

Response to the Editor

Comment E.1: *Both reviewers were very positive about the overall relevance and importance of the manuscript. This article provides a nice overview of temporal and demographic considerations for understanding and predicting plant-microbe interactions with forward-looking suggestions for future directions to develop empirical and theoretical aspects of plant-soil feedback science. The reviewers had several useful and specific suggestions to improve the manuscript, it will be important to address all of these comments while revising the manuscript.*

Response E.1: We would like to thank the editor and the reviewers for such thorough, constructive, and positive comments. We have made a number of revisions to address the comments made by the reviewers. We believe these changes have improved the clarity of our manuscript. Please see below the compilation of all reviewer comments (*italicized*) and our point-by-point responses (revised text highlighted in the text box and line numbers refer to those in the revised manuscript).

Response to Reviewer 1

Comment R1.1: *The authors of “Time will tell: the temporal and demographic contexts of plant-soil microbe interactions” highlight timely considerations for the field of plant-soil feedback theory. They identify various temporal and demographic nuances that have historically been omitted from plant-soil feedback experiments, review what research has been done to address these neglected processes, and propose specific research designs, theoretical frameworks, and larger scientific practices to further address such processes. Overall, I found this to be an enjoyable read, synthesizing ideas from a broad span of research and skillfully communicating their ideas with an impressive blend of writing, equations, and figures. Here, I offer just a couple suggestions for clarifying certain points followed by a list of smaller comments.*

Response R1.1: Thank you for the thought-provoking comments! We have revised the manuscript based on your comments; please see below our responses to your helpful suggestions.

Comment R1.2: *First, I found it difficult to determine exactly how the authors are conceptually integrating “time” and “demography”. Some of the writing seemed to indicate that these are two separate categories of processes which need to be included in PSF research practices. More so, however, the writing seems to suggest that demographic detail is an example of how ecologists can work toward more temporally explicit PSF research. The title itself seems to suggest both that time and demography are separate topics (the use of “temporal and demographic”), but also that these topics fall under a larger umbrella of time (“Time will tell.”). I do not think that my confusion about this point significantly affected my reading of this paper, but I do think that a sentence or two answering the question of “how are these temporal concerns related to these demographic concerns” might make the format of this paper more digestible for some readers.*

Response R1.2: We appreciate the reviewer’s observation regarding the integration of “time” and “demography” in our manuscript. To clarify, while we present these as distinct dimensions for analytical clarity, our intent is to highlight that detailed demographic data serve as a concrete example of making PSF research more temporally explicit. By incorporating demographic detail, we can capture how changes in plant life stages and their corresponding responses to microbial effects unfold over time. We have revised the text (Lines 99–104) to explicitly state this link and to clarify that demography is an essential facet of the temporal dimension in PSF research.

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.

Comment R1.3: *Second, I commend the authors for an interesting exposition about theory and empiricism in PSF research, but I was left wanting a bit more. Section VI introduces the authors’ pitch for an “empirical-theoretical feedback loop” and describes how theoretical models of PSFs (in particular, those which incorporate more temporal and demographic detail) can be refined through empirical methods. By the end of the first paragraph (L616-620), I was left wondering “to what end”. I would really love to hear what the authors believe this empirical-theoretical feedback loop works toward. Is the argument that we will ultimately have mathematical models of PSF that better predict field dynamics? Or is the argument that this feedback loop positions us to better test big theories or answer important questions, and if so, which ones? A perhaps low hanging fruit way to contextualize this would be to ground this discussion in our continued inability to identify the relevant axes of variation in PSF dynamics in the field (ie why are PSFs so seemingly idiosyncratic?). Of course, the authors may have other ideas about what are the big goals of PSF research, so I would love to hear how their empirical-theoretical feedback loop addresses these goals.*

Response R1.3: We thank the reviewer for motivating us to think more deeply about the ultimate goals of our proposed research program. We think the iterative process between empirical and theoretical approaches can allow us to reach both goals. We have added a sentence at the end of the first paragraph of Section VI to first provide a general statement of the goal (Line 672–675):

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.

Next, we elaborate on these goals and provide an example (i.e., the impact of drought on plant–soil microbe interactions) in the last paragraph of Section VI (Line 752–763):

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 that time itself may serve as a hidden axis of variation: the same environmental shift alters temporal trajectories differently depending on its timing. The temporal dimensions also underscore the significance of phenological mismatches among plants and soil microbes driven by climate change (Rudgers et al., 2020; e.g., late-germinating plants may be more affected by pathogens). As experiments incorporate environmental shifts and employ models to generate predictions (e.g., the impact of drought on plant diversity; Dudenhöffer et al., 2022), embracing the empirical–theoretical feedback loop can further refine the experimental design and enhance our ability to predict responses under real-world settings (e.g., changes in the degree of precipitation variability).

Comment R1.4: *At L89-91, the authors introduce the idea that different demographic processes might respond differently to microbes. I was surprised that the authors did not seem to contextualize this in ideas about demographic compensation or generally about the covariance of demographic sensitivities to microbes. This seems like a potentially fruitful framework for thinking about different demographic responses.*

Response R1.4: Thanks for this fantastic suggestion. While working to revise our manuscript in light of this idea, we realized that it may be ideal to introduce the possibility of microbes underlying demographic compensation in plants in a later section rather than in the introduction. Specifically, we realized that this suggestion is closely related to the Reviewer’s comment R1.9, related to our subsection on the effects of microbes beyond early life stages. We have now revised that section (Line 470–478) to specify the possibility that microbes can have opposing effects on different vital rates of plants, thus potentially underlying observed demographic compensation in population dynamics.

Further complicating efforts to project microbial consequences across a plant’s lifetime are that these effects can be uncorrelated or even contradictory across a plant’s lifetime (Dostalek et al., 2022). For example, Dudenhöffer et al. (2018) found that conspecific-conditioned soil microbes promote juvenile plant growth but hinder adult growth. Integrating these effects across the plant’s lifetime reveals a net negative impact of conspecific soil in plant fitness – a result that would contradict inferences based on the juvenile stage alone. Thus, variable impacts of soil microbes across plant ontogeny and/or demographic processes could contribute to demographic compensation in plant population dynamics (Villellas et al., 2015).

Comment R1.5: *L163: What does “short” mean? Relative to the growing seasons of these plants?*

Response R1.5: We agree that “short” is ambiguous. As we do not have accurate information regarding the longevity of each plant species, we have revised the sentence as follows (Line 171):

..., we showed that the length of the conditioning and response phases is under a few months in most studies.

Comment R1.6: *The authors seem to suggest that nearly all variation in plant responses to soil microbes can be tied to modifications to the microbial community composition. Is there a reason why variation can't be due to plant sensitivity to microbes per se? So in the absence of compositional variation in the soil microbial community, I would expect that variation in plant physiology (potentially due to ontogeny, genetic variation, or complex interactions with abiotic properties) induces variable sensitivity to microbes. The authors come close to making this point in L227-230, but still bring up modifications in pathogen abundance.*

Response R1.6: We agree that changes in plant physiology can lead to varying plant responses even in the absence of compositional shifts in the soil microbial community. We have revised the paragraph (Line 223–243) to adopt a more nuanced tone and added the following sentence (Line 233–235):

Even in the absence of detectable shifts in soil microbial community composition, ontogenetic changes in plant physiology can drive variable plant responses (Liu et al., 2025).

We also highlight this mechanism again at Line 332–334 when referencing Liu et al. (2025).

A recent study by Liu et al. (2025) utilized such experimental design to illustrate the importance of conditioning and response duration as well as the underlying mechanisms (i.e., changes in plant sensitivity to microbes or soil re-conditioning by the responding plant).

Comment R1.7: *L282: “communities”?*

Response R1.7: Yes, thank you, typo corrected.

Comment R1.8: *Section III.3: This section seems to neglect the potential for modern molecular methods to advance our understanding of the temporal dynamics of plant-microbe interactions. Many questions related to how cultivation time impacts plant performance may*

be enhanced from understanding how the microbial community changes during cultivation. I would've loved to hear a bit more about how traditional greenhouse experiments could be integrated with molecular methods in this section.

Response R1.8: Thank you for the suggestion. We revised this section (Line 330–337) to highlight the usefulness of molecular methods, using the study system of Steineour et al. (2023) and Liu et al. (2025) as an example.

Moreover, throughout greenhouse experiments, the concurrent application of modern molecular methods can provide critical insights linking microbial changes to variations in plant performance. A recent study by Liu et al. (2025) utilized such experimental design to illustrate the importance of conditioning and response duration as well as the underlying mechanisms (i.e., changes in plant sensitivity to microbes or soil re-conditioning by the responding plant). They found that the soil bacterial community in conspecific and heterospecific soils converged over the course of the response phase, partially explaining why differences in plant performance diminished with longer experimental duration (see also Steinauer et al., 2023).

We also note that a discussion of how molecular approaches can enhance our understanding of the dynamics of the microbial community was provided in Section VI (Line 371–349). We believe that placing this material later in the manuscript allows us to maintain a focused narrative in Section III while still addressing these important advances in the subsequent section.

Comment R1.9: *Section IV.2: I was a bit surprised that the authors included a section on the indirect effects of microbes on plant demography through modifying plant-pollinator or plant-herbivore interactions. Section IV goes from exposition on “early life demography” to “modification of other plant species interactions” to “experimental design”. I would’ve expected more exposition on the direct effects of microbes on other demographic parameters such as adult survival and reproductive processes (perhaps especially those nonsexual reproductive processes) before they went into the indirect demographic consequences via other species interactions.*

Response R1.9: Thanks for raising this point; we appreciate the concern. To our knowledge, explicit experimental studies of soil microbial impacts on mortality and reproduction of adult plants remain somewhat scarce, particularly for long-lived plants. We have added citations to the forest pathology literature on the role of soilborne fungi and oomycetes in causing tree mortality before mentioning indirect effects involving other trophic levels (Line 452–455).

For example, studies from forest pathology have shown that soilborne fungi and oomycetes can directly cause adult mortality via root rot diseases, often with long-term impacts on spatial structure and gap dynamics in forest communities (Hansen and Goheen, 2000, Liu et al., 2007, Das et al., 2016, Ruiz Gomez et al., 2019). Experimental studies have also shown that soil microbes can influence the fruit production of herbaceous species (Dostalek et al., 2022), but such direct evidence is notably scarce in natural forest systems.

Moreover, in Section IV.3, we again highlight the difficulty of experimentally demonstrating the direct linkage between soil microbes and adult demography in forest systems, and point to a potential alternative approach to move forward (Line 495–498).

Finally, while the longevity of forest trees precludes direct experimental evidence, one may leverage natural experiments to observe differences in demographic rates across sites with varying disease severity (Cobb et al., 2020).

Comment R1.10: *L667: Is there supposed to be a period between “design” and “Recent”?*

Response R1.10: Fixed. Thank you for catching this typo.

Comment R1.11: *L667-676: Related to my larger point about the authors explaining the broader context for the empirical-theoretical feedback loop, I think this anecdote could use more detail. I’m curious as to whether the revised experimental design came about because empiricists tried fitting the Ke and Wan (2020) model using their proposed design, or whether empiricists simply criticised the omission of facilitative interactions (without attempting to fit the model/conduct the proposed experimental design). This seems like an important distinction for clarifying the authors’ vision of an ideal theoretical-empirical feedback loop.*

Response R1.11: Thank you for the comment. We have used this opportunity to provide more details on this personal anecdote (Line 706–712):

For example, Ke and Wan (2020) initially proposed a simplified experimental design based on the premise that plant–plant interactions are exclusively competitive. However, when empiricists implemented the experimental design with low neighbor density, they sometimes found facilitative interactions that rendered our original analytical approach inapplicable (e.g., Wang et al., 2024, Willing et al., 2024). This feedback prompted us to develop a revised density gradient design as a solution with greater flexibility for untangling facilitative or nonlinear microbial effects (Ke and Wan, 2023).

Comment R1.12: *Figure 1: A perhaps negligible concern, but I am a bit confused about what “Plant response” indicates on the y-axis. It seems that the information being displayed above ground in the figure is simply the plant life cycle and succession of that patch. It is unclear to me what information represents the plant response to the microbial effects.*

Response R1.12: Point well taken. We have revised the figure so that plant response (y-axis) is now represented by the size of the seedling and tree icons. Additionally, we adjusted the sizes of seedlings and trees across panels (a) and (b) to illustrate the effects of the temporal dimension (see also **Response R2.12**). We also updated the figure legend with the following sentence:

Different seedling and tree sizes across the panels indicate varying plant responses (increasing upwards) to soil microbial effects (increasing downwards).

Response to Reviewer 2

Comment R2.1: *The manuscript makes a compelling case for explicitly testing the temporal aspects of plant-soil feedback to deepen our understanding of when and why these feedback mechanisms matter most. Overall, this work is a refreshing wake-up call for plant-soil feedback researchers and an excellent contribution to the field.*

Response R2.1: Thank you for the positive assessment and thorough comments! We have revised the manuscript based on your comments; please see below our responses to your helpful suggestions.

Comment R2.2: *In the Introduction, it’s worth mentioning that plants do not just interact with soil microbes but also with a variety of other groups of soil biota, including micro-, meso-, and macrofauna. These groups of soil fauna can all feed back to plant performance and demography. Nematodes are particularly known for their role in plant-soil feedback and there is a large body of literature on this.*

Response R2.2: We have added a sentence in the Introduction (Line 23–26):

Plants interact with a diverse array of soil biota that function as herbivores, pathogens, mutualists, and decomposers. In addition to the contributions of soil fauna (ranging from micro- to macrofauna; Ehrenfeld et al., 2005, Kulmatiski et al., 2014, Wilschut and Geisen, 2021), studies have highlighted the importance of plant–soil microbe interactions.

Comment R2.3: *Throughout the manuscript there is a slight bias towards North-American literature and there’s lots of self-citations. This is not necessarily wrong, but please check carefully.*

Response R2.3: Thanks for pointing out a potential bias in our citations. We have gone through each section of the manuscript to ensure that the studies we draw on are representative of the field as a whole, and have added a number of citations to studies conducted by authors outside of North America (and/or studies reporting on plant-microbe interactions from systems outside of North America; see list below). We would be glad to add additional citations should the Reviewer know of important contributions that we may have missed.

- Liu, D., M. Kelly, P. Gong, and Q. Guo, 2007. Characterizing spatial-temporal tree mortality patterns associated with a new forest disease. *Forest Ecology and Management* **253**:220–231.
- Lu, T., M. Ke, M. Lavoie, Y. Jin, X. Fan, Z. Zhang, Z. Fu, L. Sun, M. Gillings, J. Peñuelas, et al., 2018. Rhizosphere microorganisms can influence the timing of plant flowering. *Microbiome* **6**:1–12.
- Krishnadas, M., and L. S. Comita, 2019. Edge effects on seedling diversity are mediated by impacts of fungi and insects on seedling recruitment but not survival. *Frontiers in Forests and Global Change* **2**:76.
- Ruiz Gómez, F. J., R. M. Navarro-Cerrillo, A. Pérez-de Luque, W. Oßwald, A. Vannini, and C. Morales-Rodríguez, 2019. Assessment of functional and structural changes of soil fungal and oomycete communities in holm oak declined dehesas through metabarcoding analysis. *Scientific reports* **9**:5315.
- Krishnadas, M., K. Agarwal, and L. S. Comita, 2020. Edge effects alter the role of fungi and insects in mediating functional composition and diversity of seedling recruits in a fragmented tropical forest. *Annals of Botany* **126**:1181–1191.
- Lebrija-Trejos, E., A. Hernandez, and S. J. Wright, 2023. Effects of moisture and density-dependent interactions on tropical tree diversity. *Nature* **615**:100–104.
- Steinauer, K., M. P. Thakur, S. Emilia Hannula, A. Weinhold, H. Uthe, N. M. van Dam, and T. Martijn Bezemer, 2023. Root exudates and rhizosphere microbiomes jointly determine temporal shifts in plant-soil feedbacks. *Plant, cell & environment* **46**:1885–1899.
- Yin, R., W. Qin, X. Wang, D. Xie, H. Wang, H. Zhao, Z. Zhang, J.-S. He, M. Schädler, P. Kardol, et al., 2023. Experimental warming causes mismatches in alpine plant-microbe-fauna phenology. *Nature Communications* **14**:2159.
- Wang, W., H. Wu, T. Wu, Z. Luo, W. Lin, H. Liu, J. Xiao, W. Luo, Y. Li, Y. Wang, et al., 2024. Soil microbial influences over coexistence potential in multispecies plant communities in a subtropical forest. *Ecology* **105**:e4415.
- Cheng, C., M. J. Gundale, B. Li, and J. Wu, 2024. Deciphering the drivers of plant-soil feedbacks and their context-dependence: A meta-analysis. *Plant and Soil*:1–15.

More broadly, we appreciate the reviewer’s point that geographic biases are a problem in the literature. This is one of the main issues that led us to organize a recent special issue in *American Journal of Botany* (Volume 111, Issue 12): *The Role of Plant–Microbe Interactions in Plant Community Dynamics of Tropical and Subtropical Ecosystems*. In the course of organizing the special issue, we realized that fewer than 5% of the species

pairs in a recent comprehensive meta-analysis of > 175 PSF studies come from outside of the temperate latitudes (see Figure 1 in our editorial of the special issue), which underscores the issues raised by the Reviewer.

Comment R2.4: *When referring to Bennett et al. (2017), it probably should be mentioned that they also measured feedback effects on percentage mycorrhizal colonization and the number of root lesions. To some extent, this moves away from the typical plant-centric view (L 692).*

Response R2.4: We thank the reviewer for suggesting responses such as percentage colonization, which we agree can help bridge plant-centric and microbe-centric viewpoints. We have incorporated this perspective in the revised paragraph (Lines 740–742). In particular, we chose to cite Bennett et al. (2023) because they measured how percentage colonization varied with host tree status (i.e., live or dead), aligning with the temporal perspective of our manuscript:

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).

Comment R2.5: *Section VI is a bit long and repetitive. Some of it seems to better fit in sections V.1 and V.2.*

Response R2.5: We have shortened Section VI. The most noteworthy revision is that we moved the original second paragraph in Section VI to Section V (as the last paragraph; Line 635–654). With this revision, we attempt to focus on the theoretical framework in Section V and discuss the challenges related to empirically parameterizing the models in Section VI.

Comment R2.6: *L125 replace ‘plant’ with ‘species’.*

Response R2.6: Thank you. We have revised it.

Comment R2.7: *L185 But, Lepinay et al. (2018) focused in soil chemical properties (not microbial). If the microbial effects differ, the plant response should also differ. Right?*

Response R2.7: We agree and have decided to highlight another recent study that is more suitable in this context. The revised sentence (Line 193–199) is as follows:

For example, Liu et al. (2025) found that *Jacobaea vulgaris* performed worse in conspecific soil than in heterospecific soils, and that this performance difference increased as soil conditioning time extended from two to five weeks. However, the differences between soil treatments diminished after a longer conditioning duration of eight weeks. Similarly, while focusing on soil chemical properties, Lepinay et al. (2018) showed that the relative negative impact of conspecific versus heterospecific soils varied with conditioning duration over a span of two to eight weeks.

Comment R2.8: L282 ‘the microbial community’.

Response R2.8: Thank you for catching the typo. As we meant to describe a general phenomenon that may apply across various ecosystems, we have revised the sentence using “microbial communities”.

Comment R2.9: L321 What is a ‘Magenta box’?

Response R2.9: We realized that such jargon is not necessary; we now simply use the term “autoclavable container” (Line 328).

Comment R2.10: L454 Elaborate a bit on these ‘system-specific models’?

Response R2.10: During revision, we felt that the focal sentence was no longer suitable and removed it. We now mention system-specific models at Line 591–593 as we think it better fits the context of the paragraph on complex demographic models.

Although this approach demands extensive parameterization, it allows for system-specific tailoring and may prove to be especially valuable in demographically complex systems.

Towards the end of Section V, within the new paragraph where we discuss the flexibility of the two theoretical models, we added a new example of such system-specific models by David et al. (2019) (Line 647–654):

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 relative 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.

Comment R2.11: *L483 Here, it would help to briefly explain the basic concept of ‘modern coexistence theory’.*

Response R2.11: We have revised the sentence as follows to incorporate the basic concept of modern coexistence theory (Line 507–513):

Furthermore, one can add a heterospecific treatment designed to assess heterospecific effects, as well as a reference treatment in randomly located field soil to estimate the frequency-independent microbial impact on survival. These additional treatments allow the interpretation of plant–soil microbe interactions 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).

Comment R2.12: *In Figure 1, I do not understand why the plants depicted in panel A and panel B look exactly the same.*

Response R2.12: We have revised the figure so that seedling and tree icon sizes now represent plant responses (y-axis). To reflect the effects of the temporal dimension, we adjusted the sizes of seedlings and trees across panels (a) and (b), ensuring that plant responses are visually distinct between the two panels (see also **Response R1.10**).

Comment R2.13: *In Figure 2, what are the ‘highlighted points’?*

Response R2.13: We assume that the reviewer is referring to the legend of Figure 3, where we imprecisely described monochromatic pie charts as “points”. We have revised the sentence in the figure legend as follows:

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).

Alternatively, if the reviewer is referring to the gray and brown seed icons in Figure 2, we have clarified this with the following sentence:

Brown and grey seeds represent viable and dead seeds, respectively.