). The process of litter decomposition can introduce phyllosphere
297 microbes to the soil (Fanin et al., 2021, Minás et al., 2021) and release chemicals and nutrients
298 that shift microbial communities (Veen et al., 2021). Additionally, different causes of plant death
299 (e.g., herbivory, fire, and disease) are often associated with further changes in abiotic factors,
300 with potential effects on the composition and function of microbial communities. For example,

301 canopy gaps caused by wind disturbances modify nearby light and moisture levels in a way
302 that suppresses pathogens (Augspurger, 1984, Reinhart et al., 2010, Nagendra and Peterson, 2016).
303 Finally, stochastic drift could decouple microbial ~~community~~ communities from plant conditioning
304 influence if the soil remains uncolonized over an extended period of time due to plant propagule
305 limitation. In these scenarios, immediate transplant experiments fail to capture the microbial
306 effects experienced by the responding plant in nature.

307 III.3 Implications for experimental design

308 While an increasing number of studies have recognized the temporal dimensions of plant–soil
309 microbe interactions, synthesizing the factors contributing to this variability, e.g., the life history
310 of plants and functional groups of microbes involved, requires more targeted studies. Here, we
311 recommend a path forward for understanding these context dependencies. First, the temporal
312 ~~settings~~ setting of the experiment should guide our interpretation of the results. For instance,
313 in Mediterranean plant communities where the growing season only lasts a few months, tra-
314 ditional experiments in which a short-term conditioning phase is immediately followed by the
315 response phase may adequately reflect potential microbial effects on concurrently growing neigh-
316 bors that unfold within one growing season. However, such a design may not be adequate to
317 project microbial effects on population dynamics across years because it overlooks the temporal
318 lag associated with the clear seasonality of plant growth in nature (~~Ou et al., 2024~~). Second, we
319 encourage modification of the classic two-phase design (Fig. 4A) to reflect the temporal aspects of
320 a focal plant–soil system in nature. For Mediterranean annual plant communities, mirroring the
321 temporal dynamics of the natural system by incorporating a decay phase during which the con-
322 ditioned soils are exposed to a prolonged drought with no vegetative growth (red vertical arrow
323 (iii) in Fig. 4B) may provide a better understanding of how soil microbes shape plant community
324 dynamics across years (Ou et al., 2024). Moreover, researchers can build on long-term monitoring
325 plots and historical information to account for ~~variation~~ variations in conditioning duration, host
326 plant age, or time since host tree death. This approach may be especially applicable in studies that
327 focus on long-lived plants, which often source field-conditioned soils for greenhouse experiments
328 (44%; 47 out of 106 studies in Fig. 3). For example, ~~Ke et al. (2021)~~ estimated plant age with plant

329 age estimated from historical aerial photos and employed a chronosequence approach to study
330 the influence of soil conditioning length. Other examples include using (Ke et al., 2021) and host
331 tree size obtained from forest census (Chen et al., 2019) can be used as a proxy of conditioning
332 time (Chen et al., 2019) and utilizing and chronosequences of abandoned fields or agricultural
333 harvest times can be utilized to study the persistence of microbial effects (van de Voorde et al.,
334 2012, Esch and Kobe, 2021).

335 One can also design experiments that isolate a particular facet of temporal variability to
336 help disentangle the mechanisms behind observed temporal patterns. Current studies on the
337 temporal development of microbial effects typically employ sequential harvesting, where the
338 observed temporal changes result from the combination of varying plant physiological responses
339 and any changes to the soil community that are due to the effects of the responding plant itself
340 (red diagonal arrow (ii) in Fig. 4B). To isolate the effects associated with changing soil microbial
341 communities during soil conditioning, studies could plant seedlings of the same age in soils with
342 different conditioning duration durations (red vertical arrow (i) in Fig. 4B). Alternatively, if the goal
343 is to isolate the effects caused by changing plant physiology, an experiment could instead grow
344 plants of different ages/sizes (kept in a relatively sterilized environment such as a Magenta box
345 an autoclavable container before transplanting) in soils with identical conditioning duration (red
346 horizontal arrow (iv) in Fig. 4B). Moreover, throughout greenhouse experiments, the concurrent
347 application of modern molecular methods can provide critical insights linking microbial changes
348 to variations in plant performance. A recent study by ? utilized such Liu et al. (2025) utilized
349 such an experimental design to illustrate the importance of conditioning and response duration
350 as well as the underlying mechanisms. In addition, (i.e., changes in plant sensitivity to microbes
351 or soil re-conditioning by the responding plant). They found that the soil bacterial community
352 in conspecific and heterospecific soils converged over the course of the response phase, partially
353 explaining why differences in plant performance diminished with longer experimental duration
354 (see also Steinauer et al., 2023). Finally, mutants or cultivars with different developmental rates
355 can also be used to separate the effects of plant developmental stage (e.g., vegetative growth or
356 flowering) and age per se (Dombrowski et al., 2016). While the above scenarios are deliberately
357 artificial, such experiments can provide important mechanistic insights into the observed temporal

358 patterns of plant–soil microbe interactions.

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

376 IV. Assessing multiple demographic consequences of soil microbes

377 Most two-phase ~~studies~~ experiments of plant–soil microbe interactions are designed to evaluate
378 how different soil microbial contexts influence plant biomass performance. Experimentally, the
379 implicit assumption is that individual biomass at the end of the experiment integrates all critical
380 impacts of the microbial community and that variation in individual biomass growth is predic-
381 tive of variation in population growth rates. This assumption corresponds well with the classic
382 feedback model of Bever et al. (1997), where microbes regulate the intrinsic growth rate of an expo-
383 nentially growing plant population. However, soil microbes can also alter other key demographic
384 processes throughout the plant life cycle that are not directly correlated with biomass accumula-

385 tion (e.g., seed germination and pollinator visitation in Dudenhöffer et al., 2018). Dostálek et al.
386 (2022) demonstrated that it can be difficult to predict plant coexistence by using the microbial
387 effect measured at a single life stage — while biomass performance suggests self-limitation of
388 both *Bromus erectus* and *Inula salicina*, including microbial effects on seed germination and fruit
389 production suggests that both species in fact benefited from self-conditioned soil. Here, we high-
390 light key studies that provide insights into microbial control over non-biomass plant demographic
391 processes, with a particular focus on early life stage transitions.

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

393 Soil microbes can have drastic consequences on the early life stages of plants. While these effects can
394 arise from microbial effects on distinct life history processes (i.e., seed survival, germination, and
395 early seedling survival; Fig. 5), empirical studies often group them together given the logistical chal-
396 lenges of separating these effects in field settings. For example, when studying long-lived plants
397 such as forest trees, repeated demographic censuses are often used to monitor seed-to-seedling
398 transitions (e.g., Harms et al., 2000, Swamy et al., 2011). A large body of evidence for microbial ef-
399 fects on plant early life stages comes from field studies finding that fungicide applications alter pat-
400 terns of seed and seedling demography (e.g., [Bell et al., 2006](#), [Bagchi et al., 2014](#), [Krishnadas et al., 2018](#), [Song and](#)
401 [Bell et al., 2006](#), [Bagchi et al., 2014](#), [Krishnadas et al., 2018, 2020](#), [Song and Corlett, 2022](#)). Many of
402 these studies are conducted to evaluate soil microbes as potential drivers of the Janzen–Connell
403 hypothesis (Janzen, 1970, Connell, 1971) and conspecific negative density-dependence (CNDD).
404 These hypotheses suggest that the aggregation of host-specific enemies around adult plants re-
405 duces the survival probability of seedlings that disperse close to adults and under high conspecific
406 densities. While evaluating the compound microbial effect across multiple early life stages can
407 yield important insights, studies that isolate microbial effects on specific underlying demographic
408 transitions (Fig. 5) can enable a nuanced and mechanistic understanding of microbial effects on
409 plant population dynamics ([Krishnadas and Comita, 2019](#)).

410 Soil-borne pathogens can cause substantial mortality at the seed stage across biomes (e.g.,
411 Kotanen, 2007, Sarmiento et al., 2017, Li et al., 2019). One system where the impact of fungal seed
412 pathogens has been systematically dissected is that of pioneer tree species in neotropical forests,

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

Soil microbes can also affect the rates and timing of germination. Such regulation primarily arises due to the production and/or metabolism of key germination-related phytohormones like gibberellins (reviewed in Keswani et al., 2022 and Bottini et al., 2004) or ethylene (reviewed in Ravanbakhsh et al., 2018 and Ishaq, 2017). While studies of how soil microbes regulate germination have historically focused on managed settings, evidence that microbes also affect germination in natural settings is now accumulating. In one of the few two-phase experiments focused on pairwise feedback effects on germination, Miller et al. (2019) found species-specific effects of conditioned microbes on germination. Specifically, the legume *Desmodium illinoense* achieved lower germination rates in conspecific-conditioned soils than in sterilized or heterospecific-conditioned soils, while germination of *Bromus inermis* and *Solidago canadensis* was unaffected by soil microbes. Across a large-scale microcosm experiment, Eldridge et al. (2021) found that soil bacterial and fungal

communities help explain substantial variation in patterns of seed germination across nine plant species, suggesting a relationship between soil microbes and plant germination that is not explained simply by their shared responses to abiotic soil properties. Even when soil microbes do not affect overall rates of germination, they can alter the phenology of germination (Keeler and Rafferty, 2022) which could either harm (e.g., if later germination reduces seedlings' performance due to competition; Orrock and Christopher, 2010) or benefit population growth (e.g., if later germinants germinating seedlings escape severe competition ~~at the seedling stage~~ or avoid abiotic stress; Leverett et al., 2018)population growth.

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

IV.2 Microbial effects beyond early life stages

As seedlings establish and grow into reproductive adults, the soil microbial community continues to affect their performance in various ways that are not captured by experiments ~~that focus~~focusing only on plant biomass. ~~While an exhaustive review of all such effects of soil~~

470 ~~microbes is beyond the scope of this study, we briefly highlight soil microbial regulation of~~
471 ~~flowering phenology and susceptibility to herbivores. Over~~ For example, studies from forest
472 pathology have shown that soilborne fungi and oomycetes can directly cause adult mortality via
473 root rot diseases, often with long-term impacts on spatial structure and gap dynamics in forest
474 communities (Hansen and Goheen, 2000, Liu et al., 2007, Das et al., 2016, Ruiz Gómez et al., 2019)
475 . Experimental studies have also shown that soil microbes can influence the fruit production of
476 herbaceous species (Dostálek et al., 2022), but such direct evidence is notably scarce in natural
477 forest systems. In other cases, soil microbes might have equally important implications for
478 plant population dynamics through less direct pathways. For example, over the past decade,
479 evidence of microbial regulation of flowering phenology across systems has become widespread
480 (Lau and Lennon, 2012, Wagner et al., 2014, Igwe et al., 2021)(Lau and Lennon, 2012, Wagner et al., 2014, Igwe et
481 . Although the consequences of such phenological shifts at the population level are seldom quanti-
482 fied, the few-day differences reported in these studies could in principle have drastic consequences
483 for plant fitness, especially under abiotic stress when earlier flowering can be crucial to repro-
484 ductive success and fitness (reviewed in Kazan and Lyons, 2016, O'Brien et al., 2021). The soil
485 community can also regulate plant susceptibility to invertebrate herbivores (e.g., Howard et al.,
486 2020, Pineda et al., 2020, Kalske et al., 2022), with such effects likely arising due to soil microbe-
487 induced changes in leaf metabolomes or volatile organics (Kalske et al., 2022, Huberty et al.,
488 2022). The consequences of microbe-mediated shifts in plant–herbivore interactions on insect
489 population dynamics are becoming increasingly well-studied (reviewed in Shikano et al., 2017),
490 but whether these changes affect plant population dynamics is less well established. ~~Soilborne~~
491 ~~pathogens can also contribute to inter-specific and spatial variability in rates of adult tree mortality~~
492 ~~(Das et al., 2016)~~ Further complicating efforts to project microbial consequences across a plant's
493 lifetime are that these effects can be uncorrelated or even contradictory across a plant's lifetime
494 (Dostálek et al., 2022). For example, Dudenhöffer et al. (2018) found that conspecific-conditioned
495 soil microbes promote juvenile plant growth but hinder adult growth. Integrating these effects
496 across the plant's lifetime reveals a net negative impact of conspecific soil in plant fitness — a result
497 that would contradict inferences based on the juvenile stage alone. Thus, variable impacts of soil
498 microbes across plant ontogeny and/or demographic processes could contribute to demographic
499 compensation in plant population dynamics (Villellas et al., 2015). The integration of these micro-

500 bial effects remains an ongoing challenge. ~~In light of this, we propose that a promising approach is~~
501 ~~to combine experiments with system-specific models that can assess their long-term consequences~~
502 ~~on plant population dynamics, particularly in long-lived plants.~~

503 IV.3 Implications for experimental design

504 While incorporating all aforementioned demographic impacts of soil microbes is logistically chal-
505 lenging, we also see a path forward. Current experimental studies of plant–microbe interactions
506 often transplant pre-germinated seeds into conditioned soils, thereby neglecting the impact of soil
507 microbes on seed survival and germination. Accordingly, a first step in enhancing our under-
508 standing of this phenomenon is for two-phase studies to plant ungerminated seeds and report
509 germination rates along with the biomass performance and survival rates of germinated plants.
510 Studies can employ statistical approaches (Dudenhöffer et al., 2022, Chung et al., 2023) or other
511 population demographic models (David et al., 2019, Dostálek et al., 2022) to integrate the impact
512 of microbes on multiple ~~early stage~~ ~~early-stage~~ transitions (see also section V.). Moreover, for
513 short-lived plants, one can aim to follow the entire plant life cycle. For example, Dostálek et al.
514 (2022) documented seedling establishment and biomass dynamics for two growing seasons, and
515 recorded final fruit production of plants in different soil microbial backgrounds. While such an
516 experiment is more challenging, the matrix population model parameterized by Dostálek et al.
517 (2022), where soil microbes modulate transition probabilities across states, enables a more nuanced
518 estimate of microbial impact compared to solely relying on biomass-based metrics. ~~Finally, while~~
519 ~~the longevity of forest trees precludes direct experimental evidence, one may leverage natural~~
520 ~~experiments to observe differences in demographic rates across sites with varying disease severity~~
521 ~~(Cobb et al., 2020).~~

522 Compared to greenhouse-based plant–soil feedback studies that focus on biomass per-
523 formance, CNDD studies using field census data are arguably more directly linked to population
524 growth due to their emphasis on individual survival. However, observational CNDD studies can
525 be limited as it ~~can be is~~ challenging to attribute demographic patterns to soil microbes, and the im-
526 pact of heterospecifics, which are necessary to infer coexistence outcomes, is sometimes overlooked.
527 We propose that controlled experiments could complement census data for more mechanistic in-

sights. For example, field-based biocide experiments have been used to identify soil microbes as key drivers of Janzen–Connell effects in seed and seedling mortality (Bell et al., 2006, Bagchi et al., 2010, Song and Corlett, 2022, Krishnadas and Comita, 2018). Furthermore, ~~adding a one can add a heterospecific treatment designed to assess heterospecific effects, as well as a~~ reference treatment in randomly located field soil ~~allows one to estimate to estimate the~~ frequency-independent microbial ~~impacts on survival, aligning with recent studies that emphasize impact on survival. These additional treatments allow the interpretation of plant-soil microbe interactions within with the framework of~~ modern coexistence theory, ~~which emphasizes that coexistence requires stabilization (niche difference) to be greater than the competitive hierarchy (fitness difference) between species~~ (Kandlikar et al., 2019, Ke and Wan, 2020). Greenhouse experiments can also be adapted to capture the density-dependent microbial effects implicit in CNDD studies. To this end, one can use field-conditioned soil from locations with varying adult densities or perform a pot experiment with varying seedling densities (Ke and Wan, 2023). These modifications in study design can help bridge the gap between microbial impacts inferred from experiments and field census data.

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

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

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

568 **V.1 Patch occupancy models**

569 Patch occupancy models represent a relatively straightforward framework for studying plant–soil
570 microbe interactions (Pacala and Tilman, 1994, Mouquet et al., 2002). In this group of models,
571 plants compete for unoccupied sites (patches) and the probability that a particular plant species
572 establishes in a local site depends on the site’s microbial legacy (Stump and Comita, 2018, Miller and
573 Allesina, 2021, Ke and Levine, 2021). Such models can either be spatially implicit, which assumes
574 that the landscape can be divided into an infinite number of patches and tracks the proportion of
575 different plant–soil microbe states (e.g., Miller and Allesina, 2021, Ke and Levine, 2021), or spa-
576 tially explicit, which considers a fixed-size arena and allows one to consider spatial proximity when
577 modeling microbial impact (e.g., the diffusion of microbial effects from live individuals nearby;
578 Bever et al., 1997, Mack and Bever, 2014, Bauer et al., 2015). Detailed formulation aside, a common
579 assumption in such models is that plants only indirectly influence each other by modifying soil
580 microbial legacies. This assumption aligns well with two-phase experiments that grow individual
581 plants in soils with different conditioning histories, and as such, patch occupancy models can
582 be readily parameterized with biomass measurements from pot experiments (e.g., by assuming
583 establishment probability scales with the relative biomass performance). Alternatively, patch oc-

cupancy models can also be parameterized with recruitment data from repeated censuses, thereby incorporating microbial effects on multiple early life stages (e.g., seed survival, germination, and seedling survival in Fig. 5; Krishnadas and Stump, 2021). Due to this connection with empirical data, patch occupancy models are commonly used in the PSF literature when studies wish to extrapolate predictions based on pairwise biomass-based metrics to multi-species communities (e.g., Mangan et al., 2010, Teste et al., 2017, Dudenhöffer et al., 2022). [Recent theoretical studies have also suggested that patch occupancy models, through competition for limited colonization sites, generate more interpretable frequency-based dynamics for multi-species communities than do direct extensions of the classic pairwise feedback model \(Miller et al., 2022\).](#)

The patch occupancy framework offers a pathway to effectively incorporate various temporal aspects of plant–soil microbe interactions ([Fig. 6; see also see](#) an example in Box 1 [and Fig. 6](#)). This is because such models can treat different developmental stages of the soil microbial community as distinct states so that the transitions between states reflect the conditioning and decay rates of soil microbes. The explicit inclusion of microbial legacies in the form of an unoccupied but conditioned patch state differs from previous feedback models, which usually assume tight coupling between plants and microbes (Eppinga et al., 2018, Mack et al., 2019). For example, Ke et al. (2021) modified a previous model (Fukami and Nakajima, 2013) by making microbial effects vary with the duration of soil conditioning, which in turn influences the transient trajectory of community assembly. In another example, Ke and Levine (2021) used a spatially implicit model to show that the strength of stabilization driven by host-specific pathogens depends on how quickly the conditioning effects of plants erode. The above models directly track the changes of microbial impact on plants through time, and can thus be parameterized with the type of experiments mentioned in subsection III.3. Alternatively, one can build simulation-based models that explicitly track the population size of microbes at each local site, allowing the temporal development and decay of microbial effects to emerge naturally (Schroeder et al., 2020). However, such models are harder to parameterize with empirical data since they require detailed knowledge of microbial traits and population dynamics (Jiang et al., 2020).

611 V.2 Models incorporating multiple demographic processes

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

639 In addition to integrating multiple microbial effects, a demographically explicit model can

640 help identify the most critical microbial effect via simulations. For instance, in the annual–perennial
641 plant model in Uricchio et al. (2019), foliar pathogens have little impact but seed pathogens can
642 have a more significant effect on perennial competitors in the system. Such a sensitivity analysis
643 is particularly useful when models include many mechanistic parameters for microbial dynamics
644 (e.g., Ke et al., 2015, Schroeder et al., 2020) and represents another reason why isolating microbial
645 effects on specific demographic transitions can be enlightening. Even for models that do not
646 explicitly incorporate microbial dynamics, identifying the bottleneck for population growth can
647 provide insights for future studies and guide more targeted experiments. Using an integral
648 projection model parameterized with long-term demographic data, Chu and Adler (2015) showed
649 that feedback loops during the recruitment stage contributed most to plant coexistence compared
650 to ~~that those~~ during the growth and survival stages. The authors speculated ~~that~~ this is due to the
651 recruitment stage involving many demographic transitions that are susceptible to soil pathogens
652 (Chu and Adler, 2015). In Box 2, with an annual–perennial plant model incorporating microbial
653 effects as qualitative switches in parameter values, we also demonstrate how sensitivity analysis can
654 help identify the relative importance of different microbial effects on the perennial plant – (Fig. 7).
655 In sum, formulating demographic models not only allows smooth integration of the temporal
656 and demographic dimensions of plant–soil microbe interactions but also provides an opportunity
657 to explore their consequences in multi-species communities. Nonetheless, parameterizing such
658 models for long-lived plants remains a significant ongoing challenge.

659 While we presented two separate modeling frameworks for incorporating temporal and
660 demographic components, in practice, both approaches are flexible and can be used to answer
661 multiple research questions. For instance, decay dynamics and time-dependent feedback can
662 also be built into a demographically explicit model (e.g., (Senthilnathan and D'Andrea, 2023);
663 see also Zou et al., 2024 for a discrete-time model with explicit consideration of the temporal
664 dynamics of soil microbes). Ultimately, the choice depends on the research question and the
665 focal plant–soil system. For example, in systems affected by wind (Nagendra and Peterson, 2016)
666 or fire disturbances (Senior et al., 2018) that may truncate soil conditioning at different timings,
667 or those where low propagule availability prevents immediate recolonization of conditioned
668 soils, investigating the temporal dimension can yield valuable insights; such analyses can also

669 be performed using individual-based models (Zee and Fukami, 2015). On the other hand, when
670 different soil microbes are known to impact different phases of the plant life cycle, integrating
671 these microbial effects into a demographic model may be more important. For example, in the
672 pyrogenic Florida scrub ecosystem, David et al. (2019) parameterized an integral projection model
673 (IPM) for the endangered perennial herb *Hypericum cumulicola*, incorporating positive microbial
674 effects on germination estimated via a greenhouse experiment. Their simulations indicated that
675 soil microbes increased the number of post-fire years with positive population growth, particularly
676 in high-elevation and low-nutrient patches. Together, these examples illustrate that system-specific
677 models are key to tailoring predictions to the ecological contexts that shape plant–soil microbe
678 interactions.

679 VI. Conclusion: moving forward with an empirical-theoretical feed- 680 back loop

681 Since its introduction to community ecology, the study of plant–soil microbe interactions has long
682 been shaped by a tight link between empirical and theoretical approaches. By showing how
683 empirically tractable greenhouse experiments can yield data to calculate theory-derived metrics,
684 the approach from Bever et al. (1997) has motivated more than two decades of research to predict the
685 long-term consequences of soil microbes (Crawford et al., 2019a). To date, new studies continue to
686 follow this integration, proposing new theories to capture different impacts of soil microbes as well
687 as new experimental designs to quantify them (e.g., Kandlikar et al., 2019, 2021, Yan et al., 2022a).
688 Two key assumptions of this approach are that ~~plant-soil~~ plant-soil microbe interactions follow a
689 simplified temporal trajectory – and that measuring microbial impact on plant biomass captures
690 the population dynamic consequences of soil microbes. While such abstractions have helped make
691 models generalizable, growing evidence has proven the relevance of the two knowledge gaps when
692 predicting the role of soil microbes in natural communities (Chung, 2023). ~~Explicit consideration~~
693 ~~of the temporal and demographic aspects not only leads to new research questions but also allows~~
694 ~~researchers to draw conclusions grounded on relevant experimental settings.~~ As such, we see
695 tremendous value in future efforts that aim to (1) develop theoretical models that can explicitly

696 incorporate the temporal and demographic components of plant–soil microbe interactions, and
697 (2) parameterize such models with corresponding observational data or experiments aimed at
698 quantifying these past-missing components.

699 ~~New modeling frameworks should be developed in order to incorporate the aforementioned~~
700 ~~temporal and demographic components. Here, we identify two paths moving forward. First,~~
701 ~~patch occupancy models can be used to study the temporal dimensions of Advancing research~~
702 ~~through the integration of empirical and theoretical approaches not only brings us closer to the~~
703 ~~long-standing goal of precisely predicting microbial effects in the field but also sharpens our~~
704 ~~ability to identify the key axes of variation underlying plant–soil microbe interactions by tracking~~
705 ~~the transition between different soil microbial states, which impact the subsequent establishment~~
706 ~~of plants in that patch. This framework also echoes recent theoretical studies suggesting that~~
707 ~~competition for limited colonization sites generates more interpretable frequency-based dynamics~~
708 ~~for multi-species communities than do extensions of the classic pairwise feedback model (Miller et al., 2022)~~
709 ~~. Second, instead of tracking species' occupancy frequency, one can also build demographic~~
710 ~~models that explicitly track plant population densities; this approach offers the opportunity~~
711 ~~to easily incorporate microbial effects on multiple plant demographic stages. We note that in~~
712 ~~practice, these modeling approaches are both flexible and can be used to answer more than one~~
713 ~~research question (e.g., decay dynamics and time-dependent feedback can also be built into a~~
714 ~~demographically explicit model; Senthilnathan and D'Andrea, 2023, Zou et al., 2024). Ultimately,~~
715 ~~the choice depends on the research question and the focal plant–soil system. For example, in~~
716 ~~systems with disturbances that may truncate soil conditioning at different timings (Nagendra and Peterson, 2016)~~
717 ~~, or those with low propagule availability such that conditioned soils are not immediately recolonized,~~
718 ~~investigating the temporal dimension can provide great insights into the role of soil microbes~~
719 ~~in nature; this can also be done by simulations of time-discrete models (Zou et al., 2024) and~~
720 ~~individual-based models (Zee and Fukami, 2015). On the other hand, when different soil microbes~~
721 ~~are known to impact different parts of the plant life cycle, integrating multiple microbial effects~~
722 ~~into a single demographic model may be more important. microbe interactions.~~

723 ~~While We have argued that~~ patch occupancy models can be parameterized with either
724 biomass measurements (e.g., Mangan et al., 2010, Teste et al., 2017, Dudenhöffer et al., 2022)

725 or census data (e.g., Stump and Comita, 2018). However, we caution that the model itself is
726 agnostic to the demographic details of plant–soil microbe interactions and will encompass different
727 microbial effects depending on the data used for parameterization (Fig. 5). For instance, Stump
728 and Comita (2018) parameterized their patch occupancy model with CNDD patterns based on
729 5-year seedling survival (Comita et al., 2010), which correspond to microbial effects on the survival
730 of established older seedlings. On the other hand, Krishnadas and Stump (2021) parameterized a
731 similar model with CNDD patterns based on the seed-to-seedling transition, thereby representing
732 microbial effects on recruitment and earlier life stages. Moreover, using different types of data
733 to parameterize the model implies different assumptions on how microbial effects operate. In
734 particular, using performance measurements from single-individual greenhouse experiments (e.g.,
735 Teste et al., 2017, Dudenhöffer et al., 2022) to parameterize a patch occupancy model implies that
736 the plant community is driven by how soil microbes affect the density-independent growth rate of
737 plant populations, whereas using CNDD patterns from observational census incorporates how soil
738 microbes and other non-microbial mechanisms modify the nature of density dependence among
739 plants.

740 Designing new experiments that provide the necessary information to parameterize ~~the~~
741 new plant demographic models of plant–soil microbe interactions is another frontier of research.
742 Some models require experiments that are similar to ~~the~~ current two-phase experiments. For
743 instance, to depict temporal development patterns, one can repeat an experiment along natu-
744 rally occurring variations in the duration of soil conditioning; ~~to track multiple early life stage~~
745 ~~microbial effects, one can directly plant ungerminated seeds into cultivated soils~~. However, some
746 microbial effects cannot be reliably estimated by classic two-phase experiments with a single-
747 growing plant individual. For example, if microbes are expected to affect not only plant in-
748 trinsic growth rate but also the nature of density dependence among plants, then estimating
749 microbial effects requires additional treatments beyond the classic two-phase design. Recent
750 studies linking plant–soil microbe interactions and coexistence theory specifically highlight this
751 scenario where soil microbes influence the model’s density dependence parameters (Kandlikar
752 et al., 2019, Ke and Wan, 2020, Zou et al., 2024), which require employing experiments that directly
753 manipulate plant density and soil origin (~~Chung and Rudgers, 2016, Cardinaux et al., 2018~~). (e.g.,

754 Chung and Rudgers, 2016, Cardinaux et al., 2018). An empirical–theoretical feedback loop is also
755 central to the design of such theory-driven experiments. For example, a proposed Ke and Wan (2020)
756 initially proposed a simplified experimental design based on the premise that plant–plant inter-
757 actions are competitive (Ke and Wan, 2020) was challenged by the observation that facilitation
758 is common, leading to exclusively competitive. However, when empiricists implemented the
759 experimental design with low neighbor density, they sometimes found facilitative interactions that
760 rendered our original analytical approach inapplicable (e.g., Wang et al., 2024, Willing et al., 2024).
761 This feedback prompted us to develop a revised density gradient design as a solution with greater
762 flexibility for untangling facilitative or nonlinear microbial effects (Ke and Wan, 2023). Again,
763 the optimal approach depends on feasibility and reflects which research question can provide a
764 fundamental understanding of the focal plant–soil system.

765 Recent Understanding the temporal dimensions of plant–soil microbe interactions in forest
766 systems remains a difficult challenge. Fortunately, recent census-based CNDD studies have in-
767 troduced a promising approach to investigate how microbe-mediated plant demography interacts
768 with the three temporal aspects, namely, the duration of soil conditioning, the life stage of respond-
769 ing plants, and the time delay between consecutive colonizing plants. Current CNDD studies often
770 calculate size-weighted abundance when estimating conspecific densities, thereby implicitly con-
771 sidering soil conditioning time by linking plant size to microbial effects. Additionally, microbial
772 communities associated with plants of different ages can be sequenced to examine the relationship
773 between pathogen accumulation and species' CNDD strength (Chen et al., 2019). Long-term obser-
774 vational data should also allow us to test whether conspecific effects change with the age/stage of
775 the responding focal individual (Bagchi et al., 2014, Zhu et al., 2015, 2018). For instance, Zhu et al.
776 (2015) showed that the CNDD effects attenuated as individuals mature from seedlings to adults.
777 Finally, a recent study also pioneered the inclusion of dead tree individuals into the abundance
778 calculation (i.e., the effects of decay; Magee et al., 2024). Insights from such CNDD studies can be
779 used to parameterize patch occupancy models with corresponding temporal aspects, offering new
780 insights by integrating the two overlooked components for long-lived plants.

781 One of the remaining challenges is to move away from a plant-centered viewpoint towards
782 a better understanding of the dynamics and functionality of soil microbial communities (Jiang

et al., 2020). ~~Theoretical models often assume simplified microbial dynamics (e.g., separation of timescales) or treat soil microbes as a qualitative modifier of plant parameters.~~ Incorporating microbial community assembly processes, ~~as outlined in section II~~, can help inform which processes need to be prioritized when building mechanistic models of microbial community dynamics (e.g., Schroeder et al., 2020; see also Zou et al., 2024 for a discrete-time model with explicit consideration of the temporal dynamics of soil microbes Schroeder et al., 2020, Zou et al., 2024). Empirically, experiments that establish the causal relationship between measured microbial dynamics and plant demographic responses can help feed theory with realistically parameterized temporal patterns. To this end, a starting point is to simultaneously measure shifts in both plant response and microbial community composition within studies that vary the temporal components (e.g., Esch and Kobe, 2021, Ke et al., 2021, Hannula et al., 2021, ~~but see Carini et al., 2016 for technical challenges related to erroneously detecting DNA from dead microbes in sequencing time series~~). Moreover, Measuring responses such as mycorrhizal percentage colonization and how they vary over time can also help bridge plant-centric and microbe-centric viewpoints (e.g., Bennett et al., 2023). However, given the functional plasticities and redundancies of microbial communities, improvements in identifying microbial functionality beyond that based on taxonomic information are also needed (see also Carini et al., 2016 for technical challenges related to erroneously detecting DNA from dead microbes in sequencing time series). Explicit quantification of microbial activity, such as measurements through multi-omics outputs, can allow for better modeling of functional microbial dynamics. Future studies balancing both the plant and microbe perspectives can further facilitate the empirical–theoretical feedback loop when studying the two missing components of plant–soil microbe interactions.

In summary, we conclude that studying the temporal dimension and the multiple demographic consequences of plant–soil microbe interactions provides a better understanding of their natural context. ~~In addition to the maintenance of plant diversity, the two knowledge gaps can also be important for other ecological processes (e.g., recovery following disturbance and gap dynamics).~~ One outstanding question in the literature is how to predict the seemingly idiosyncratic nature of plant–soil microbe interactions (i.e., its context dependency; De Long et al., 2019, Cheng et al., 2024). Recognizing that soil conditioning and plant response are temporally varying processes suggests

812 that time itself may serve as a hidden axis of variation: the same environmental shift alters temporal
813 trajectories differently depending on its timing. The temporal dimensions highlighted here also
814 underscore also underscore the significance of phenological mismatch mismatches among plants
815 and soil microbes driven by climate change (Rudgers et al., 2020; e.g., late-germinating plants
816 may be more vulnerable to affected by pathogens). Recognizing that soil conditioning and plant
817 response are temporally varying processes also provides insights into the context dependency of
818 plant-soil-microbe interactions: shifts in the abiotic environment can occur throughout a plant's
819 lifetime, and the timing of these shifts can alter the temporal trajectory differently. As experiments
820 incorporate environmental shifts and employ models to generate predictions (e.g., the impact of
821 drought on plant diversity; Dudenhöffer et al., 2022), embracing the empirical-theoretical feedback
822 loop can further refine the experimental design and enhance our ability to predict responses under
823 real-world settings (e.g., changes in the degree of precipitation variability). Ultimately, knowledge
824 of the system's natural history should guide researchers to recognize which aspects of the temporal
825 and demographic components are important for the focal system and the research question. With
826 the most critical aspect being identified, we believe that parameterizing new demographic mod-
827 els provides an avenue to predict the long-term consequences of plant-soil-microbe interactions
828 against a the backdrop of real-world conditions in which these interactions unfold.

829 Boxes

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

Here, we demonstrate how the temporal decay of microbial effects can be studied with a multi-species patch occupancy model. We considered three different plant–soil microbe states (Box Fig. 6A): unconditioned soil (P_{00}), soils colonized and conditioned by plant i (P_{ii}), and uncolonized soils with a microbial legacy (P_{0i}). The transition among these different states can be described as follows (see also Ke and Levine, 2021 and Miller and Allesina, 2021):

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

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

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

Specifically, state transitions occur due to plant colonization/soil conditioning (r_i), plant mortality (m_i), and the decay of microbial effects (d_i , black arrows in Box Fig. 6A). Here, soil microbes affect the ability of plants to recolonize conditioned soils (red arrows in Box Fig. 6A). N represents the total number of species within the community.

To illustrate the consequences of variable decay rates of microbial effects, we simulated the microbial effects (σ_{ij}) for 16 plant species with data from Teste et al., 2017, which measured soil microbial effects on plant biomass accumulation. We randomly drew species' fecundity (r_i) from a uniform distribution between 0.2 to 0.25. This simulation illustrates how the decay rates of microbial effects determine the overall consequences of soil microbes on plant communities (Box Fig. 6B & C). Specifically, with this parameterization and when microbial effects persist after host death (i.e., low d_i ; left panels in Box Fig. 6B & C), plant–soil microbe interactions mostly ~~result~~resulted in the dominance of a single species, overwhelming

Box 1 (continued)

species' variation in fecundity. However, if the conditioned microbial effect decayed rapidly after the death of host plants (i.e., high d_i ; right panels in Box Fig. 6B & C), variation in species' fecundity allowed higher diversity in each simulation and more equal persistence probability across species. Therefore, predicting the consequences of plant-soil microbe interactions in nature also requires quantifying the decay rate of greenhouse-measured microbial effects.

831

For Review Only

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

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

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

$$N_p(t+1) = \underbrace{s_p(1-g_p)N_p(t)}_{\text{survival of ungerminated seeds}} + \underbrace{A_p(t)\frac{\lambda_p}{1+\alpha_{pp}A_p(t)+\alpha_{pa}g_aN_a(t)}}_{\text{seed production by adult plants}} \quad (2)$$

$$A_p(t+1) = \underbrace{A_p(t)\xi}_{\text{survival of existing adults}} + \underbrace{N_p(t)\frac{g_p v}{1+\beta_{p,A_p}A_p(t)+\beta_{p,N_p}g_pN_p(t)+\beta_{p,N_a}g_aN_a(t)}}_{\text{maturation of seeds into adult plants}} \quad (3)$$

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

For the perennial plant, there are five demographic parameters that can be affected by soil microbes (g_p , s_p , λ_p , v , and ξ). As demonstrated in section II., the first strength of a demographic model is that it can integrate multiple microbial effects. For example, if in the case where soil pathogens decreased all parameters of the perennial plant by 20%, the model suggests suggested that it would nearly be outcompeted by the annual plant (i.e., from grey to blue dashed line; Fig. 7). By only quantifying the impact of pathogens on the intrinsic fecundity (λ_p), as is commonly done in studies that grow individual plants in conditioned

Box 2 (continued)

soils, we would have underestimated the impacts of soil microbes in this system. The second strength of a demographic model is that it helps identify the most critical microbial effect for competitive outcomes. For example, sensitivity analysis (see Box figure Fig. 7 legend for details) revealed that, compared to other demographic parameters, the impact of pathogens on adult survival probability (ξ) had the strongest impact on the perennial plant population (Fig. 7).

834

For Review Only

835 **Figure legends**

836 **Figure 1.** Temporal dimensions of plant–soil microbe interactions throughout the repeated
837 process of plant establishment, growth, death, and recolonization by another individual. (A) The
838 common assumptions regarding plant–soil microbe interactions implied by the design of classic
839 experiments: microbial communities develop relatively quickly, with resulting microbial effects
840 that are constant throughout different plant life stages and remain as long-lasting legacies after
841 plant senescence to impact the next generation. (B) The dynamic plant–soil microbe interaction
842 perspective highlighted in our review: microbial communities change continuously throughout the
843 conditioning process, with impacts on plant performance that depend on both the duration of plant
844 conditioning and response (subsection III.1). Moreover, microbial communities and their impacts
845 on plant performance may diminish with time after the senescence of the previous conditioning
846 individual (subsection III.2) or undergo different trajectories depending on the previous rounds of
847 conditioning (mentioned as a future direction in subsection III.3). Different seedling and tree sizes
848 across the panels indicate varying plant responses (increasing upwards) to soil microbial effects
849 (increasing downwards). Created in BioRender (<https://BioRender.com/a8tl9rj>).

850 **Figure 2.** An example demonstrating how incorporating the temporal and demographic aspects
851 of plant–soil microbe interactions can generate different competitive outcomes in the annual
852 plant model. (A) A graphical representation of the Beverton–Holt annual plant model, which
853 tracks the density of seeds prior to germination. Demographic processes influenced by soil
854 microbes in this simulation are highlighted in red, including seed survival and the fecundity
855 of germinated plants. Brown and grey seeds represent viable and dead seeds, respectively. (B)
856 Abundance time series of N_1 (solid line) and N_2 (dashed line) under different microbial effect
857 scenarios: no pathogenic effect (grey), pathogens decrease the seed survival of N_1 (s_1 ; blue), and
858 pathogens decrease the fecundity of N_1 (λ_1 ; orange). The left panel assumes a 10% decrease
859 in N_1 's demographic parameters, whereas the right panel assumes that the initial 10% decrease
860 after one generation aggravates to an 80% decrease after eight generations (i.e., a 10% decrease
861 after every generation). Note that the blue lines often overlap the grey lines due to the minor
862 impact of s_1 . Parameters are obtained from the species pair *Festuca microstachys* (N_1) versus
863 *Hordeum murinum* (N_2) in Van Dyke et al. (2022): $g_1 = 0.752$, $g_2 = 0.667$, $s_1 = 0.134$, $s_2 = 0.045$,
864 $\lambda_1 = 2129.950$, $\lambda_2 = 736.667$, $\alpha_{11} = 0.588$, $\alpha_{12} = 1.411$, $\alpha_{21} = 0.109$, and $\alpha_{22} = 0.948$. Panel (A)

865 created in BioRender (<https://BioRender.com/0kwj3z5>).

866 **Figure 3.** A summary of the experimental duration and life history information of the study species
867 in the Crawford et al. (2019b) and Yan et al. (2022b) data sets. Since the two studies focused on the
868 pairwise plant–soil feedback, we compiled information on plant life history and categorized each
869 pairwise comparison as different “pair types”: annual (both plants are annuals; orange), perennial
870 (both plants are perennials; green), or annual–perennial (match of an annual versus a perennial;
871 blue). Fully opaque pie charts represent studies that evaluated plant–soil feedback between annual
872 and perennial plants, with slice colors representing the percentage of different pair types within
873 the study (translucent points are single-color pie charts, representing studies that included only
874 annual or only perennial species). The position of each pie chart indicates the duration of a study’s
875 conditioning (x-axis; field-conditioned soil as a separate category) and response phase (y-axis). The
876 upper and right stacked histograms depict the same information but are based on the number of
877 experimental pairs across all studies. Note that one study with a conditioning length of 48 months
878 and a response length of 32 months (Kulmatiski, 2019) was excluded from the figure to improve
879 visualization. Data compiled from the publicly available dataset in Crawford et al. (2019b) and
880 Yan et al. (2022b) are available at <https://github.com/pojuke/DemographicReviewPSF>.

881 **Figure 4.** Experiments for studying plant–soil microbe interactions. (A) The classic two-phase
882 experimental design, consisting of a conditioning phase during which plants modify the soil
883 microbial community and a response phase during which plants respond to the soil modification.
884 Depicted here in the response phase is the case of negative frequency-dependent feedback where
885 conditioned soils favor the performance of heterospecifics over conspecifics. (B) Proposed experimental
886 designs to study the various temporal dimensions in the main text (measuring the orange plant’s
887 performance in soils conditioned by the blue plant as an example): (i) isolating changes in the soil
888 microbial community by varying the duration of soil conditioning, (ii) sequential harvesting with
889 both conditioning effect and plant age advancing simultaneously, (iii) isolating the decay process
890 by incorporating a time lag after soil conditioning, and (iv) isolating changes in plant physiology
891 by transplanting individuals of different age in the same conditioned soil. Created in BioRender
892 (<https://BioRender.com/yisnt7l>).

893 **Figure 5.** Conceptual diagram depicting multiple demographic consequences of soil microbes,
894 with a particular focus on early plant life stages following most empirical studies. The inner

895 circle (black arrows) indicates the distinct demographic processes that can be affected by soil
896 microbes; in the main text, we highlight empirical evidence on seed mortality, germination, and
897 early seedling survival. The outer circle (grey dashed arrows) indicates the life stages included
898 in different studies on conspecific negative density dependence (CNDD). Created in BioRender
899 (<https://BioRender.com/cyus4c6>).

900 **Figure 6.** An example demonstrating how the temporal decay of microbial effects can be studied
901 with a patch occupancy model. (A) Transitions among different plant-soil microbe states occur
902 due to plant colonization/conditioning, plant death, and the decay of microbial effects. Here, soil
903 microbes affect the ability of plants to recolonize conditioned soil (red arrows). (B & C) Diversity
904 of the plant community when microbial effects decay slowly ($d_i = 0.01$; left panels) or rapidly
905 ($d_i = 0.99$; right panels). We simulated the dynamics of 16 plant species (depicted with different
906 colors and letters). We ran 100 simulations; each time we randomly generated a new fecundity
907 value for each species (i.e., $r_i \sim U(0.2, 0.25)$) while fixing the microbial effect parameters based on
908 data from Teste et al. (2017). Panel (B) shows a representative time series of the relative abundance
909 of different plant species (frequencies of empty patches are omitted). Panel (C) shows the number
910 of times (out of 100 simulations) the focal species (x-axis; different species labeled with different
911 capitalized letters) persisted in the final community. Mortality (m_i) is set to 0.05 for all plants and
912 initial conditions are: $P_{00} = 0.2$, $P_{ii} = 0.05$ for $i = 1 \dots 16$, and $P_{0i} = 0.0$. See Box 1 for additional
913 details.

914 **Figure 7.** Detecting the most critical microbial effect within an annual-perennial plant competition
915 model (modified from Uricchio et al., 2019). Here, soil microbes can impact five demographic
916 parameters of the perennial plant: seed germination rate (g_p), seed survival rate (s_p), intrinsic
917 fecundity (λ_p), seedling survival rate (v) and adult survival rate (ξ). The grey dashed line
918 represents the relative abundance of the perennial plant in the absence of any pathogenic effects
919 from the microbes (i.e., unperturbed baseline parameters), while the dashed blue line shows the
920 perennial's relative abundance when the pathogen simultaneously causes a 20% reduction in all
921 five parameters. To evaluate the demographic consequences of microbes primarily impacting one
922 demographic process, we sequentially decreased the value of each parameter by 20%, while the
923 other four non-focal parameters were randomly decreased by 0% to 5% (assuming weaker microbial
924 impact). For each focal parameter, we repeated this process in 100 simulations (translucent grey

925 points; red points and error bars represent the means and standard deviations) and ran each
926 simulation for 200 generations. These simulations reveal that soil pathogens that primarily reduce
927 adult survival (ξ) have substantially stronger demographic consequences than pathogens that
928 primarily affect other demographic processes. See Box 2 for model description. The baseline
929 parameters are obtained from the species pair *Elymus glaucus* (our perennial) versus *Bromus*
930 *diandrus* (our annual) in Uricchio et al. (2019) – perennial plant parameters: $g_p = 0.125$, $s_p = 0.515$,
931 $\lambda_p = 282.127$, $\xi = 0.920$, $v = 0.292$; annual plant parameters: $g_a = 0.168$, $s_a = 0.443$, $\lambda_a = 47.594$;
932 competitive reduction of seed production: $\alpha_{aa} = 0.066$, $\alpha_{ap} = 0.143$, $\alpha_{pp} = 0.018$, $\alpha_{pa} = 0.104$;
933 competitive reduction of perennial survival: $\beta_{p,N_p} = 0.086$, $\beta_{p,A_p} = 0.063$, $\beta_{p,N_a} = 0.002$.

For Review Only

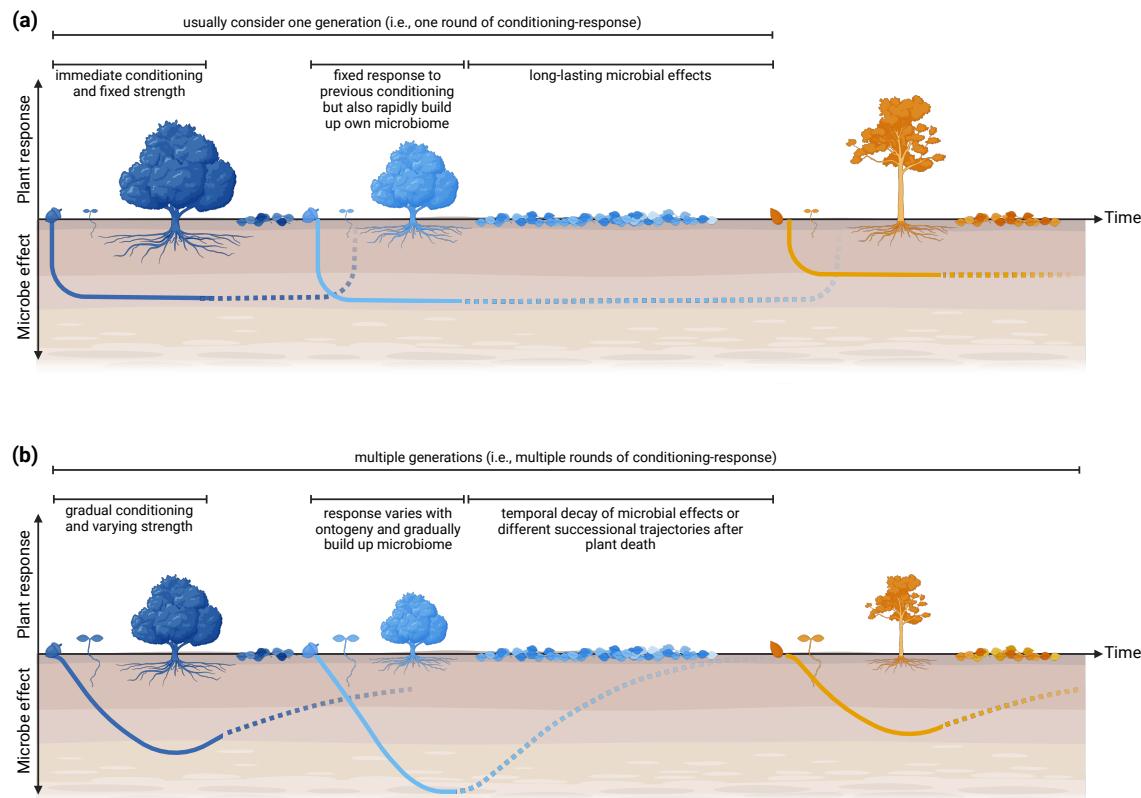


Figure 1 Temporal dimensions of plant–soil microbe interactions throughout the repeated process of plant establishment, growth, death, and recolonization by another individual. (A) The common assumptions of regarding plant–soil microbe interactions implied by the design of classic experiments: microbial communities develop relatively quickly, with resulting microbial effects that are constant throughout different plant life stages and remain as long-lasting legacies after plant senescence to impact the next generation. (B) The dynamic plant–soil microbe interaction perspective highlighted in our review: microbial communities change continuously throughout the conditioning process, with impacts on plant performance that depend on both the duration of plant conditioning and response (subsection III.1). Moreover, microbial communities and their impacts on plant performance may diminish with time after the senescence of the previous conditioning individual (subsection III.2) or undergo different trajectories depending on the previous rounds of conditioning (mentioned as a future direction in subsection III.3). Different seedling and tree sizes across the panels indicate varying plant responses (increasing upwards) to soil microbial effects (increasing downwards). Created in BioRender (<https://BioRender.com/a8tl9rj>).

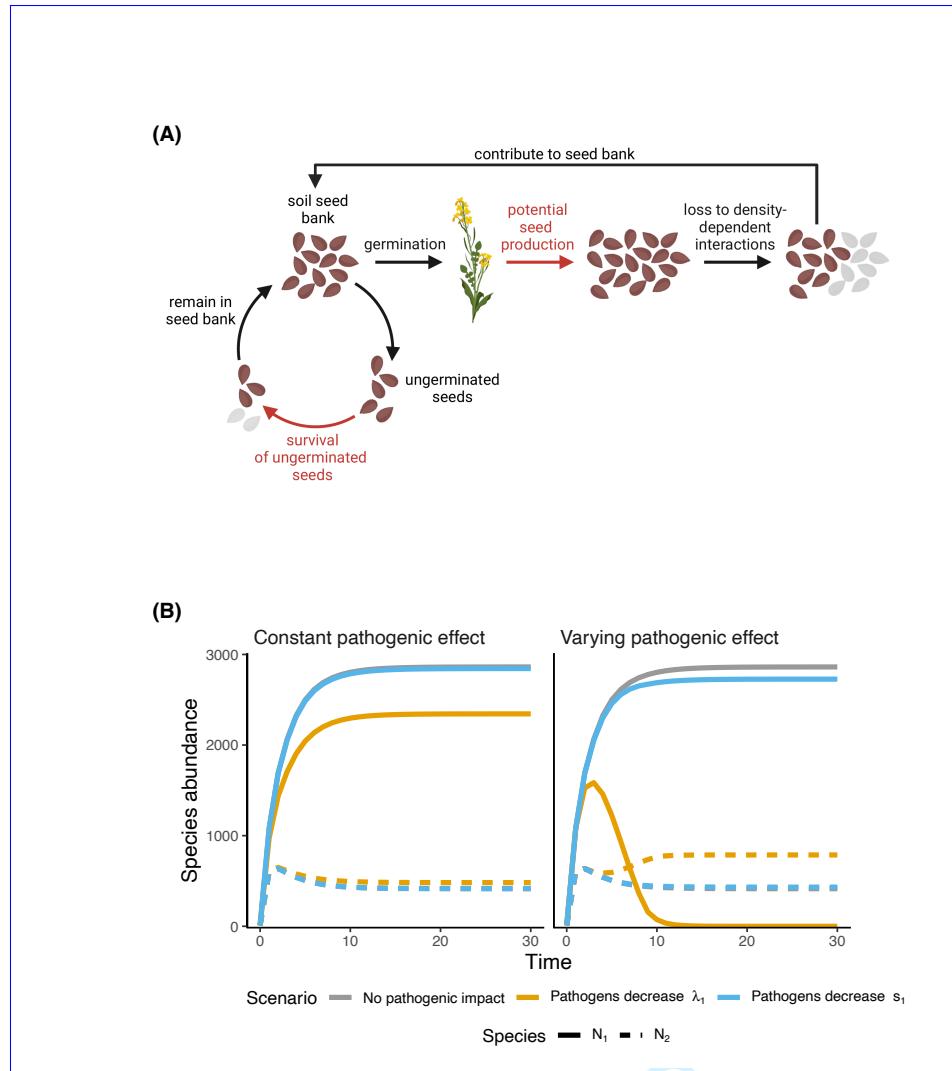


Figure 2 An example demonstrating how incorporating the temporal and demographic aspects of plant-soil microbe interactions can generate different competitive outcomes in the annual plant model. (A) A graphical representation of the Beverton-Holt annual plant model, which tracks the density of seeds prior to germination. Demographic processes influenced by soil microbes in this simulation are highlighted in red, including seed survival and the fecundity of germinated plants. Brown and grey seeds represent viable and dead seeds, respectively. (B) Abundance time series of N_1 (solid line) and N_2 (dashed line) under different microbial effect scenarios: no pathogenic effect (grey), pathogens decrease the seed survival of N_1 (s_1 ; blue), and pathogens decrease the fecundity of N_1 (λ_1 ; orange). The left panel assumes a 10% decrease in N_1 's demographic parameters, whereas the right panel assumes that the initial 10% decrease after one generation aggravates to an 80% decrease after eight generations (i.e., a 10% decrease after every generation). Note that the blue lines often overlap the grey lines due to the minor impact of s_1 . Parameters are obtained from the species pair *Festuca microstachys* (N_1) versus *Hordeum murinum* (N_2) in Van Dyke et al. (2022): $g_1 = 0.752$, $g_2 = 0.667$, $s_1 = 0.134$, $s_2 = 0.045$, $\lambda_1 = 2129.950$, $\lambda_2 = 736.667$, $\alpha_{11} = 0.588$, $\alpha_{12} = 1.411$, $\alpha_{21} = 0.109$, and $\alpha_{22} = 0.948$. Panel (A) created in BioRender (<https://Biorender.com/0kwj3z5>).

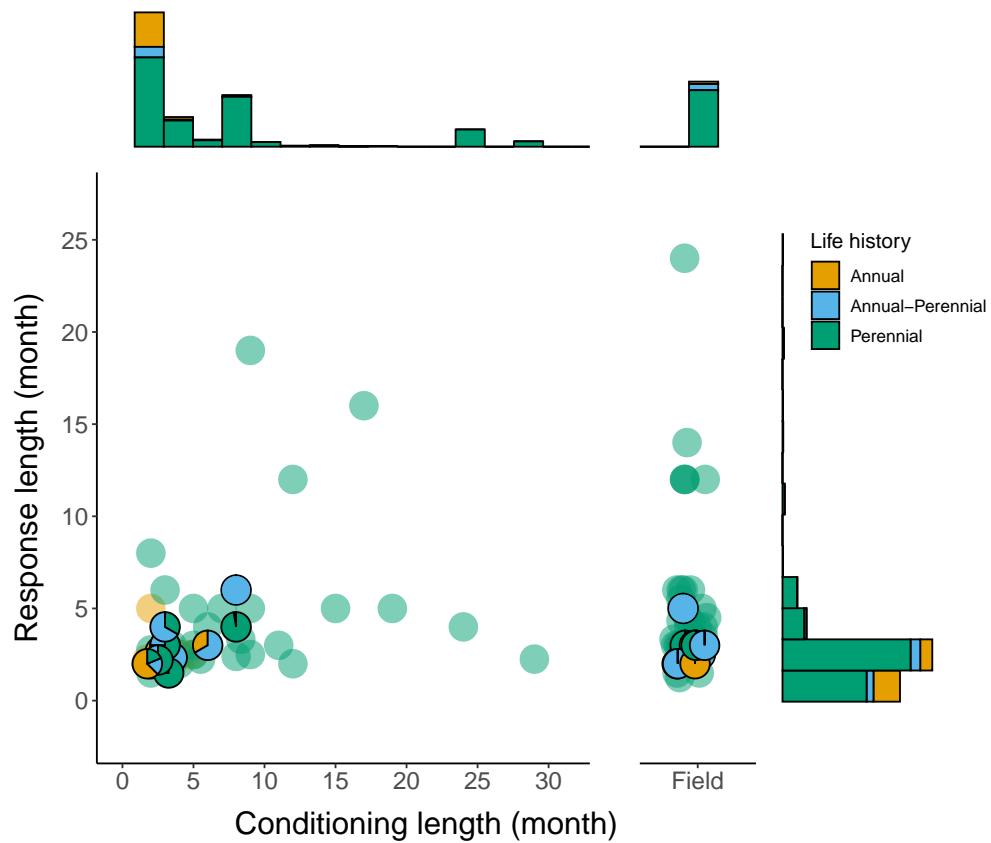


Figure 3 A summary of the experimental duration and life history information of the study species in the [Crawford et al. \(2019a\)](#) [Crawford et al. \(2019b\)](#) and [Yan et al. \(2022a\)](#) [Yan et al. \(2022b\)](#) data sets. Since the two studies focused on the pairwise plant-soil feedback, we compiled information on plant life history and categorized each pairwise comparison as different “pair types”: annual (both plants are annuals; orange), perennial (both plants are perennials; green), or annual-perennial (match of an annual versus a perennial; blue). [Highlighted points](#) [Fully opaque pie charts](#) represent studies that evaluated plant-soil feedback between annual and perennial plants, with [each pie chart slice colors](#) representing the percentage of different pair types within the study (translucent points [indicate are single-color pie charts](#), [representing](#) studies that included only annual or only perennial species). The position of each pie chart indicates the duration of a study’s conditioning (x-axis; field-conditioned soil as a separate category) and response phase (y-axis). The upper and right stacked histograms depict the same information but are based on the number of experimental pairs across all studies. Note that one study with a conditioning length of 48 months and a response length of 32 months (Kulmatiski, 2019) was excluded from the figure to improve visualization ([see supplementary data](#)). [Data compiled from the publicly available dataset in Crawford et al. \(2019b\) and Yan et al. \(2022b\) are available at <https://github.com/pojuke/DemographicReviewPSF>.](#)

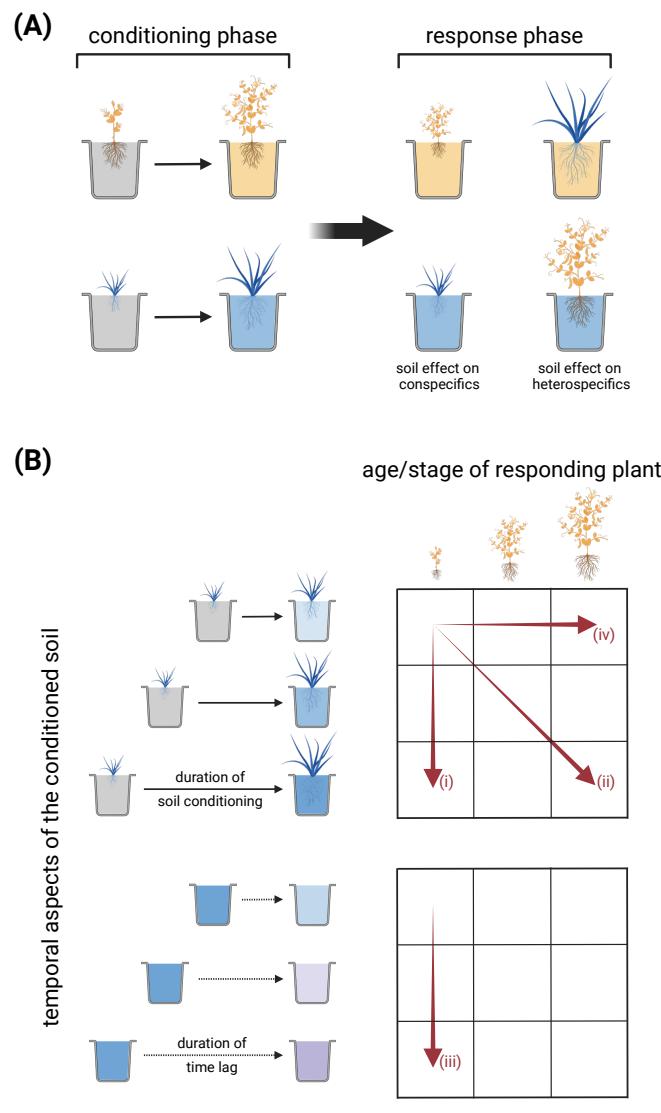


Figure 4 Experiments for studying plant–soil microbe interactions. (A) The classic two-phase experimental design, consisting of a conditioning phase during which plants modify the soil microbial community and a response phase during which plants respond to the soil modification. Depicted here in the response phase is the case of negative frequency-dependent feedback where conditioned soils favor the performance of heterospecifics over conspecifics. (B) Proposed experimental designs to study the various temporal dimensions in the main text (measuring the orange plant’s performance in soils conditioned by the blue plant as an example): (i) isolating changes in the soil microbial community by varying the duration of soil conditioning, (ii) sequential harvesting with both conditioning effect and plant age advancing simultaneously, (iii) isolating the decay process by incorporating a time lag after soil conditioning, and (iv) isolating changes in plant physiology by transplanting individuals of different age in the same conditioned soil. [Created in BioRender \(https://BioRender.com/yisnt7l\)](https://BioRender.com/yisnt7l).

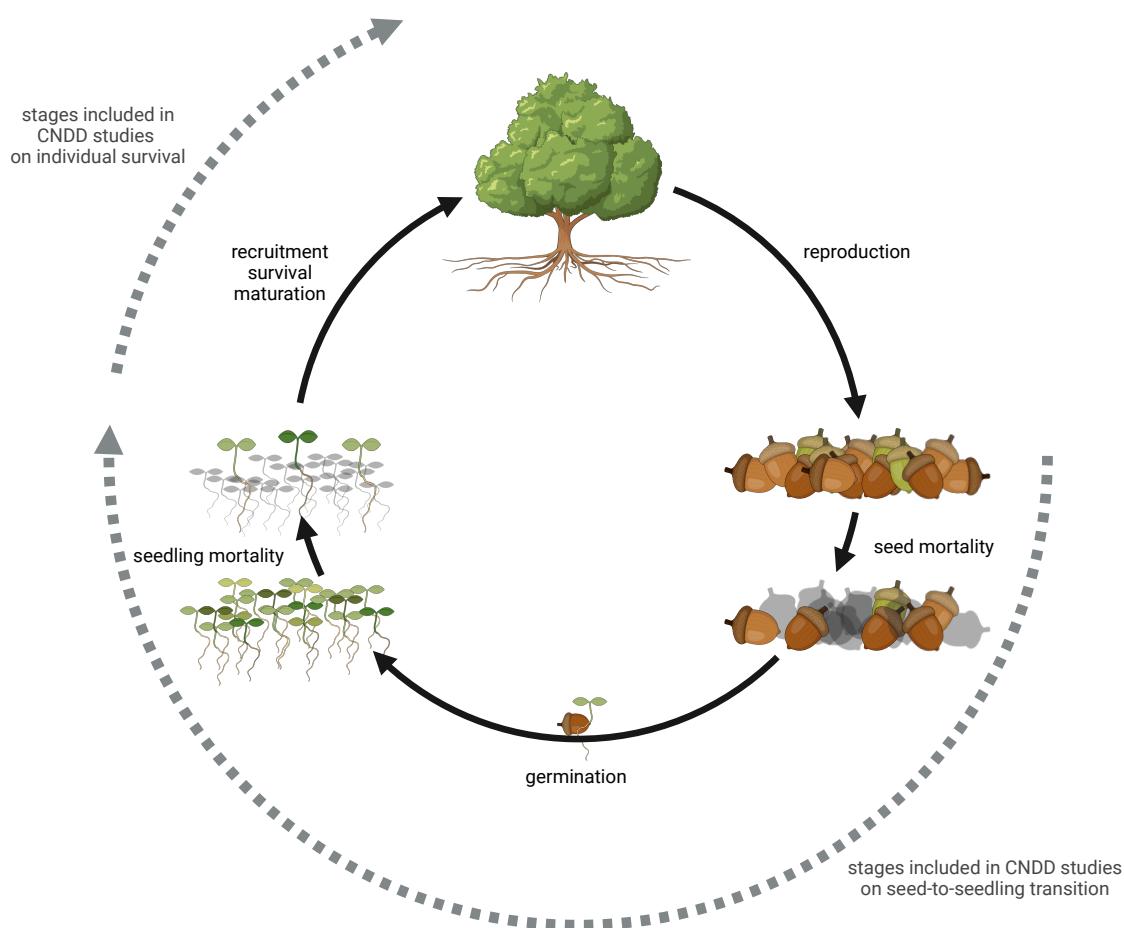


Figure 5 Conceptual diagram depicting multiple demographic consequences of soil microbes, with a particular focus on early plant life stages following most empirical studies. The inner circle (black arrows) indicates the distinct demographic processes that can be affected by soil microbes; in the main text, we highlight empirical evidence on seed mortality, germination, and early seedling survival. The outer circle (grey dashed arrows) indicates the life stages included in different studies on conspecific negative density dependence (CNDD). [Created in BioRender](https://BioRender.com/cyus4c6) (<https://BioRender.com/cyus4c6>).

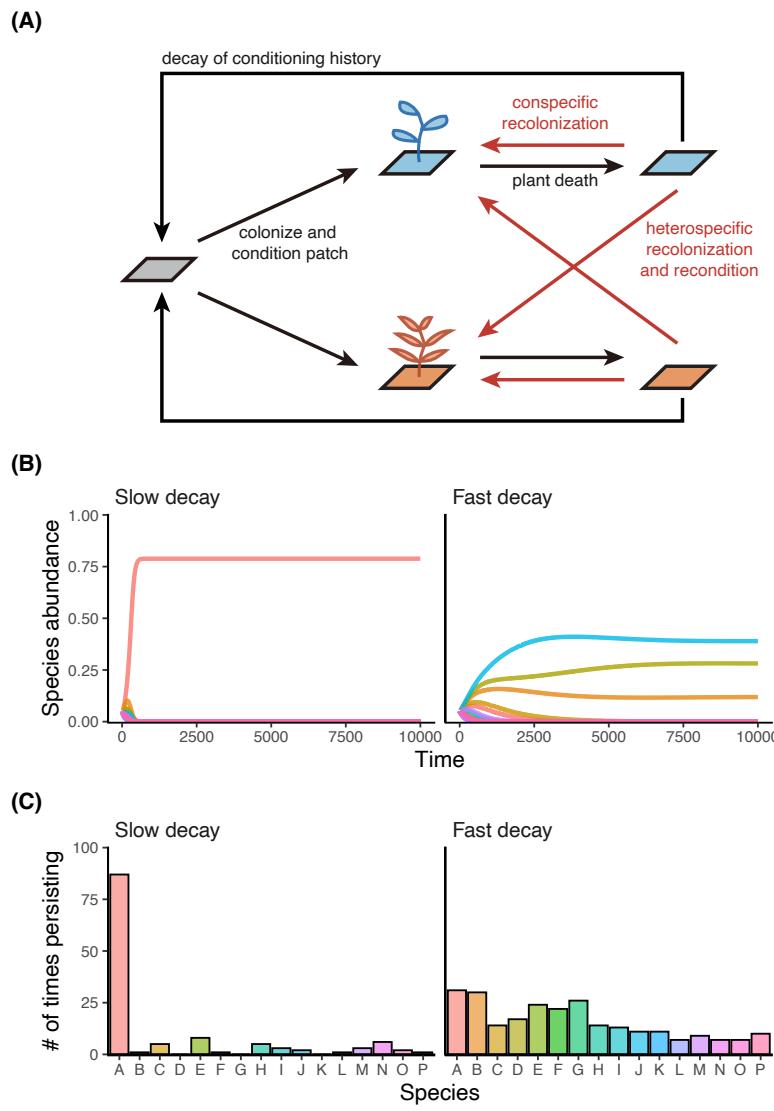


Figure 6 An example demonstrating how the temporal decay of microbial effects can be studied with a patch occupancy model. (A) Transitions among different plant-soil microbe states occur due to plant colonization/conditioning, plant death, and the decay of microbial effects. Here, soil microbes affect the ability of plants to recolonize conditioned soil (red arrows; [modified from Ke and Levine, 2021](#)). (B & C) Diversity of the plant community when microbial effects decay slowly ($d_i = 0.01$; left panels) or rapidly ($d_i = 0.99$; right panels). We simulated the dynamics of 16 plant species (depicted with different colors and letters). We ran 100 simulations; each time we randomly generated a new fecundity value for each species (i.e., $r_i \sim U(0.2, 0.25)$) while fixing the microbial effect parameters based on data from Teste et al. (2017). Panel (B) shows a representative time series of the relative abundance of different plant species (frequencies of empty patches are omitted). Panel (C) shows the number of times (out of 100 simulations) the focal species (x-axis; different species labeled with different capitalized letters) persisted in the final community. Mortality (m_i) is set to 0.05 for all plants and initial conditions are: $P_{00} = 0.2$, $P_{ii} = 0.05$ for $i = 1 \dots 16$, and $P_{0i} = 0.0$. See Box 1 for additional details.

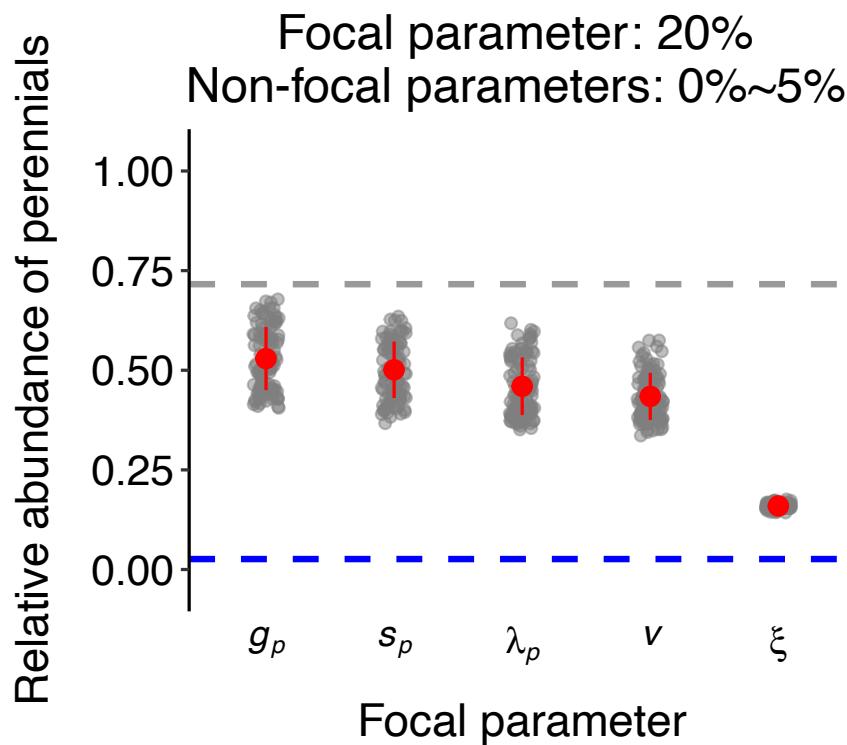


Figure 7 Detecting the most critical microbial effect within an annual–perennial plant competition model (modified from Uricchio et al., 2019). Here, soil microbes can impact five demographic parameters of the perennial plant: seed germination rate (g_p), seed survival rate (s_p), intrinsic fecundity (λ_p), seedling survival rate (v) and adult survival rate (ξ). The grey dashed line represents the relative abundance of the perennial plant in the absence of any pathogenic effects from the microbes (i.e., unperturbed baseline parameters), while the dashed blue line shows the perennial’s relative abundance when the pathogen simultaneously causes a 20% reduction in all five parameters. To evaluate the demographic consequences of microbes primarily impacting one demographic process, we sequentially decreased the value of each parameter by 20%, while the other four non-focal parameters were randomly decreased by 0% to 5% (assuming weaker microbial impact). For each focal parameter, we repeated this process in 100 simulations (translucent grey points; red points and error bars represent the means and standard deviations) and ran each simulation for 200 generations. These simulations reveal that soil pathogens that primarily reduce adult survival (ξ) have substantially stronger demographic consequences than pathogens that primarily affect other demographic processes. See Box 2 for model description. The baseline parameters are obtained from the species pair *Elymus glaucus* (our perennial) versus *Bromus diandrus* (our annual) in Uricchio et al. (2019) – perennial plant **parameterparameters**: $g_p = 0.125$, $s_p = 0.515$, $\lambda_p = 282.127$, $\xi = 0.920$, $v = 0.292$; annual plant parameters: $g_a = 0.168$, $s_a = 0.443$, $\lambda_a = 47.594$; **competitioncompetitive** reduction **on-of** seed production: $\alpha_{aa} = 0.066$, $\alpha_{ap} = 0.143$, $\alpha_{pp} = 0.018$, $\alpha_{pa} = 0.104$; **competitioncompetitive** reduction **on-of** perennial survival: $\beta_{p,N_p} = 0.086$, $\beta_{p,A_p} = 0.063$, $\beta_{p,N_a} = 0.002$.

934 Acknowledgments

935 We thank Xinyi Yan for contributing to the dataset used for Figure 3 and for insightful comments
936 that improved the manuscript. We thank Lawrence Uricchio and Erin Mordecai for help with
937 the model and parameter estimates used in ~~Box~~ Figure 7. We thank Hengxing Zou, Chia-Hao
938 Chang-Yang, Y. Anny Chung, ~~Hengxing Zou~~, Ching-Lin Huang, Yu-Pei Tseng, Yi Sun, and Shuo
939 Wei for their discussions. P.-J. Ke and J.W. are funded by the Taiwan Ministry of Education
940 Yushan Fellow Program (MOE-110-YSFAG-0003-001-P1) and the Taiwan Ministry of Science and
941 Technology (MOST 111-2621-B-002-001-MY3 and NSTC 113-2811-B-002-118). J.W. is also supported
942 by NTU postdoctoral grant 112L4000-1. G.S. Kandlikar, M. Krishnadas, and P.-J. Ke acknowledge
943 support from sDiv, the Synthesis Centre of iDiv (DFG FZT 118, 202548816).

944 Author Contributions

945 Author Contributions

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

948 Data Availability

949 The dataset used in Figure 3 and code used to generate model simulations are available on GitHub
950 (<https://github.com/pojuke/DemographicReviewPSF>) and will be made available on Zenodo
951 with a DOI upon publication. Figures 1, 2A, 5, and ~~Box~~ Figure 6A are created with BioRender.com.

952

953 References

- 954 Augspurger, C. K., 1984. Seedling survival of tropical tree species: interactions of dispersal
955 distance, light-gaps, and pathogens. *Ecology* **65**:1705–1712.
- 956 Bagchi, R., R. E. Gallery, S. Gripenberg, S. J. Gurr, L. Narayan, C. E. Addis, R. P. Freckleton, and O. T.
957 Lewis, 2014. Pathogens and insect herbivores drive rainforest plant diversity and composition.
958 *Nature* **506**:85–88.
- 959 Bagchi, R., T. Swinfield, R. E. Gallery, O. T. Lewis, S. Gripenberg, L. Narayan, and R. P. Freckle-
960 ton, 2010. Testing the Janzen-Connell mechanism: pathogens cause overcompensating density
961 dependence in a tropical tree. *Ecology Letters* **13**:1262–1269.
- 962 Barret, M., M. Briand, S. Bonneau, A. Préveaux, S. Valière, O. Bouchez, G. Hunault, P. Simoneau,
963 and M. A. Jacques, 2015. Emergence shapes the structure of the seed microbiota. *Applied and*
964 *Environmental Microbiology* **81**:1257–1266.
- 965 Bauer, J. T., K. M. L. Mack, and J. D. Bever, 2015. Plant-soil feedbacks as drivers of succession:
966 evidence from remnant and restored tallgrass prairies. *Ecosphere* **6**:art158.
- 967 Bell, T., R. P. Freckleton, and O. T. Lewis, 2006. Plant pathogens drive density-dependent seedling
968 mortality in a tropical tree. *Ecology Letters* **9**:569–574.
- 969 Bennett, J. A., J. Franklin, and J. Karst, 2023. Plant-soil feedbacks persist following tree death,
970 reducing survival and growth of *populus tremuloides* seedlings. *Plant and Soil* **485**:103–115.
- 971 Bennett, J. A., H. Maherli, K. O. Reinhart, Y. Lekberg, M. M. Hart, and J. Klironomos, 2017. Plant-
972 soil feedbacks and mycorrhizal type influence temperate forest population dynamics. *Science*
973 **355**:181–184.
- 974 Bever, J. D., 1994. Feedback between plants and their soil communities in an old field community.
975 *Ecology* **75**:1965–1977.
- 976 Bever, J. D., 2003. Soil community feedback and the coexistence of competitors: conceptual
977 frameworks and empirical tests. *New Phytologist* **157**:465–473.

- 978 Bever, J. D., I. A. Dickie, E. Facelli, J. M. Facelli, J. Klironomos, M. Moora, M. C. Rillig, W. D.
979 Stock, M. Tibbett, and M. Zobel, 2010. Rooting theories of plant community ecology in microbial
980 interactions. *Trends in Ecology & Evolution* **25**:468–478.
- 981 Bever, J. D., S. A. Mangan, and H. M. Alexander, 2015. Maintenance of plant species diversity by
982 pathogens. *Annual Review of Ecology, Evolution, and Systematics* **46**:305–325.
- 983 Bever, J. D., T. G. Platt, and E. R. Morton, 2012. Microbial population and community dynamics on
984 plant roots and their feedbacks on plant communities. *Annual Review of Microbiology* **66**:265–283.
- 985 Bever, J. D., K. M. Westover, and J. Antonovics, 1997. Incorporating the soil community into plant
986 population dynamics: The utility of the feedback approach. *Journal of Ecology* **85**:561–573.
- 987 Bezemer, T. M., J. Jing, J. M. T. Bakx-Schotman, and E.-J. Bijleveld, 2018. Plant competition alters
988 the temporal dynamics of plant–soil feedbacks. *Journal of Ecology* **106**:2287–2300.
- 989 Bingham, M. A. and S. W. Simard, 2011. Do mycorrhizal network benefits to survival and growth of
990 interior douglas-fir seedlings increase with soil moisture stress? *Ecology and Evolution* **1**:306–316.
- 991 Bittleston, L. S., Z. B. Freedman, J. R. Bernardin, J. J. Grothjan, E. B. Young, S. Record, B. Baiser,
992 and S. M. Gray, 2021. Exploring microbiome functional dynamics through space and time with
993 trait-based theory. *mSystems* **6**:10–1128.
- 994 Bonanomi, G., V. Antignani, M. Capodilupo, and F. Scala, 2010. Identifying the characteristics of
995 organic soil amendments that suppress soilborne plant diseases. *Soil Biology and Biochemistry*
996 **42**:136–144.
- 997 Bottini, R., F. Cassán, and P. Piccoli, 2004. Gibberellin production by bacteria and its involvement
998 in plant growth promotion and yield increase. *Applied Microbiology and Biotechnology* **65**:497–503.
- 999 Brinkman, E. P., W. H. van der Putten, E.-j. Bakker, and K. J. F. Verhoeven, 2010. Plant–soil feedback:
1000 experimental approaches, statistical analyses and ecological interpretations. *Journal of Ecology*
1001 **98**:1063–1073.
- 1002 Bulgarelli, D., K. Schlaepi, S. Spaepen, E. V. L. Van Themaat, and P. Schulze-Lefert, 2013. Structure
1003 and functions of the bacterial microbiota of plants. *Annual Review of Plant Biology* **64**:807–838.

- 1004 Callaway, R. M., G. C. Thelen, A. Rodriguez, and W. E. Holben, 2004. Soil biota and exotic plant
1005 invasion. *Nature* **427**:731–733.
- 1006 Cardinaux, A., S. P. Hart, and J. M. Alexander, 2018. Do soil biota influence the outcome of novel
1007 interactions between plant competitors? *Journal of Ecology* **106**:1853–1863.
- 1008 Carini, P., P. J. Marsden, J. W. Leff, E. E. Morgan, M. S. Strickland, and N. Fierer, 2016. Relic DNA
1009 is abundant in soil and obscures estimates of soil microbial diversity. *Nature Microbiology* **2**:1–6.
- 1010 Chang-Yang, C.-H., J. Needham, C.-L. Lu, C.-F. Hsieh, I.-F. Sun, and S. M. McMahon, 2021. Clos-
1011 ing the life cycle of forest trees: The difficult dynamics of seedling-to-sapling transitions in a
1012 subtropical rainforest. *Journal of Ecology* **109**:2705–2716.
- 1013 Chaparro, J. M., D. V. Badri, and J. M. Vivanco, 2013. Rhizosphere microbiome assemblage is
1014 affected by plant development. *The ISME Journal* **8**:790–803.
- 1015 Chen, L., N. G. Swenson, N. Ji, X. Mi, H. Ren, L. Guo, and K. Ma, 2019. Differential soil fungus
1016 accumulation and density dependence of trees in a subtropical forest. *Science* **366**:124–128.
- 1017 Cheng, C., M. J. Gundale, B. Li, and J. Wu, 2024. Deciphering the drivers of plant-soil feedbacks
1018 and their context-dependence: A meta-analysis. *Plant and Soil* pages 1–15.
- 1019 Chu, C. and P. B. Adler, 2015. Large niche differences emerge at the recruitment stage to stabilize
1020 grassland coexistence. *Ecological Monographs* **85**:373–392.
- 1021 Chung, Y. A., 2023. The temporal and spatial dimensions of plant–soil feedbacks. *New Phytologist*
1022 **237**:2012–2019.
- 1023 Chung, Y. A., T. A. Monaco, J. B. Taylor, and P. B. Adler, 2023. Do plant–soil feedbacks promote
1024 coexistence in a sagebrush steppe? *Ecology* **104**:e4056.
- 1025 Chung, Y. A. and J. A. Rudgers, 2016. Plant–soil feedbacks promote negative frequency dependence
1026 in the coexistence of two aridland grasses. *Proceedings of the Royal Society B* **283**:20160608.
- 1027 Clark, C., J. Poulsen, D. Levey, and C. Osenberg, 2007. Are plant populations seed limited? A
1028 critique and meta-analysis of seed addition experiments. *The American Naturalist* **170**:128–142.

- 1029 Cobb, R. C., S. E. Haas, N. Kruskamp, W. W. Dillon, T. J. Swiecki, D. M. Rizzo, S. J. Frankel, and
1030 R. K. Meentemeyer, 2020. The magnitude of regional-scale tree mortality caused by the invasive
1031 pathogen *Phytophthora ramorum*. *Earth's Future* **8**:e2020EF001500.
- 1032 Comita, L. S., H. C. Muller-Landau, S. Aguilar, and S. P. Hubbell, 2010. Asymmetric density
1033 dependence shapes species abundances in a tropical tree community. *Science* **329**:330–332.
- 1034 Connell, J., 1971. On the role of natural enemies in preventing competitive exclusion in some
1035 marine animals and in rain forest trees. In P. Den Boer and G. Gradwell, editors, *Dynamics of
1036 Populations*, pages 298–312. Centre for Agricultural Publishing and Documentation, Wageningen,
1037 The Netherlands.
- 1038 Crawford, K. M., J. T. Bauer, L. S. Comita, M. B. Eppinga, D. J. Johnson, S. A. Mangan, S. A.
1039 Queenborough, A. E. Strand, K. N. Suding, J. Umbanhowar, et al., 2019a. When and where
1040 plant-soil feedback may promote plant coexistence: a meta-analysis. *Ecology Letters* **22**:1274–
1041 1284.
- 1042 Crawford, K. M., J. T. Bauer, L. S. Comita, M. B. Eppinga, D. J. Johnson, S. A. Mangan, S. A.
1043 Queenborough, A. E. Strand, K. N. Suding, J. Umbanhowar, et al., 2019b. When and where
1044 plant-soil feedback may promote plant coexistence: a meta-analysis: raw data and citations for
1045 the meta-analysis. *Figshare Repository*: <https://doi.org/10.6084/m9.figshare.7985195.v1>.
- 1046 Dalling, J. W., M. Swaine, and N. C. Garwood, 1998. Dispersal patterns and seed bank dynamics
1047 of pioneer trees in moist tropical forest. *Ecology* **79**:564–578.
- 1048 Das, A. J., N. L. Stephenson, and K. P. Davis, 2016. Why do trees die? characterizing the drivers of
1049 background tree mortality. *Ecology* **97**:2616–2627.
- 1050 David, A. S., P. F. Quintana-Ascencio, E. S. Menges, K. B. Thapa-Magar, M. E. Afkhami, and C. A.
1051 Searcy, 2019. Soil microbiomes underlie population persistence of an endangered plant species.
1052 *The American Naturalist* **194**:488–494.
- 1053 Day, N. J., K. E. Dunfield, and P. M. Antunes, 2015. Temporal dynamics of plant–soil feedback and
1054 root-associated fungal communities over 100 years of invasion by a non-native plant. *Journal of
1055 Ecology* **103**:1557–1569.

- 1056 De Long, J. R., E. L. Fry, G. Veen, and P. Kardol, 2019. Why are plant–soil feedbacks so unpredictable,
1057 and what to do about it? *Functional Ecology* **33**:118–128.
- 1058 Diez, J. M., I. Dickie, G. Edwards, P. E. Hulme, J. J. Sullivan, and R. P. Duncan, 2010. Negative soil
1059 feedbacks accumulate over time for non-native plant species. *Ecology Letters* **13**:803–809.
- 1060 Dombrowski, N., K. Schlaeppi, M. T. Agler, S. Hacquard, E. Kemen, R. Garrido-Oter, J. Wunder,
1061 G. Coupland, and P. Schulze-Lefert, 2016. Root microbiota dynamics of perennial *Arabis alpina*
1062 are dependent on soil residence time but independent of flowering time. *The ISME Journal*
1063 **11**:43–55.
- 1064 Dostál, P., 2021. The temporal development of plant-soil feedback is contingent on competition
1065 and nutrient availability contexts. *Oecologia* **196**:185–194.
- 1066 Dostál, P., J. Müllerová, P. Pyšek, J. Pergl, and T. Klinarová, 2013. The impact of an invasive plant
1067 changes over time. *Ecology Letters* **16**:1277–1284.
- 1068 Dostálek, T., J. Knappová, and Z. Münzbergová, 2022. The role of plant–soil feedback in long-term
1069 species coexistence cannot be predicted from its effects on plant performance. *Annals of Botany*
1070 **130**:535–546.
- 1071 Dudenhöffer, J.-H., A. Ebeling, A.-M. Klein, and C. Wagg, 2018. Beyond biomass: Soil feedbacks
1072 are transient over plant life stages and alter fitness. *Journal of Ecology* **106**:230–241.
- 1073 Dudenhöffer, J.-H., N. C. Luecke, and K. M. Crawford, 2022. Changes in precipitation patterns
1074 can destabilize plant species coexistence via changes in plant–soil feedback. *Nature Ecology &*
1075 *Evolution* **6**:546–554.
- 1076 Edwards, J. A., C. M. Santos-Medellín, Z. S. Liechty, B. Nguyen, E. Lurie, S. Eason, G. Phillips, and
1077 V. Sundaresan, 2018. Compositional shifts in root-associated bacterial and archaeal microbiota
1078 track the plant life cycle in field-grown rice. *PLOS Biology* **16**:e2003862.
- 1079 Ehrenfeld, J. G., B. Ravit, and K. Elgersma, 2005. Feedback in the plant-soil system. *Annual Review*
1080 *of Environment and Resources* **30**:75–115.

- 1081 Eldridge, D. J., S. K. Travers, J. Val, J. Ding, J.-T. Wang, B. K. Singh, and M. Delgado-Baquerizo,
1082 2021. Experimental evidence of strong relationships between soil microbial communities and
1083 plant germination. *Journal of Ecology* **109**:2488–2498.
- 1084 Eppinga, M. B., M. Baudena, D. J. Johnson, J. Jiang, K. M. L. Mack, A. E. Strand, and J. D. Bever,
1085 2018. Frequency-dependent feedback constrains plant community coexistence. *Nature Ecology
& Evolution* **2**:1403–1407.
- 1087 Esch, C. M. and R. K. Kobe, 2021. Short-lived legacies of *Prunus serotina* plant–soil feedbacks.
1088 *Oecologia* **196**:529–538.
- 1089 Esch, C. M., C. M. Medina-Mora, R. K. Kobe, and M. L. Sakalidis, 2021. Oomycetes associated with
1090 *Prunus serotina* persist in soil after tree harvest. *Fungal Ecology* **53**:101094.
- 1091 Fanin, N., D. Lin, G. T. Freschet, A. D. Keiser, L. Augusto, D. A. Wardle, and G. F. Veen, 2021.
1092 Home-field advantage of litter decomposition: from the phyllosphere to the soil. *New Phytologist*
1093 **231**:1353–1358.
- 1094 Forero, L. E., A. Kulmatiski, J. Grenzer, and J. M. Norton, 2021. Plant-soil feedbacks help explain
1095 biodiversity-productivity relationships. *Communications Biology* **4**:789.
- 1096 Fukami, T. and M. Nakajima, 2013. Complex plant–soil interactions enhance plant species diversity
1097 by delaying community convergence. *Journal of Ecology* **101**:316–324.
- 1098 Gallery, R. E., D. J. Moore, and J. W. Dalling, 2010. Interspecific variation in susceptibility to
1099 fungal pathogens in seeds of 10 tree species in the neotropical genus *Cecropia*. *Journal of Ecology*
1100 **98**:147–155.
- 1101 Gao, C., L. Montoya, L. Xu, M. Madera, J. Hollingsworth, E. Purdom, R. B. Hutmacher, J. A.
1102 Dahlberg, D. Coleman-Derr, P. G. Lemieux, et al., 2019. Strong succession in arbuscular mycor-
1103 rhizal fungal communities. *The ISME journal* **13**:214–226.
- 1104 Gilbert, G. S., 2002. Evolutionary ecology of plant diseases in natural ecosystems. *Annual Review
of Phytopathology* **40**:13–43.

- 1106 Grove, S., I. M. Parker, and K. A. Haubensak, 2015. Persistence of a soil legacy following removal
1107 of a nitrogen-fixing invader. *Biological Invasions* **17**:2621–2631.
- 1108 Gundale, M. J. and P. Kardol, 2021. Multi-dimensionality as a path forward in plant-soil feedback
1109 research. *Journal of Ecology* **109**:3446–3465.
- 1110 Hannula, S. E., R. Heinen, M. Huberty, K. Steinauer, J. R. De Long, R. Jongen, and T. M. Bezemer,
1111 2021. Persistence of plant-mediated microbial soil legacy effects in soil and inside roots. *Nature
1112 Communications* **12**:5686.
- 1113 Hannula, S. E., A. M. Kielak, K. Steinauer, M. Huberty, R. Jongen, J. R. De Long, R. Heinen, and
1114 T. M. Bezemer, 2019. Time after time: temporal variation in the effects of grass and forb species
1115 on soil bacterial and fungal communities. *MBio* **10**:10–1128.
- 1116 Hansen, E. M. and E. M. Goheen, 2000. *Phellinus weiri* and other native root pathogens as determi-
1117 nants of forest structure and process in western north america. *Annual review of phytopathology*
1118 **38**:515–539.
- 1119 Harms, K. E., S. J. Wright, O. Calderón, A. Hernandez, and E. A. Herre, 2000. Pervasive density-
1120 dependent recruitment enhances seedling diversity in a tropical forest. *Nature* **404**:493–495.
- 1121 Harper, J. L., 1977. Population biology of plants. Academic Press.
- 1122 Hawkes, C. V., S. N. Kivlin, J. Du, and V. T. Eviner, 2013. The temporal development and additivity
1123 of plant-soil feedback in perennial grasses. *Plant and Soil* **369**:141–150.
- 1124 Herrera Paredes, S. and S. L. Lebeis, 2016. Giving back to the community: microbial mechanisms
1125 of plant–soil interactions. *Functional Ecology* **30**:1043–1052.
- 1126 Horton, T. and M. van der Heijden, 2008. The role of symbioses in seedling establishment and
1127 survival. *Seedling Ecology and Evolution* pages 189–214.
- 1128 Howard, M. M., J. Kao-Kniffin, and A. Kessler, 2020. Shifts in plant–microbe interactions over com-
1129 munity succession and their effects on plant resistance to herbivores. *New Phytologist* **226**:1144–
1130 1157.

- 1131 Huang, L.-F., L.-X. Song, X.-J. Xia, W.-H. Mao, K. Shi, Y.-H. Zhou, and J.-Q. Yu, 2013. Plant-soil
1132 feedbacks and soil sickness: from mechanisms to application in agriculture. *Journal of Chemical*
1133 *Ecology* **39**:232–242.
- 1134 Huberty, M., K. Steinauer, R. Heinen, R. Jongen, S. E. Hannula, Y. H. Choi, and T. M. Bezemer,
1135 2022. Temporal changes in plant–soil feedback effects on microbial networks, leaf metabolomics
1136 and plant–insect interactions. *Journal of Ecology* **110**:1328–1343.
- 1137 Igwe, A. N., B. Quasem, N. Liu, and R. L. Vannette, 2021. Plant phenology influences rhizosphere
1138 microbial community and is accelerated by serpentine microorganisms in *plantago erecta*. *FEMS*
1139 *Microbiology Ecology* **97**:85.
- 1140 Ishaq, S. L., 2017. Plant-microbial interactions in agriculture and the use of farming systems to
1141 improve diversity and productivity. *AIMS Microbiology* **3**:335.
- 1142 Janzen, D. H., 1970. Herbivores and the number of tree species in tropical forests. *The American*
1143 *Naturalist* **104**:501–528.
- 1144 Jiang, J., K. C. Abbott, M. Baudena, M. B. Eppinga, J. A. Umbanhowar, and J. D. Bever, 2020.
1145 Pathogens and mutualists as joint drivers of host species coexistence and turnover: implications
1146 for plant competition and succession. *The American Naturalist* **195**:591–602.
- 1147 Johansen, A. and E. S. Jensen, 1996. Transfer of N and P from intact or decomposing roots of
1148 pea to barley interconnected by an arbuscular mycorrhizal fungus. *Soil Biology and Biochemistry*
1149 **28**:73–81.
- 1150 Kalske, A., J. D. Blande, and S. Ramula, 2022. Soil microbiota explain differences in herbivore
1151 resistance between native and invasive populations of a perennial herb. *Journal of Ecology*
1152 **110**:2649–2660.
- 1153 Kandlikar, G. S., 2024. Quantifying soil microbial effects on plant species coexistence: A conceptual
1154 synthesis. *American Journal of Botany* **111**:e16316.
- 1155 Kandlikar, G. S., C. A. Johnson, X. Yan, N. J. Kraft, and J. M. Levine, 2019. Winning and losing with
1156 microbes: how microbially mediated fitness differences influence plant diversity. *Ecology Letters*
1157 **22**:1178–1191.

- 1158 Kandlikar, G. S., X. Yan, J. M. Levine, and N. J. Kraft, 2021. Soil microbes generate stronger
1159 fitness differences than stabilization among California annual plants. *The American Naturalist*
1160 **197**:E30–E39.
- 1161 Kardol, P., M. T. Bezemer, and W. H. van der Putten, 2006. Temporal variation in plant–soil feedback
1162 controls succession. *Ecology Letters* **9**:1080–1088.
- 1163 Kardol, P., G. B. De Deyn, E. Laliberté, P. Mariotte, and C. V. Hawkes, 2013. Biotic plant–soil
1164 feedbacks across temporal scales. *Journal of Ecology* **101**:309–315.
- 1165 Kazan, K. and R. Lyons, 2016. The link between flowering time and stress tolerance. *Journal of*
1166 *Experimental Botany* **67**:47–60.
- 1167 Ke, P.-J. and J. M. Levine, 2021. The temporal dimension of plant–soil microbe interactions:
1168 mechanisms promoting feedback between generations. *The American Naturalist* **198**:E80–E94.
- 1169 Ke, P.-J. and T. Miki, 2015. Incorporating the soil environment and microbial community into plant
1170 competition theory. *Frontiers in Microbiology* **6**:1066.
- 1171 Ke, P.-J., T. Miki, and T. Ding, 2015. The soil microbial community predicts the importance of plant
1172 traits in plant–soil feedback. *New Phytologist* **206**:329–341.
- 1173 Ke, P.-J. and J. Wan, 2020. Effects of soil microbes on plant competition: a perspective from modern
1174 coexistence theory. *Ecological Monographs* **90**:e01391.
- 1175 Ke, P.-J. and J. Wan, 2023. A general approach for quantifying microbial effects on plant competition.
1176 *Plant and Soil* **485**:57–70.
- 1177 Ke, P.-J., P. C. Zee, and T. Fukami, 2021. Dynamic plant–soil microbe interactions: the neglected
1178 effect of soil conditioning time. *New Phytologist* **231**:1546–1558.
- 1179 Keeler, A. M. and N. E. Rafferty, 2022. Legume germination is delayed in dry soils and in sterile
1180 soils devoid of microbial mutualists: Species-specific implications for upward range expansions.
1181 *Ecology and Evolution* **12**:e9186.
- 1182 Keswani, C., S. P. Singh, C. García-Estrada, S. Mezaache-Aichour, T. R. Glare, R. Borriss, V. D.
1183 Rajput, T. M. Minkina, A. Ortiz, and E. Sansinenea, 2022. Biosynthesis and beneficial effects

- 1184 of microbial gibberellins on crops for sustainable agriculture. *Journal of Applied Microbiology*
1185 **132**:1597–1615.
- 1186 Kotanen, P. M., 2007. Effects of fungal seed pathogens under conspecific and heterospecific trees
1187 in a temperate forest. *Botany* **85**:918–925.
- 1188 Koziol, L., P. A. Schultz, G. L. House, J. T. Bauer, E. L. Middleton, and J. D. Bever, 2018. The plant
1189 microbiome and native plant restoration: the example of native mycorrhizal fungi. *BioScience*
1190 **68**:996–1006.
- 1191 Krishnadas, M., K. Agarwal, and L. S. Comita, 2020. Edge effects alter the role of fungi and insects
1192 in mediating functional composition and diversity of seedling recruits in a fragmented tropical
1193 forest. *Annals of Botany* **126**:1181–1191.
- 1194 Krishnadas, M., R. Bagchi, S. Sridhara, and L. S. Comita, 2018. Weaker plant-enemy interac-
1195 tions decrease tree seedling diversity with edge-effects in a fragmented tropical forest. *Nature*
1196 *Communications* **9**:1–7.
- 1197 Krishnadas, M. and L. S. Comita, 2018. Influence of soil pathogens on early regeneration success
1198 of tropical trees varies between forest edge and interior. *Oecologia* **186**:259–268.
- 1199 Krishnadas, M. and L. S. Comita, 2019. Edge effects on seedling diversity are mediated by impacts
1200 of fungi and insects on seedling recruitment but not survival. *Frontiers in Forests and Global*
1201 *Change* **2**:76.
- 1202 Krishnadas, M. and S. M. Stump, 2021. Dispersal limitation and weaker stabilizing mechanisms
1203 mediate loss of diversity with edge effects in forest fragments. *Journal of Ecology* **109**:2137–2151.
- 1204 Kulmatiski, A., 2019. Plant-soil feedbacks predict native but not non-native plant community
1205 composition: a 7-year common-garden experiment. *Frontiers in Ecology and Evolution* **7**:326.
- 1206 Kulmatiski, A., A. Anderson-Smith, K. H. Beard, S. Doucette-Riise, M. Mazzacavallo, N. E. Nolan,
1207 R. A. Ramirez, and J. R. Stevens, 2014. Most soil trophic guilds increase plant growth: a meta-
1208 analytical review. *Oikos* **123**:1409–1419.

- 1209 Kulmatiski, A., K. H. Beard, and J. Heavilin, 2012. Plant–soil feedbacks provide an additional
1210 explanation for diversity–productivity relationships. *Proceedings of the Royal Society B: Biological
1211 Sciences* **279**:3020–3026.
- 1212 Kulmatiski, A., K. H. Beard, J. M. Norton, J. E. Heavilin, L. E. Forero, and J. Grenzer, 2017. Live
1213 long and prosper: plant–soil feedback, lifespan, and landscape abundance covary. *Ecology*
1214 **98**:3063–3073.
- 1215 Lau, J. A. and J. T. Lennon, 2012. Rapid responses of soil microorganisms improve plant fitness in
1216 novel environments. *Proceedings of the National Academy of Sciences* **109**:14058–14062.
- 1217 Lebrija-Trejos, E., A. Hernández, and S. J. Wright, 2023. Effects of moisture and density-dependent
1218 interactions on tropical tree diversity. *Nature* **615**:100–104.
- 1219 Lennon, J. T. and S. E. Jones, 2011. Microbial seed banks: the ecological and evolutionary implica-
1220 tions of dormancy. *Nature Reviews Microbiology* **9**:119–130.
- 1221 Lepinay, C., Z. Vondráková, T. Dostálék, and Z. Münzbergová, 2018. Duration of the conditioning
1222 phase affects the results of plant–soil feedback experiments via soil chemical properties. *Oecologia*
1223 **186**:459–470.
- 1224 Leverett, L. D., G. F. Schieder IV, and K. Donohue, 2018. The fitness benefits of germinating later
1225 than neighbors. *American Journal of Botany* **105**:20–30.
- 1226 Li, Y. M., J. P. Shaffer, B. Hall, and H. Ko, 2019. Soil-borne fungi influence seed germination and
1227 mortality, with implications for coexistence of desert winter annual plants. *PLoS One* **14**:e0224417.
- 1228 Liang, M., X. Liu, G. S. Gilbert, Y. Zheng, S. Luo, F. Huang, and S. Yu, 2016. Adult trees cause
1229 density-dependent mortality in conspecific seedlings by regulating the frequency of pathogenic
1230 soil fungi. *Ecology Letters* **19**:1448–1456.
- 1231 Liu, D., M. Kelly, P. Gong, and Q. Guo, 2007. Characterizing spatial–temporal tree mortality
1232 patterns associated with a new forest disease. *Forest Ecology and Management* **253**:220–231.
- 1233 Liu, X., K. Steinauer, K. van der Veen-van Wijk, and T. M. Bezemer, 2025. Zooming in on the

- 1234 temporal dimensions of plant–soil feedback: Plant sensitivity and microbial dynamics. *Journal*
1235 *of Ecology* **113**:39–52.
- 1236 Lu, T., M. Ke, M. Lavoie, Y. Jin, X. Fan, Z. Zhang, Z. Fu, L. Sun, M. Gillings, J. Peñuelas, et al., 2018.
1237 Rhizosphere microorganisms can influence the timing of plant flowering. *Microbiome* **6**:1–12.
- 1238 Mack, K. M. and J. D. Bever, 2014. Coexistence and relative abundance in plant communities are
1239 determined by feedbacks when the scale of feedback and dispersal is local. *Journal of Ecology*
1240 **102**:1195–1201.
- 1241 Mack, K. M., M. B. Eppinga, and J. D. Bever, 2019. Plant-soil feedbacks promote coexistence and
1242 resilience in multi-species communities. *PLoS One* **14**:e0211572.
- 1243 Magee, L. J., J. A. LaManna, A. T. Wolf, R. W. Howe, Y. Lu, D. Valle, D. J. Smith, R. Bagchi,
1244 D. Bauman, and D. J. Johnson, 2024. The unexpected influence of legacy conspecific density
1245 dependence. *Ecology Letters* **27**:e14449.
- 1246 Mangan, S. A., S. A. Schnitzer, E. A. Herre, K. M. L. Mack, M. C. Valencia, E. I. Sanchez, and J. D.
1247 Bever, 2010. Negative plant–soil feedback predicts tree-species relative abundance in a tropical
1248 forest. *Nature* **466**:752–755.
- 1249 Miller, E. C., G. G. Perron, and C. D. Collins, 2019. Plant-driven changes in soil microbial communi-
1250 ties influence seed germination through negative feedbacks. *Ecology and Evolution* **9**:9298–9311.
- 1251 Miller, Z. R. and S. Allesina, 2021. Metapopulations with habitat modification. *Proceedings of the*
1252 *National Academy of Sciences* **118**:e2109896118.
- 1253 Miller, Z. R., P. Lechón-Alonso, and S. Allesina, 2022. No robust multispecies coexistence in a
1254 canonical model of plant–soil feedbacks. *Ecology Letters* **25**:1690–1698.
- 1255 Minás, A., P. A. García-Parisi, H. Chludil, and M. Omacini, 2021. Endophytes shape the legacy
1256 left by the above- and below-ground litter of the host affecting the establishment of a legume.
1257 *Functional Ecology* **35**:2870–2881.
- 1258 Mordecai, E. A., 2013a. Consequences of pathogen spillover for cheatgrass-invaded grasslands:
1259 coexistence, competitive exclusion, or priority effects. *The American Naturalist* **181**:737–747.

- 1260 Mordecai, E. A., 2013b. Despite spillover, a shared pathogen promotes native plant persistence in
1261 a cheatgrass-invaded grassland. *Ecology* **94**:2744–2753.
- 1262 Mordecai, E. A., 2015. Pathogen impacts on plant diversity in variable environments. *Oikos*
1263 **124**:414–420.
- 1264 Mouquet, N., J. L. Moore, and M. Loreau, 2002. Plant species richness and community productivity:
1265 why the mechanism that promotes coexistence matters. *Ecology Letters* **5**:56–65.
- 1266 Müller, A., E. George, and E. Gabriel-Neumann, 2013. The symbiotic recapture of nitrogen from
1267 dead mycorrhizal and non-mycorrhizal roots of tomato plants. *Plant and Soil* **364**:341–355.
- 1268 Nagendra, U. J. and C. J. Peterson, 2016. Plant-soil feedbacks differ in intact and tornado-damaged
1269 areas of the southern Appalachian mountains, USA. *Plant and Soil* **402**:103–116.
- 1270 Neytcheva, M. S. and L. W. Aarssen, 2008. More plant biomass results in more offspring production
1271 in annuals, or does it? *Oikos* **117**:1298–1307.
- 1272 O'Brien, A. M., N. A. Ginnan, M. Rebollo-Gómez, and M. R. Wagner, 2021. Microbial effects on
1273 plant phenology and fitness. *American Journal of Botany* **108**:1824–1837.
- 1274 Orrock, J. L. and C. C. Christopher, 2010. Density of intraspecific competitors determines the
1275 occurrence and benefits of accelerated germination. *American Journal of Botany* **97**:694–699.
- 1276 Ou, S. X., G. S. Kandlikar, M. L. Warren, and P.-J. Ke, 2024. Realistic time-lags and litter dynamics
1277 alter predictions of plant-soil feedback across generations. *bioRxiv* pages 2024–01.
- 1278 Pacala, S. W. and D. Tilman, 1994. Limiting similarity in mechanistic and spatial models of plant
1279 competition in heterogeneous environments. *The American Naturalist* **143**:222–257.
- 1280 Pajares-Murgó, M., J. L. Garrido, A. J. Perea, Á. López-García, J. M. Bastida, J. Prieto-Rubio,
1281 S. Lendínez, C. Azcón-Aguilar, and J. M. Alcántara, 2024. Intransitivity in plant-soil feedbacks
1282 is rare but is associated with multispecies coexistence. *Ecology Letters* **27**:e14408.
- 1283 Peay, K. G., 2018. Timing of mutualist arrival has a greater effect on *Pinus muricata* seedling growth
1284 than interspecific competition. *Journal of Ecology* **106**:514–523.

- 1285 Pepe, A., M. Giovannetti, and C. Sbrana, 2018. Lifespan and functionality of mycorrhizal fungal
1286 mycelium are uncoupled from host plant lifespan. *Scientific Reports* **8**:10235.
- 1287 Pineda, A., I. Kaplan, S. E. Hannula, W. Ghanem, and T. M. Bezemer, 2020. Conditioning the
1288 soil microbiome through plant–soil feedbacks suppresses an aboveground insect pest. *New
1289 Phytologist* **226**:595–608.
- 1290 Ravanbakhsh, M., R. Sasidharan, L. A. Voesenek, G. A. Kowalchuk, and A. Jousset, 2018. Microbial
1291 modulation of plant ethylene signaling: ecological and evolutionary consequences. *Microbiome*
1292 **6**:1–10.
- 1293 Reinhart, K. O., J. T. Bauer, S. McCarthy-Neumann, A. S. MacDougall, J. L. Hierro, M. C. Chiuffo,
1294 S. A. Mangan, J. Heinze, J. Bergmann, J. Joshi, et al., 2021. Globally, plant-soil feedbacks are
1295 weak predictors of plant abundance. *Ecology and Evolution* **11**:1756–1768.
- 1296 Reinhart, K. O., A. A. Royo, S. A. Kageyama, and K. Clay, 2010. Canopy gaps decrease microbial
1297 densities and disease risk for a shade-intolerant tree species. *Acta Oecologica* **36**:530–536.
- 1298 Rudgers, J. A., M. E. Afkhami, L. Bell-Dereske, Y. A. Chung, K. M. Crawford, S. N. Kivlin, M. A.
1299 Mann, and M. A. Nuñez, 2020. Climate disruption of plant-microbe interactions. *Annual Review
1300 of Ecology, Evolution, and Systematics* **51**:561–586.
- 1301 Ruiz Gómez, F. J., R. M. Navarro-Cerrillo, A. Pérez-de Luque, W. Oßwald, A. Vannini, and
1302 C. Morales-Rodríguez, 2019. Assessment of functional and structural changes of soil fungal
1303 and oomycete communities in holm oak declined dehesas through metabarcoding analysis.
1304 *Scientific reports* **9**:5315.
- 1305 Sarmiento, C., P.-C. Zalamea, J. W. Dalling, A. S. Davis, S. M. Stump, J. M. U'Ren, and A. E.
1306 Arnold, 2017. Soilborne fungi have host affinity and host-specific effects on seed germination
1307 and survival in a lowland tropical forest. *Proceedings of the National Academy of Sciences USA*
1308 **114**:11458–11463.
- 1309 Schroeder, J. W., A. Dobson, S. A. Mangan, D. F. Petticord, and E. A. Herre, 2020. Mutualist and
1310 pathogen traits interact to affect plant community structure in a spatially explicit model. *Nature
1311 Communications* **11**:2204.

- 1312 Senior, J. K., J. M. O'Reilly-Wapstra, J. A. Schweitzer, J. K. Bailey, and B. M. Potts, 2018. Forest fire
1313 may disrupt plant–microbial feedbacks. *Plant Ecology* **219**:497–504.
- 1314 Senthilnathan, A. and R. D'Andrea, 2023. Niche theory for positive plant-soil feedbacks. *Ecology*
1315 **104**:e3993.
- 1316 Shade, A., H. Peter, S. D. Allison, D. Baho, M. Berga, H. Bürgmann, D. H. Huber, S. Langenheder,
1317 J. T. Lennon, J. B. Martiny, et al., 2012. Fundamentals of microbial community resistance and
1318 resilience. *Frontiers in Microbiology* **3**:417.
- 1319 Shemesh, H., T. D. Bruns, K. G. Peay, P. G. Kennedy, and N. H. Nguyen, 2023. Changing balance
1320 between dormancy and mortality determines the trajectory of ectomycorrhizal fungal spore
1321 longevity over a 15-yr burial experiment. *New Phytologist* **238**:11–15.
- 1322 Shikano, I., C. Rosa, C.-W. Tan, and G. W. Felton, 2017. Tritrophic interactions: microbe-mediated
1323 plant effects on insect herbivores. *Annual Review of Phytopathology* **55**:313–331.
- 1324 Song, X. and R. T. Corlett, 2022. Do natural enemies mediate conspecific negative distance-and
1325 density-dependence of trees? a meta-analysis of exclusion experiments. *Oikos* **2022**:e08509.
- 1326 Steinauer, K., M. P. Thakur, S. Emilia Hannula, A. Weinhold, H. Uthe, N. M. van Dam, and T. Mar-
1327 tijn Bezemer, 2023. Root exudates and rhizosphere microbiomes jointly determine temporal
1328 shifts in plant-soil feedbacks. *Plant, cell & environment* **46**:1885–1899.
- 1329 Stump, S. M. and L. S. Comita, 2018. Interspecific variation in conspecific negative density depen-
1330 dence can make species less likely to coexist. *Ecology Letters* **21**:1541–1551.
- 1331 Suding, K. N., W. Stanley Harpole, T. Fukami, A. Kulmatiski, A. S. MacDougall, C. Stein, and
1332 W. H. van der Putten, 2013. Consequences of plant–soil feedbacks in invasion. *Journal of Ecology*
1333 **101**:298–308.
- 1334 Swamy, V., J. Terborgh, K. G. Dexter, B. D. Best, P. Alvarez, and F. Cornejo, 2011. Are all seeds
1335 equal? spatially explicit comparisons of seed fall and sapling recruitment in a tropical forest.
1336 *Ecology Letters* **14**:195–201.

- 1337 Teste, F. P., P. Kardol, B. L. Turner, D. A. Wardle, G. Zemunik, M. Renton, and E. Laliberté, 2017.
1338 Plant–soil feedback and the maintenance of diversity in Mediterranean-climate shrublands.
1339 *Science* **355**:173–176.
- 1340 Uricchio, L. H., S. C. Daws, E. R. Spear, and E. A. Mordecai, 2019. Priority effects and nonhierar-
1341 chical competition shape species composition in a complex grassland community. *The American*
1342 *Naturalist* **193**:213–226.
- 1343 van de Voorde, T. F., W. H. van der Putten, and T. M. Bezemer, 2012. The importance of plant–soil
1344 interactions, soil nutrients, and plant life history traits for the temporal dynamics of jacobaea
1345 vulgaris in a chronosequence of old-fields. *Oikos* **121**:1251–1262.
- 1346 van der Putten, W. H., R. D. Bardgett, J. D. Bever, T. M. Bezemer, B. B. Casper, T. Fukami, P. Kardol,
1347 J. N. Klironomos, A. Kulmatiski, J. A. Schweitzer, K. N. Suding, T. F. J. van der Voorde, and
1348 D. A. Wardle, 2013. Plant–soil feedbacks : the past, the present and future challenges. *Journal of*
1349 *Ecology* **101**:265–276.
- 1350 Van Dyke, M. N., J. M. Levine, and N. J. Kraft, 2022. Small rainfall changes drive substantial
1351 changes in plant coexistence. *Nature* **611**:507–511.
- 1352 Veen, C., E. Fry, F. ten Hooven, P. Kardol, E. Morriën, and J. R. De Long, 2019. The role of plant
1353 litter in driving plant-soil feedbacks. *Frontiers in Environmental Science* **7**:168.
- 1354 Veen, G. F., F. C. ten Hooven, C. Weser, and S. E. Hannula, 2021. Steering the soil microbiome by
1355 repeated litter addition. *Journal of Ecology* **109**:2499–2513.
- 1356 Villegas, J., D. F. Doak, M. B. García, and W. F. Morris, 2015. Demographic compensation among
1357 populations: what is it, how does it arise and what are its implications? *Ecology Letters* **18**:1139–
1358 1152.
- 1359 Wagner, M. R., D. S. Lundberg, D. Coleman-Derr, S. G. Tringe, J. L. Dangl, and T. Mitchell-Olds,
1360 2014. Natural soil microbes alter flowering phenology and the intensity of selection on flowering
1361 time in a wild arabidopsis relative. *Ecology Letters* **17**:717–726.

- 1362 Wang, W., H. Wu, T. Wu, Z. Luo, W. Lin, H. Liu, J. Xiao, W. Luo, Y. Li, Y. Wang, et al., 2024.
1363 Soil microbial influences over coexistence potential in multispecies plant communities in a
1364 subtropical forest. *Ecology* **105**:e4415.
- 1365 Willing, C. E., J. Wan, J. J. Yeam, A. M. Cessna, and K. G. Peay, 2024. Arbuscular mycorrhizal
1366 fungi equalize differences in plant fitness and facilitate plant species coexistence through niche
1367 differentiation. *Nature Ecology & Evolution* **8**:2058–2071.
- 1368 Wilschut, R. A. and S. Geisen, 2021. Nematodes as drivers of plant performance in natural systems.
1369 *Trends in Plant Science* **26**:237–247.
- 1370 Wubs, E. R. J. and T. M. Bezemer, 2018. Temporal carry-over effects in sequential plant–soil
1371 feedbacks. *Oikos* **127**:220–229.
- 1372 Wubs, E. R. J., W. H. van der Putten, M. Bosch, and T. M. Bezemer, 2016. Soil inoculation steers
1373 restoration of terrestrial ecosystems. *Nature Plants* **2**:16107.
- 1374 Yan, X., J. M. Levine, and G. S. Kandlikar, 2022a. A quantitative synthesis of soil microbial effects
1375 on plant species coexistence. *Proceedings of the National Academy of Sciences* **119**:e2122088119.
- 1376 Yan, X., J. M. Levine, and G. S. Kandlikar, 2022b. A quantitative synthesis of soil microbial effects
1377 on plant species coexistence: code and data. *Zenodo*: <https://doi.org/10.5281/zenodo.6513066>.
- 1378 Yin, R., W. Qin, X. Wang, D. Xie, H. Wang, H. Zhao, Z. Zhang, J.-S. He, M. Schädler, P. Kardol,
1379 et al., 2023. Experimental warming causes mismatches in alpine plant-microbe-fauna phenology.
1380 *Nature Communications* **14**:2159.
- 1381 Younginger, B. S., D. Sirová, M. B. Cruzan, and D. J. Ballhorn, 2017. Is biomass a reliable estimate
1382 of plant fitness? *Applications in plant sciences* **5**:1600094.
- 1383 Zalamea, P.-C., C. Sarmiento, A. E. Arnold, A. S. Davis, A. Ferrer, and J. W. Dalling, 2021. Closely
1384 related tree species support distinct communities of seed-associated fungi in a lowland tropical
1385 forest. *Journal of Ecology* **109**:1858–1872.
- 1386 Zee, P. C. and T. Fukami, 2015. Complex organism–environment feedbacks buffer species diversity
1387 against habitat fragmentation. *Ecography* **38**:370–379.

- 1388 Zhelnina, K., K. B. Louie, Z. Hao, N. Mansoori, U. N. Da Rocha, S. Shi, H. Cho, U. Karaoz, D. Loqué,
1389 B. P. Bowen, et al., 2018. Dynamic root exudate chemistry and microbial substrate preferences
1390 drive patterns in rhizosphere microbial community assembly. *Nature Microbiology* **3**:470–480.
- 1391 Zhu, Y., L. S. Comita, S. P. Hubbell, and K. Ma, 2015. Conspecific and phylogenetic density-
1392 dependent survival differs across life stages in a tropical forest. *Journal of Ecology* **103**:957–966.
- 1393 Zhu, Y., S. Queenborough, R. Condit, S. Hubbell, K. Ma, and L. Comita, 2018. Density-dependent
1394 survival varies with species life-history strategy in a tropical forest. *Ecology Letters* **21**:506–515.
- 1395 Zou, H.-X., X. Yan, and V. H. Rudolf, 2024. Time-dependent interaction modification generated
1396 from plant–soil feedback. *Ecology Letters* **27**:e14432.