

Opinion

Plant–soil feedback under drought: does history shape the future?

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Plant–soil feedback (PSF) is widely recognised as a driver of plant community composition, but understanding of its response to drought remains in its infancy. Here, we provide a conceptual framework for the role of drought in PSF, considering plant traits, drought severity, and historical precipitation over ecological and evolutionary timescales. Comparing experimental studies where plants and microbes do or do not share a drought history (through co-sourcing or conditioning), we hypothesise that plants and microbes with a shared drought history experience more positive PSF under subsequent drought. To reflect real-world responses to drought, future studies need to explicitly include plant–microbial co-occurrence and potential co-adaptation and consider the precipitation history experienced by both plants and microbes.

PSF

Plants and soil microbes interact in myriad ways, from mutualistic relationships between roots and mycorrhizal fungi to pathogenic fungi attacking plant roots, parasitic plants capitalising on mycorrhizas to access their carbon (C) supply, and decomposer microbes increasing nutrient availability to plants. During their life cycle, plants change their associated soil microbial communities, which can in turn affect their own fitness and that of their neighbours or successors. This **microbe-mediated PSF** (see *Glossary*) can be negative when a plant grows worse in its own soil, with its own selected microbes, compared with sterilised soil or soil from another species; conversely, a plant experiences positive **PSF** when it grows better in its own soil (Figure 1). Negative PSF has been linked to the accumulation of fungal pathogens, while positive PSF is thought to be caused by mutualistic symbionts and plant-specific decomposer communities [1]. Several decades of research have identified PSF as an important driver of plant coexistence, vegetation dynamics, and ecosystem functioning [2,3]. New theoretical frameworks show that microbes can stabilise or destabilise plant communities via frequency-dependent feedback as well as by generating fitness differences [4]. While it is often assumed that PSF is driven by host-specific microbes, recent work challenges this and instead suggests that generalist microbes can have plant-specific effects, with the outcome depending on the environmental context, plant and microbial genotype, and plant traits [5–7].

The effects of climate change on PSF, and the implications for plant community composition, are increasingly being investigated [8–10]. **Drought** is widespread and strongly affects both plant and microbial communities and plant–microbe interactions, but recent PSF studies including drought do not show consistent results. Here, we synthesise how drought affects plant–microbe interactions and what the consequences are for PSF, specifically focusing on the roles of plant traits, plant and microbial drought histories, and plant–microbe **co-adaptation** in shaping PSF responses to novel climatic disturbances. We draw on these initial findings to provide a predictive framework for how PSF might respond to drought and identify future research directions to

Highlights

Drought, which is increasing in intensity and frequency with climate change, can severely affect plant growth and alter vegetation dynamics.

Plants modify microbial communities in their rhizosphere, which in turn affect plant productivity and local persistence, creating so-called plant–soil feedback (PSF).

As droughts impact both plant and soil microbial attributes, PSF is likely to change under and following drought events, but limited experimental tests produce widely diverging results regarding the direction and magnitude of changes.

Combined evidence from a range of related research fields suggests that PSF response to drought may be predicted by plant traits, the intensity of drought, and the drought histories of both plants and microbes.

Explicit inclusion of coexistence history and the local adaptation of plants and soil microbes at local and regional scales will enable more realistic predictions about the contribution of plant–microbial associations to plant community response to climate change.

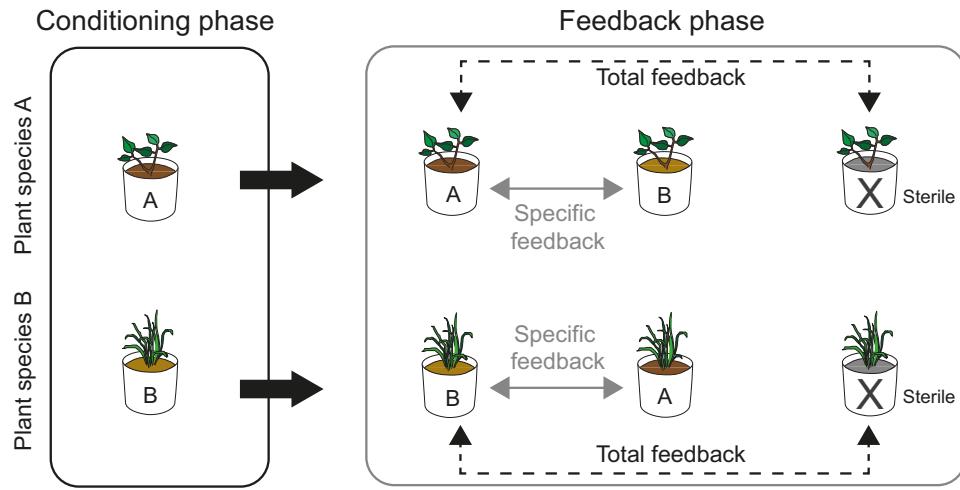
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Figure 1. Experimental approach for testing plant–soil feedback (PSF). Testing for PSF involves taking soil from a specific plant species or genotype growing in the field or greenhouse ('conditioning phase') and using that soil (either as a whole soil or using microbial inoculum from that soil) to grow a second set of plants ('feedback phase'). The conditioning phase can occur in the field with the collection of soils from beneath naturally occurring plant populations, which might be particularly useful for long-lived species. Species-specific feedback measures the effect that a plant has on its own growth [plant (A) in soil (A) and plant (B) in soil (B)] compared with the effect that another species has [plant (A) in soil (B) and plant (B) in soil (A)]; total feedback measures the effect that a plant has on its own growth [plant (A) in soil (A) and plant (B) in soil (B)] compared with a sterile soil (marked with a cross). In the species-specific feedback approach, PSF is positive when a plant species grows better in its own soil than in soil conditioned by other species and negative when it grows worse in its own soil. Total feedback is positive when a species grows better in its own live soil than in sterile soil.

advance our understanding of the role of feedback between plants and microbes in mediating plant response to drought.

Effects of drought on plant–microbe interactions and implications for PSF

Drought affects plants and microbes directly, but also indirectly by altering their interactions. Interest in the effect of drought on plant growth and fitness via changes in plant–microbe interactions has steeply increased because of the increasing recognition that microbes can extend the plant phenotype [11]. PSF is the net outcome of all positive and negative effects of soil microbes on plant growth, and thus either a shift in the balance of microbes that elicit positive versus negative effects on plant growth or a change in the effect that these microbes have (their mode of action) is required for drought to have an effect on this net outcome [6]. The former is likely to occur because many soil-borne pathogens rely on soil moisture and their abundance might be reduced as a result of drought [12], while the relative abundance of mycorrhizal fungi can increase during drought [13,14]. The latter may be realised through altered plant traits or physiological processes that render plants more or less susceptible to pathogens or attractive to mutualists. For example, drought-induced increases in tissue H_2O_2 concentrations might increase plant resistance to pathogens [15], while drought-induced accumulation of amino acids, tissue die-off, or increases in tissue nitrogen (N) content as a result of the rewetting-induced peak in soil N availability would increase plant susceptibility to pathogens [12,16]. Importantly, drought-induced changes in plant physiological processes can affect soil microbes, and these changes can in turn feed back to plant growth. For example, plants alter their root exudation during and after drought, which may change the rhizosphere microbiome and associated biogeochemistry. Altered exudates can select for beneficial microbial taxa or communities that promote plant growth, induce early flowering [17], or facilitate plant regrowth through increasing N availability [18]. Drought can

also reduce C allocation to microbial mutualists and affect soil nutrient availability, altering the balance of trade and mycorrhizal or rhizobial nutrient supply to the plant [19] and potentially introducing competition for these resources. Associations with mycorrhizal fungi can also alleviate plant drought stress through inducing systemic changes, as well as through direct transport of water to the plant [20].

In cases where microbial responses to drought help to maintain plant fitness under drought ('microbe-mediated adaptation' *sensu* Petipas *et al.* [21]; see also 'microbial rescue' *sensu* Mueller *et al.* [22]) effects may be specific to individual plant species (or even genotypes) or more generalised, likely depending on the underlying mechanism. At least three processes may produce changes in microbial communities that benefit plants: (i) an increase in microbial traits that alter the abiotic environment in ways that ameliorate the effects of drought on plants (e.g., increased soil water-holding capacity or nutrient availability); (ii) an increase in microbial traits that alter the expression of plant traits that improve plant drought tolerance; or (iii) an increase in the relative abundance of mutualists that are particularly beneficial under drought conditions (e.g., mycorrhizas) compared with pathogens. Of these three mechanisms, the first (microbial effects on the abiotic environment) is likely to be the most general across all plant taxa [21], assuming that the microbial behaviour is at least partly independent of specific plant traits (but see [23]). Drought effects on microbes that modulate plant traits or that change the abundance of mutualists are more likely to be species specific because only certain plant species may have the genetic machinery to respond [6,24]. Ultimately, because PSF depends on both the capacity for different plant species to condition for different microbial communities and the relative effects of soil microbial shifts on different species, even mechanisms that should benefit all species, like increased biofilm production increasing soil moisture-holding capacity, may have greater relative benefits for some plant taxa and thus alter PSF. In such cases, while **total feedback** would always become more positive (less negative), the effect on **species-specific feedback** would depend on the relative magnitudes of these plant growth effects, and the implication for plant community composition would depend on both components.

PSF responses to drought: hypotheses and evidence

Drought effects on PSF will depend on the duration and severity of drought as well as plant growth strategy and the drought history of both the test plant population and the microbial inocula [9,10] (Figure 2). PSF studies can impose a drought in the conditioning phase, in the feedback phase, or in both, which can complicate interpretation because these approaches test different mechanisms (Figure 3). While drought is not well defined in the majority of PSF experiments [25], we would expect **moderate drought** during the conditioning and the feedback phase to cause a shift towards more positive PSF across species. Such conditions should restrain pathogen spread and enhance plant defence traits (e.g., increased H₂O₂ concentrations as discussed above) and mycorrhizal associations compared with wet conditions [26,27]. When a moderate drought follows a wet conditioning phase, this pattern may be less pronounced. However, **severe drought** can limit plants' ability to allocate C both to mutualists and to defence against pathogens [26–28]. Under such conditions, plants may experience a more negative impact of the soil microbiome on their performance and hence more negative PSF (Figure 2). This is particularly likely when a severe drought in the conditioning phase is followed by a wet feedback phase, when enhanced nutrient availability on rewetting can reduce antagonistic microbe–microbe interactions, including those involved in the suppression of soil-borne plant pathogens [29]. Phenotypic responses to higher nutrient availability following soil rewetting, such as higher nutrient tissue content and lower tissue density [13,30], can also make plants more susceptible to pathogen attack and less dependent on mycorrhiza, and hence result in less positive or more negative PSF (Figure 2).

Glossary

Co-adaptation: simultaneous adaptation in two (or more) species in the context of a given environment. While coevolution references the reciprocal selection (and corresponding evolutionary responses) that occurs between two species, co-adaptation also incorporates both species responding in parallel to external selective agents (e.g., drought).

Drought: below-normal precipitation. The degree of drought is defined in various ways, but is often related to the duration and extent of water deficit and the resulting stress to natural or agricultural ecosystems. The degree of drought also depends on the drought history of the community. Consequently, mild and extreme drought in a wetland ecosystem will be defined differently from these conditions in a semi-arid grassland. The Standardized Precipitation Index is one way to consistently represent drought across ecosystems (as used by the US Drought Monitor to represent abnormal to exceptional drought conditions; <https://droughtmonitor.unl.edu/About/AbouttheData/DroughtClassification.aspx>).

Legacy effects: biotic or abiotic conditions created by prior environments that persist when the environment changes.

Local adaptation: evolutionary process by which organisms become better suited to their local environment, resulting from natural selection.

Microbe-mediated PSF: occurs when PSF is caused by changes in the abundance and community composition of soil microbes, and is the focus of this opinion article.

Moderate drought: defined here as a moderate reduction in rainfall or soil water content that affects plant and microbial growth and processes but does not result in plant wilting or death.

Plant–soil feedback (PSF): the legacy that growing plants leave behind in the soil, which subsequently affects the growth of future plants in that soil. Different experimental designs allow the calculation of total feedback or species-specific feedback (Figure 1).

Severe drought: defined here as a severe reduction in rainfall or soil water content that halts plant and microbial growth and processes and results in plant wilting or death.

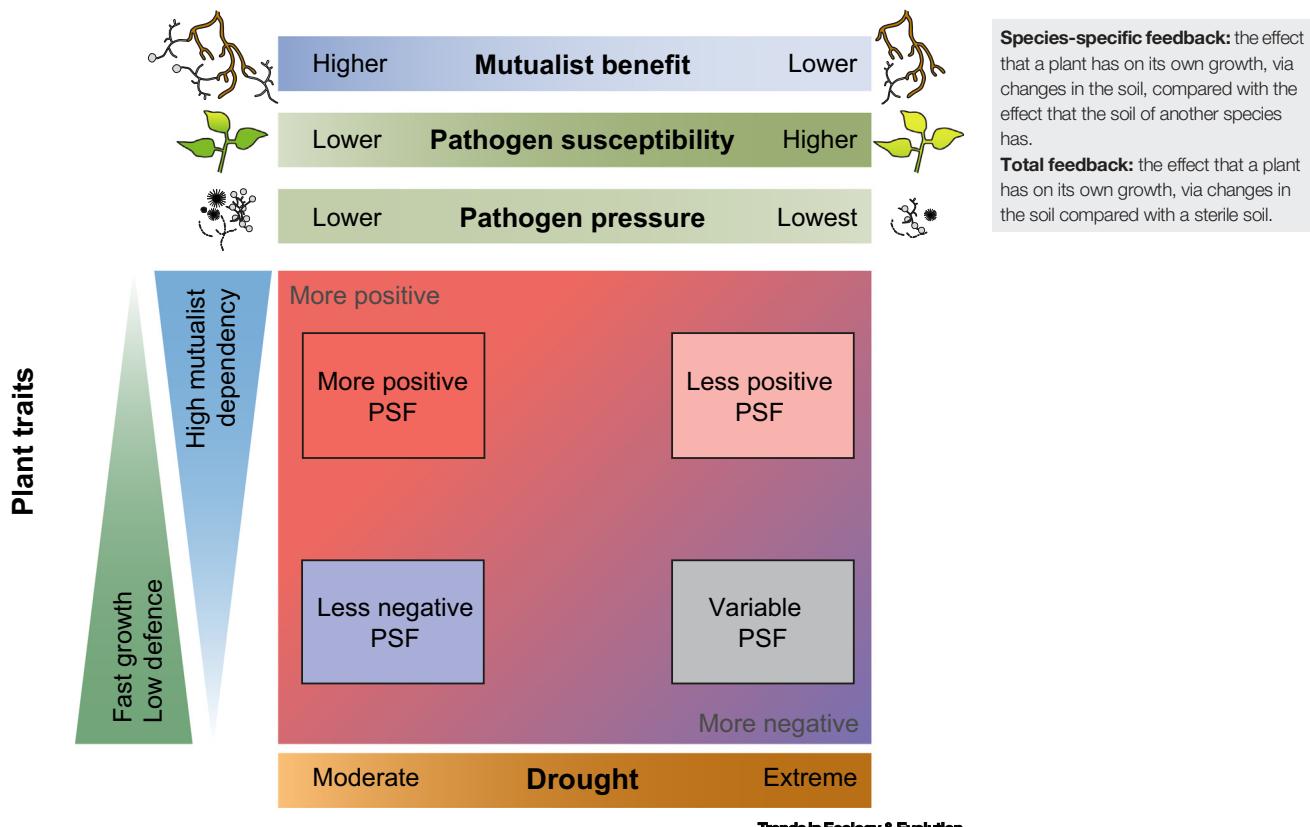
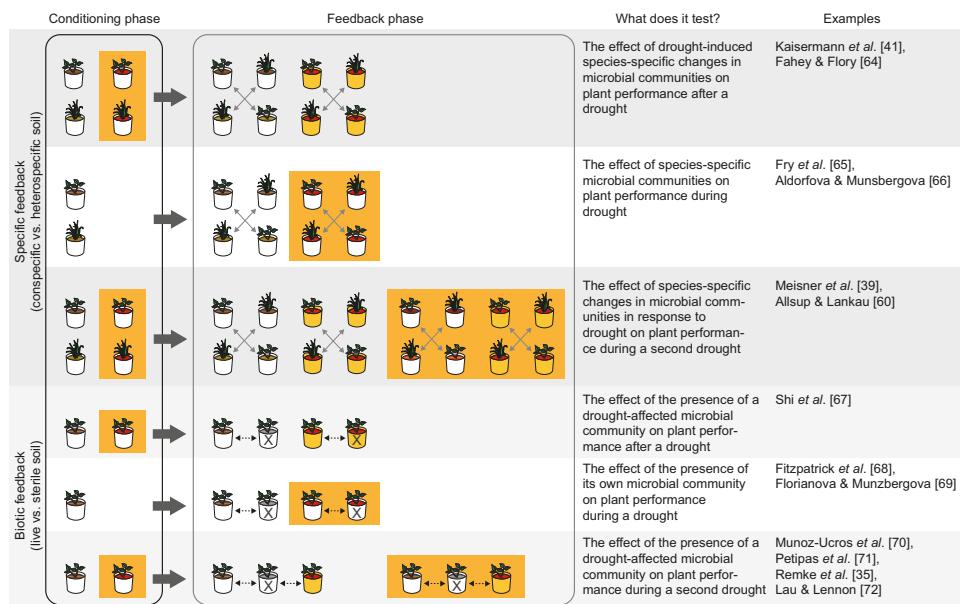


Figure 2. Diagram of hypothesised total plant–soil feedback (PSF) responses (Figure 1) to drought for fast-growing, poorly defended plants vs slow-growing, highly defended plants with high mycorrhizal dependence (y-axis) under moderate or extreme drought (x-axis). Boxes represent PSF under non-co-adapted scenarios; background indicates PSF with co-adapted plants and microbes. Species more reliant on mutualists are predicted to experience more positive PSF under moderate drought compared with moist conditions, as mutualists can increase plant drought tolerance. Extreme drought may weaken these effects, however, as the ability of plants to support mutualists and reciprocal benefits to the plants decline. Well-defended species are also expected to shift towards more positive PSF and fast-growing species should shift towards less negative PSF under moderate drought, given that moderate drought can reduce pathogen pressure and allow more investment in defence due to relaxed competitive pressure. Fast-growing taxa may respond variably to extreme drought depending on the balance of drought effects on pathogen susceptibility vs pathogen abundance, which should respectively increase and decrease under extreme drought. Overall, PSF responses to drought should be more positive when plants and microbes are co-adapted, especially under moderate drought and for species reliant on mutualists (background shading). For fast-growing, poorly defended species, PSF should be more negative under drought when pathogens and plants are co-adapted (due to shorter generation times and hence faster adaptation in pathogens than in plants). All comparisons in the figure (more or less positive or negative PSF, lower or higher mutualist and pathogen properties) are compared with moist conditions.

We examined 37 studies testing for the effects of drought on PSF in the widest sense (see supplemental information and Datafile 1 online) and found widely varying PSF in response to drought (Figure 4). When we split between studies in which plants and microbes have no shared history and those that do, we found that, in studies that used both soils and plants from the conditioning phase – the latter either as seeds (offspring) or as cuttings (clones) – and thus allowed for microbial adaptation to or filtering by the particular plant populations considered, nearly all studies found that drought in the conditioning phase and in the feedback phase resulted in more positive PSF as we predicted (Figure 4B). While these counts are too low to justify any conclusions, they



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Figure 3. Various experimental designs used to test the effects of drought on plant–soil feedback (PSF). Experiments can test species-specific feedback (grey arrows) or total feedback (broken arrows; Box 1) and can impose drought in the conditioning phase, the feedback phase, or both (drought is indicated by orange background). Not indicated in this figure are differences in (the number of) plant species, drought duration, and whether the conditioning phase is field based or pot based [35,39,41,59,60,63–72].

lead us to hypothesise that more positive PSFs under drought conditions are not only driven by the responses to contemporary conditions but further strengthened by microbial adaptation or community turnover in response to previous or historical drought. Moreover, we suspect that positive PSF may be strongest when plants and microbes with a history of coexistence are used, due to coevolutionary responses (reciprocal genetic or epigenetic responses of plants and microbes) to historical drought. While these findings are not quantitative and are based on a low number of studies, we propose that the historical drought needs to be considered when explaining PSF responses to drought, which has not been done in recent meta-analyses [31,32].

Highly variable drought effects on PSF were also observed in past meta-analyses and multispecies experiments. For example, a recent meta-analysis found that PSF became more positive under drought conditions (plants were less affected by drought when grown in conspecific soil or unsterilised/untreated soil) [31]. However, in an experiment across 21 plant species, soil inoculum from dry conditions triggered more negative PSF (better plant growth in heterospecific than conspecific soil) than inoculum from wet conditions in the majority of species, while some species experienced more positive PSF instead [33]. The discrepancy in PSF responses was not clearly related to the responses of microbial communities to drought [13]. Another recent meta-analysis showed that species with typically negative PSFs (reduced growth in conspecific soil compared with sterile control) show both negative and positive responses to drought, while species with positive PSF tend to have more positive PSF under drought [32].

Explanations for varying PSF responses to drought

We suggest that the variation in PSF responses observed among studies may be caused by variation in plant traits, plant or microbial adaptation to past drought, varying intensity and timescales

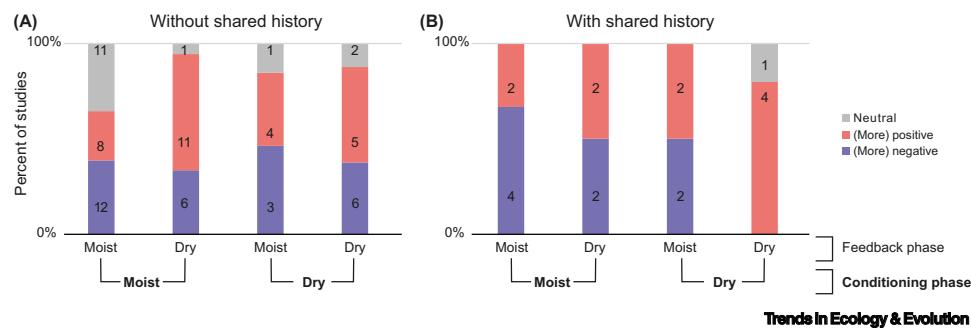


Figure 4. Overview of studies assessing the effect of drought on plant soil feedback (PSF), including (A) studies that lack any shared history and (B) experiments that include shared plant and microbial drought history through local co-adaptation or the inclusion of conditioned microbes and plants in the feedback phase. On the x-axis, studies are further grouped by whether the conditioning phase and the feedback phase were dry or moist (Figure 1). Numbers in coloured bars are the total number of studies that find that particular PSF response (neutral, positive, negative) under the specific experimental conditions. See the supplemental information online for more detail on studies and analysis.

of drought (i.e., drought history), or the disruption of coevolved plant–microbe interactions when using naïve combinations of plants and soils.

Plant traits

We predict that species with high allocation to defence and mycorrhizal fungi will experience stable or enhanced positive PSF under mild or short-term drought (Figure 3), given that moderate drought ensures continued C allocation to the soil microbiome, and mycorrhizal fungi confer drought resistance on their host [27,34,35]. Once drought starts to severely limit plant photosynthesis, beneficial interactions with symbionts are likely to collapse and result in less positive PSF. By contrast, PSF in fast-growing and non-mycorrhizal species will be primarily driven by interactions with pathogens [6,30,36], leading to less negative PSF under mild drought due to a reduction in pathogen pressure but variable PSF under severe drought (Figure 2). The outcome will depend on the balance between decreasing pathogen abundance and increasing plant susceptibility to pathogens due to physiological stress [26,28]. The overall reduction in pathogen pressure under drought conditions and the superior ability to benefit from enhanced nutrient availability on rewetting may also boost the performance of fast-growing species over slow-growing species [14], leading to positive PSF following drought. The previously described meta-analysis finding that species with positive PSF (likely due to their associations with mutualists) typically experience even more positive PSF under drought while species with negative PSF show more variable PSF responses to drought supports these predictions [32].

Drought history

In drought-adapted ecosystems, we expect a smaller change in PSF with drought compared with mesic ecosystems, because in these systems plant and microbial communities show **local adaptation** in which drought-resistant traits are selected; in other words, the same reduction in precipitation will be a less severe drought and cause less pronounced shifts in plant–microbial interactions and PSF in a drought-adapted system than in a mesic system (Figure 2). For example, in a central Texas, USA grassland ecosystem that historically experienced frequent drought, extreme decreases in rainfall limited C4 grass size and physiology, with rates of photosynthesis, conductance, and water-use efficiency reduced by 40–55% [37], but microbial community composition and function remained unchanged [38]. By contrast, even one drought event in mesic systems can affect subsequent microbial function, plant community assembly, and PSF

(e.g., [39–41]). For example, over 10 years, recurrent drought increased microbial community compositional and functional divergence compared with soils with one or no drought event in a mesic mountain grassland [42]. Further supporting this prediction, a 25-year drought manipulation in a mesic grassland resulted in microbial communities that were less sensitive to phytohormones that are commonly increased in response to drought [43].

Plant adaptation to drought

Evolutionary divergence in plant traits across arid to mesic environments is also likely to contribute to variation in PSF responses to drought. As discussed earlier, many plant traits ranging from flowering time to morphological and physiological traits can be adaptive under drought. For example, given that mycorrhizas often increase plant drought tolerance, we might predict that plant populations from xeric environments would evolve increased dependence on mycorrhizas, similar to the observed increased plant dependence on mycorrhizas in low-nutrient environments (e.g., [44]). If so, plants from xeric environments that are highly dependent on these mutualists may experience more positive PSF under drought, provided that these xeric plant populations also allocate more resources to mycorrhizal mutualists (Figure 2). Maternal effects could also contribute to **legacy effects** of drought on PSF. In one case, offspring from mothers grown under well-watered conditions showed greater mycorrhizal colonisation when grown under drought conditions than offspring from mothers grown under drought stress [34]. Such shifts in interactions with mutualists are likely to lead to altered PSF.

The role of plant–microbial co-adaptation to drought

The majority of PSF studies do not use co-sourced or co-adapted plant–microbial combinations (Figure 3), but genotype-specific effects on soil communities and genotype-specific responses to soil communities are common [45,46]. This means that PSF responses to drought are likely to be affected by the particular plant genotypes or ecotypes used in the experiment [47], more so when those genotypes are locally adapted to climate. Moreover, PSF outcomes might be affected by co-adaptation between plant populations and diverse microbial communities. For example, the growth of individual plants and species coexistence differ significantly when assessed in the presence of local versus distant soil microbial communities [48,49]. Gehring and coauthors [50] explicitly investigated how plant genotype-specific microbial communities affected drought tolerance. Pinyon pines (*Pinus edulis*) are polymorphic for drought tolerance, and this polymorphism largely results because drought-tolerant genotypes condition microbial communities with increased abundance of ectomycorrhizal fungi in the *Geopora* genus. While *Geopora* spp. are associated with increased drought tolerance in both drought-tolerant and -intolerant plant genotypes, plant control of the microbial community is so strong that the benefits are primarily observed for drought-tolerant plant genotypes that enrich this taxon. Similarly, Remke *et al.* [35] found that local soil biota enhanced plant drought tolerance, and local mycorrhizal fungi were more beneficial for plant hosts under drought conditions. However, it is also possible that pathogens in co-adapted systems have an advantage over plants because of their shorter generation times, which results in more negative feedback for fast-growing species (Figure 2). Thus, microbial effects and total PSF (and potentially species-specific PSF) can vary dramatically when co-evolutionary relationships are disrupted (Figure 2).

Concluding remarks and future directions

PSF responses to drought in existing studies are highly variable. However, we take the observation that PSF was mostly positive when co-sourced plants and microbes both experienced drought in the conditioning as well as the feedback phase, to suggest that a shared history under the conditions that the system is challenged with matters. Carryover due to plant and microbial responses, and possibly even (co-)adaptation, may have an important role in determining

Outstanding questions

How do drought history, intensity, and duration affect PSF responses to drought? Historical climate seems to matter, but PSF studies vary widely in the intensity and duration of drought, which is likely to affect the strength and direction of the PSF response.

How do plant traits determine PSF responses to drought? We understand the plant traits that underlie the direct effects of drought on plant growth, such as rooting depth. However, how these traits influence microbes that lead to PSF responses is unclear.

What are the microbial traits that confer benefit on plants under drought and how do these result in PSF responses? Benefits from microbial traits may be incidental, but the discovery of beneficial traits that apply broadly across plant species could lead to new strategies for enhanced drought tolerance in managed ecosystems.

What are the molecular and genetic mechanisms through which plants and microbes interact in response to changes in soil moisture? Increasingly, we recognise that microbes can extend plant phenotypes in ways that enhance drought tolerance, but understanding of how that happens requires interdisciplinary studies that link ecology and omics.

What is the relative importance of microbial community change and microbial adaptation in mitigating plant responses to drought? Identifying the role of these different processes will be fundamental for the engineering of plant–microbe interactions for resistance to climate change.

Ultimately, the effects of PSF on coexistence and the maintenance of plant diversity depend on the strength of PSF as a stabilising mechanism and how soil communities affect fitness differences between competing plant species (i.e., their role as an equalising mechanism in modern coexistence theory terms). What are the long-term consequences of more positive PSF as a result of drought and how long does it take for changes in coexistence to occur?

the outcome of PSF. We only have a limited understanding of how plant genetics and plant-microbe co-adaptation mediate PSF. However, it seems likely that variation in PSF responses to drought could be driven in part by genetic variation among plants and/or plant-microbe co-adaptation. Testing for the importance of plant-microbe co-adaptation requires multigeneration conditioning phases either in the field or in the greenhouse (Box 1). Such

Box 1. Co-adaptation of plants and microbes under drought and the implications for PSF

Plant-microbe co-adaptation has the potential to strengthen (or weaken) PSF responses to drought. Testing for such effects requires multigenerational conditioning phases where plant populations and their associated microbes are propagated under drought (yellow) or ambient (unshaded) conditions for multiple plant generations. To date, studies that track PSF over multiple plant generations remain rare, and none has been crossed with variation in environmental conditions such as drought. Some studies use space-for-time substitutions to extend the conditioning phase (e.g., selecting soils [60,61] or both seeds and soils from gradients with different drought histories [62]). Such approaches may be especially useful for long-lived taxa. Although single plants are shown in Figure 1 rather than the conditioning of soil with one or a few plants as is typically undertaken in PSF experiments, plant populations comprising many individuals are used, so that plant populations can evolve and the effects of selection exceed the effects of drift. The conditioning phase could use naturally occurring field populations or experimental evolution approaches where replicate populations are planted into dry versus wet conditions for multiple generations and allowed to evolve. Offspring from the conditioned (evolved) plant populations are then grown reciprocally under moist and dry conditions in the presence of microbes conditioned in the same environment or the alternative environment or in sterilised soils (pots marked X). In the scenario depicted here, microbes conditioned to drought alleviate the effect of drought on plant growth, particularly when drought-adapted plants are combined with drought-adapted microbial communities, resulting in stronger positive total PSF [(g) vs (h) and (e) vs (f); drought-evolved plants are indicated by orange leaves, drought-conditioned microbes are indicated by orange pots]. Similarly, plant populations adapted to wet conditions experience less negative PSF in wet environments than plant populations adapted to drought [(a) vs (b) and (c) vs (d)]. Such effects might occur if plant populations adapted to wetter environments have evolved increased pathogen defences due to stronger pathogen pressure in such environments.

This approach differentiates between potential mechanisms mediating drought effects on PSF. First, the main effects of microbial history would indicate that microbial populations and/or communities have shifted in response to drought (via evolution or community assembly). Second, the main effects of plant history would indicate that plants have evolved rapidly in response to drought (or that drought has strong maternal effects [63]). Plant evolutionary effects can be differentiated from maternal effects by including a common garden generation between the conditioning and the feedback phase. Both evolutionary shifts in microbial and plant traits can lead to altered total PSF. The interactive effects of microbial and plant history on PSF indicate the role of co-adaptation. If such effects are sufficiently species specific, drought legacy can also alter species-specific PSF.

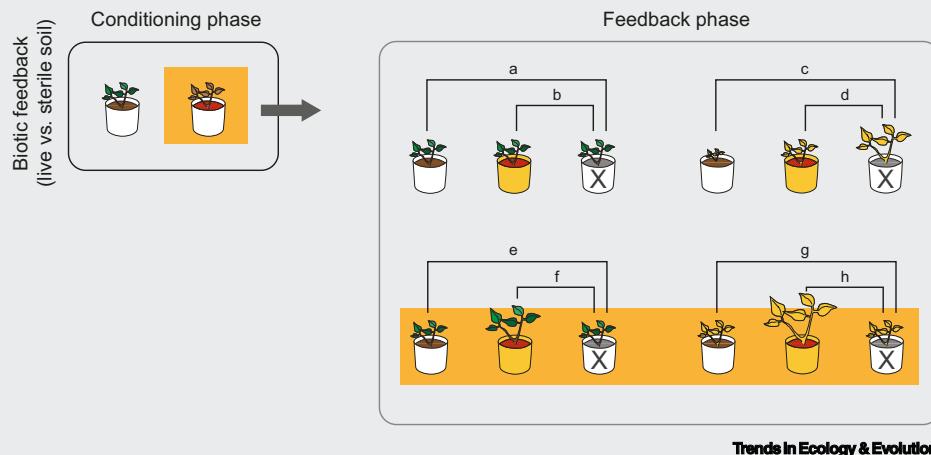


Figure 1. Hypothesised role of co-adaptation in determining total PSF responses to drought. Orange background shading indicates current drought treatment, orange plants indicate drought adaptation, orange pot colour indicates soils with past drought, X on the pot indicates sterilised soil, plant size in the feedback phase indicates plant growth response.

studies may inform on: (i) how rapid adaptation of plants to drought influences plant–microbe interactions and PSF; (ii) how coevolution between plants and microbes influences PSF; and even (iii) how maternal environmental effects influence PSF.

Many studies have assessed the role of plant traits in driving PSF and while the results of these studies are also variable, the general consensus is that fast-growing plants that rely less on arbuscular mycorrhizal fungi and are more vulnerable to pathogens generally experience more negative PSF, whereas slow-growing plants that rely more on mycorrhizal fungi experience more positive PSF [6,36,51]. Here we clarified the likely role of those plant traits in driving PSF responses during or after drought. However, predicting the consequences of drought for PSF and the implications for plant community composition will require more explicit consideration of drought history, duration, and intensity as well as soil and seed sources. In addition, experiments need to include multiple plant species of various drought coping strategies and a feedback phase that includes not just single species but also multispecies communities (see [Outstanding questions](#)).

How can we overcome these challenges to ensure that future studies of PSF reflect likely real-world responses to climate change? First, we suggest that PSF studies need to routinely co-source plant seeds and soil microbes to avoid breaking locally structured interactions, regardless of whether these are the result of parallels in habitat filtering or host–microbe co-adaptation. Exceptions are when source divergence is meaningful, as in tests of range expansion [52]. Along the same lines, drought treatments should consider the drought history of the site as well as the nature of changes in precipitation patterns expected to occur in the region [25]. For example, the potential for adaptive evolutionary changes might be greater in regions expected to experience a consistent reduction in mean precipitation than in regions that will experience more extreme drought events. The latter scenario can lead to genetic bottlenecks in species that experience high mortality under extreme droughts and fluctuation in selective pressures in dry and wet years, which can slow or alter the trajectory of evolutionary changes, although it is also possible for single extreme drought events to cause rapid evolutionary change [53].

In addition, explicit tests of mechanisms are needed to understand why PSF responses to drought occur or do not occur. Assessment of changes in microbial community composition has become routine, but making causal inferences about the effect of such changes on plant performance is no easy task. For example, coupling PSF studies with stable isotope probing of soil microbial metatranscriptomes [54] or metaproteomes [55] would provide insight into *in situ* community function by identifying the individual taxa responsible for specific mechanisms of plant–microbial interactions. Follow-up studies of key isolates will provide in-depth understanding of the relevant microbial traits [56] and signalling pathways (see [Outstanding questions](#)), which could then feed into predictive or conceptual frameworks [18,57]. Moreover, disentangling the role of microbial species turnover versus adaptation in driving changes in PSF under drought – a distinction that is rarely explicitly mentioned (see [Outstanding questions](#)) – will provide further mechanistic insight, which may be accomplished by temporal tracking of microbial strains rather than taxa [58].

A more mechanistic understanding of the pathways through which plants and microbes co-adapt and coevolve, including the role of plant and microbial traits, will help us understand the outcomes of PSF in response to changing environmental conditions. Together with an understanding of the conditions that favour or prevent these processes [59], this will strengthen our ability to predict PSF responses to drought and the resulting consequences for plant community composition.

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Author contributions

F.d.V. brought together the author team. All authors together devised the focus and content of the manuscript and all authors wrote the text and edited the final text.

Declaration of interests

No interests are declared.

Supplemental Information

Supplemental Information: contains Supplemental Methods detailing search criteria and method of assessing PSF response to drought in selected studies as presented in [Figure 4](#). Supplemental Data File 1: contains details of all studies used for generating [Figure 4](#). Supplemental information associated with this article can be found online at <https://doi.org/10.1016/j.tree.2023.03.001>

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