Multi-dimensionality as a path forward in plant-soil feedback research

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Abstract

1. Feedback between plants and their associated soil biota is an important driver of plant distribution, abundance and community composition with consequences for ecosystem functioning. The field of plant-soil feedback (PSF) research has become an integral subdiscipline of terrestrial ecosystem ecology, and in recent decades has rapidly evolved by deepening and broadening its scope.

2. We review the major developments in the field, discuss methodological considerations and present a way forward for new approaches to PSF research that will lead to a more generalized and predictive understanding of PSFs. We illustrate that the field of PSF research has pursued multiple dimensions, including temporal scales, biogeographic perspectives, environmental context and the level of biological resolution.

3. Plant-soil feedbacks have been related to successional species turnover, but our inferences are often constrained by experimental time-scales, and anthropogenic impacts can alter or disrupt the temporal interactions between plants and soil biota. Plant-soil feedbacks also have been used to explain spatial patterns of plant recruitment, coexistence and diversity, and have increasingly been linked to the patterns of spread and abundance of non-native and invasive plants.

4. In recent years, more consideration also has been given to the sensitivity of PSF to environmental context, in particularly to gradients of resource availability and changing climatic conditions (including extreme events). Here, of particular interest are the differential responses of mutualistic and antagonistic soil biota. How plants interact with different groups of soil biota has further been predicted from species' phylogenetic relatedness and increasingly also from plant chemical and morphological shoot, root and litter traits.

5. Synthesis. In moving the field forward, future PSF research should take a multidimensional approach by explicitly considering cross-connections between dimensions, including, for example, spatio-temporal variation in resource availability, and trait–environment relationships across taxonomic and functional groups of plants.
INTRODUCTION

The interactions between plants, soils and soil biota have been studied for centuries, initially mostly from an agricultural or forestry perspective, but more recently also from a more fundamental and theoretical ecology perspective (Kulmatiski et al., 2008; Mariotte et al., 2018; van der Putten et al., 2013). These studies have focused, one way or another, on how plants influence soil chemical, physical and biological properties, and how these plant effects on soil properties in turn influence plant performance. About 50 years ago, Janzen (1970) and Connell (1970) proposed the idea that plant density and coexistence patterns could be explained by negative effects of host-specific seed predators and herbivores on the establishment of conspecific seedlings in the vicinity of adult trees. In the late 1970s and more so in the 1980s, this principle of self-intolerance was then explicitly extended to soil pathogens and root herbivores (Augspurger & Kelly, 1984; van der Putten et al., 1988) which paved the way for more formal testing of reciprocal plant-soil interactions. This resulted in the development of a recognized field of research focused on ‘plant-soil feedbacks’ (PSFs; Bever, 1994). This field of research studies how plants affect soil properties and how the resultant changes in soil properties in turn affect the performance of plants from the same species (i.e. conspecific feedbacks) or plants from other species (i.e. heterospecific feedbacks).

Under the umbrella of ‘PSF’ research, most studies have experimentally separated feedbacks operating through physicochemical soil properties versus feedbacks operating through biological soil properties, and in many cases have explicitly tested for so-called biotic PSFs, which are effects mediated through plant-associated communities of soil microbes and fauna, including root pathogens, mutualists and litter decomposers (van der Putten et al., 2013). This specific focus can be traced back to a small number of early milestone studies and the methodology these studies employed (Bever, 1994; van der Putten et al., 1993; indicated by the horse and buggy in Figure 1).

From a cobble stone road to a high speed rail system: accelerating towards a more predictive framework for plant-soil feedbacks

FIGURE 1 Accelerating the development of plant-soil feedback research. The horse and buggy represent seminal early studies that founded and shaped the plant-soil feedback (PSF) research field mostly by running short-term experiments under controlled conditions testing conspecific and heterospecific feedbacks. These early studies informed on the role of PSF in local community dynamics, laying the foundation for new branches of PSF to develop, first by focusing on succession covering broader temporal scales. Later (during the past two decades), the field of PSF research rapidly accelerated and broadened, by adopting ideas from other fields of research: spatial ecology, environmental biology, functional ecology, taxonomy and phylogeny (indicated by the coloured lines). These fields of PSF research are accelerating rapidly, which has been aided by some methodological advances. For future PSF research, we foresee greater multidimensionality in research focus (i.e. addressing cross-connections between dimensions) which will lead the research field to a higher level of generality.
Since these early studies, PSF studies typically consist of two phases: (a) a soil conditioning or training phase where plants ‘condition’ their associated soils, either in the field or in a greenhouse setting, and (b) a test phase where plants are grown on soil conditioned by the same or by other species. In this test phase, researchers commonly use soil sterilization and re-inoculation procedures to tease apart the abiotic and biotic feedback pathways. Then, multiple metrics have been developed and applied to calculate feedback values based on plant biomass on ‘conspecific’ versus ‘heterospecific’ or ‘own’ versus ‘foreign’ or ‘home’ versus ‘away’ soils (Bates et al., 2020; Brinkman et al., 2010; van der Putten et al., 2013).

Since the 1990s, research into PSFs using these types of approaches has increased exponentially (Crawford et al., 2019; Lekberg et al., 2018; Mariotte et al., 2018; van der Putten et al., 2013), and the PSF concept and methodological approach have been applied to a wide range of research questions. While the original studies mainly tested for heterospecific or conspecific feedbacks within local communities at a given point in time, their findings had obvious implications for understanding the organization of plant communities across broader spatial and temporal scales. As such, PSF research quickly picked up speed, expanded in scale and began to explore a greater range of ecological dimensions (Figure 1, multicoloured lines). For example, studies began to explicitly test the implications of PSF on vegetation dynamics across successional stages (De Deyn et al., 2003; Kardol et al., 2006). Plant-soil feedback research also began to explore a broader spatial dimension (Ollff et al., 2000). This has included PSF research addressing the Janzen–Connell hypothesis, the success of some invasive and range-expanding plants (Hierro et al., 2005; Klironomos, 2002; van der Putten et al., 2016), as well as the responses of plant and soil communities to abiotic properties across space and time (i.e. environmental context; De Long, Fry, et al., 2019; Pugnaire et al., 2019; Smith-Ramesh & Reynolds, 2017; van der Putten et al., 2016). Further, while initial research was focused at the species level within local communities, research since has explored a broader breadth of biological organization, including at the subspecies scale where PSFs have been compared among contrasting genotypes (Felker-Quinn et al., 2011; Lankau et al., 2011; Van Nuland et al., 2017), as well as coarser scales, where PSFs have been evaluated across functional groupings or spectra of plant species (Bezemer et al., 2006; van de Voorde et al., 2011).

This brings us to the present, where formal, two-phase PSF studies are being published at a rapidly increasing rate (multicoloured lines leading to the bullet train in Figure 1). In this review, we describe four primary dimensions that PSF research has followed in recent years, including time, space, environmental context and biological resolution. Each of these fields of PSF research has been prolific in their own right, and have given us a much better understanding of how PSFs impact plant communities and vice versa; however, we still have a long way to go in order to achieve a more generalized understanding regarding where and when PSFs are important. We highlight that relatively little PSF research to date has attempted to cross these primary dimensions. Recent work has already broken new ground in moving beyond uni-dimensional approaches, and we propose that many future breakthroughs in PSF will involve more explicit consideration of a greater range of cross-connections among these primary dimensions (i.e. multidimensional PSF research, depicted by the bullet train in Figure 1), which will require new methodological and conceptual considerations. We propose that following a more multidimensional research approach will lead to greater generality of our understanding of when and where PSFs are likely to matter.

2 | TEMPORAL PERSPECTIVES ON PLANT-SOIL FEEDBACKS

From the onset of this field of research, PSFs have been studied to understand the patterns of temporal species turnover, first in the context of primary succession (van der Putten et al., 1993) but later also in the context of secondary succession (e.g. Kardol et al., 2007; Koziol & Bever, 2019). Here, negative feedbacks accelerate the rate of succession, while positive feedbacks slow the rates down (Kardol et al., 2006). It has been shown that early successional plant species are often particularly sensitive to the build-up of soil pathogens and root herbivores, accelerating their replacement by later successional species. Even though PSF experiments typically only capture short-term, transient dynamics, these studies have suggested that PSFs may cause plant community composition to diverge, at least temporally (Kardol et al., 2007). In linking PSFs to successional shifts in plant species composition, most studies have focused on feedbacks with root-associated soil biota. However, recent work has also emphasized the role of plant shoot and root litter as drivers of PSFs and as mediators of feedbacks with root-associated microbes (Laughlin et al., 2015; Keller & Phillips, 2019; Manrubia et al., 2020; Veen et al., 2019; Zhang et al., 2016). Litter-mediated PSFs may act on different time-scales than feedbacks with root-associated soil biota, and could thus further and for longer influence plant successional trajectories. At larger time-scales, the complex temporal dynamics of conspecific and heterospecific PSF events may maintain plant community diversity (Teste et al., 2017) or delay community convergence (Fukami & Nakajima, 2013) rather than change the direction of the trajectory.

In recent years, temporal dynamics in ecology have gained traction in understanding biotic interactions across time-scales (Rigal et al., 2020; Ryo et al., 2019; Wolkovich et al., 2014; Yang, 2020), and this development has important ramifications for how we position current and future PSF research. In relating PSFs to community succession (as discussed above), ecologists are increasingly aware that PSF experiments should address time-scales relevant to species dispersal and colonization, life-history strategy and after-life effects. But, there are many other time-scales also relevant for the study of PSFs that could give direction to future research in this field (Figure 2). Long-term evolutionary processes have shaped how organisms are adapted to their environment, including co-evolution between plants and soil biota (Govaert et al., 2019). New evidence shows that evolution across angiosperm species shapes the root
microbiome (Fitzpatrick et al., 2018). This sets the stage for the species acting in our experiments, that is, the traits and trait plasticity of plants and soil biota driving their reciprocal interactions. The design and experimental time-scales of most PSF studies, however, strongly constrain the scope of our inferences regarding the evolutionary basis of plant-soil organism relationships but also regarding the role of longer term soil legacies. For example, plant species responses to the soil community depend on how preceding plant species have changed the soil community (Bezemer et al., 2018; Wubs & Bezemer, 2018b) and on how environmental conditions have changed along the way (Figure 2).

Plant-soil feedback experiments test how plants respond to changes in soil properties resulting from previous presence of conspecific or heterospecific individuals (see ‘two-phase approach’ above). When neutral or common soils are conditioned in the greenhouse, the duration of the conditioning phase is often relatively short (Lepinay et al., 2018), typically shorter than a plant’s full life cycle. As plant effects on soil biota and soil abiotic properties vary with plant life stage (Chaparro et al., 2014; Dinnage et al., 2019), the short duration of the conditioning phase set by experimental constraints can result in erroneous estimation of the true feedback strength. Although confounding factors may come into play, soil conditioning in the field allows longer conditioning times, bridging experimental time-scales and more realistic successional time-scales (Figure 2).

For planted forests and cropping systems, conditioning times can be precisely set, but for natural ecosystems conditioning times by specific species are often unknown; but, see Ke et al. (in press) for a novel approach using high-resolution aerial photos. Similarly, the strength of PSF can depend on the length of the response phase, that is, plant age and ontological stage (Bezemer et al., 2018; Kardol et al., 2013). Moreover, PSFs in natural ecosystems are more complex and less predictable than most two-phase experiments suggest, as plants can leave soil legacies that persist beyond (Wubs & Bezemer, 2018b) and well beyond the plant’s life span (Heinen et al., 2020).

Finally, anthropogenic climate change and other human activities alter the temporal interactions between plants and soil biota (De Long, Fry, et al., 2019; van der Putten et al., 2016; Figure 2). Plants and soil biota experience time differently, and therefore changes in temporal climatic variability and the frequency of climatic extremes can alter the relationship between driver and responder in PSF relationships, which could slow down, speed up or redirect PSFs. For example, longer growing seasons may disrupt ‘synchronized’ plant-soil biota dynamics as within-year and across-year life cycle seasonality differ between plants and soil biota. Shifts in the phenologies of interacting species may lead to shifts in their synchrony (Kharouba et al., 2018; Rudolf, 2018). In the short term, plants can show phenological responses to altered seasonal events, while within the same time frame soil communities may not only change

**FIGURE 2** Conceptual diagram depicting four different time-scales that each are relevant to testing, understanding and predicting conspecific and heterospecific plant-soil feedbacks (PSFs). Examples are given (in italics) of why and how each of the time-scales is relevant. Relationships between plants and soil biota shaped by evolution, or soil legacies resulting from previous plant communities determine ‘what was before’, that is, the local pools of species and their traits and trait relationships. Our actual measurements of PSFs (centre box) are strongly dependent on experimental time-scales which do not always align with the life cycles and population dynamics of the plants and soil biota under study. Longer, successional time-scales are important in making inferences on ‘what comes next’, that is, how do PSFs influence plant species turnover or larger scale biogeochemical processes? Many previous PSF studies have explicitly or implicitly focused on successional time-scales. In recent years, increased emphasis has been put on the role of current and future-predicted anthropogenic influences on PSFs, for example by testing the effects of global change factors on the strength of feedback through shifts in organismal activity and community dynamics. We argue that in moving the field of PSF research forward it is important to explicitly consider the different time-scales at which the relevant processes occur, that is, look both backward and forward. The illustration of the successional time-scales is adapted from an original drawing by Greg Crutsinger.
their phenology but also population size or turn over community composition (Hannula et al., 2019; Lauber et al., 2013). Further, over time, changing environmental conditions and accumulative effects of increased frequencies of occurrence of extreme events (drought, heatwaves) may push plant and soil communities across tipping points that are irreversible through positive feedback loops. However, the time points at which thresholds and tipping would be crossed differ between plant and soil communities as soil organisms may have wider tolerance ranges for extreme climatic conditions. This challenges the predictions of long-term consequences of environmental change on PSFs.

3 | SPATIAL PERSPECTIVES ON PLANT-SOIL FEEDBACKS

Just as many of the first PSF studies were inherently temporal in focus (i.e. focused on community succession), they were also inherently spatial. The concept of 'self-intolerance' proposed by Janzen (1970) and Connell (1970) was a springboard for PSF research (Bever, 1994), which had an explicit spatial focus by proposing that diversity may be maintained in some communities if offspring growing closer to parent plants experience stronger negative interactions than offspring growing further away (Figure 3, left panel). It was proposed that negative PSFs that play out over relatively small spatial scales might help explain the patterns of diversity across broader spatial scales (e.g. hyper-diverse tropical forests versus low-diverse northern biomes). A notable early study addressing the Janzen–Connell hypothesis, by Packer and Clay (2000), showed that seedlings of a temperate tree species, *Prunus serotina*, experienced negative PSFs when grown in soils originating near parent trees, due to higher prevalence of *Pythium* pathogens. Many additional PSF studies have provided support for the Janzen–Connell hypothesis (Mangan et al., 2010; McCarthy-Neumann & Ibanez, 2013), although a thorough meta-analysis of PSF across biomes to explain global biodiversity patterns has yet to be done. However, some patterns have emerged that are suggestive that PSFs may serve as a diversifying force in some biomes more than others, such as more negative PSFs often found for grasses and annual forbs compared to trees or shrubs (Kulmatiski et al., 2008), or differential feedbacks based on nutrient-acquisition strategy (Bennett et al., 2017; Teste et al., 2017).

As research addressing the local-scale spatial PSF patterns predicted by the Janzen–Connell hypothesis was developing, another branch of local-scale spatial PSF research quickly diverged, where the focus was put on comparisons between native and exotic species within local communities, which often differ substantially in their relative abundances (Vila et al., 2011). Klironomos (2002) is recognized as the first study explicitly comparing PSF between a suite of native and exotic species, and showed in a Canadian prairie ecosystem that many rare native species showed negative PSF, whereas many abundant exotic species showed strong positive feedbacks. Many studies have subsequently made similar comparisons between native and exotic species within local communities, and this remains an active area of research today (Aldorfova et al., 2020; Kulmatiski, 2019). A majority of these studies have pointed to the same conclusion as Klironomos (2002), that is, that abundant exotic species within local communities often exhibit more positive or less negative PSFs than less abundant native species (Aguilera et al., 2017; Aldorfova et al., 2020; Ba et al., 2018; Kulmatiski et al., 2017; Lau & Suwa, 2016; de Souza et al., 2018). However, studies have also shown that exotic species can have no PSF advantage (Crawford & Knight, 2017; Dukes et al., 2019; Kulmatiski, 2019), or even in some cases can achieve a high local abundance despite exhibiting more negative PSFs than natives (Callaway et al., 2013).

![Figure 3](image-url)  
**Figure 3** Diagrams depicting how plant-soil feedbacks can differ for a species in its native and two contrasting introduced environments. In the native environment, we depict negative conspecific feedbacks (− sign) and positive heterospecific feedbacks (+ sign), which are proposed to serve as a diversifying force that promotes stable coexistence (Bever, 2003). These hetero- and conspecific feedbacks can shift when a species is introduced to a new environment. When an introduced species experiences positive (+) feedbacks relative to native species, establishment and invasion may be more successful, whereas negative (−) feedbacks relative to native species may result in unsuccessful establishment and invasion.
As studies comparing PSFs for native and exotic species within local communities became more numerous, a distinct line of PSF research focused on explicitly comparing the strength and directions of PSF across species' native and new ranges began (Beckstead & Parker, 2003), which eventually addressed species range expansions as well (Engelkes et al., 2008; Ramirez et al., 2019). Given that PSFs are the net effect of antagonistic and beneficial soil organisms, more positive PSF could develop for a species in a new environment if soil pathogens are less abundant (i.e. the enemy release hypothesis; Elton, 1958), or if a species is able to establish more positive soil mutualisms (Reinhart & Callaway, 2006; Figure 3, centre panel). This could occur if co-evolution of plant–microbe mutualisms in native environments has evolved a stable and equal benefit for plant–microbe partners, whereas novel combinations of plants and microbe mutualists in new environments may sometimes result in a temporary and disproportionate benefit for plant growth (McGinn et al., 2018; Nijjer et al., 2007). Conversely, PSF may become more negative in a species' new range, which could occur if exotic plants are unable to find and associate with obligate mutualists that they depend upon in their native range, or if they encounter more virulent pathogens (Figure 3, right panel). The random recombination of plants with both beneficial and antagonistic organisms in new environments may lead to idiosyncratic success in different receiving environments (Figure 3).

Comparisons of PSFs in species' native and new environments are a rapidly expanding area of research, and one in which there has been some methodological debate (discussed under ‘Methodological challenges and advances’). One of the first studies of this type was conducted by Beckstead and Parker (2003), which compared soil pathogen effects in native European soils relative to introduced California soils. The work showed fungal pathogens were present in both native and introduced ranges, but pathogenic nematodes were absent from the introduced range, which was partially suggestive of enemy release. Numerous additional studies have provided further evidence that escape from soil pathogens may serve as an important mechanism for enhanced performance in plant species' new environments (Callaway et al., 2004; Gundale, Pauchard, et al., 2014; McGinn et al., 2018; Nunes et al., 2019). Evidence has also grown to support that changes in PSF between a species' new and introduced environments can involve a whole suite of interaction types, including shifts in the strength of mutualisms (Callaway et al., 2011; Mitchell et al., 2006). For instance, plants sometimes are (Nuñez et al., 2009) and sometimes are not (Callaway et al., 2011; Gundale et al., 2019; Policelli et al., 2019; Yang et al., 2013) limited by the presence of suitable mutualists in new environments, impacting their ability to establish positive feedbacks (Figure 3). Further, some studies have suggested more positive mutualisms can develop in a plant's new environment (Gundale et al., 2016; Gundale, Kardol, et al., 2014; Yang et al., 2013).
Further research is needed within this research dimension, as we still lack generality in knowing how the strength and direction of PSF is likely to shift for which types of species and in which types of environments (Gundale, Pauchard, et al., 2014; Kueffer et al., 2013; Novoa et al., 2020; Nuske et al., 2021).

## 4 | ENVIRONMENTAL PERSPECTIVES ON PLANT-SOIL FEEDBACKS

As PSF research began to explore temporal and spatial dimensions, a further pathway that eventually developed was to understand how sensitive PSFs are to environmental context. Environmental context can vary across space (e.g. an elevation gradient) and time (e.g. climate change), and thus shares some overlap with the previous two dimensions; however, we consider environmental context a distinctly unique dimension, because it explicitly refers to variation in the abiotic and biotic conditions in which plants and soil biota interact across space or time. More specifically, key factors such as resource availability (e.g. nitrogen or water), abiotic stress (e.g. extreme climates; Bennett & Klironomos, 2019; De Long, Fry, et al., 2019; Smith-Ramesh & Reynolds, 2017) or other key biotic interactions (e.g. competition or herbivory; Bezemer et al., 2013; Heinze et al., 2016, 2020; Kardol et al., 2007; Mommer et al., 2018) have a strong potential to independently or interactively impact the strength by which plants interact with beneficial and antagonistic soil organisms. Regarding soil mutualists, it is frequently hypothesized that plants invest their photosynthate to optimize the capture of the most limiting resource (e.g. optimal allocation model or stress gradient hypothesis; Alexander, 1991; Bertness & Callaway, 1994; Johnson, 2010; Revillini et al., 2016). Thus, plants are expected to invest in and rely upon soil mutualists to a greater degree in environmental contexts where soil resources are scarce (Figure 4). There have also been a myriad of hypotheses suggesting how plant interactions with antagonistic biota may change across environmental gradients (e.g. Aerts & Chapin, 2000; Herms & Mattson, 1992). Such hypotheses generally propose that plants are better defended against antagonists when resource availability is low (van der Putten, 2003); however, the reverse has also been hypothesized (Smith-Ramesh & Reynolds, 2017). Thus, hypotheses related to both plant mutualistic and antagonistic soil biota have pointed to the expectation that the net PSFs should be more positive in resource-poor or stressful environments (Figure 4, position A), and more negative in resource-rich or low-stress environments (Figure 4, position B).

Studies evaluating the sensitivity of PSFs to environmental context have primarily focused on soils collected from local or regional productivity gradients, which are often caused by variation in underlying geology, soil parent material or topography. Another common approach to study environmental context has been to cross abiotic factors, such as nutrients, water or treatments simulating climate change, with PSF treatments in order to determine if the strength or direction of PSF shifts in response to specific environmental drivers that are known or expected to vary across space or time. One of the first studies to explicitly address environmental context, by Johnson et al. (2010) investigated whether a North American grass, *Andropogon gerardii*, was locally adapted to soil resource limitation through its association with arbuscular mycorrhizal fungal communities. The study showed that combinations of local soil communities and local plants achieved maximum plant growth when soil biota and plants originated from the same environment, indicating local adaptation. Subsequent research has since shown that soil pathogenicity can also drive variation in PSFs across environmental gradients (Bennett & Klironomos, 2018; Dominguez-Begines et al., 2020; Hersh et al., 2012; Spear et al., 2015). There is now growing evidence that spatial variation in a wide range of environmental factors can alter the strength or direction of PSFs, including soil nutrients (Gustafson & Casper, 2004; Larios & Suding, 2015; McCarthy-Neumann & Kobé, 2019), water (Rasmussen et al., 2020), light (McCarthy-Neumann & Ibanez, 2013; Smith & Reynolds, 2015), elevation (Fry et al., 2018; Lynn et al., 2020; Van Nuland et al., 2017) and biotic factors including competition and herbivory (Kostenko et al., 2012; Lekberg et al., 2018). However, it is also important to note that not all studies have found PSFs to be responsive to these types of environmental factors (e.g. De Long et al., 2015; Gundale, Kardol, et al., 2014; Shannon et al., 2014).

In addition to the focus on spatial environmental gradients, it is recognized that climate change drivers (i.e. temporal environmental gradients) can alter plant and microbial communities (Evans & Wallenstein, 2014; Isobe et al., 2020), which may influence the strength or direction of PSFs. While this area of research started later than other major dimensions of PSF research, there has been much speculation and uncertainty about how altered precipitation, rising levels of atmospheric CO₂ and rising temperatures will impact PSFs (Bardgett et al., 2013; Classen et al., 2015; De Long, Fry, et al., 2019; van der Putten, 2012; van der Putten et al., 2016). Importantly, plants and their associated soil organisms may not respond in synchrony to climatic changes, and hence, climate may disrupt or decouple interactions among coexisting and co-evolved species (Bardgett et al., 2013; Rudgers et al., 2020). This may have unforeseen consequences for PSFs.

Precipitation and drought have been among the most studied climate change drivers on PSFs. One of the first studies of this type focused on drought impacts on PSFs was by Lau and Lennon (2012), who showed that plants achieved their highest fitness when their contemporary environmental conditions were matched with microbial communities sourced from similar environmental conditions, suggesting that positive PSFs may to some degree help plants adapt to water limitation. Subsequent studies have shown that experimental drought treatments can cause PSFs to be positive or less negative (Fry et al., 2018; Snyder & Harmon-Threatt, 2019), more negative (Crawford & Hawkes, 2020; Kaiermann et al., 2017) or more variable (Valliere & Allen, 2016). Regarding rising CO₂ levels and temperature, very little empirical work has thus far been done, and evidence remains very limited (but, see De Long et al., 2015; Duell et al., 2019), Hines et al. (2017) and van Grunsven et al. (2010). It has been hypothesized that rising CO₂ may enrich plants and their
litter with carbon relative to nutrients, which has been hypothesized to reduce nutrient availability and stimulate plant investment into mutualists to improve their nutrient acquisition (i.e. more positive PSF; Figure 4 position D), whereas warming may reduce reliance on mutualists by stimulating saprotrophic nutrient mineralization rates (Figure 4, position B; van der Putten et al., 2016). However, both atmospheric CO₂ and temperature may interact with other resources such as water availability or other types of biotic interactions, which may change the direction or magnitude of these hypothesized responses (Valliere & Allen, 2016).

In addition to key abiotic factors that can vary across space or time, key biotic interactions such as competition or herbivory differ in different environmental contexts can influence the strength or direction of PSFs (Bezemer et al., 2013; Casper & Castelli, 2007; Kardol et al., 2007). For example, a recent study in a German grassland by Heinke et al. (2020) showed that insect herbivores made conspecific feedbacks less positive, and that correlations between species’ PSFs and their abundances in the local community only occurred when PSFs were assessed in the presence of herbivory. Here, it is important to note that microbes associated with above-ground plant parts can also result in species-specific feedbacks (Whitaker et al., 2017). Regarding competition, a study by Xi et al. (2020) showed that conspecific feedbacks for two tropical tree species native to southwest China were impacted by an interaction between competition with one another and the amount of light available. Specifically, they found that under high-light conditions, positive PSFs shifted to negative in the presence of heterospecific neighbours. Even intraspecific competition has been shown to interact with PSFs to control plant growth. A study by Chung and Rudgers (2016) showed intraspecific competition (i.e. density-dependent growth) was impacted by whether soils had been trained by conspecifics or heterospecifics. These studies illustrate that biotic interactions such as herbivory and competition likely have important direct and interactive effects with abiotic factors to control how PSFs play out in different environmental contexts, and it still remains uncertain how this impacts the patterns of plant community coexistence and diversity (Figure 4, depicted as a potential change in community composition from position A to B).

Despite an increasing number of studies describing the responsiveness of PSFs to abiotic or biotic variation across space or time, there remains limited evidence at this point for consistent or general patterns. A recent meta-analysis by Beals et al. (2020) showed that environmental factors do on average impact PSFs; however, their study revealed that drought experiments were the primary driver of this significant response and that other factors showed no consistent effects. They also found that when studies include both interspecific competition and PSF treatments, interspecific competition often reduced the positivity of heterospecific PSFs. As there still remains relatively few studies evaluating the impact of different types of abiotic factors and biotic interactions on PSFs, responses currently appear very idiosyncratic between study systems and environmental factors. This highlights that further research is needed to elucidate general patterns in this research area (Bennett & Klironomos, 2019; De Long, Fry, et al., 2019; Smith-Ramesh & Reynolds, 2017). A path forward for studying the relationship between PSFs and environmental context may be through the plant economic spectrum framework, which will help us clarify whether coordinated relationships between abiotic factors (e.g. nutrients, light, climate), community-level interactions (competition or herbivory) and PSFs are predictable across species and environments (Figure 4; and discussed further in the next section).

5 | BIOLOGICAL RESOLUTION PERSPECTIVES ON PLANT-SOIL FEEDBACKS

Rooted in agricultural research, initial PSF studies had a strong focus on species-specific responses. There is indeed a large and still increasing body of research showing how individual plant species differentially affect the abundance and composition of associated communities of microbes (Bever et al., 2015), protists (Wilschut et al., 2019), nematodes (Wilschut et al., 2019) and probably also saprotrophs (Veen et al., 2019). There is a similarly large body of research showing how individual plant species differ in their responses to various groups of soil biota. The general idea that species-specific PSFs have consequences for plant-competitive interaction and coexistence is now rather well-established, as discussed above. However, in explaining the variation in PSFs both among and within species, an increasing range of resolutions is now being explored. Depending on the question or intended application, recent studies have further advanced our understanding of PSFs at both lower and higher levels of taxonomic resolution than the species level (Bukowski et al., 2018; Cortois et al., 2016; Figure 5). The wider range of resolutions considered has not only broadened and deepened the concept of PSF but has also already led to increased integration with other fields of research (Mariotte et al., 2018).

At the lowest level of biological resolution, intraspecific variation and diversity is an increasingly recognized driver of community dynamics and ecosystem functioning (Raffard et al., 2019) and observed within-species variation in the strength of PSF has led to increased interest in how PSFs vary at the population or plant genotype level (Van Nuland et al., 2019; Ware et al., 2019; Figure 5). For example, for a tropical tree species (Virola surinamensis, Myristicaceae) in Panama, Eck et al. (2019) showed that seedlings less well when soils were inoculated with soil biota from their maternal tree compared to soil biota from non-maternal conspecific trees. This points at negative within-species PSF, likely driven by highly specialized, genotype-specific soil microbes, which could further contribute to the maintenance of genetic diversity within plant populations. At the community level, plant genetic diversity may also buffer against the build-up of soil pathogens and, thereby, moderate negative PSF (Semchenko et al., 2017).

Further, plant interactions with mutualistic soil organisms, and hence, positive PSF, can also be genetically controlled. For example, Gehring et al. (2017) showed that pine seedlings selected for ectomycorrhizal communities resembling those of their mother tree,
and this further affected seedling responses to drought. In agricultural research, it has been shown that different crop varieties of the same species can greatly differ in their feedback with soil biota (Wang et al., 2019), and that domesticated varieties are more vulnerable to negative PSFs than their wild relatives (Carrillo et al., 2019). If genotype-level PSFs are common, this would shed new light on the Janzen–Connell hypothesis (Liu et al., 2015), and it would also challenge how we select soils and seeds for ‘classic’ species-level PSF experiments. Recently, further progress also has been made by linking plant gene functions and expression profiles to metabolic pathways (Song et al., 2020; Wang et al., 2018). In combination with metatranscriptomic analysis of rhizosphere communities (Turner et al., 2013), this opens new avenues to explore the physiological links between plant roots and rhizosphere microbial communities at the level of root metabolic diversity (Fitzpatrick et al., 2020; van Dam & Bouwmeester, 2016; Figure 5). For example, Li et al. (2019) showed how the soil legacies from previous crops can influence the composition and metabolic function of microbial rhizosphere communities and the up- and down-regulation of plant genes involved in the production of hormones which may further influence plant performance. Thus, understanding the molecular pathways of how plant genetic variation translates to variation in the root microbiome will get us closer to mechanistically understanding PSFs.

The great variation observed in how different species and genetic lineages vary in their feedbacks with soil biota has increasingly led researchers to question the role of phylogeny (e.g. in ’t Zandt et al., 2021). These could arise if the pool of species used in the experiment share a certain degree of co-evolution with pathogenic or mutualistic soil biota (Wandrag et al., 2020): closely related plant species often show morphological and chemical resemblance which may shape plant interactions with soil biota. The strength of pairwise PSF may thus weaken if closely related species share mutualists and/or pathogens (Koyama et al., 2019). However, a global meta-analysis of PSFs across life-forms, life cycles and phylogenetic scales did not find evidence that feedbacks can be explained by phylogenetic distance (Mehrabi & Tuck, 2015),

**FIGURE 5** Plant-soil feedback (PSF) studies initially had a strong focus on species-level feedbacks with, more recently, using phylogenetic similarity as one possible explanation of observed difference in pairwise feedbacks. For example, species A may share co-evolved mycorrhizal fungi with phylogenetically closely related species B but not with distantly related species E. The field has further broadened by also studying feedbacks at lower and higher levels of taxonomic resolution. At the lower level of resolution, intraspecific variation may influence the strength or direction of PSFs, and we are slowly starting to understand the relationships between gene expression, metabolic profiles of root exudates and the rhizosphere microbiome. Much progress has also been made by moving away from taxonomy and instead looking at the functional traits of the species involved; here the focus has so far largely been on plant shoot and root traits and much less so on the traits of soil organisms. For plants traits, it has been argued that the sign of feedbacks could shift from negative to positive along the plant economic spectrum (i.e. resource-acquisitive vs. resource-conservative species), but little is known about how heterospecific feedbacks vary along economic spectra.
while a more recent meta-analysis only showed a very weak correlation between phylogenetic distance and the strength of PSF (Crawford et al., 2019). This could at least partly be explained by the mixed evidence for phylogenetic signals from individual studies (e.g. Brandt et al., 2009; Fitzpatrick et al., 2017; Münzbergová & Surinova, 2015; Senior et al., 2018). Phylogenetic signals in PSF could however have consequences for plant community assembly in the field (Anacker et al., 2014). For example, if closely related plant species share more soil pathogens than more distantly related species, this could stimulate phylogenetic diversity at the community level (Kempel et al., 2018; Liu et al., 2012). This further emphasizes the potential importance of considering phylogenetic relatedness in PSF studies, and in crop selection in case of ‘phylogenetic farming’ (Kaplan et al., 2020). However, all in all it is evident that the strength of PSF is not consistently predicted from phylogenetic relationships alone (Wandrag et al., 2020), and other explanatory variables are needed.

Moving away from taxonomic and phylogenetic explanations, in recent years functional trait-based approaches, including those focusing on litter and root traits, have become an integral part of PSF research (Bardgett, 2017; Cortois et al., 2016; Kardol et al., 2015; Veen et al., 2019)—this line of research has evolved from earlier work looking at how PSF varies with life cycle length and among plant functional groups (Kulmatiski et al., 2008). As shown in community ecology, there is congruence between phylogeny and function (Cadotte et al., 2019), but plant traits more directly and explicitly link plants to their associated soil biota, and hence, would be expected to be more powerful in explaining variation in the direction and strength of PSFs among and between species, and also might shed light on the relationship between PSFs and abiotic factors and other community-level interactions (e.g. competition and herbivory). Here, the initial focus was on comparing plant species traits associated with the plant economic spectrum, that is comparing resource-conservative slow-growing species and resource-acquisitive fast-growing species, showing that species from these coarse trait groups differed in how they influence soil properties as well as how they respond to the resultant changes in soil properties (Baxendale et al., 2014). Typically, fast-growing species experience more negative PSF (Figure 5). This has also been shown in studies including root traits. Most notably, ‘fast’ species with high specific root length (SRL) may be particularly susceptible to fungal pathogens (Bergmann et al., 2016; Cortois et al., 2016). Recent studies have included a larger suite of root traits, to further explore how root anatomy, morphology, chemistry and physiology influence plant interactions with soil microbes and broad groups of soil fauna (Leff et al., 2018; Moreau et al., 2015; Spitzer et al., 2021; Wilschut et al., 2019). However, in most cases root traits only explained a small portion, if any, of the variation in associated soil communities. Moreover, so far only few studies have used root traits, or root economic spectra, as explanatory variables of PSF, and those who did, found that root traits only explained a small proportion of the variation in feedback effects (e.g. C.M. Spitzer, unpubl. data). This indicates that we are not still far from a widely applicable trait-based framework to predict PSF. Here, it could be that we are not measuring the right traits or that PSFs are largely driven by species-specific interactions that cannot be captured by generic traits. However, an improved understanding of the functional links between plants and soil biota would also assist in further establishing possible coordinated relationships between PSFs and environmental context.

6 | METHODOLOGICAL CHALLENGES AND ADVANCES

As each of the four major dimensions of PSF research progress, it is inevitable that new methodological tools and approaches will be needed to maintain forward momentum. Here, we highlight some specific methodological considerations within each research dimension.

6.1 | Temporal considerations

As described earlier, temporal factors spanning many scales can influence the outcome of PSF experiments. Thus, a major methodological challenge is to consider the appropriate temporal scales in our experimental designs (Figure 2). We know that PSFs in the field are not the same as in the greenhouse—greenhouse-measured PSFs are typically stronger (Beals et al., 2020; Forero et al., 2019; Heinze et al., 2016; Kulmatiski et al., 2008; Morris et al., 2007; Schmittko et al., 2016). However, most PSF experiments have been and are still being conducted under greenhouse conditions (Beals et al., 2020; Kulmatiski & Kardol, 2008), largely because of the difficulty of disentangling plant-soil biota interactions under realistic field conditions. For two-phase PSF experiments, the conditioning phase can take place in the field, that is collecting soils beneath individuals or patches of certain plant species. These soils can be considered ‘species-specific’ soils for testing plant growth responses in the second, testing phase. Particularly for long-lived species, using field-conditioned soil better represents the overall effect of a plant on soil properties during its life span. Field-conditioned soils also better represent the soil biota associated with local environmental conditions (Beals et al., 2020). However, to keep species-specific soils separate, provide sterile control treatments and also to control for other drivers of plant growth, the testing phase typically involves growing plants in pots under controlled greenhouse conditions. This approach is powerful in testing plant responses to naturally conditioned soils, but it does not account for the multiple, re-occurring series of feedback events that occur in real-life plant community dynamics. In this light, the addition of additional greenhouse conditioning phases has gained new insights in ‘sequential feedbacks’, that is, how soil legacies can carry over and interact with the conditioning effects of succeeding species (Wubs & Bezemer, 2018b). Studies like this better link observations in greenhouse studies to the patterns of plant community assembly under field conditions.
6.2 | Spatial considerations

PSF studies that have some spatial aspect typically also rely upon controlled greenhouse experiments to serve as models of complex space. Given that soil and plant communities can be highly heterogeneous across space, such experiments need to carefully consider how spatial variation is or is not represented, and how it impacts interpretation. In this light, a recent series of manuscripts debated whether pooling of samples across space to create soil inoculum treatments is appropriate or not (Cahill et al., 2017; Gundale et al., 2017; Reinhart & Rinella, 2016). While it appears there is general agreement that pooling versus not pooling inoculum treatments do not have the exact same meaning, there remains substantial disagreement over the ‘correctness’ of the two approaches. We maintain that both approaches are appropriate for different types of questions, because they address different aspects of soil community diversity, that is, alpha versus gamma diversity (Gundale et al., 2019; Teste et al., 2019). These two components of community diversity provide different yet legitimate representations of space (Whittaker, 1960), and both remain useful for different types of research questions and goals that consider space differently. Seeking to understand when and where these two types of experiments show convergent or divergent results, which could be sensitive to beta-diversity or soil community-level interactions, is a more fruitful pathway towards gaining new knowledge about PSFs than claims that only one approach is ‘correct’ (Gundale et al., 2019; Peach & Meiners, 2020).

There remain many other spatial aspects of PSF experiments that need to be developed and discussed (e.g. Ware et al., 2019). A notable example is that PSF greenhouse experiments usually alter the natural three-dimensional structure of soil during transfer of soils from the conditioning phase to the testing phase, when soils are typically homogenized and sieved to remove stones, large roots or other debris. It has been shown that physically altered soil can lead to more negative PSF for some plant species (Bergmann et al., 2016). We suggest a useful strategy to address this uncertainty is to intentionally vary soil physical properties within greenhouse PSF studies, independently of soil communities, so that interactions between soil abiotic and biotic components on plant performance can be explicitly understood. Further, evaluating the role of PSFs in a natural community context requires consideration of the competitive neighbourhood (Casper & Castelli, 2007; Kardol et al., 2007) and, hence, the spatial structure of plant communities. Some studies have used creative designs of greenhouse experiments to account for this by growing plants on spatially diverse conditioned soils, by testing for the interactive effects of different soil legacies with the root system of a single plant (Hendriks et al., 2015) or by varying the spatial grain of soil conditioning (Wubs & Bezemer, 2018a).

6.3 | Environmental context considerations

As we noted earlier, environmental context can include both spatial and temporal aspects, which means many of the temporal and spatial methodological considerations discussed above are equally relevant for studying environmental context. In addition to these, researchers should consider some methodological challenges specific to studying environmental context. For spatial environmental gradients, we propose that research would benefit if local environmental gradients were described to a greater degree in absolute rather than relative terms. The influence of productivity on diversity has been a long discussed relationship in ecology (Chase & Knight, 2013), and it has been noted that some of the variation in relationships between individual study systems may be because not all gradients span the same environmental scales within or between sites (Chase & Knight, 2013), a concern that is equally legitimate for PSF research. More thorough description of within- and across-site variation of nutrient and carbon fluxes in standardized units (e.g. kg C ha−1 yr−1 or mg of N mineralized g−1 soil yr−1) would help researchers compare and contrast PSF studies across different local gradients. Further, generalization could be greatly enhanced if PSF treatments were applied in a more standardized way across different study systems in order to facilitate cleaner comparisons, such as is done in some other coordinated global-scale experimental networks, such as the Nutrient Network (www.nutnet.org; Borer et al., 2014), Drought-Net (www.drought-net.org; Knapp et al., 2017) and the recently founded Bug-Network (www.bug-net.org; A. Kempel and E. Allen).

6.4 | Biological resolution considerations

Thus far, a majority of PSF studies develop interpretations solely on comparisons of plant growth in sterilized versus unsterilized or inoculated soils, and provide little detail about the community of soil organisms that drive plant growth responses. Responses are usually attributed to pathogens or mycorrhizae specifically, whereas these approaches provide little evidence for the role of any particular taxa. We propose that future PSF studies should strive for a higher level of resolution regarding which components of the soil communities influence plants and vice versa within PSF experiments. For starters, the field needs to thoroughly evaluate to what degree inoculation approaches are successful at establishing intended soil communities (Howard et al., 2017). Further, we propose that more groups of taxa need to be considered as drivers of PSF responses (e.g. fungi and bacteria, but particularly also protists, nematodes and for litter-mediated feedbacks also collembola, mites and soil macrofauna). These goals could be achieved by simply applying well-established microscopic techniques at the beginning and end of a PSF experiments, as well as using sequencing approaches that have made quantifying the relative and absolute abundances of many different components of the soil food web more affordable and accessible (Geisen et al., 2018; de Groot et al., 2016; Waeyenberge et al., 2019). In particular, the sequencing of bulk soil microbial communities and the root microbiome informs how individual plant species or genotypes acquire certain microbial taxa and functional genes, that is, microbial enrichment, which can then be linked to plant performance (and ecosystem function; Edwards et al., 2019; Fitzpatrick et al., 2018).
But, in addition to better describing soil biota in PSF experiments, we also suggest a greater use of experimental approaches that independently manipulate different components of the soil community (Bradford et al., 2002; Xiong et al., 2020). These types of manipulation will provide greater clarity on which types of soil organisms are the main driver of PSFs, and how those organisms are influenced by other components of the soil food web. Finally, just as PSF research has begun to look at the patterns of PSFs across many levels of plant classification and organization, we also foresee greater need to consider soil communities associated with plants across these levels of organization. In particular, greater generalization will be gained when soil microbial and faunal functional groups and traits can be linked to plant groups and traits to explain when and where PSFs matter (Fry et al., 2019; Spitzer et al., 2021; Sweeney et al., 2021).

## 7 | CROSS-CONNECTIONS AND NOVEL DIMENSIONS

In the preceding sections, we described four major dimensions that PSF research has followed, including time, space, environmental context, and biological resolution. Currently, there are many new studies emerging in each of these individual areas, all of which are contributing to a growing knowledge of when, where and how PSFs matter; however, very few studies thus far have explicitly spanned more than one of these dimensions [but, see Diez et al. (2010), Dostal et al. (2013) and Nuske et al. (2021) for good examples]. We argue that a major pathway forward to gain the next level of generality in PSF research is to strive for a greater range of cross-connections between these four primary dimensions, that is, ‘multidimensional PSF research’ (Figure 1), which will require new conceptual and methodological considerations. Here, we highlight how cross-connections could be improved for each primary dimension.

### 7.1 | Temporal dimensions

As described earlier, temporal PSF research seeks to understand its role in driving plant community composition through time. Clearly, evidence is accumulating that PSFs indeed can influence successional trajectories (van der Putten et al., 2016). However, a primary challenge and frontier within this dimension is integrating generality across multiple time-scales of influence. Beyond this immediate challenge, temporal PSF research still lacks generality across complementary PSF dimensions. PSFs can be considered as re-occurring series of relatively short-term events of reciprocal plant-soil biota interactions, which are shaped by environmental processes. In the absence of external disturbances, this series of events keeps recurring with possible and to some extent predictable shifts in the composition of plant and soil communities. However, anthropogenic alteration in environmental processes may speed up, slow down or disrupt the occurrence of PSF events. This could, for example, occur if plants and soil organisms do not respond synchronously to environmental changes (Bardgett et al., 2013). We also know little about how our understanding of PSFs as drivers of succession would be influenced by spatial considerations such as variation in soil type or the presence or movement of above-ground herbivores (Veen et al., 2014). Key questions moving forward include: Does the impact of PSFs in driving community-level succession vary across biogeographic or environmental contexts, and can different levels of biological organization be useful in predicting these patterns? Do PSFs drive community stability in some contexts, and successional change in others, and can plant functional groups, traits and phylogeny predict how these community-level interactions play out? As cross-dimension work of this type develops further, we expect to learn that interactions between plant resource acquisition strategy (i.e. the plant economic spectrum) and local resource availability or environmental stress will determine whether PSF promotes temporal species coexistence or serves as a successional force.

### 7.2 | Spatial perspectives

Thus far it is clear that PSFs sometimes do and sometimes do not help explain key biogeographical patterns such as Janzen–Connell parent-sibling feedbacks, or species invasions and range expansions. This current idiosyncratic picture regarding where PSFs seem to matter may be greatly improved through cross-connections with the other three primary PSF research dimensions. For example, biogeographic PSF studies usually provide only a snapshot perspective (e.g. Gundale, Kardol, et al., 2014), and rarely provide any temporal context (Olff et al., 2000). Understanding how temporal drivers such as time since introduction or soil legacies could strongly influence the soil communities present (Diez et al., 2010; Dostal et al., 2013; Nunes et al., 2019), or the degree that exotic species have become adapted to their new environment (Blossey & Notzold, 1995), which likely influence whether PSFs are positive or negative. Environmental context (e.g. resource availability or stress) is another dimension that can vary across space and interact with the biogeographic novelty of species (Nuske et al., 2021; Ramirez et al., 2019), and thus may alter the relative contribution of pathogens versus mutualists to PSFs. A greater focus on how variation in abiotic conditions across biogeographic settings interacts with soil communities is likely key for understanding where and when PSF are likely to promote diversity, as well as impact the success of invasive and range-expanding species (Nuske et al., 2021). As with temporal PSF, biogeographic PSF research still lacks generality across different levels of biological organization, in order to predict whether success or failure of exotic and range-expanding species mediated through PSF differ among genotypes, phylogenies or functional groups or traits, which will greatly enhance the generality of this research dimension. As research of this type develops further, we anticipate learning that positive PSFs that are often observed for some biogeographically novel species are likely to diminish through time, and that these temporal dynamics in PSFs are likely greatest for species or genotypes at the acquisitive end of the economic trait spectrum.
7.3 | Environmental context

There have already been several reviews highlighting the need to better understand how environmental context influences PSFs (Bennett & Klironomos, 2019; De Long, Fry, et al., 2019; Smith-Ramesh & Reynolds, 2017), and clearly more studies are needed to address this single dimension. Within the dimension of environmental context, many new frontiers need to be crossed. For example, we need to reconcile how PSFs are predicted to impact community composition and diversity along environmental gradients, with other long-standing hypotheses explaining these same patterns. For example, it has long been speculated that vegetation diversity along gradients follows a hump-shaped or negative relationship with increasing fertility and productivity. However, it appears that the PSF research field commonly predicts the opposite, where negative feedbacks that serve as a diversifying force are predicted to be stronger in more fertile and less stressful environments (Bennett & Klironomos, 2019; De Long, Fry, et al., 2019). Thus, reconciling these predictions and patterns should be a focal point moving forward. Drawing upon other dimensions of PSF research may be helpful in doing this, for instance by considering how regional communities have assembled over different time-scales, the biogeographic context of community members (i.e. did the dominant community members recently arrive or not?) or the different levels of biological organization contributing to regional community diversity (i.e. genotypic, species, functional group vs. trait diversity). We anticipate that as cross-dimensional research focused on environmental context develops further, it will become clearer that great variation in conspecific feedbacks occurs in resource-rich environments, and that the biogeographic novelty and traits of community members will be important determinants of this variation, whereas we anticipate that factors causing abiotic stress (e.g. nutrient limitation or extreme climates) will more universally show positive conspecific PSFs.

7.4 | Biological resolution

As we noted above, broadening our understanding of temporal, spatial and environmental dimensions of PSF research will be enhanced when such processes are considered across more levels of biological organization and classification. Complementary to this, we suggest that PSF research focused at different levels of biological organization will also be enhanced when stronger connections to spatial and temporal dimensions of PSF research are made. For example, genetic variation within some plant populations is spatially structured, sometimes providing local adaptation to environmental factors and sometimes not (Parchman et al., 2011; Ricono et al., 2020). Does spatial structuring of intraspecific genetic variation, or in microbial community composition impact where and when intraspecific PSFs are important? Regarding phylogeny and taxonomy, we foresee research probing deeper into whether phylogenetic similarity or dissimilarity impacts the strength or direction of PSFs in different environmental, biogeographic and temporal contexts. For example, does the phylogenetic relatedness between an exotic and native species in different types of environments determine the strength and direction of PSFs, and ultimately influence invasiveness? Regarding the highest level of biological organization, it is already recognized that plant functional groups and traits can help explain the strength or direction of PSFs in some environments, but it remains unknown whether these relationships hold up across different spatio-temporal contexts, or if different suits of traits are needed to explain PSFs in different context? Many breakthroughs are expected as we strive for this higher level of generality about when and where different levels of biological organization are useful in predicting the strength and direction of PSFs. As this type of multidimensional research progresses, we anticipate that the lowest levels of biological organization will emerge as most useful in explaining PSFs when environmental context is considered at relatively small spatial or temporal scales (e.g. plot-level or site-level, or species turnover time), as plant population level or plastic responses may be most relevant at those scales; in contrast, we anticipate that species or plant functional traits will be most useful in understanding the strength or direction of PSFs at course scales (e.g. regional gradients, across biomes or across successional time).

7.5 | Multidimensional methodological considerations

Whereas individual research dimensions may benefit from applying both fine and coarse resolution approaches, multidimensional PSF research will likely require some-trade-offs in the resolution at which each individual dimension is considered. Further, researchers will need to consider whether the time, space and biological organization scales considered are appropriately aligned. We foresee that the most valuable multidimensional PSF studies that will lead to the greatest level of generalization will be those operating at relatively coarse scales in each dimension. This will be inherently challenging given that a majority of PSF studies are focused on species in small greenhouse pots over short time spans. Complementary experimental approaches are needed to more successfully cross major dimensions of PSF research.

One promising path forward is to a greater extent move PSF studies from the greenhouse to the field. Meta-analyses have shown that PSFs are often stronger in greenhouse settings than out in nature (Beals et al., 2020; Kulmatiski et al., 2008). While greenhouse experiments will always remain a useful tool in PSF research, an increasing number of field-based PSF experiments replicated across space (e.g. native vs. introduced ranges or along environmental gradients) are needed as a complementary inference tool. For example, species removal treatments can be imposed on naturally assembled communities, or monocultures can be planted to condition soils in the field (Phase 1) prior to investigating reciprocal effects on subsequent plant generations (Phase 2). While these types of experiments do not allow for the same mechanistic insights that greenhouse experiments using sterilization and inoculation techniques provide, the trade-off is that they can be run for a much longer period of time, allow for
bigger experimental unit sizes, can potentially cover more space and also may allow for coarser levels of biological organization to be considered. A recent PSF experiment described by De Long, Heinen, et al. (2019) provides a good example of this, whereby 2.5 × 2.5 m replicated grassland plots were used to capture realistic levels of spatial heterogeneity in plant community composition. Explicit focus was put on plant functional groups and economic trait spectra, and soils were conditioned for 1 or 2 years to account for temporal effects. Initial findings of this experiment showed that soil legacy effects on the later establishing plant communities were largely mediated by shifts in fungal communities (Heinen et al., 2020).

8 | CONCLUSIONS

As we describe in this paper, during the past two to three decades we have seen a proliferation of research that has begun to inform us about how PSFs vary across time, space, environmental context and levels of biological organization. While we clearly need more research within each of these dimensions, we foresee that PSF research in the future will become increasingly multi-dimensional (Figure 1). This multi-dimensional research will require the development of new hypotheses and methods, but will eventually lead to a higher level of generalization regarding the feedback interactions between plant and soil communities. Greater generalization in the field is in high demand. Generalization regarding the feedback interactions between plant and soil communities (Heinen et al., 2020).

DATA AVAILABILITY STATEMENT

This study does not include data or use data.

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