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MARSCHNER REVIEW

Plant-soil feedback: incorporating untested influential drivers and reconciling terminology

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Abstract
Background Plants condition the soil in which they grow, thereby altering the performance of subsequent plants growing in this soil. This phenomenon, known as plant-soil feedback (PSF), has garnered increasing interest. Experiments are moving from single species soil pairings in the glasshouse to community-level field trials. Consequently, our knowledge of the role PSF plays in shaping ecosystem functions has advanced. However, knowledge gaps remain.
Scope Here, we explore intrinsic and extrinsic abiotic and biotic drivers of PSF such as maternal effects, plant functional traits, self-DNA, plant-plant competition, herbivory, interactions between soil organisms, temperature, drought, flooding, greenhouse gases, (micro)nutrients, plant-litter-soil feedback and priority effects. These drivers have begun to feature in experiments, thereby increasing our mechanistic understanding of PSF. Nonetheless, many of these topics have received insufficient coverage to determine general principles across larger temporal and spatial scales. Further, conflicting terminology has excluded PSF studies from reviews and meta-analyses. We review terms such as soil sickness, Janzen-Connell hypothesis, soil-related invasive species work, soil legacies, allelopathy and soil-related succession that overlap with PSF but are generally not named as such.
Conclusion Holistic experimental designs that consider the continual reciprocal feedback between the extrinsic environment, plants and soil, as well as the

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unification of terminologies are necessary if we are to realise the full potential of PSF for understanding and steering ecosystem processes. Here, we compile outstanding questions related to PSF research that emphasis the aforementioned topics and suggest ways to incorporate them into future research in order to advance plant-soil ecology.

Keywords Above-belowground interactions · Allelopathy · Decomposition · Herbivory · Invasive species · Janzen-Connell · Maternal effects · Plant functional traits · Plant-soil-litter feedback · Priority effects · Self-DNA · Soil legacies · Soil sickness · Succession

Introduction

As plants grow, they shape the soil environment. Rooting patterns change the soil structure (Canadell et al. 1996), root exudation recruits the soil microbial community (Canarini et al. 2019) and nutrient uptake can deplete soil pools (Bennett and Klironomos 2019), while senesced root and shoot litter may return or add nutrients, facilitate the build-up of soil organic matter (SOM) and alter soil physical characteristics (Hassan et al. 2021b). In turn, these plant-induced alterations to the soil affect the growth of subsequent generations of plants, a phenomenon termed plant-soil feedback (PSF) (Bever 1994; van der Putten et al. 2013). Such PSF can range from positive to negative and the effects can vary between individuals of the same species (i.e., conspecific feedback) or between species (i.e., heterospecific feedback) (van der Putten et al. 2016). Although this process has been known since the dawn of agriculture (i.e., soil sickness: (Cesarano et al. 2017; Huang et al. 2013; Schreiner and Reed 1907), the complexity of the myriad interactions involved means that understanding and predicting PSF remains difficult (Bennett and Klironomos 2019). Recent decades have seen an uptick in PSF research interest (Fig. 1a). Plant-soil feedback research has evolved from glasshouse work focused on single plant-soil conditioning followed by single plant responses (Kulmatiski and Kardol 2008) to multi-factor studies seeking to understand the mechanisms and context-dependencies of PSF in mixed, natural plant communities (Beals et al. 2020; Casper and Castelli 2007; De Long et al. 2019a; Heinen et al. 2020b; Heinze et al. 2016). As our knowledge base has expanded, it is increasingly recognized that PSF plays a pivotal role in shaping plant community development and ecosystem function (Crawford et al. 2019; Suding et al. 2013; van der Putten et al. 2013).

Despite increased attention, finding general principles of PSF impacts on plant communities remains challenging due to the fact that several potentially important abiotic and biotic drivers have received limited attention (Bennett and Klironomos 2019; De Long et al. 2018; Smith-Ramesh and Reynolds 2017) and due to inconsistent terminology across disciplines (De Long et al. 2018; Smith-Ramesh and Reynolds 2017; Veen et al. 2019). The influences of intrinsic biotic drivers, as well as extrinsic abiotic and biotic drivers, have begun to receive attention in PSF experiments. A better understanding of the impacts of such drivers may help explain the influence of interactions with the wider environment and the mechanisms behind PSF (Beals et al. 2020; De Long et al. 2018; Smith-Ramesh and Reynolds 2017). Further, PSF has gone by many names throughout the years, such as soil sickness. Therefore, results going by another name are often being overlooked during meta-analyses (Crawford et al. 2019; Kulmatiski et al. 2008; but see Meisner et al. 2014) and could greatly add to the mechanistic understanding of PSF.

In this review, we have two aims. The first is to highlight intrinsic (biotic) and extrinsic (abiotic and biotic) drivers that have received minimal attention in PSF studies, but are up and coming areas of interest (Fig. 1b, c). We have deliberately chosen to include drivers that have received minimal attention in previous reviews and those that are underrepresented in PSF research based on literature searches (Fig. 1b, c). The second aim is to discuss research fields that may be considered as part of PSF, but have gone by different names over the years, which has limited inclusion of these topics in PSF experiments and meta-analyses (Fig. 1a). Overall, whenever possible, we have chosen to focus predominantly on the most recent literature published, namely studies published within the last 5 years, to emphasise the state of the art in PSF research. We present a conceptual framework demonstrating the developmental trajectory of PSF research

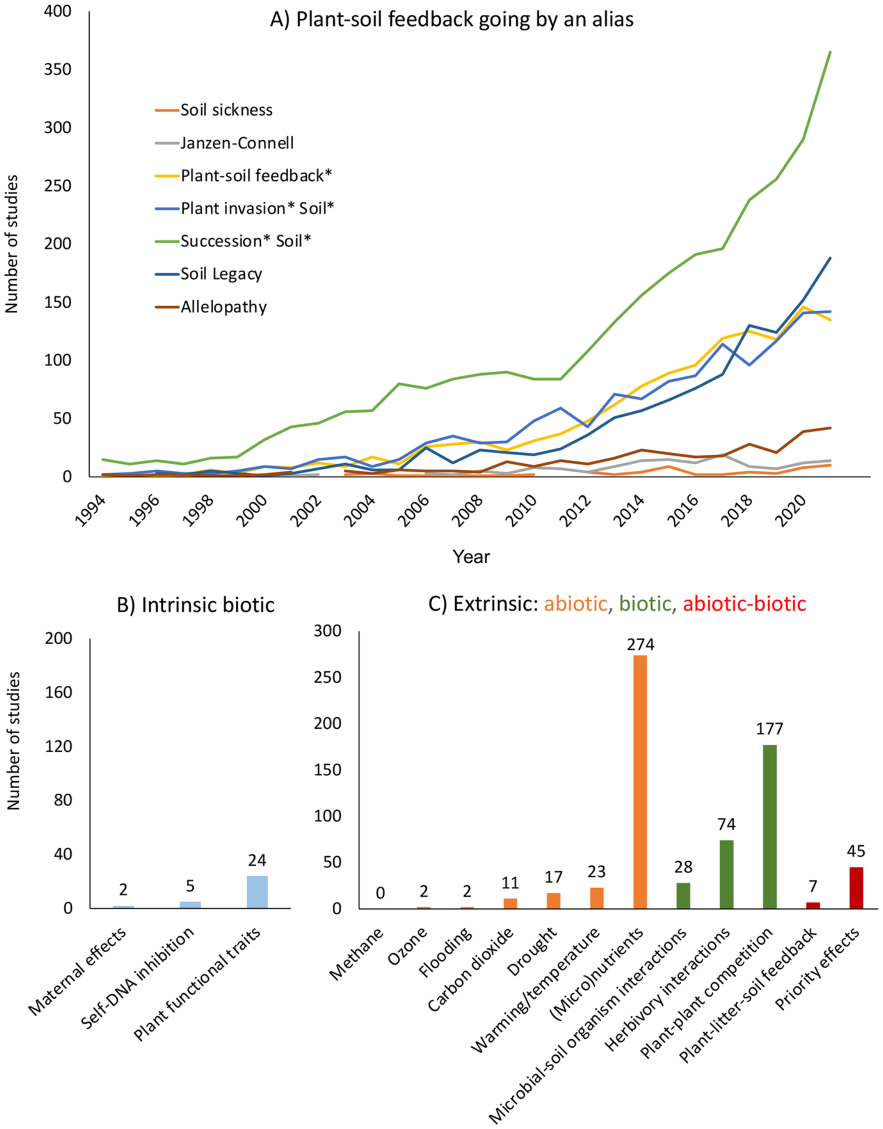
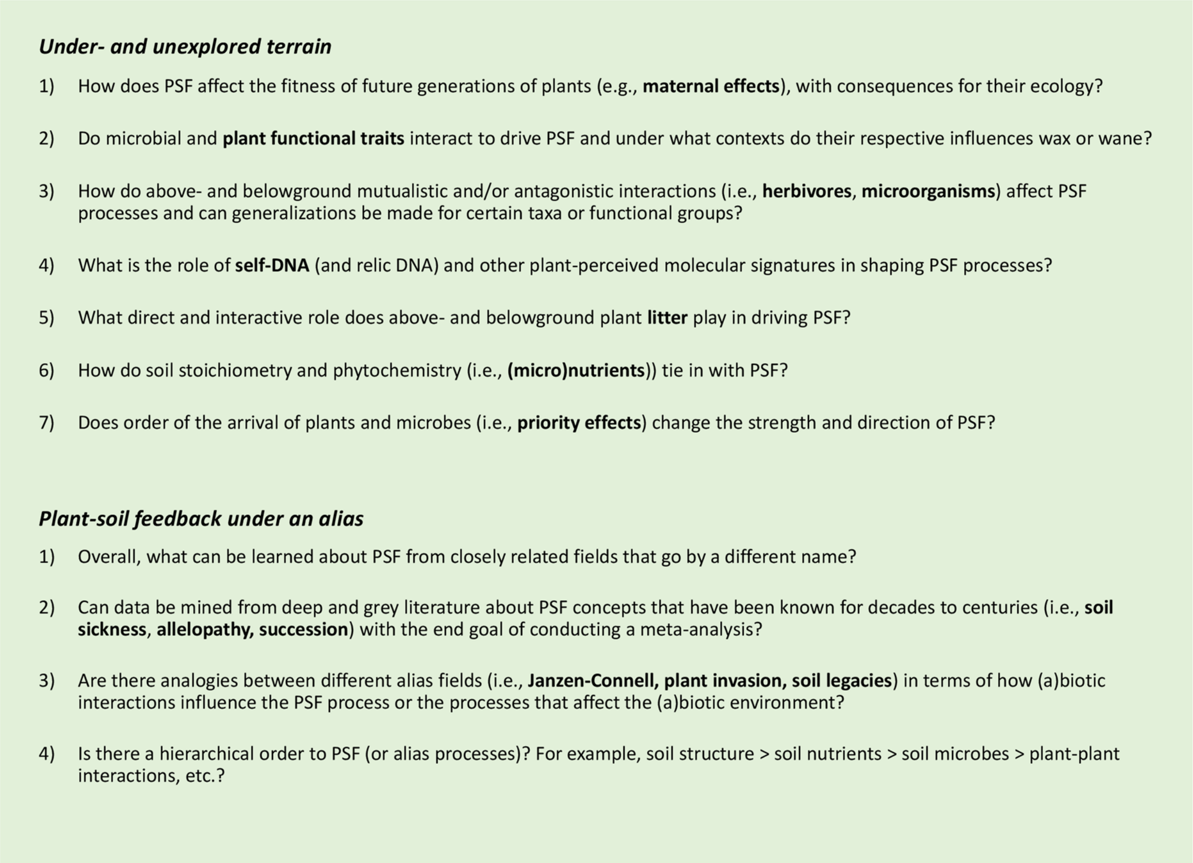


Fig. 1 Panel A shows the number of articles published each year in plant-soil feedback (PSF) and other related topics that fall under the umbrella of plant-soil feedback, but are listed under an alias. The trends demonstrates that many of the research topics showed a steady uptick in publication over time, but PSF seems to be plateauing, indicating that calling topics that are actually PSF by another name might lead to under- or misrepresentation in the literature and meta-analyses. The year 1994 was chosen as a start year because this is when the term plant-soil feedback was coined (Bever 1994). Panels B and C show the total number of studies published that included under- and unexplored drivers of PSF according to Web of Science searches. Drivers are grouped by intrinsic (panel B) and extrinsic (panel C). Within extrinsic, drivers are further subdivided into abiotic, biotic or a combination of abiotic and biotic. The studies were searched by including the "driver" AND "plant-soil feedback*" or "driver" AND "plant soil feedback*" and all resultant hits were controlled to ensure that the article actually looked at PSF. Literature searches were performed in Scopus and Web of Science in April and October 2022

and the necessity to harmonise terminology across fields of related research, whilst expanding study foci to encompass neglected or lesser explored themes. We conclude with a list of outstanding questions that the aforementioned drivers and merging of existing terminologies can help to answer (Box 1).



Under- and unexplored terrain

1) How does PSF affect the fitness of future generations of plants (e.g., **maternal effects**), with consequences for their ecology?

2) Do microbial and **plant functional traits** interact to drive PSF and under what contexts do their respective influences wax or wane?

3) How do above- and belowground mutualistic and/or antagonistic interactions (i.e., **herbivores**, **microorganisms**) affect PSF processes and can generalizations be made for certain taxa or functional groups?

4) What is the role of **self-DNA** (and relic DNA) and other plant-perceived molecular signatures in shaping PSF processes?

5) What direct and interactive role does above- and belowground plant **litter** play in driving PSF?

6) How do soil stoichiometry and phytochemistry (i.e., **(micro)nutrients**)) tie in with PSF?

7) Does order of the arrival of plants and microbes (i.e., **priority effects**) change the strength and direction of PSF?

Plant-soil feedback under an alias

1) Overall, what can be learned about PSF from closely related fields that go by a different name?

2) Can data be mined from deep and grey literature about PSF concepts that have been known for decades to centuries (i.e., **soil sickness**, **allelopathy, succession**) with the end goal of conducting a meta-analysis?

3) Are there analogies between different alias fields (i.e., **Janzen-Connell, plant invasion, soil legacies**) in terms of how (a)biotic interactions influence the PSF process or the processes that affect the (a)biotic environment?

4) Is there a hierarchical order to PSF (or alias processes)? For example, soil structure > soil nutrients > soil microbes > plant-plant interactions, etc.?

Box 1 Outstanding questions for consideration in future plant-soil feedback (PSF) research

Under- and unexplored PSF terrain

Most early PSF experiments grew a single plant species in soils under glasshouse conditions and then used soils to grow the same plants (i.e., conspecifics), as well as other, usually co-occurring species (i.e., heterospecifics) (Kulmatiski and Kardol 2008). This was a necessary first step in developing the over-arching concept behind PSF: plants change the soils and these (abiotic and biotic) changes to the soil impact on plants that grow in the soil at a later date. However, the full picture is much more complex. Plant growth is influenced by myriad other drivers such as temperature, moisture, competition, herbivory, priority effects, genetic adaptation and maternal effects, which interact to alter plant growth, reproductive performance and functional trait expression in subsequent generations. While literature is amassing on these drivers, many topics are only now reaching the level of understanding that allows us to make cross-linkages for a holistic picture of influences on plants. Here, we highlight a selection of intrinsic biotic drivers, as well as extrinsic abiotic, biotic and abiotic-biotic drivers that are likely to bear strong, direct influences on PSF, as demonstrated by what is known about plant-soil interactions in general and the recent emergence of these topics in published PSF studies. We focus on understudied drivers that have been rarely or never considered in other reviews and opinion pieces on PSF and provide an assessment of certain other drivers which have been considered previously (e.g., herbivory, plant-soil-litter feedback), but still require further research (Fig. 1b, c). Finally, we suggest ways to take the field forward in each instance.

Intrinsic biotic drivers

Maternal effects

The influences of the genotype or phenotype of a maternal plant on the phenotype of the offspring is referred to as maternal effects (Wolf and Wade 2009). The result of maternal effects could be that plants produce offspring better adapted to cope with the stressful conditions experienced by their mother (Herman and Sultan 2011; Roach and Wulff 1987). Such effects can manifest through changes to seed constitution (e.g., size, dispersal characteristics, nutrient content) (Germain and Gilbert 2014), seed microbiomes (Nelson 2018; Shade et al. 2017) and/or via DNA methylation that switches genes off or on that are related to, e.g., plant height (Hu et al. 2015) or reproduction (Alonso et al. 2018). Therefore, maternal effects are an intrinsic biotic driver that may affect PSF. For example, *Taraxacum officinale* L. exposed to root herbivory produced seeds with a better dispersal capacity (i.e., lower biomass), thereby enabling their progeny to "escape" hostile soils (Bont et al. 2020). Plants grown with a specific, beneficial soil microbial community may also produce offspring better adapted to grow with this particular soil microbial community, leading to enhanced performance of the next generation of plants in the same soil (Wagg et al. 2015).

However, soil-related maternal effects may not always be adaptive. Specifically, maternal plants that experience negative PSF may produce seeds with lower germination rates (De Long et al. 2021). There is also evidence that soil-induced maternal effects can be overridden by interactions with soil abiotic and biotic properties. For example, Stotz et al. (2018) found that plants originating from maternal lines grown with an invasive plant had decreased competitive ability, but when plants were grown in soil conditioned by the invader, competitive ability was increased. Further, De Long et al. (2019b) showed that maternal plants exposed to drought produced offspring that performed worse (i.e., smaller offspring) under ambient moisture (i.e., negative maternal effect), but this effect disappeared under drought conditions. This means that although PSF-related maternal effects are being detected, their relative importance in driving plant community composition may be limited due, in part, to a greater importance of environmental drivers. However, a comparison between the relative importance of environmental drivers versus PSF-induced maternal effects has yet to be carried out. To date, most studies on PSF maternal effects have focused on a limited number of herbaceous, temperate grassland species. Consequently, general conclusions as to the role PSF maternal effects play across plants with different growth habits and across ecosystems cannot be made.

Plant functional traits

Plant functional traits comprise the morphological, physiological or phenological features measurable at the plant individual level (Violle et al. 2007). It is widely recognized that plant traits determine how plants respond to their abiotic and biotic environment, impact on other above- and belowground trophic levels and affect functions and processes (e.g., nutrient cycling) in ecosystems (Kattge et al. 2020). Plant traits influence abiotic soil properties, as well as the soil biological community, indicating that plant traits are an intrinsic biotic driver that plays an important role in PSF (Bergmann et al. 2016; Xi et al. 2021). Chemical (e.g., plant nutrient and defence compound concentrations) and structural (e.g., specific root length and root diameter) plant traits can determine PSF processes by directly affecting the composition of rhizosphere microbial communities (Spitzer et al. 2021; Wilschut et al. 2019) and the decomposition of root (Zhang et al. 2016) and shoot (Eppinga et al. 2011; Ke et al. 2015; Laughlin et al. 2015) litter.

Despite the uptick of research looking at how plant traits influence PSF, most studies have focused on the individual effects of either shoot or root traits on PSF. However, under natural conditions, shoot and root traits interact to determine the outcome of PSF. A recent meta-analysis revealed that dissimilarities in shoot and root traits have the potential to influence the individual feedback of two plant species in each other's soil (i.e., pairwise PSF; Xi et al. 2021). This study also provided evidence that plant traits along the fast- to slow-growing plant economic spectrum (Reich 2014) might be a powerful tool to predict the outcome of PSF and ties into other work demonstrating the influence of traits on

PSF processes (Baxendale et al. 2014; Heinen et al. 2020a; Orwin et al. 2010; Teste et al. 2017).

The relationship between plant traits and PSF is not unidirectional and interactions with other organisms and environmental factors occur in natural settings. For example, floral traits and fecundity have been shown to be under the influence of PSF (Jiao et al. 2021), demonstrating this bidirectional relationship. Plant and microbial traits also exist in a bidirectional relationship. This has been investigated, particularly in the context of soil nutrient cycling (Fry et al. 2018a). Plant traits such as litter quality are known to impact on microbial traits such as carbon use efficiency (Allison 2012; Manzoni 2017). In turn, microbial traits such as colonization efficiency can also influence plant traits involved in nutrient uptake (de Souza et al. 2020; Laliberté 2017), potentially leading to knock-on effects for PSF.

Plant traits can also be driven by environmental factors (Lienin and Kleyer 2012; Milanović et al. 2020), thus affecting PSF processes. For example, Werger et al. (2020) found wind-induced changes in root morphological traits affected the strength and direction of PSF. Similar to wind, aboveground herbivory was found to influence root morphology, which would most likely affect PSF (Heinze 2020). Although the first steps have been made, the next challenge in PSF research is to integrate plant trait-based approaches and to understand how interactions with the wider environment affect the relationship between plant functional traits and PSF.

Self-DNA inhibitory effects

DNA carries the instructions that control cell functioning and genetic inheritance. However, there is an additional functional role for extracellular DNA (ex-DNA): after fragmentation, either by natural or artificial decomposition, small DNA molecules (between ~50 and ~2000 base pairs) can exert an inhibitory effect on individuals of the same species (Mazzoleni et al. 2015a). Although for a long time the exact mechanism was unclear, Mazzoleni et al. (2015b) showed for the first time that exposure to fragmented self-DNA (i.e., conspecific) inhibits root growth in plants, while non-self-DNA does not trigger these effects. This inhibitory effect of ex-DNA is not only found in plants (Singh et al. 1999), but also in bacteria (Trinick and Parker 1982), fungi (Bottone et al. 1998) and animals (from insects to humans (Monticolo et al. 2020)). Such inhibitory effects could depend on the similarity of the plant DNA with the fragmented molecules: the self-DNA toxic effect remained to a lesser extent when exposing plants to decomposing litters of phylogenetically similar plants (Mazzoleni et al. 2015b). Self-DNA effects have been proposed as a contributing mechanism to soil sickness effects in agriculture (Cesarano et al. 2017) and therefore is likely an important intrinsic biotic driver influencing PSF. In support of this, Barbero et al. (2016) showed that fragments of self-DNA induced intracellular calcium signalling and plasma membrane depolarization in *Phaseolus lunatus* L. and *Zea mays* L., thereby resolving a potential mechanism by which autotoxicity of self-DNA could work. However, Cartenì et al. (2016) proposed additional mechanisms such as a DNA-sensor that orchestrates a wide variety of innate cellular immune responses that could also explain inhibitory effects of extracellular DNA. To complicate this even further, Carini et al. (2016) showed that "relic DNA" could even make-up to 40% of DNA in soils, remaining un-degraded for years, and be involved in legacy effects for the next generation of both plants and microbes. With regards to the implications for PSF, self- or non-self DNA could be an overlooked driver of intergenerational shifts in plant performance and warrants more exploration.

Extrinsic biotic drivers

Plant-plant competition

Virtually all plants are engaged in intra- and/or interspecific above-belowground competition, making it highly likely that this extrinsic biotic factor is playing a pivotal role in PSF. Aggressively competitive plants often dominate an ecosystem, meaning that soil pathogens or herbivores may come to specialise in exploiting such an ample resource. In line with this, it has been proposed that negative PSF is responsible for maintaining species diversity in systems where competitive exclusion would otherwise dominate (Bever 2003; van der Putten et al. 2013). Although there is empirical and modelling support for this hypothesis, (Chung et al. 2019; Mack et al. 2019), such competitive interactions can only explain co-existence under real world conditions for certain species, under certain circumstances (Fitzpatrick et al. 2017; Maron et al. 2016) and the short-term nature of most PSF experiments has limited extrapolation to the field (Beckman et al. 2022). In addition, according to a recent meta-analysis (Crawford et al. 2019), most studies to date have typically considered species pairs and modelling studies suggest that such dynamics are unlikely to occur under scenarios where a multitude of species interact (Miller et al. 2022). Another meta-analysis suggests that competition renders PSF effects inconsequential (Lekberg et al. 2018), calling into question the true influence of PSF in the field. However, real world studies have indeed demonstrated that species coexistence can be predicted in part by PSF and competition (Chung et al. 2019; Kulmatiski 2019). Such mixed evidence inhibits general conclusions to be drawn regarding the role of competition in altering PSF.

Variation can also occur when the type, intensity and circumstances of competition are considered. Further, interspecific competition between co-occurring natives was found to exacerbate negative PSF relative to intraspecific competition, but this effect was species-specific and held over both live and sterile soils (Xue et al. 2018b). A recent meta-analysis showed that interspecific competition in heterospecific soils reduced plant growth more than when plants were exposed to intraspecific competition (Beals et al. 2020). There may be no effects of PSF at low levels of competitive density and positive feedbacks realised at the highest levels (Buerdsell et al. 2021). Heterogeneity in the soil can also dictate the outcome of PSF on a species-specific basis (Xue et al. 2018a), which further complicates our ability to apply PSF-competition dynamics to real world scenarios. Interspecific plant competition with native plants has been shown to effectively short-circuit positive PSF induced by invasive species (Crawford and Knight 2017). However, beneficial synergistic effects between positive PSF in invasive plants and interspecific competition with natives have also been observed (Oduor et al. 2022). Taken together, these findings have implications on the management of plant invasions, which require tailor-made management strategies depending on the species considered.

Studies have begun to consider the mechanisms behind PSF-competitive interactions and to tease apart the relative importance of above- versus belowground competition. For example, Shannon et al. (2014) found that arbuscular mycorrhizal fungi colonisation can be reduced both by previous heterospecific soil conditioning, as well as under directly competitive circumstances. Whether the direct competitive circumstances led to the reduced arbuscular mycorrhizal fungi colonisation as the result of, e.g., allelopathic effects versus direct competition for arbuscular mycorrhizal fungi symbionts remains to be tested. Ectomycorrhizal fungi generate more positive PSF versus arbuscular mycorrhizal fungi under competition in the field, which could help explain patterns of diversity and community assembly (Kadowaki et al. 2018). Competition for light can also affect microbial-driven PSFs, with high light conditions increasing plant competitive intensity in the presence of soil microbes, while this effect disappeared under low light (Xi et al. 2019). Nutrient availability can affect the outcome of PSF and competition, with higher nutrient levels alleviating negative biotic effects under competitive scenarios (Klinerova and Dostal 2020). Root competition can be alleviated by conspecific feedbacks, thereby creating niche space for enhanced root growth of an inferior competitor (Hendriks et al. 2015). In sum, it remains unresolved as to the contexts and ecosystems under which PSF is overridden or enhanced by competition, as well as the precise mechanisms that drive these effects.

Interactions with herbivory

Herbivory is a major driving process in ecosystems. As most plant species are potential food sources for a multitude of organisms, herbivory is an important extrinsic biotic factor shaping PSF. Herbivory changes plant-soil interactions mediated via plant physiological processes (e.g., shifts in leaf primary and secondary metabolites, root exudation (reviewed in Biere and Goverse (2016)), which can determine the strength and direction of PSF processes. It has been shown that herbivory by polyphagous caterpillars can alter soil fungal community composition possibly via changes to plant exudation patterns (Bezemer et al. 2013), and that this modifies PSF dynamics in response plants (Kostenko et al. 2012). Several studies suggest that herbivory may mask or alleviate PSF (Bennett et al. 2020; Dietterich et al. 2019; Heinze and Joshi 2018), and that the importance of PSF for plant species increases along a gradient of diminishing herbivory (Heinze et al. 2019). In addition, a large-scale PSF study using 20 herbaceous plant species demonstrated that the individual PSFs experienced by plants exposed to herbivores during the conditioning phase were better predictors of plant landscape abundance and diversity than those of plants that were shielded from herbivory (Heinze et al. 2020). This may indicate that considering the role of PSF independent of herbivory may be insufficient to predict in situ feedbacks.

Taken from the perspective of the herbivore, considerable evidence suggests that PSF also affects the herbivores that feed on the affected plants (Kos et al. 2015; Kostenko et al. 2012). For instance, PSF of twelve different plant species affected consumption and growth of the polyphagous caterpillar *Mamestra brassicae* L. on individual plants (Heinen et al. 2019) and determined its overall feeding patterns in plant communities (Heinen et al. 2018). Further, PSF is positively correlated with herbivore performance (Heinen et al. 2019), indicating that soils that generate more vigorous plants help improve plant resources for herbivores. On the other hand, various studies have shown strong shifts in phytohormonal defences (Zhu et al. 2018), and shifts in the plant metabolomic profile that can repel herbivores (Huberty et al. 2020; Mutyambai et al. 2019; Ristok et al. 2019). These processes also seem to have a strong successional component, with plants inducing successional changes belowground (e.g., decreases in nutrient availability and increasingly fungal-dominated microbial communities), which feedback on plant growth and tissue quality over time, and subsequently, the performance of herbivores (Howard et al. 2020; Huberty et al. 2022).

Finally, herbivory can interact with other environmental factors. In a mesocosm study, Sveen et al. (2021) illustrated that herbivory and nitrogen deposition interact to influence PSF and arbuscular mycorrhizal fungal colonization, with the surprising finding that herbivory was actually a strong, plant species-specific mediator of the negative effect of nitrogen deposition. These complex relationships indicate that herbivory can be beneficial to the plant in some instances, which has implications for our understanding of PSF in real-world conditions.

Although herbivores can affect PSF and vice versa, how this interaction affects ecosystem dynamics is not fully understood (Smith-Ramesh and Reynolds 2017). The effects of herbivory seem to mask PSF partially and may fade as complexity in interactions with other environmental factors increases. Unravelling how the different components of PSF (i.e., microbial, nutritional, allelopathic) relate to herbivory from the individual to the community level in the field will increase our understanding of these processes, and their importance for ecosystem functioning (Bennett and Klironomos 2019).

Microbial and soil organism interactions

Soil mutualists, saprotrophs and pathogens play important roles as extrinsic biotic drivers of PSF. (Note: microorganisms that inhabit the soil, but also inhabit plant tissue (e.g., mycorrhizae, other endophytes) could be considered *intrinsic* biotic drivers.) Mutualists and saprotrophs tend to have synergistic interactions that aid in plant growth, whereas pathogens tend to be antagonistic for plant growth (Hannula et al. 2020). Soil pathogens are considered the main drivers behind negative PSF (Bever et al. 2015; Domínguez-Begines et al. 2021) and most PSF studies have largely focused on broad pathogen groups rather than the interactions within and between different functional groups of microorganisms. Further, it has recently been proposed that generalist microbiota can have species-specific PSF effects that correlate with phylogenetic relatedness and plant functional diversity in the wider plant community (Semchenko et al. 2022). Essentially, this suggests that generalist soil organisms can have context-dependent, species-specific effects. Given that soil-borne plant pathogens are expected to become an increasingly pressing global problem (Delgado-Baquerizo et al. 2020), it is important to understand how interactions with mutualists may ameliorate the negative effects of pathogens.

Both pathogens and mutualists vary in their host specificity, ranging from highly specific to a single host to generalists, which can affect PSF (Domínguez-Begines et al. 2021; Hannula et al. 2020). For example, the invasive oomycete pathogen *Phytophthora cinnamomi* (Rands) drove negative PSF in the highly susceptible, dominant *Quercus suber* L., but not in the coexisting *Olea europaea* L. in Mediterranean mixed forests (Domínguez-Begines et al. 2021). These disparate responses could partly be due to their symbiotic associations with contrasting types of mycorrhizal fungi: *Q. suber* is ectomycorrhizal, while *O. europaea*, associates with arbuscular mycorrhizal fungi (Domínguez-Begines et al. 2020). These results are somewhat surprising because evidence suggests that ectomycorrhizal fungi are better at protecting their plant hosts against pathogens in comparison to arbuscular mycorrhizal fungi because ectomycorrhizal fungi produce a mantle around the host root, while arbuscular mycorrhizal fungi grow predominantly within the roots (Tedersoo et al. 2020). Alternatively, it could be due to inherent differences in susceptibility or that mycorrhizal colonisation primed a stronger defence response in *O. europaea* versus *Q. suber* (Jung et al. 2012).

Considering interactions between mutualists is also gaining traction. For example, it is known that saprotrophic and ectomycorrhizal fungi both decompose organic matter and have been shown to compete with one another (Fernandez and Kennedy 2016; Lindahl et al. 2021). In line with this, studies have shown that *Pinus* spp. L. co-invade with beneficial ectomycorrhizal fungi from their native range (Dickie et al. 2010; Policelli et al. 2020; Sapsford et al. 2022). As the density of the co-invading pines and ectomycorrhizae increases, saprotrophic diversity decreases drastically, suggesting this loss is due to competitive exclusion of saprotrophs by ectomycorrhizae (Sapsford et al. 2022). The result is correlated with losses in plant community diversity (Nuñez et al. 2017). In contrast, it has been demonstrated in a growth chamber study that native *Nothofagus* (Blume) trees and non-native pine trees grown in pine-invaded soils and non-invaded soils grew equally well in both soils in terms of biomass and ectomycorrhizal root colonisation, suggesting the presence of each host (and their mutualists) did not necessarily hinder the other (Policelli et al. 2020). The implications of such interactions on future plant communities and the subsequent PSF remains relatively unknown, particularly when designing invasive species management plans (Dickie et al. 2022).

Plant-associated soil organisms (both microbes and soil animals) exist in a complex, heterogeneous environment where myriad interactions occur. Therefore, considering the entire soil community beyond interactions between microbial functional groups is critical. Recent research showed that conditioning plant species can leave long-term impacts on the soil fungal community (in comparison to bacterial communities that fade faster) and both fungal and bacterial legacies are stored inside plant roots, which can affect the growth of the next plant (Hannula et al. 2021; Heinen et al. 2020b). Soil animals such as nematodes have also been implicated in negative PSF (Brinkman et al. 2015; Wilschut and Geisen 2021; Wilschut et al. 2019), but their interactions with the rhizosphere microbial community can induce positive effects on plants (Wilschut and Geisen 2021). Interactions between nematodes and soil microarthropods can also change PSF effects, but effects depend on plant species identity and the previous conditioning plant species (Kuťáková et al. 2018). The logical follow up is to consider additional microbial functional groups and soil animals (Geisen et al. 2022), eventually building to soil food web analyses that can identify all the major players involved behind PSF.

Extrinsic abiotic drivers

Temperature

Temperature is an extrinsic abiotic factor that strongly influences the physiology and enzyme activities of plants (Bita and Gerats 2013; Moore et al. 2021) and soil (micro)organisms (Nottingham et al. 2019; Walker et al. 2018). Hence, temperature impacts on processes like decomposition (Li et al. 2021; Wang et al. 2021) and nutrient uptake (Pregitzer and King 2005) and thus the growth of, and interactions between, plants and soil (micro)organisms (De Long et al. 2018; Hassan et al. 2022). As these interactions affect ecosystem functioning, it is necessary to understand the effects of temperature on PSF (Hassan et al. 2022), especially because temperature is expected to increase during climate change (Pörtner et al. 2022).

Increasing temperatures impact on soil water availability (Osakabe et al. 2014), but to date many studies on PSFs investigated only the direct effects of drought without including temperature (Fry et al. 2018b; Kaisermann et al. 2017; Martorell et al. 2021; Wilschut and van Kleunen 2021). However, some studies have tested the interacting effects of drought and warming on PSFs (Duell et al. 2019; Pugnaire et al. 2019) or the direct effects of temperature on feedback processes between plants and soils (De Long et al. 2015;

van Grunsven et al. 2010). For example, increasing temperature was found to affect PSFs in a native forb (Rasmussen et al. 2020) and native grasses along an elevational gradient (De Long et al. 2015). Further studies that tested whether native and non-native plant species showed different PSF responses to increased temperature showed conflicting results. For instance, van Grunsven et al. (2010) found no overall effect of a 5 °C temperature increase on PSF in both native and non-native plants. In contrast, Duell et al. (2019) observed that warmer growing conditions resulted in more positive PSF for non-native species. This finding was also supported by a recent meta-analysis (Hassan et al. 2022). However, the mechanisms behind these temperature-related PSFs, remain open and partly contradictory. For example, it was found that increasing temperature increased arbuscular mycorrhizal colonization (Rasmussen et al. 2020), but negatively affected their activity (Mohan et al. 2014). Warming was also found to affect fungal to bacterial ratios in soils (Cregger et al. 2014), thereby changing interactions between soil biota and plants. Furthermore, there is empirical evidence that increasing soil temperature impacts the effects of soil biota on plants (Heinze et al. 2017; Pineda et al. 2013) and nutrient cycling (Burns et al. 2013; De Long et al. 2018), with potential consequences for plant-litter-soil feedbacks (Veen et al. 2019).

However, two recent meta-analyses revealed no overall effect of temperature on PSF (Beals et al. 2020; Hassan et al. 2022), although plants with different life-cycle traits (De Long et al. 2018) or invasion status (Duell et al. 2019) might differ in their PSF response to warming. Potential differences in PSF might be due to dissimilarities in nutrient uptake rates between fast- and slow-growing species and the fact that temperature impacts on nutrient cycling (Burns et al. 2013; De Long et al. 2018). Furthermore, increasing temperature was found to enhance pathogen accumulation (Crawford et al. 2019; Romero et al. 2022), thus increasing negative PSFs experienced by native plant species and potentially enhancing the enemy release experienced by non-natives (Duell et al. 2019; Hassan et al. 2022).

Besides direct effects on soil biota and thus PSFs, temperature is likely to interact with other drivers of PSFs. For instance, it can be assumed that increasing temperature impacts on PSF via effects on herbivores. Warmer environmental conditions influence the growth and feeding activity of insect herbivores (Lemoine et al. 2014). Such temperature-related effects on herbivory might result in changes in root exudation or plant litter quality via accumulation of defence compounds (Massey et al. 2007) as plants respond to herbivory - that in turn feedback on plant growth via effects on soil biota. Furthermore, by influencing photosynthesis and thus plant functional traits like specific leaf area and leaf dry matter content (Zhu et al. 2020), increasing temperature will likely impact plant-litter-soil feedbacks. As plants species differ in their growth responses to temperature (Gremer et al. 2012), it is also possible that temperature effects might affect competition between plant species and subsequently their relative contribution to PSFs. Overall, more research is needed to get a comprehensive picture of temperature effects on PSF.

Drought and flooding

There has been increasing interest in the effects of drought on PSF. Given that severe drought events are expected to increase as climate change advances (Pörtner et al. 2022), understanding the effect of this extrinsic abiotic driver on PSF has become paramount. Drought leaves a strong signature in the soil, changing nutrient availability and stoichiometry (Gao et al. 2020) and soil microorganism community composition (Canarini et al. 2021; Meisner et al. 2018), consequently influencing plant growth (Buchenau et al. 2022). Such drought effects can have implications for ecosystem processes such as carbon cycling (Fuchslueger et al. 2016). It has also been demonstrated that drought can effectively override PSF (Fry et al. 2018b), create a positive PSF (Rutten and Gomez-Aparicio 2018) or shift PSF in a way that alters plant-plant competition (Kaisermann et al. 2017). Including interactions between drought and PSF can better predict plant landscape abundance versus considering PSF in isolation (Xi et al. 2022). Drought can interact with other global change factors, such as N deposition, leading to disruption in mycorrhizal colonisation, shifts in plant biomass allocation and more negative PSF (Valliere and Allen 2016). In addition, plants from different functional groups can show disparate responses to drought legacies (Hassan et al. 2021a), leading to potential shifts in plant community composition in the long-term. A recent meta-analysis showed that soil microbial feedbacks can enhance plant growth under drought conditions (Beals et al. 2020). However, these results were based on only seven papers, which indicates that no broad conclusions about drought and PSF can be reached as of yet.

In contrast to drought, the impact of flooding on PSF has received very limited attention. Flooding can have direct damaging effects on the soil by enhancing erosion (Julian and Torres 2006) or washing away nutrients and organic matter (Talbot et al. 2018; Yarwood 2018). Positive effects can occur, however, when flood waters recede and deposit nutrient-rich soils (Talbot et al. 2018). With flooding there tends to be a shift from aerobic- to anaerobic-dominated soil microbial communities, with likely cascade effects on plants if these microorganisms produce phytotoxic chemicals or induce shifts in root metabolic profiles (Hartman and Tringe 2019). Enhanced soil moisture after flooding could generate a proliferation of pathogens (Martínez-Arias et al. 2022), with potentially synergistic effects on negative PSF. From the perspective of the plant, flooding changes virtually all aspects and functions, including metabolism, stress hormone production, respiration and overall growth during all life stages (Zhou et al. 2020). The strongest directive negative effect of flooding on plants is the deprivation of oxygen in the soil (Jackson 1985). Species-rich plant communities can mitigate the effect of these anoxic flooding conditions by generating greater soil porosity via diverse rooting strategies (Wright et al. 2017), which could lead to future PSF. One of the few PSF studies that included a flooding component found that negative feedbacks in rice (*Oryza sativa* L.) increased with time since land conversation to rice paddies (Edwards et al. 2019). However, this study was conducted in a permanently flooded field and did not explicitly explore changes to the soil between flooded versus unflooded fields. Thus, how flooding drives PSF remains unclear.

Greenhouse gases: carbon dioxide, methane, nitrogen oxides and ozone

Anthropogenic greenhouse gas (GHG) emissions (e.g., carbon dioxide (CO_2), methane (CH_4), nitrous oxides (NO_X)) are increasing and there is abundant evidence that many of these have direct effects on plant function and plant-soil interactions (Maček et al. 2019; Rosado-Porto et al. 2022). These GHGs are likely to directly affect PSF through alteration of litter quality, shifts in plant growth or by changing the strength and direction of plant-microbial relationships (Maček et al. 2019). Elevated CO_2 (eCO_2) has been shown to increase above- and below-ground plant biomass (Terrer et al. 2021), photosynthetic rates (Li et al. 2018) and labile carbon inputs to soil (Kuzyakov et al. 2019). Resultantly, more carbon is being fixed without a concomitant increase in (micro)nutrients and long-term CO_2 experiments (e.g., Free Air Carbon Dioxide Enrichment (FACE)) have shown a significant decrease in concentrations of nutrients in plant tissue. This can have cascading effects through the soil food web, potentially changing litter decomposition rates (Loladze 2014; Penuelas et al. 2020). The decomposition of previously stable soil carbon (i.e., carbon priming) can occur with eCO_2, likely due to increased competition between microbes and plants for resources, the activation of different microbial groups or preferential substrate consumption (Reich et al. 2006). eCO_2 also has direct effects on soil microbial community composition. For example, in a scrub-oak system, carbon-degrading fungi and associated enzymatic activities were increased, leading to reduced carbon storage (Carney et al. 2007). Further, there is evidence of the up-regulation of genes related to nitrogen cycling, indicating that PSF could be positive under eCO_2 through increased soil nitrogen availability (Yu et al. 2018). All of these effects are likely to have strong intergenerational impacts on plant growth and community dynamics. Given the contrasting effects of eCO_2 on carbon storage and the microbial community composition, it is still unclear if net PSF will be positive or negative. It seems likely that there will be high context dependency, and various interactions with other global change drivers such as drought and flooding (Walker et al. 2021).

While CH_4 is commonly studied in light of its role in radiative forcing, recent evidence has come to light that plants can produce CH_4 independently of microbes in response to cell damage from reactive oxygen species. CH_4 is produced during the breakdown of plant structural materials such as pectin and lignin (Keppler et al. 2008; Messenger et al. 2009). Methane could play the role of an antioxidant in plant cells, protecting against a range of abiotic stresses (Li et al. 2020). The breakdown of these large molecules and the CH_4-induced resilience to abiotic stress could have interesting implications for plant-litter-soil feedback (PLSF). The resultant alterations to litter quality, plus interspecific variation in the magnitude of these effects, could change decomposition rates and thereby PLSF. Further, CH_4 is implicated in root organogenesis, which would have further effects on the rhizosphere, increasing its breadth and potentially offering more opportunities for root foraging and microbial association (Kou et al. 2018; Zhao et al. 2019). An increased sphere of influence could further increase PSF effects, whether positive or negative.

Ground level ozone (O_3) is an increasing risk to plant health. It forms from NO_x and volatile organic compounds, entering plants through their stomata. There, it will react with the membrane or form reactive oxygen species, which damage cell apparatus (Cho et al. 2011). O_3 is highest on hot sunny days and causes visible injury to the plant. In a timely review, Agathokleous et al. (2020) showed that leaf thickness and other leaf traits can inform vulnerability to O_3 damage, as can plant functional type, with resultant cascading consequences across trophic levels likely. Therefore, the effect of O_3 on PSF could be partly predictable by these criteria. Further, elevated O_3 reduces plant carbon allocation to the soil, which could indirectly affect the soil microbial community. Currently, it is unclear if and how O_3 can directly impact soil microbial communities to influence PSF, and this could form the basis of an important research area. It is clear nevertheless, that GHGs alone and in combination with other drivers can have strong impacts on PSFs and it is urgent that the less studied GHGs are incorporated into PSF experiments.

The role of (micro)nutrients

The role of base cations (e.g., calcium, magnesium and potassium), plant macronutrients (e.g., nitrogen, phosphorus, potassium), plant micronutrients (e.g., iron, manganese and zinc), and important elements such as sulphur and silicon (hereafter collectively plant nutrients) constitute important extrinsic abiotic drivers that have been overlooked in most PSF studies (but see the section on soil sickness). Nitrogen and phosphorus are considered to be the main drivers and often the immediate limiting factors for plant growth (Wang et al. 2018a). Soil nitrogen can change PSF via impacts on the microbial community and soil organic matter (Wang et al. 2022). However, research on individual plant nutrients is increasing, particularly in an agricultural context (Kaspari 2021). For example, necrosis of crop leaves can occur as a result of potassium, sulphur, copper or nitrogen deficiency, which can affect the quality and quantity of carbon exudates and litter (Grundon 2006), likely resulting in alterations to the rhizosphere community composition and changes to PSF.

Micronutrients help determine the quality of the litter and speed of its turnover. There is evidence that micronutrients, when added to soils, can catalyse release of plant-available nitrogen, phosphorus and potassium, which can increase plant and invertebrate abundance (Prather et al. 2020). Measuring local plant nutrients in the rhizosphere to a high resolution has begun to gain momentum (Capstaff et al. 2021; Clode et al. 2009). Some research has linked changes in the plant community with ecosystem scale plant nutrient shifts, although such changes are often not characterised as PSF. For example, woody encroachment in savannah landscapes is associated with an accumulation of copper, sulphur, calcium and strontium in the soil, as well as nitrogen and phosphorus (Zhou et al. 2021). The increase in concentration and availability of these nutrients can create a positive PSF that enables further encroachment (but see D'Angioli et al. (2021)). Nutrient-related PSF is also at play in other regions where shrub encroachment is an issue, namely, in the arctic tundra (Myers-Smith et al. 2011; Wookey et al. 2009).

In order to understand how micronutrients drive PSF, detailed information on plant responses to micronutrients alone and in combination is needed. For example, Wang et al. (2018b) demonstrated a close link between concentrations of plant nutrients in soils and plant tissues on an elevational gradient, finding that soil was a stronger determinant of plant magnesium, calcium, manganese and zinc than elevation, while potassium and iron were decoupled. Further, litter decomposition in a range of forests was found to be tightly correlated with micronutrient concentration. Specifically, in a range of *Pinus* species, manganese constrains late successional stage litter breakdown because of its importance in the production of lignolytic enzymes by Basidiomycota fungi (Berg et al. 2007), while in tropical tree litter, single micronutrients can have strong effects, either accelerating (zinc; (Powers and Salute 2011);

sodium; (Kaspari et al. 2009)) or delaying (magnesium; (Powers and Salute 2011)) decomposition. Shifts in litter decomposition rates can affect PSF by either altering seedling establishment rates through litter thatch or increasing plant growth through rapid release of micronutrients (Veen et al. 2019). Soil pH is also an important determinant of bioavailability of cations and micronutrients, (Wang et al. 2018a). Finally, recent work indicates that there is widespread nutrient dilution in food webs (iron, zinc, manganese, etc.) as a consequence of anthropogenic global change (Kaspari 2021). This is likely to have long-term impacts on plant community dynamics, and it is important to begin to understand the role of heretofore overlooked plant (micro)nutrients in PSF.

Abiotic-biotic extrinsic drivers

Plant-litter-soil feedback (PLSF)

Above- and belowground plant litter impacts various ecosystems processes such as nutrient cycling, carbon sequestration and plant community composition (Xu et al. 2013). Although the importance of litter is recognized as an important extrinsic driver that can have both abiotic and biotic effects on PSF, placing its effects into PSF research has only recently become recognized (Hobbie 2015; Veen et al. 2019). Feedbacks caused by physical, chemical or biotic components of litter could result in broader implications for the dominance of a species within the ecosystem (Capellesso et al. 2016; Mazzoleni et al. 2010).

Physical effects of litter can lead to both negative and positive PLSFs. It is long known that a layer of litter insulates the ground, thereby reducing fluctuations of temperature (MacKinney 1929). Such buffering effects are stronger in grasslands versus forests (Xu et al. 2013), suggesting that the potential feedbacks vary by ecosystem. A thick litter layer can inhibit seeds that require specific wavelengths of light in order to germinate (Vázquez-Yanes et al. 1990), but could also prevent moisture loss under drought (Wellstein 2012). However, whether these effects are seen as negative versus positive remains a question of perspective. For example, suppression of one species could have benefits for another via the alleviation of competitive exclusion (Vaccaro et al. 2009). Further, Wang et al. (2013) found that a layer of pine needle litter impaired atmospheric methane uptake by the soil, but this trend reversed when soil moisture reached a certain threshold (i.e., the soil became a methane sink), suggesting a possible link between litter physio-dynamics and climate change.

Chemical-mediated litter feedback pathways can range from allelochemical influences to nutrient sequestration or release. The section above on allelopathy covers the former, thus here we focus on the latter: nutrient dynamics. As litter decomposes, it can provide valuable nutritional resources for plants (Hobbie 2015). Shifts towards fast-growing herbaceous vegetation that produces labile litter with higher litter nitrogen and lower carbon and lignin content can impact on the soil community, thereby leading to increases in soil nitrogen and generating positive feedbacks (Zhang et al. 2022). In fact, litter traits associated with decomposability (i.e., leaf dry matter and nitrogen content) have been shown to influence landscape-level plant community composition via soil nutrient availability (Laughlin et al. 2015) (see section above on plant functional traits). Typically, shoot litter is more labile than root litter (Freschet et al. 2013), suggesting that root litter might be more likely to generate neutral or negative PLSFs. Belowground biomass allocation tends to be higher compared to aboveground (particularly in harsh ecosystems such as boreal forests and the arctic) (Poorter et al. 2012; Qi et al. 2019), but root decomposition remains underrepresented in the literature.

Biological pathways also play a significant role in shaping the PLSF pathway. The “home-field advantage” (HFA) hypothesis proposes that plant litter will break down faster in “home” versus “away” soils due, in part, to co-evolved specialised decomposer communities in “home” soils (Ayres et al. 2009; Veen et al. 2015a). This can result in the release of nutrients, which the plant can rapidly recycle, thereby initiating a positive PSF. Although many studies have found evidence for HFA (Asplund et al. 2018; Milcu and Manning 2011; Vivanco and Austin 2008), others have not (Ayres et al. 2006; Gießelmann et al. 2011; Veen et al. 2015a). On occasion, a reverse HFA has been found, where litter breaks-down more easily away from the plant from which it originated (Ding and Wang 2019). Taken together, it appears that HFA is not a universally applicable theory and the mechanisms behind such effects remain unresolved

(Austin et al. 2014; Palozzi and Lindo 2017; Veen et al. 2015b). Theories postulate that other factors outside of the soil microbiome could be driving HFA, such as litter traits (Veen et al. 2015a) and soil abiotic properties. Further, fungal endophytes present in leaves that remain active after senescence can begin to function as saprotrophs after the leaf senesces, which could have implications for decomposition, nutrient release from organic matter and thereby act as one of the mechanisms behind HFA (Fanin et al. 2021; Wolfe and Ballhorn 2020). There is evidence that phyllosphere-derived microbiota can remain dominant in abscised leaves for up to eight months, after which this litter becomes dominantly colonised by soil biota (Voříšková and Baldrian 2013). On the other hand, recent work has also shown that repeated introduction of litter can shape the soil fungal community structure (Veen et al. 2021). What precisely these reciprocal influences on soil and litter microbiomes have for PLSFs is beginning to be understood. For example, it has been shown that litter inoculum with no direct contact with the soil or plant can drive negative feedbacks in multiple Asteraceae species (Zaret et al. 2021). Similarly, inoculation of unsterilised conspecific leaf material had positive feedback effects on *Leymus chinensis* (Trin.) grass grown under sterile conditions (Li et al. 2022). Root litter is also postulated to harbour pathogens capable of infecting the next generation of plants (Aldorfová et al. 2022). The enhanced understanding of PLSF demonstrates that litter microbiota have the potential to mediate plant species coexistence via, e.g., species-specific negative feedbacks caused by the phyllosphere microbiome (Whitaker et al. 2017).

Priority effects

Priority effects explain how the order or timing of species arrival affects the establishment, growth or reproduction of subsequent later-arriving species. Priority effects are extrinsic abiotic and/or biotic driver(s) that can add an extra layer of complexity to determining PSF effects. In essence, priority effects relate to PSF in that the first species to arrive will be the soil "conditioning" species and subsequent species will act as the "response" species". Priority effects can play important roles in the assembly of communities of various trophic-levels at different scales (Debray et al. 2022; Fukami 2015; Grainger et al. 2019; Kardol et al. 2013b), such as dictating the order of colonization of microorganisms on plant litter that consequently influences litter degradation rates (Veen et al. 2019) and plant community assembly via sequential soil conditioning (Grman and Suding 2010; van de Voorde et al. 2011; Weidlich et al. 2017).

The investigation of priority effects resulting from soil conditioning by a plant species on the subsequent species growing in that same soil (van de Voorde et al. 2011) is akin to the two phases of a typical PSF experiment – "conditioning" and "feedback" phases. Therefore, priority effects could change plant performance in the succeeding plant community (Grman and Suding 2010; van de Voorde et al. 2011; Weidlich et al. 2017). For example, priority effects caused by legumes that arrived before grasses in an experimental grassland in Germany consistently improved belowground productivity of the successive plant community (Weidlich et al. 2018). Thus, the identification of species or plant functional traits that create positive priority effects that allow for successful establishment of target plants or those that create detrimental priority effects can help us to facilitate restoration (Weidlich et al. 2021; Wolfsdorf et al. 2021) or prioritise the removal of certain plants that generate undesirable soil legacies (Grman and Suding 2010). As such, active management of the plant community composition and their priority effects may be required to achieve desirable soil legacy effects in degraded ecosystems.

The incorporation of priority effects into PSF studies could be expanded by having more than two experimental phases and/or varying the intervals of measurements for each phase (Wubs and Bezemer 2017). Certain plant species may generate highly persistent soil legacies that interact with or override the conditioning effects by subsequent later-arriving species (Hannula et al. 2021). For example, in a long-term mesocosm experiment utilising grassland plants of the Netherlands, Hannula et al. (2021) showed that the influence of an initial plant species on the soil fungal community can be persistent in the endosphere of new plants growing in the soil, which temporarily obscured the soil conditioning effects of these new plants. Future studies should consider the order of plant species' soil conditioning and the persistence of their effects to improve the predictability of PSF (Hannula et al. 2021; van de Voorde et al. 2011).

Plant-soil feedback going by an alias

Soil sickness

After humans began to settle and cultivate crops for subsistence, it quickly became evident that planting the same crop repeatedly in the same soils usually resulted in diminished yields over time. Colloquially, this phenomenon became known as soil sickness. In essence, soil sickness is negative PSF. Soil sickness is widespread within agriculture, with at least 111 species documented as demonstrating negative responses when grown in their "own" soils (Cesarano et al. 2017). Historically, the mechanisms behind soil sickness have been attributed to a combination of nutrient depletion, the build-up of soil-borne pathogens and the release of allelopathic compounds from the crops directly or via their residue. In modern agriculture, nutrients are likely to play a secondary role, due to high fertilisation rates (Cesarano et al. 2017; Kumar et al. 2017). Soil pathogens and autotoxic chemicals released from the crop can play important individual and interactive roles in driving soil sickness (Huang et al. 2013). However, emerging evidence suggests soil biota and autotoxicity caused by litter (i.e., crop residues) cannot fully explain soil sickness, with self-DNA (i.e., the DNA of the same species that remains in the environment after decomposition) being proposed as an additional driving mechanism (Cesarano et al. 2017; Mazzoleni et al. 2015a) (see section on self-DNA). Given that the underpinning mechanisms behind soil sickness and PSF are the same, recent calls have emerged to better integrate these concepts (Cesarano et al. 2017; Mariotte et al. 2018). Creating cross-discipline knowledge exchange offers opportunities to better understand and manage natural and agricultural ecosystems.

Janzen-Connell hypothesis

In the 1970's, Daniël Janzen and Joseph Connell developed, in parallel, a theory to help explain tropical tree diversity distribution (Connell 1971; Janzen 1970). Specifically, they observed that host-specific herbivores and pathogens make the areas near a parent tree inhospitable for the survival of conspecific seedlings. These herbivores and pathogens were named "distance-responsive predators" if they kill seeds or seedlings near the parent tree or "density-dependent predators" if they kill seeds or seedlings where a particular species was most abundant (typically near the parent tree). These negative distance and density dependence effects are widespread in lowland tropical rainforests (Comita et al. 2010; Harms et al. 2000; Metz et al. 2010). Such effects can prevent any one tree species from dominating the landscape, because if that species is too common, there will be fewer safe places for its seedlings to survive. However, since these natural enemies are host-specific, they will not harm other tree species. As a result, if a species becomes very rare, then more enemy-free areas will become available, giving that species' seedlings a competitive advantage. This negative feedback allows tree species to coexist and provides a partial explanation for the high levels of biodiversity in tropical rainforests (Terborgh 2012; Wright 2002). This mechanism is also at play across different ecosystems (Comita et al. 2014) such as grasslands (Petermann et al. 2008), temperate forests (Deniau et al. 2018; Packer and Clay 2000; Ramage et al. 2017; Seiwa et al. 2019; Yao et al. 2020) and savannahs (Rutten et al. 2016). Conversely, host-specific mutualists can increase the abundance of a particular host species, hence reducing community diversity, in line with the mutualistic effects seen in positive PSF, thereby comprising a "reverse Janzen-Connell effect" (Connell and Lowman 1989; Zahra et al. 2021). The Janzen-Connell hypothesis is essentially a PSF process except in cases when aboveground herbivory is the main driver (Norghauer et al. 2016).

Although the importance of soil-borne pathogens are one mechanism behind the Janzen-Connell hypothesis (Bagchi et al. 2010; Bell et al. 2006; Laliberté et al. 2015), it is not fully known which microorganisms are responsible for this strong negative PSF. Thus far, oomycete pathogens (e.g., *Phytophthora*, *Pythium* (Pringsheim)) are suggested to be important causal agents of negative distance- and density-dependent seedling mortality in species-rich tropical rainforests (Bell et al. 2006; Du et al. 2017; Harms et al. 2000) and temperate forests (Comita et al. 2014; Ramage et al. 2017), but perhaps not in Mediterranean woodlands (Teste and Laliberté

2021). Although oomycete-driven mortality of seedlings in Mediterranean woodland was found regardless of proximity to conspecific trees, short-term seedling recruitment patterns in fire-prone ecosystems did not follow the Janzen-Connell hypothesis, with positive density-dependent survival occurring under conspecific trees (Teste and Laliberté 2021). Instead, the seedlings may have benefited from more nutrient-rich litter under conspecific versus heterospecific trees, have been facilitated under conspecific trees via increased nutrients or have been more negatively affected by generalist soil fungal pathogens found away from conspecific trees.

The role of plant-soil feedback in plant invasion

Soil-driven mechanisms are involved in making plant communities more resistant or vulnerable to non-native plant species invasion, with PSF featuring as the underlying mechanism (Dawson and Schrama 2016; Klironomos 2002; Levine et al. 2006). Soil chemical properties can explain invasions and could be considered a component of PSF (Slesak et al. 2022). Recent reviews point to large variation in the effects non-native invasive species have on soil properties (Lee et al. 2017; Lone et al. 2019; Xu et al. 2022). Native species can (but not always) develop soil microbial communities that suppress the growth of non-native species, while soils modified under non-native species tend to benefit recruitment of their own seedlings (Perkins and Nowak 2013; Reinhart and Callaway 2006). However, relationships between non-natives and soil properties are not straightforward. Studies have explicitly used PSF to demonstrate that invasive plants can escape specific soil pathogens from their native range, leading to increased invasibility in the introduced range (Aldorfová et al. 2021; Reinhart et al. 2003); a phenomenon known as The Enemy Release Hypothesis (Keane and Crawley 2002). However, competition between invaders can interact with soil conditioning to generate idiosyncratic release responses from above- and belowground herbivores (Lucero et al. 2020). This finding puts focus on the importance of including multiple drivers (in this case, competition and herbivory) in order to fully understand PSF effects.

Invasive plants can impact on soil biota and physiochemical properties interactively, leading to PSF effects. Invasive plants can affect soil biota via litter and rhizosphere inputs and, with time, support greater abundances of soil decomposers that stimulate nutrient release (Zhang et al. 2019). As a result of these litter or rhizosphere loops, positive feedbacks can develop, which then can facilitate more invasion (Zhang et al. 2019). However, consideration of other interactions is needed. For example, chemical compounds (e.g., allelopathic) released by invasive plants can promote considerable shifts in soil bacteria, that then impact on nutrient cycling, enzymatic activity, mineralization, soil carbon and nitrogen content (Torres et al. 2021).

It is becoming clearer that the important role of PSF in plant invasion is context- and temporally-dependent. For example, the study of Slesak et al. (2022) on Scotch broom (*Cytisus scoparius* L.) suggests strong context-dependency since the effects of Scotch broom on soil physiochemical properties were more pronounced in less fertile sites. In this case, identifying context-dependency of the effects of plant invasion on PSF can help focus management efforts on removing Scotch broom from low-quality sites first. Other studies have demonstrated the role of biotic interactions in regulating early invasion processes at the root level. For example, native tree species (*Quercus acutissima* Carruth.) can create a negative PSF against non-native invading plants, likely due to the production of allelopathic litter and a distinct soil microbial community (Chen et al. 2021). These interactions were also noted to be context-dependent, in this case the production of allelopathic compounds depended on the degree of landscape openness. The context of competitive interactions can also affect the end result of invasion. For example, the invasive legume, *Lespedeza cuneata* (Dum.Cours), benefited from positive PSF effects when interspecific competition was mostly absent, but when root competition from native species was present, PSF effects were neutralized (Crawford and Knight 2017). There is also evidence that positive PSF wanes over time as more generalist soil-borne pathogens colonize the non-native-conditioned soil (Gruntman et al. 2017).

We require more long-term tests or assessments of the ongoing role of PSF (i.e., soil legacy effects; see next section) after non-native plant removal has been done by land managers. Recent work suggests the importance of removing non-native plant invaders rapidly during the establishment phase (Chen et al. 2021; de la Peña et al. 2010; Slesak et al. 2022). The strength, direction, context dependency and temporal stability of invasion-related PSF, as well as the biological, chemical, and physical mechanisms behind them, must be taken into account after non-native plant removal to better inform restoration efforts.

Soil legacy effects

The broad definition of soil legacy considers any event that leaves an influence or "legacy" in the soil that can have subsequent impacts on anything occurring in or on that soil. Drivers of soil legacies can be of anthropogenic or natural origin. The effects they generate can change both abiotic and biotic soil properties and, resultantly, may be directly responsible for PSF or indirectly by initiating alternative plant community developmental trajectories. All soil legacies may not technically be a form of PSF. For example, mine tailings (i.e., the waste soils and substrates of metal and mineral extraction) can leave a legacy of toxic elements (e.g., arsenic, lead, nickel, zinc), extremes in pH and poor water infiltration, creating soils that are ruined for agricultural use and poisonous to a plethora of organisms (Kossoff et al. 2014; Xu et al. 2019). Agricultural practices can leave soil legacies leading to knock-on effects for the plant community and how PSF operates. Nonetheless, in many instances, the term soil legacy is used in place of PSF. Numerous examples exist (Cong et al. 2015; De Long et al. 2019b; Heinen et al. 2020b; Nsikani et al. 2017). Gathering literature on soil legacies and bringing it into the main sphere of PSF studies is essential. Including search terms such as "soil legacy" in meta-analyses on PSF is one way that this can be accomplished.

Soil-associated allelopathy

Allelopathy is a biological phenomenon by which one organism has harmful effects on the growth of surrounding organisms, through the production of secondary metabolites (i.e., allelochemicals) (Whittaker and Feeny 1971). Such effects have been explicitly studied in plants, and their role in PSF is becoming more appreciated (Latif et al. 2017). However, allelopathy clearly has an important role in intergenerational plant performance, which makes it an important component of PSF. Allelopathic effects are usually the direct result of plant chemical impacts (Weston and Duke 2003), but can also be generated directly or interactively via microbes (Cipollini et al. 2012; Inderjit 2005). For example, allelopathic compounds may selectively inhibit certain species of mycorrhizal fungi, with consequences for plant species dominance and overall community composition. Chemical transport via common mycorrhizal hyphal networks allows for systemic defence signalling across plant populations and directed allelochemical delivery to target plants (Achatz and Rillig 2014; Barto et al. 2012; Gorzelak et al. 2015). This process is mainly known from ectomycorrhizal networks where plants can warn each other of herbivore attacks or other potential threats (Delaux 2017; Souto et al. 2000). However, arbuscular mycorrhizal fungi are also able to perform this function and even saprobic or parasitic fungi might have the ability to pass allelochemicals through their hyphae (Barto et al. 2012). In plant-fungus mutualistic interactions, the fungus can benefit if adjacent plants are warned of potential threats and therefore remain healthy, allowing them to continue providing resources for the fungus. In recent years, research on the mechanisms associated with allelopathic interactions has increased exponentially (Zhang et al. 2021). In particular, allelopathic mechanisms play a large role in explaining PSF associated with plant invasiveness (Callaway and Ridenour 2004; Hierro and Callaway 2003; Lankau et al. 2009). Further, the rise of *-omics* techniques has allowed us to unravel the identity of the secondary metabolites involved in these PSF interactions (Scognamiglio et al. 2015). Allelopathy is one of the mechanisms that may lead to soil sickness (Huang et al. 2013) (see section above for further details), but it can also play a beneficial feedback role in agricultural systems by promoting weed suppression (Birkett et al. 2001; Mariotte et al. 2018). Moreover, certain chemical compounds produced by plant roots such as strigolactones can attract mycorrhizal fungi, but also inhibit stem division and even attract parasitic plants such as broomrape (*Orobanche* spp. L.) (Bouwmeester et al. 2021). Such chemical compounds could result in PSF if they remain active in the soil over longer periods. Collectively, allelochemicals can play a pivotal role in PSF, even though their effects are not always specifically categorized as such.

Primary and secondary plant community succession

Primary and secondary succession of terrestrial plant communities occurs when plants colonise the land after the formation of a new substrate or a significant disturbance event occurs in a pre-existing ecosystem, respectively. Over time, plant community composition changes, generally as a result of the effects the plants have on themselves and each other, as well as their interactions with the wider environment. Changes to the plant community typically occur in concert with changes in soil abiotic and/or biotic properties (Bardgett and Wardle 2010; Peltzer et al. 2010; Walker et al. 2010). By definition, these concomitant changes in the soil and the plant community fit within the PSF framework (Jiang et al. 2010; Kardol et al. 2013a). Studies investigating PSF dynamics during secondary succession show that negative feedbacks typically occur during early stages, which facilitates species turnover, and neutral or positive feedbacks in later stages that promote plant community stability (Bauer et al. 2015; Jing et al. 2015; Kardol et al. 2006; Koziol and Bever 2015; Kulmatiski et al. 2008). Some examples include studies on secondary succession after agricultural abandonment (Kardol et al. 2006), restoration of tallgrass prairies (Bauer et al. 2015), mine site remediation (Orozco-Aceves et al. 2015) and shifts from a tree- to a shrub-dominated ecosystem following pest-induced tree mortality (Pfennigwerth et al. 2018). The drivers of PSF among most of these examples are linked with soil microorganisms, in particular, mycorrhizal and pathogenic fungi (Bauer et al. 2015; Kardol et al. 2006; Pfennigwerth et al. 2018). Types of secondary succession may vary depending on the ecosystem age or form(s) of disturbance. This can lead to disparities in strength and/or direction of PSF effects (Kardol et al. 2022; van de Voorde et al. 2011) and interactions with other factors (e.g., herbivory, water or nutrient availability, climate) that may override the feedback effects (de la Peña et al. 2016; Dietterich et al. 2019; Heinze and Joshi 2018; Yelenik and Levine 2011).

By contrast, primary succession involves a predictable shift from nitrogen to phosphorus limitation, which may strongly favour plant species of certain nutrient-acquisition strategies at each successional stage (Laliberté et al. 2013; Lambers et al. 2008; Peltzer et al. 2010; Walker et al. 2010). This could hypothetically render PSF more predictable during primary versus secondary succession (Cortois et al. 2016; Kardol et al. 2013a). For example, during early stages of primary succession, negative abiotic PSF, due to soil conditioning by pioneer symbiotic nitrogen-fixing plants, is expected to promote the growth and establishment of non-nitrogen-fixing plants in nitrogen-poor soil (Chapin et al. 1994; Png et al. 2019; Titus and del Moral 1998). Increased N fixation early on in succession can also be induced by invasive species (e.g., *Myrica faya* Ait.), which could have repercussions for subsequent plant community development (Vitousek et al. 1987). On the other hand, owing to a conspecific negative density dependence mechanism assumed in the Janzen-Connell hypothesis (see section above), negative biotic PSF is expected to become more important in primary late-successional ecosystems, thereby promoting species coexistence (Bever et al. 2015; Kardol et al. 2013a; Laliberté et al. 2015).

However, studies examining PSF of plant communities during early- and late primary succession revealed unpredictable effects. For example, negative abiotic and biotic PSF was found to be important during very early stages of sand dune ecosystem development (van der Putten et al. 1993). Furthermore, Castle et al. (2016), Teste et al. (2017), Png et al. (2019) and Trevenen et al. (2022) showed that negative PSF was not predominant during late primary succession of plant communities in glacial forefield and costal dune ecosystems, and that positive and neutral PSF were also commonly detected. The uncertainties of how the type and direction of feedback effects may present or shift during succession encumbers our ability to utilise PSF as a management tool to predict and steer successional trajectories. Experimental designs should consider the use of field-conditioned soil for *ex situ* greenhouse studies or the use of phytometer plants in situ, which can incorporate a greater range of “latent” effects (De Long et al. 2018, 2019a). Overall, most literature (see references mentioned above in this subsection) on plant community succession does not explicitly consider the soil-mediated turnover effects to be PSF, despite that these effects play a pivotal role in shifts in plant community composition. However,

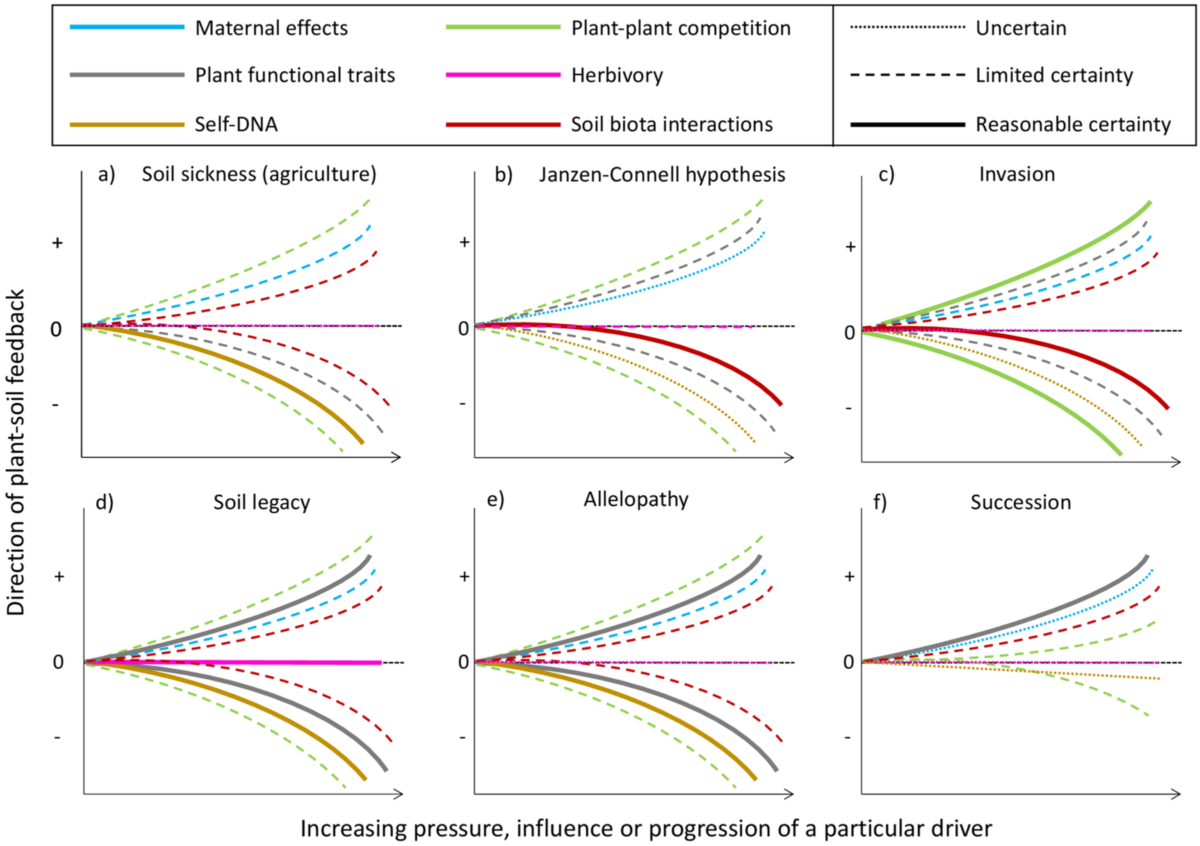


Fig. 2 Conceptual diagram showing how different intrinsic (i.e., maternal effects, plant functional traits and self-DNA) and extrinsic (i.e., plant-plant competition, herbivory and soil biota interactions) biotic drivers could be shaping plant-soil feedback (PSF) within the different research areas that are actually PSF but have been called by an alias in the literature. The x-axis shows the increasing pressure, influence or progression of a particular driver, while the y-axis shows the direction of feedback and its increasing or decreasing strength. Certain drivers have the capacity to shift the direction of PSF towards either positive or negative, depending on the context. Predictions are made based on the current knowledge body, as reviewed in the text. Relative certainty of the predictions based upon available evidence is indicated by a gradient of certainty, with solid, dashed and dotted lines indicating reasonable certainty, limited certainty and uncertainty, respectively. Note: there are many exceptions to the predictions here and this figure is not meant to be a definitive predictor of how drivers influence PSF under these circumstances. Rather, this figure is meant to provide the best possible predictions based on state of the art knowledge and stimulate further research to test these hypotheses

the increasing body of literature on PSF and succession demonstrates the benefits of continuing to integrate PSF into understanding soil-mediated turnover effects in plant succession.

Conclusions and future directions

Given the aforementioned knowledge gaps, it is evident that deeper, holistic experiments and meta-analyses are needed in order for substantial gains in PSF research to be realised. We hope that the papers presented here in this Special Issue on Plant-Soil Feedback (S98) will inspire others in PSF research and tangential fields to build upon these results and suggestions. It is important to point out that the topics covered here are not an exhaustive review of the facets and drivers involved in PSF, but here we covered what we consider to be some of the most pressing future research directions, based on what has been emerging in the literature and basic knowledge about drivers of plant-soil interactions. For example, other phenomenon such as hydraulic lift (Horton and Hart 1998), nurse plant facilitation (Di Bella et al.

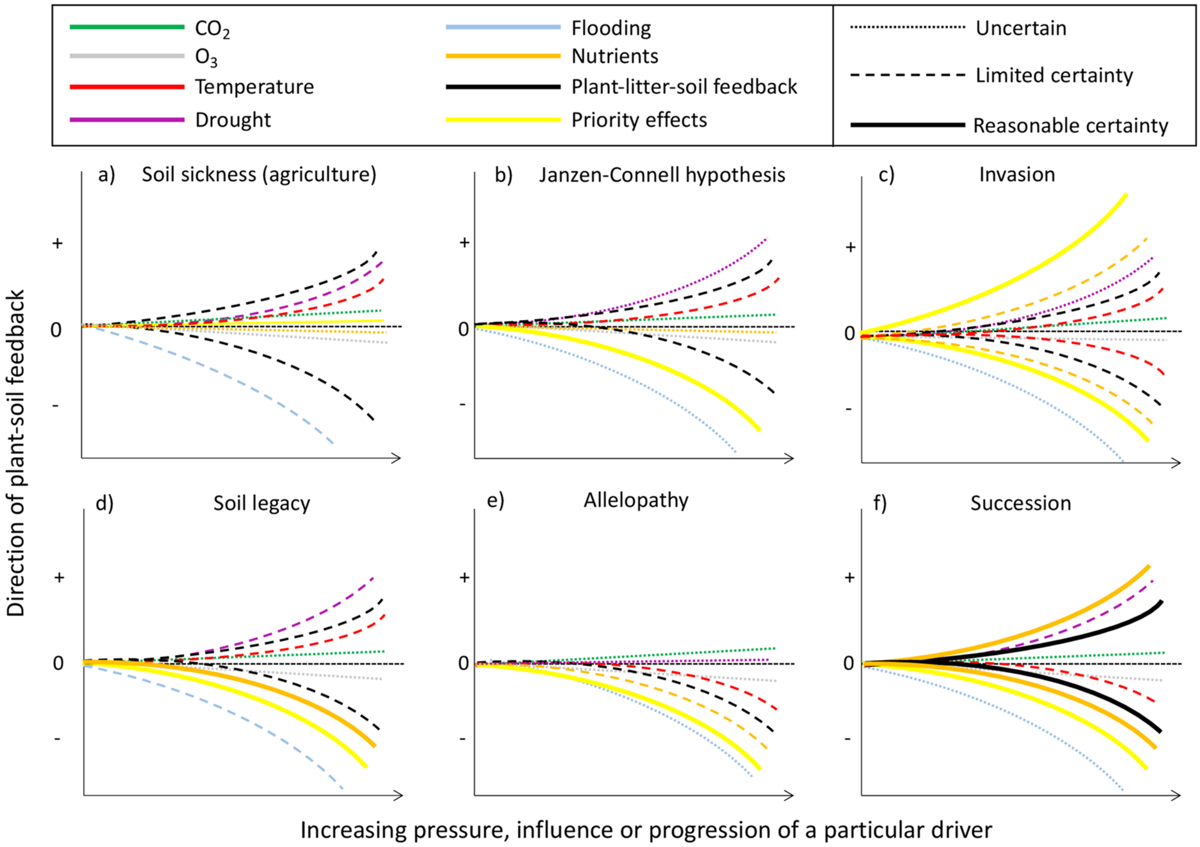


Fig. 3 Conceptual diagram showing how different extrinsic abiotic drivers (i.e., CO_2, O_3, temperature, drought, flooding, nutrients) and extrinsic drivers that can be both abiotic and biotic (i.e., plant-litter-soil feedbacks and priority effects) could be shaping plant-soil feedback (PSF) within the different research areas that are actually PSF but have been called by an alias in the literature. The x-axis shows the increasing pressure, influence or progression of a particular driver, while the y-axis shows the direction of feedback and its increasing or decreasing strength. Certain drivers have the capacity to shift the direction of PSF towards either positive or negative, depending on the context. Predictions are made based on the current knowledge body, as reviewed in the text. Relative certainty of the predictions based upon available evidence is indicated by a gradient of certainty, with solid, dashed and dotted lines indicating reasonable certainty, limited certainty and uncertainty, respectively. Note: there are many exceptions to the predictions here and this figure is not meant to be a definitive predictor of how drivers influence PSF under these circumstances. Rather, this figure is meant to provide the best possible predictions based on state of the art knowledge and stimulate further research to test these hypotheses

2019; Gómez-Aparicio et al. 2004) and resource islands (Garcia et al. 2018) no doubt play roles in PSF, but remain understudied. Fully integrating the drivers and PSF going by an alias that are discussed here is one of the next crucial steps. Making certain predictions as to the outcomes of these interactions is possible in some cases (Figs. 2 and 3), but sufficient knowledge is currently lacking in other cases. Bidirectional relationships also exist between external drivers and PSF (Fig. 4). For example, PSF can affect herbivore performance, (Heinen et al. 2018), which could change herbivore population dynamics and, in turn, further influence PSF as the next generation of herbivores consumes plant tissue and generates another round of feedbacks. Floral traits and fecundity can be driven by PSF (Jiao et al. 2021), possibly leading to long-terms shifts in plant population and community composition, resulting eventually in different PSF. Future work needs to consider the continual reciprocal feedback between the extrinsic environment, the intrinsic environment of the plant itself and the soil.

Plant-soil feedback research has been on a developmental trajectory that has sought to include

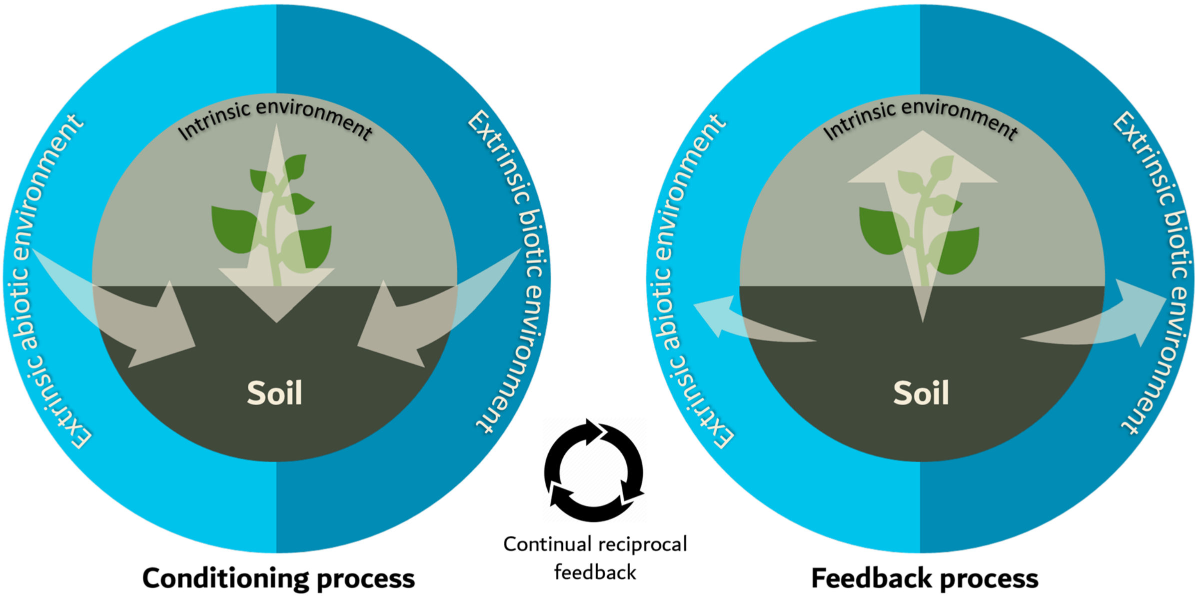


Fig. 4 Conceptual diagram showing how the extrinsic abiotic (e.g., CO_2, O_3, temperature, drought, flooding, nutrients, plant-litter-soil feedbacks and priority effects) and biotic (e.g., plant-plant competition, herbivory, soil biota interactions, plant-litter-soil feedbacks and priority effects) environments, as well as the intrinsic biotic environment (e.g., maternal effects, plant functional traits and self-DNA) affect the soil during the conditioning process. During the feedback process, the soil affects the extrinsic and intrinsic environments, resulting in a continual reciprocal feedback between environmental drivers, the soil and the plant. Future work on plant-soil feedback should consider these continual reciprocal feedback relationships. The size of the arrows indicates hypothesized relative strength of effect of a particular environmental driver

ever-increasing levels of complexity in order to better reflect how PSF operates in natural ecosystems. The first reviews on PSF called for studies outside of the greenhouse (Kulmatiski and Kardol 2008). This led to reviews and opinion pieces that highlighted context-dependency (Smith-Ramesh and Reynolds 2017), proposed frameworks to use PSF (i.e., the soil microbiome) to suppress aboveground insect herbivory (Pineda et al. 2017), encouraged merging fundamental and agricultural PSF research lines (Mariotte et al. 2018) and examined the role of temporal PSF dynamics in controlling plant community diversity (Thakur et al. 2021). Still others have pulled focus on the necessity of selecting the best soil sampling designs to answer specific questions (Allen et al. 2021; Gundale et al. 2019; Reinhart and Rinella 2016; Rinella and Reinhart 2017) and the importance of including environmental influencers such as temperature, soil moisture, aboveground herbivory and belowground interactions (De Long et al. 2018). Progress is being made to explore the influences of such external drivers, as demonstrated by a recent meta-analysis that showed specific types of competition (e.g., interspecific competition in heterospecific soils) can enhance negative PSF, while specific environmental stressors (i.e., drought) can bolster positive microbial effects (Beals et al. 2020). Another meta-analysis solidified the importance of PSF for plant coexistence, citing microbial communities (i.e., pathogens, mycorrhizae) and phylogenetic distance as some of the primary mechanisms behind pair-wise PSF (Crawford et al. 2019). Additional drivers with strong impacts on PSF will continue to emerge in the literature. For example, soil acidification can drive increases in root biomass and inhibit its subsequent decomposition (Wang et al. 2020), leading to possible consequences not only for soil carbon storage, but shifts in plant community composition. No doubt additional avenues of interest in PSF studies will continue to emerge, highlighting the need for collaborative efforts and knowledge exchange between researchers across the globe.

Ultimately, once substantial knowledge has been amassed, it will become possible to begin modelling landscape-wide patterns (Caruso and Rillig n.d.; Collins et al. 2020; Ke and Levine 2021; Mack et al. 2019). Such modelling could be used to predict when and where PSF is most important, particularly when disturbances (e.g., fire, climate, plant pathogens, anthropogenic) alter ecosystem processes. Next, steering PSF might become possible. Due to the continuous reciprocal process of plants influencing soil abiotic and biotic properties and soil properties influencing plants (Fig. 4), several possible routes exist for steering PSF: (1) Direct transplantation of soil with "healthy" microbiomes, analogous with "faecal transplants" in human guts from healthy individuals (Wubs et al. 2016; Yergeau et al. 2015); (2) Spreading of seeds and plant particles which introduces both the plant community as well as the associated plant microbiome (Elzenga et al. 2019); (3) shifting soil biotic communities by planting plant species that might alter the microbial and soil animal communities via their exudates (Clocchiatti et al. 2021; Vieira et al. 2020); (4) shaping soil communities by introducing litter or amendments (ranging from simple sugars to crop residues to manure) (Clocchiatti et al. 2020; Docherty and Gutknecht 2019; Reardon and Wuest 2016); and 5) adjusting agricultural systems in order to minimize negative PSF (Seipel et al. 2019). Various combinations of the above-listed methods can also be employed (Wubs et al. 2019). Steering of PSF can be a valuable tool in a nature restoration context (Moreno-Mateos et al. 2020; Morriën et al. 2017), facilitate soil nutrient retention (Mariotte et al. 2018) and sequester carbon (Bergmann et al. 2016; Hannula and Morriën 2022). No doubt the years to come will continue to see a massive explosion in PSF research, as numerous outstanding questions remain (Box 1). It is imperative that developing lines of research consider the underexplored, interrelated topics discussed above, as well as those that have been proposed by others, and make a concerted effort to include other areas of research that are actually PSF going by an alias. Essentially a "whole ecosystem approach" should be undertaken. Such an approach will further our understanding of the role PSF plays within ecosystem processes.

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Data availability This manuscript contains no data.

Declarations

Competing interests The authors declare no competing interests of any nature.

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