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Deciphering the role of specialist and generalist plant–microbial interactions as drivers of plant–soil feedback

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Summary

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Feedback between plants and soil microbial communities can be a powerful driver of vegetation dynamics. Plants elicit changes in the soil microbiome that either promote or suppress conspecifics at the same location, thereby regulating population density-dependence and species co-existence. Such effects are often attributed to the accumulation of host-specific antagonistic or beneficial microbiota in the rhizosphere. However, the identity and host-specificity of the microbial taxa involved are rarely empirically assessed. Here we review the evidence for host-specificity in plant-associated microbes and propose that specific plant–soil feedbacks can also be driven by generalists. We outline the potential mechanisms by which generalist microbial pathogens, mutualists and decomposers can generate differential effects on plant hosts and synthesize existing evidence to predict these effects as a function of plant investments into defence, microbial mutualists and dispersal. Importantly, the capacity of generalist microbiota to drive plant–soil feedbacks depends not only on the traits of individual plants but also on the phylogenetic and functional diversity of plant communities. Identifying factors that promote specialization or generalism in plant–microbial interactions and thereby modulate the impact of microbiota on plant performance will advance our understanding of the mechanisms underlying plant–soil feedback and the ways it contributes to plant co-existence.

I. Introduction: host specificity as the key assumption in plant–soil feedback research

Plants and their interactions with soil microorganisms drive changes in soil abiotic and biotic properties that can modify the performance of subsequent generations of plants. This process is known as plant–soil feedback (PSF) and has been the focus of intense research as an important driver of vegetation dynamics and ecosystem functioning (Bever, 2003; van der Putten *et al.*, 2013; Bever *et al.*, 2015). Plant–soil feedback is strongly shaped by plant–microbial interactions, with the effect on plant performance encompassing two components – the overall nature of a plant's relationship with its microbiome (positive and negative total PSF, corresponding to net mutualistic or parasitic relationships; Box 1) and the specificity of a plant's response to the particular soil microbes left behind by different plant species. In particular, many plant species leave a distinct microbial legacy that can either reduce or enhance the performance of conspecific individuals relative to their performance on soils previously occupied by other species (negative and positive specific PSF, respectively; Box 1). Variation among plants in total PSF reflects microbially-mediated fitness differences (e.g. variation in pathogen susceptibility), which reduce the potential for stable co-existence. However, total PSF can contribute to co-existence if it forms a trade-off with other fitness-related traits (e.g. growth-defence trade-off; Mordecai, 2011; Kandlikar *et al.*, 2019). Negative specific PSF can generate negative density-dependence in plant populations and stabilize species co-existence (Bever, 2003). Positive specific PSF, however, can destabilize co-existence by promoting dominance and may facilitate the invasion of new habitats (Klironomos, 2002; Callaway *et al.*, 2004; Suding *et al.*, 2013).

Broad manipulations of soil biota via soil sterilization, biocide treatments and microbial inoculations highlight the importance of soilborne pathogens (mainly fungi and oomycetes) as major drivers of negative PSFs (van der Putten *et al.*, 1993; Packer & Clay, 2000; Maron *et al.*, 2011). Positive feedbacks have been linked to mutualistic symbionts, especially mycorrhizal fungi, or modifications of nutrient cycling via effects on decomposer communities (Ke *et al.*, 2015; Cortois *et al.*, 2016; Crawford *et al.*, 2019). Since plants show differential growth and survival responses to soil microbiota shaped by conspecifics vs other plant species, it is often assumed that such specific PSFs are driven by host-specific symbionts (Gilbert & Webb, 2007; Bever *et al.*, 2015; van Ruijven *et al.*, 2020). However, host specificity of soil microbial taxa driving PSF is rarely empirically tested. Contrary to the expectation, studies describing the soil microbial taxa associated with different plant hosts report low levels of specialization in plant-associated microbiota (Davison *et al.*, 2015; Pöhlme *et al.*, 2018; Maciá-Vicente & Popa, 2021; Spear & Broders, 2021). Moreover, the central role of host-specific pathogens in regulating PSF and species co-existence relies on an assumption that pathogens are more host-specific than mutualists. However, host-specificity is rarely compared between different microbial functional groups (Wang *et al.*, 2019). Lastly, we lack empirical studies comparing the relative impact of specialist vs generalist soil microbiota on plant

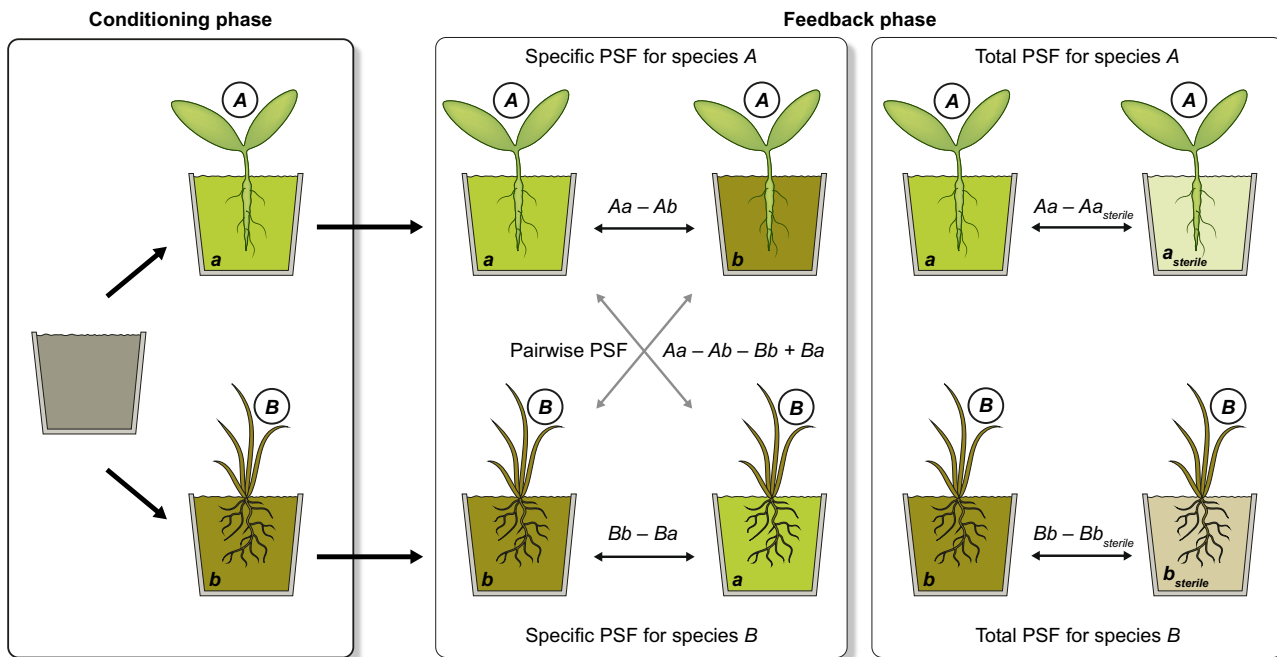
performance and vegetation dynamics. The assumption of a higher contribution of specialized microbial symbionts to PSFs is indeed challenged by observations that specialist pathogens are often biotrophs, which benefit from keeping the host alive and thus only elicit mild effects on hosts (Jarosz & Davelos, 1995). Conversely, generalists are frequently necrotrophs that cause high host mortality rates (Jarosz & Davelos, 1995; Gilbert & Parker, 2016) and likely contribute more strongly to regulating plant populations.

A clearer understanding of how specialist and generalist microbial taxa contribute to PSF will help us to predict variation in PSF across plant species and communities. If all species were equally and strongly regulated by host-specific microbes, consistently strong specific PSFs would pervade across all species in a community. At the other extreme, if all plant species were equally affected by generalist microbiota, strong total PSF would be observed, but specific PSFs should be neutral. In reality, we see wide variation between plant species in the strength and direction of total and specific PSF (e.g. Klironomos, 2002; Cortois *et al.*, 2016). We suggest three potential causes of this variation. First, such variation may be due to some species forming highly specialized relationships with their symbionts and others lacking specialist symbionts with strong impacts on their hosts. Second, generalists can display 'effective specialization' (Benitez *et al.*, 2013), where different combinations of microbial populations or genotypes generate differential impacts on host species. Lastly, variation in PSF may be driven by true generalists that effectively associate with a wide range of plant species but have a differential impact on plant performance (Klironomos, 2003; Hersh *et al.*, 2012).

Predicting whether and to what degree a particular host plant experiences PSF driven by specialist or effectively specialized microbiota will be a challenge, as such specialization is likely driven by molecular mechanisms related to specific defence or signalling genes (Gilbert & Parker, 2016; Lofgren *et al.*, 2021). More probabilistic predictions about the evolution of specialist interactions may be possible based on the local and regional abundance of host plants (Jaenike, 1990; Barrett & Heil, 2012); though the dependence of host-specificity on host abundance in soil microbiota remains untested. By contrast, robust predictions can be made about how the impacts of generalist microbiota, and resulting total and specific PSF, should vary along known axes of variation in plant function, which reflect investment towards resource acquisition (including reliance on microbial mutualisms), defence and reproduction (Diaz *et al.*, 2016; Weigelt *et al.*, 2021).

Further, PSFs driven by specialist and generalist microbiota are likely to generate distinct effects on species co-existence. Specialist pathogens can generate negative specific PSFs that stabilize plant co-existence independent of other plant traits and trade-offs. By contrast, PSFs driven by generalist interactions are more likely to form joint axes with other plant traits and have equalizing effects on species co-existence via fundamental trade-offs in resource distribution (e.g. growth-defence trade-off; Mordecai, 2011; Kandlikar *et al.*, 2019). Lastly, the strength of PSF driven by host-specific or

Box 1 Plant–soil feedback – common experimental techniques and implications for detecting specificity in plant–microbial interactions.



Plant–soil feedback experiments generally consist of a ‘conditioning phase’ and a ‘feedback phase’. In the conditioning phase, a single plant species is grown in a ‘naive’ soil with the aim of establishing a host-specific soil microbial community (soils *a* and *b* for species A and B, respectively). The effect of host-specific changes in microbial communities on plant performance is assessed in the feedback stage of the experiment, where plants are either grown in the soil conditioned by conspecifics (*Aa* and *Bb*) or in the soil conditioned by other species (*Ab* and *Ba*). In addition, conditioned soils are also frequently sterilized to assess the net effect of the whole soil microbiome on plant performance. Soil conditioning approaches and formulas used to calculate PSF vary between studies, but three main types of PSF are usually assessed. Total PSF assesses the plant response to the presence of the whole soil microbiome. It is usually assessed by comparing plant performance in nonsterilized vs sterilized soil conditioned by conspecifics ($Aa - Aa_{sterile}$ and $Bb - Bb_{sterile}$). Negative total PSF is indicative of the dominance of antagonistic interactions with soil biota (microbial competition for nutrients, pathogenic and parasitic interactions), while positive total PSF is characteristic of plants with strong mutualistic interactions with soil biota, such as mycorrhizal symbiosis. Specific PSF compares plant performance (usually biomass, sometimes germination and survival) when grown in soil conditioned by conspecifics (*Aa* and *Bb*) vs soil conditioned by other species (*Ab* and *Ba*), with negative values indicating better performance in soil of other species than of own species, and positive values indicating enhanced growth in conspecific soil. Negative specific PSF has the highest potential to generate stabilizing effects on species co-existence, because it prevents a given species from becoming dominant. However, such a stabilizing effect can only be tested by looking at pairwise PSF, which is the sum of two individual specific PSFs ($Aa - Ab - Ba + Bb$; Bever *et al.*, 1997). Pairwise PSF is negative when both species exhibit negative specific PSF, but it can also be negative when one of the species has a neutral or positive specific PSF as long as it is compensated by a strong negative specific PSF in the other species. The pairwise feedback concept can be extended to include more than two species, such that PSF can be calculated for whole communities to assess the overall role of plant–soil interactions in regulating plant community dynamics (Eppinga *et al.*, 2018).

All PSF measures assess the net effect of all soil microorganisms on plant performance and cannot differentiate between the impacts imposed by individual host-specific and generalist microbial taxa.

specialized symbionts depends primarily on host plant abundance and, if the molecular mechanisms involved in specialized signalling are phylogenetically conserved, on the phylogenetic relatedness of co-existing plant species (Gilbert & Webb, 2007; Parker *et al.*, 2015). However, plant community context will be crucial when predicting PSFs driven by generalist microbial taxa, with greater trait divergence between co-existing species resulting in more pronounced specific PSF.

In this review, we:

(1) Assess evidence for the prevalence of host specificity in plant–microbial associations and how it differs between soil-

borne fungal and oomycete pathogens, mutualists and saprotrophs.

(2) Explore how generalist microbiota can produce specific effects on plant performance.

(3) Synthesize existing theoretical and empirical evidence to identify major gradients of variation in plant traits and plant community properties that predict specificity in plant–microbial interactions and the contribution of generalist microbiota to PSF.

(4) Identify critical knowledge gaps and propose future directions to build a more comprehensive understanding of the mechanisms underlying PSF.

II. How prevalent is host specificity in belowground plant–microbial associations?

Plant associations with soil pathogens are assumed to be more host-specific than those with mutualistic microbiota, and thus held responsible for frequently observed negative specific PSFs (e.g. Schnitzer *et al.*, 2011; Crawford *et al.*, 2019). Indeed, the most widely studied mutualistic symbionts in the context of PSF – arbuscular mycorrhizal fungi (AMF) – exhibit very wide host ranges (Davison *et al.*, 2015; Lekberg & Waller, 2016). Ectomycorrhizal (EcM) fungi, however, are considered to be more host-specific (Segnitz *et al.*, 2020; but see Peay *et al.*, 2015; Pölme *et al.*, 2018). However, many pathogens, including fungi, oomycetes, bacteria, and viruses, also infect multiple hosts, frequently spanning wide phylogenetic host ranges (Gilbert & Webb, 2007; Newman & Derbyshire, 2020; Spear & Broders, 2021). Therefore, the role of host specialists in driving PSFs remains unclear due to the lack of direct comparisons of host specificity between different guilds of soil microbes (but see Wang *et al.*, 2019).

Here, we compare surrogates for host range breadth across soilborne fungal and oomycete taxa from the major ecological guilds often implicated in driving PSFs (Supporting Information Methods S1). We made a first assessment using the database provided by Pölme *et al.* (2020), which compiles global fungal

and oomycete records with information on their host associations. We retained only records of plant-associated fungi and oomycetes and calculated the mean pairwise phylogenetic distance (MPD; Webb *et al.*, 2002) between their plant hosts. MPD is often used to predict likely host breadths, with lower values indicating higher host specificity (Gilbert & Webb, 2007; Gilbert & Parker, 2016). We found significant differences in MPD across ecological guilds, with AMF and EcM fungi displaying the lowest and the highest host specificity, respectively, and other ecological guilds displaying intermediate host ranges ($\chi^2(5) = 522.1$, $P < 0.001$; Fig. 1a). Therefore, based on currently available global data, the assumption that pathogens are more specialized than other microbial guilds does not appear to hold. Although this dataset is a unique and valuable source of information at the global scale, it also has limitations. In particular, it does not contain data on locally available host species that the fungal and oomycete taxa did not colonize. We therefore cannot assess host-specificity in taxa that were only recorded in a single host or the deviation of observed specificity from that expected based on random associations.

To reduce this limitation, we also assessed three case studies from experimental mesocosms with temperate grassland plant species where the occurrence of fungal taxa, or lack thereof, was examined by high-throughput amplicon sequencing (Leff *et al.*, 2018; Francioli *et al.*, 2020; Sweeney *et al.*, 2021; Table S1).

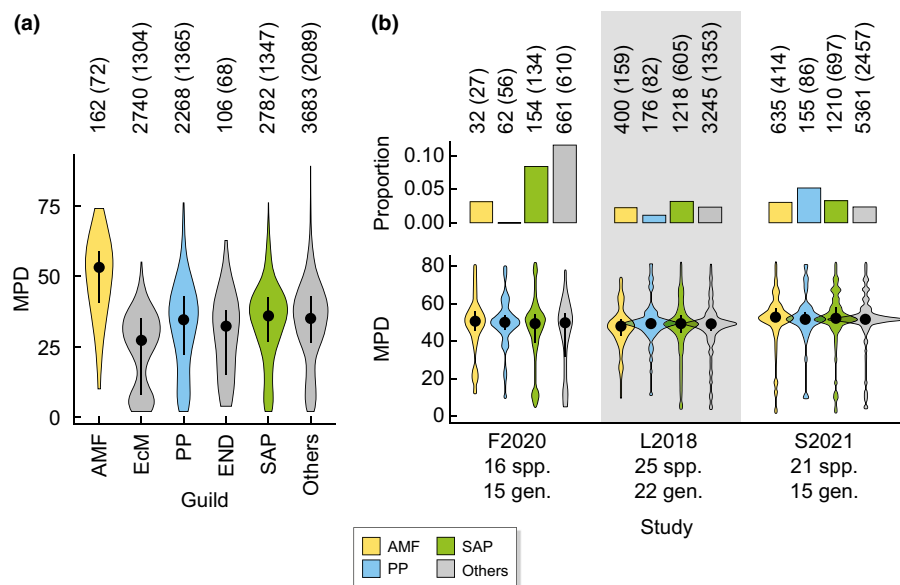


Fig. 1 Host ranges of plant-associated fungal and oomycete guilds calculated as the mean pairwise phylogenetic distance (MPD) between the plants that they colonize. (a) Global analysis using data from Pölme *et al.* (2020). (b) Analysis of case studies comprising experimental mesocosms with temperate grassland plant species (F2020: Francioli *et al.*, 2020; L2018: Leff *et al.*, 2018; S2021: Sweeney *et al.*, 2021; number of plant species and genera included are shown at the bottom of the figure). Violin plots represent the distribution of MPD values, with points and error bars indicating median values and interquartile ranges, respectively. The values at the top indicate the total number of fungal and oomycete taxa included in each dataset: species hypotheses (Kõljalg *et al.*, 2013) in (a), and of amplicon sequence variants (ASVs, Callahan *et al.*, 2017) in (b). Values within parentheses indicate taxa found in at least two host species and therefore used for the calculation of MPD. Bar plots at the top in (b) represent the proportion of fungal taxa with host MPDs significantly lower ($P < 0.05$) than those obtained by a randomized null model. The assignment of fungal and oomycete taxa to guilds was based on the FungalTraits database (Pölme *et al.*, 2020), but several guilds of saprotrophs from different substrata (litter, soil, wood, unspecified) were combined into a single saprotroph category (SAP), for simplicity. AMF, arbuscular mycorrhizal fungi; EcM, ectomycorrhizal fungi; END, root endophytes; PP, plant pathogens; SAP, saprotrophs.

Here, we found no significant differences in host associations across putative mutualists, pathogens and saprotrophs (Fig. 1b), with median MPDs for each guild indicating frequent colonization of phylogenetically distant plant lineages (Fig. S1). In all ecological guilds, less than one tenth of all taxa were more specialized than expected by chance (Fig. 1b). Low levels of specificity across these three ecological guilds were also found when using an alternative specialization index based on the relative abundance of fungal taxa across hosts (including those occurring in a single host) and independent of host phylogenetic relatedness (Fig. S2).

These data combined indicate that soil fungal and oomycete communities are dominated by generalist taxa and, although a proportion of taxa display significant host specificity, this is not more common in pathogens than other guilds. This finding raises several questions. Firstly, how can we reconcile observed species-specificity in PSFs with the high prevalence of generalist microbiota? Secondly, why do soil-borne fungal and oomycete taxa display variation in the degree of host specialization and which host traits may favour or disfavour specialization?

III. Redefining specificity in belowground plant–microbial associations

Low levels of host specialization inferred from the occurrence patterns of individual microbial taxa (Fig. 1) do not mean that such organisms cannot produce differential effects on plant performance. Specific effects in plant–pathogen interactions can also be generated via so-called ‘effective specialization’ that arises from the interaction between plant and pathogen genotypes and its modulation by environmental context (Benitez *et al.*, 2013). First, effective specialization can result from local adaptation of a pathogen or cryptic diversity, if a perceived pathogen species in fact constitutes multiple subpopulations or genotypes with preferences towards certain plant species or local plant populations (Konno *et al.*, 2011; Barrett & Heil, 2012; Eck *et al.*, 2019). Indeed, cryptic diversity within pathogenic species is well established, particularly in fungi where *formae specialis*, pathotypes and other intra-specific categories have been historically used to delineate variations in host preference (Termorshuizen, 2014). Second, effective specialization may also be driven by context dependency of biotic interactions, including the regulatory effects of the abiotic environment, host phenology and age (Laine, 2007; Alvarez-Loayza *et al.*, 2011; Grulke, 2011), and co-infection by multiple pathogens. For example, Hersh *et al.* (2012) showed that co-infection with different combinations of generalist pathogens resulted in variable outcomes across plant species. Similarly, Semchenko *et al.* (2018) found that a higher diversity of putative soilborne pathogens led to stronger negative PSF in grassland species. Together, the interplay between these factors may enhance specific host effects and pathogen-mediated plant diversity regulation.

Although originally conceived to explain plant–pathogen interactions, we argue that effective specialization also applies to other guilds of plant-associated fungi. Mycorrhizal fungi have broad host ranges but elicit differential responses across plant

hosts (Molina & Trappe, 1994; van der Heijden *et al.*, 1998; Hoeksema *et al.*, 2018), including significant variations in response to different conspecific isolates, which may reflect cryptic diversity (Klironomos, 2003; Angelard *et al.*, 2014; Koch *et al.*, 2017). Plants are also typically colonized by multiple species of mycorrhizal fungi that interact with one another (Bever, 2002; Bennett & Bever, 2009; Sepp *et al.*, 2019) and with other components of microbial communities (Deveau *et al.*, 2018). Mycorrhizal symbioses are also strongly dependent on the abiotic context (Hoeksema *et al.*, 2010). Likewise, saprotrophic microbial taxa that apparently lack host specificity may produce specific effects on litter decomposition via local adaptation processes, co-colonization of litter by multiple taxa, and interactions with microenvironmental conditions. This could explain, for example, the so-called ‘home field advantage’ phenomenon that describes the higher efficiency of litter decomposition in soils conditioned by conspecific as compared to heterospecific plants (Austin *et al.*, 2014; Veen *et al.*, 2015). However, it is unknown whether specialization in litter decomposition generates specific feedback effects on plant growth.

We currently lack a comprehensive understanding of how such variable and context-dependent interactions with generalist microbiota shape specific PSFs, and how their impacts can be predicted. Moreover, even a single pathogenic or mutualistic microbial isolate can produce variable outcomes for the performance of different plant species under controlled conditions (Klironomos, 2003; Konno *et al.*, 2011; Angelard *et al.*, 2014; Spear & Broders, 2021). Such variation cannot be attributed to effective specialization, which is mediated by cryptic variation, co-infection or abiotic environment, but it is likely underlain by differences among plant hosts in the traits reflecting their defence, resource acquisition and reproduction strategies. Below, we synthesize existing evidence to predict how plant interactions with specialist and generalist soilborne pathogens, mutualists and saprotrophs vary along known gradients of plant form and function, and collectively contribute to PSF.

IV. Plant–pathogen interactions as drivers of PSF

1. Plant traits promoting host specificity in plant–pathogen interactions

Negative specific PSF should be promoted by high pathogen host-specificity. Host-specific natural enemies, particularly insect herbivores and seed predators, are more likely found on hosts that are easily detected and colonized, e.g. those reaching high abundance (Jaenike, 1990; Barrett & Heil, 2012) and characterized by large size and limited dispersal (Janzen, 1969). However, it is unknown if the same factors can promote specialization in soil pathogens. Significant relationships between PSF measures and plant species abundance, longevity and growth rates lend some support to this prediction (Lemmermeyer *et al.*, 2015; Maron *et al.*, 2016; Kulmatiski *et al.*, 2017; Xi *et al.*, 2021), but the underlying mechanisms remain unknown. Further studies are required to establish if soil pathogens are more likely to specialize on plant hosts that are easily located.

2. Plant traits that underlie variation in the impact of pathogens on plant performance

Plants differ in their resistance to natural enemies due to a fundamental trade-off between investments into growth, reproduction and defence. Specifically, plant strategies vary along the so-called plant economic spectrum (Wright *et al.*, 2004; Diaz *et al.*, 2016) or the conservation gradient (Weigelt *et al.*, 2021), with 'slow' species investing in well-defended, long-lasting tissues at the expense of growth rate on one end of the gradient and 'fast' species investing in rapid tissue growth that prioritizes resource acquisition over tissue longevity at the other end. Multiple studies have found that total and specific PSF vary significantly along the conservation gradient, with more negative PSF detected in species with fast growth, high specific leaf area and leaf nitrogen (N) content, short life span and high competitive ability (Lemmermeyer *et al.*, 2015; Fitzpatrick *et al.*, 2017; Kulmatiski *et al.*, 2017; Lekberg *et al.*, 2018; Semchenko *et al.*, 2018; Xi *et al.*, 2021; Table S2). However, despite higher susceptibility to infection, such species may also be tolerant of pathogen infection due to their capacity for fast tissue regrowth (Parker & Gilbert, 2018), which may weaken the dependence of PSF on the conservation gradient and explain the lack of correlation between PSF and the plant economic spectrum reported in some studies (Table S2).

Plant–soil feedback may also be influenced by plant dispersal ability, which in turn is negatively related to seed size and positively related to plant height and the existence of seed dispersal adaptations (Thomson *et al.*, 2011; Tamme *et al.*, 2014). Efficient dispersal may allow escape from local pathogen pressure, and hence reduce selection for pathogen defence (Stump & Comita, 2020). Therefore, species with strong dispersal ability should experience more negative PSF. The link between plant dispersal and susceptibility to soilborne pathogens remains unexplored, but a few studies have found a positive relationship between seed size and specific PSF or conspecific density dependence consistent with this prediction (Bennett & Klironomos, 2018; Seiwa *et al.*, 2019; Spear & Broders, 2021; Xi *et al.*, 2021; Table S2).

Plant traits that explain variation in plant susceptibility to pathogens do not imply specificity. These traits underlie the overall nature of plant interactions with pathogens, which is most effectively captured in the comparison of plant growth or survival in live conspecific soil vs soil where the microbiota has been excluded by sterilization (total PSF in Box 1). Despite the lack of specificity, total PSF may play a major role in regulating plant community dynamics by contributing to fundamental life history trade-offs (Kandlikar *et al.*, 2019; Ke & Wan, 2020). For example, the dominance of highly competitive plant species may be counteracted by their high susceptibility to generalist soil pathogens (Lekberg *et al.*, 2018). However, the same traits can also underlie specific PSFs when placed in a community context, explaining why several studies report significant correlations between specific PSF and plant traits related to generic tissue conservation (Table S2).

3. Generalist pathogen interactions and specific PSFs in a community context

If plant communities are regulated by host-specific pathogens, strong negative specific PSFs should prevail, disease risk should increase with conspecific density, and heterospecific neighbours should reduce specialist pathogen transmission – a process known as pathogen dilution (Keesing *et al.*, 2006; Collins *et al.*, 2020). In contrast, the potential of generalist pathogens to induce specific PSFs will depend strongly on plant community composition (Ampt *et al.*, 2022). Because plant susceptibility to a certain pathogen tends to be phylogenetically conserved (Gilbert & Webb, 2007), plants should experience pathogen dilution in phylogenetically diverse plant communities (Fig. 2; Parker *et al.*, 2015), and the opposite effect, pathogen spillover (when neighbouring species serve as pathogen reservoirs and hence increase disease risk) in more phylogenetically homogeneous communities (Fig. 2; Gilbert & Parker, 2016).

In addition to phylogenetic diversity, variation in pathogen defence levels between co-existing species, and the relative abundance of species with high susceptibility (high infection rate, reduced plant performance) vs resistance (low infection rate, unchanged plant performance) to generalist pathogens, should also affect specific PSF. In communities with a wide range of investment into tissue defences, plants will benefit from pathogen dilution in the rhizosphere of species with higher pathogen resistance than their own, resulting in negative specific PSF (Fig. 2). In contrast, heterospecific neighbours with higher pathogen susceptibility than conspecifics will cause pathogen spillover and hence generate positive specific PSF (Fig. 2). In addition, plant communities can harbour tolerant hosts that act as pathogen reservoirs, hosting pathogens but not developing disease symptoms or accumulating high densities of pathogens with limited impact on their fitness (Mordecai, 2011; Ampt *et al.*, 2019). For example, many soilborne pathogens that cause severe disease in crops also colonize wild plants as endophytes, causing only mild negative effects on their performance (Malcolm *et al.*, 2013; Kia *et al.*, 2017; Lofgren *et al.*, 2018). The underlying mechanisms, and the importance of pathogen tolerance for PSF and plant community dynamics, are poorly understood. The limited empirical evidence suggests that plant species at the 'fast' end of the plant economic spectrum are more tolerant to pathogen infection and contribute more to pathogen transmission than slow-growing species (Parker & Gilbert, 2018; Welsh *et al.*, 2020). Hence, fast-growing plant species are not only highly susceptible to infection but can also amplify the spread of generalist pathogens to slower growing species. It has also been predicted that hosts should evolve towards higher tolerance with increasing diversity of natural enemies (Jokela *et al.*, 2000). This suggests that the diversity of both plant and pathogen communities are likely to be important drivers of pathogen dilution, spillover, and associated specific PSFs. This is particularly true when pathogen communities are dominated by taxa with wide host ranges.

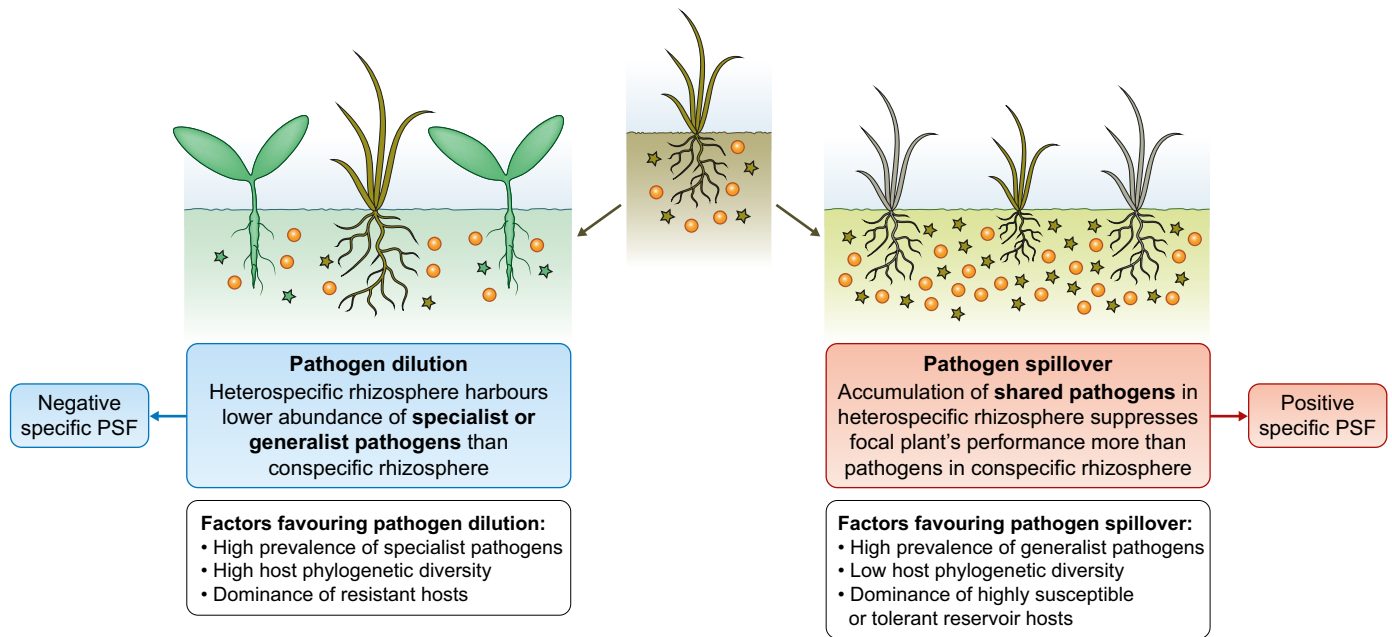


Fig. 2 Factors favouring pathogen dilution and spillover in plant communities. The focal plant species in the centre of the figure is negatively affected by a multi-host specialist pathogen with a phylogenetically restricted host range (green stars) and a generalist pathogen with a wide host range (orange circles). The focal plant species can experience pathogen dilution when inhabiting a phylogenetically diverse community or a community dominated by species that invest in defence and are hence resistant against generalist pathogens, resulting in negative specific plant–soil feedback (PSF; poorer growth in conspecific soil in the centre than heterospecific soil on the left). The focal plant species can instead experience pathogen spillover in communities with low phylogenetic diversity or dominance of plant species that are more susceptible or tolerant to shared pathogens than the focal species, promoting pathogen accumulation and resulting in positive specific PSF (higher growth in conspecific soil in the centre than heterospecific soil on the right).

V. Mutualistic interactions as drivers of PSF

In addition to pathogens, PSF is also shaped by plant interactions with potentially mutualistic symbionts, such as rhizobia and mycorrhizal fungi, as well as with free-living, plant growth-promoting rhizobacteria (PGPR) such as those in genus *Pseudomonas*. The role of mutualistic interactions in driving PSF has been most thoroughly examined for interactions with AMF, the most widespread type of mycorrhizal symbiosis. We first focus on arbuscular mycorrhizal symbiosis and then briefly discuss the applicability of the same principles to other beneficial microbiota.

1. Plant traits underlying variation in the impact of mycorrhizal fungi on plant performance

AMF symbiosis is likely the ancestral state for land plants, with a general evolutionary trend towards lower reliance on AMF for nutrient uptake in more recently diverged plant lineages (Ma *et al.*, 2018). Species characterized by stronger dependency on mycorrhizal symbiosis should exhibit a more positive relationship with the soil microbiome and consequently more positive total PSF (Box 1). Mycorrhizal dependency as a plant species trait is challenging to quantify by direct measurement, as plant growth responses to mycorrhizal colonization are highly context-dependent (van der Heijden *et al.*, 1998; Hoeksema *et al.*, 2018). Plant root morphology provides a good proxy for mycorrhizal dependency, as plants that depend strongly on arbuscular mycorrhizal symbiosis invest in larger volumes of cortex tissue to

accommodate fungal partners, resulting in larger root diameter (Valverde-Barrantes *et al.*, 2016; known as the fungal collaboration gradient, Bergmann *et al.*, 2020). Empirical evidence supports this prediction by showing that species characterized by larger root diameter and higher mycorrhizal colonization experience more positive total PSF (Cortois *et al.*, 2016; Semchenko *et al.*, 2018; Table S2).

2. Specificity in resource allocation to different fungal partners and specific PSF

Since AMF are obligate biotrophs and cannot complete their lifecycle without access to plant roots (Bonfante & Perotto, 1995), strong specialization on particular plant species is not a viable option for AMF. Plants, however, vary in their dependence on arbuscular mycorrhizal symbiosis and the frequency of root colonization by AMF, i.e. mycorrhizal status (Hempel *et al.*, 2013; Moora, 2014), which may reflect how selective plants are in allocating resources to different fungal partners. Obligately mycorrhizal species are always colonized by AMF, facultatively mycorrhizal species show variable frequencies of colonization, and nonmycorrhizal plants seemingly actively prevent colonization. Obligately mycorrhizal species are likely to have thick roots that are inefficient in nutrient uptake and hence ‘outsource’ this function to mycorrhizal fungi (Bergmann *et al.*, 2020). Such plant hosts may forego partner selectivity to safeguard mycorrhizal colonization in all situations, as even a fungal partner with a high carbon (C) to

nutrient exchange rate is better than no fungal partner (Smith *et al.*, 2009; Sepp *et al.*, 2019; Davison *et al.*, 2020). However, the absence of mycorrhizal colonization in some specimens of facultatively mycorrhizal species may be the result of colonization control by the host plant (Sepp *et al.*, 2019; Davison *et al.*, 2020). Facultatively mycorrhizal species may have refined root systems that are relatively efficient in nutrient uptake ('do-it-yourself' species within the fungal collaboration gradient; Bergmann *et al.*, 2020) and may only form mycorrhiza under certain environmental conditions or in the presence of highly mutualistic fungal partners (Grman, 2012). Finally, nonmycorrhizal hosts may have even stronger control over mycorrhizal colonization, as such species dominate in extremely nutrient-impooverished or disturbed habitats where mycorrhizal associations are no longer beneficial and may interfere with root system development (Smith *et al.*, 2009; Hempel *et al.*, 2013; Lambers & Teste, 2013).

In a community of species with differential mycorrhizal dependency and status, obligately mycorrhizal species with thick roots should experience strong positive total PSF but negative specific PSF, as low levels of symbiont discrimination will lead to the accumulation of less mutualistic fungal partners in conspecific rhizosphere compared to heterospecifics with tighter control over fungal colonization (Bever, 2002; Bennett & Bever, 2009; Kiers *et al.*, 2011; Grman, 2012). In contrast, species with fine roots and greater control over colonization by different mycorrhizal partners should exhibit neutral to negative total PSF but positive specific PSF. In addition, mycorrhizal dependency and associated PSFs may be related to seed dispersal (Bergmann *et al.*, 2017). For example, poor dispersal of large seeds may select for more mutualistic mycorrhizal interactions in the presence of closely related individuals, enhancing seedling support via mycorrhizal networks and resulting in more positive specific PSF (Pickles *et al.*, 2017; Liang *et al.*, 2021).

3. Mycorrhizal associations in a community context

As with pathogens, the role of mutualistic interactions in mediating specific PSFs likely depends on the phylogenetic and functional structure of local plant communities. Different plant clades show distinct growth responses to different clades of EcM fungi and AMF (Hoeksema *et al.*, 2018; Davison *et al.*, 2020). Hence, phylogenetically diverse plant communities, and those characterized by wide variation in host mycorrhizal dependency and ability to regulate mycorrhizal colonization, should generate stronger specific PSFs. Plant–soil feedback is also more positive in communities where hosts associate with different mycorrhizal types, such as in forests combining arbuscular mycorrhizal and EcM trees (Bennett *et al.*, 2017; Kadowaki *et al.*, 2018; Liang *et al.*, 2021). Lastly, mycorrhizal symbioses may function as a 'biological market' where plants and fungi bargain for resources at the best 'prices' they can find (Kiers *et al.*, 2011; Fellbaum *et al.*, 2014). Thus, diverse communities where both hosts and fungi can choose the most profitable partners likely generate more positive specific PSFs (Thrall *et al.*, 2007; Fellbaum *et al.*, 2014).

4. Plant–soil feedback and other types of mutualistic associations

Other mutualist groups with higher host specificity than AMF could generate stronger specific PSFs. For example, rhizobia are restricted to only a few plant lineages and involve highly specific recognition markers (Yang *et al.*, 2010; Werner *et al.*, 2014). However, PSF studies focussing specifically on plants with rhizobial associations are too limited to confirm the prediction of more specific PSFs in hosts associating with rhizobia (Bever *et al.*, 2013). Similarly, EcM fungi from the genus *Suillus* form specific associations with trees in the Pinaceae family (Lofgren *et al.*, 2021). However, this plant family does not stand out as having more specific PSFs compared to other EcM trees lacking specific fungal associations (see fig. 2 in Bennett *et al.*, 2017). High host specificity may not result in stronger PSFs because host-specific mutualists may not necessarily provide higher benefits to the plant compared to generalists, and there are many ways by which generalists can produce specific effects on their hosts. However, host-specialist interactions probably play an important role in driving PSFs under certain conditions, and more theoretical and empirical research is needed to identify where and when it could be expected.

VI. Soil microbial decomposers as drivers of PSF

1. Plant traits underlying variation in soil microbial decomposer communities

Plants can strongly regulate soil decomposer communities and their activity via litter quality, with litter rich in nutrients and labile C sources enhancing decomposition rates and high concentrations of structural and chemical defences, such as lignin and secondary metabolites, inhibiting decomposition (Chen *et al.*, 2017; Barel *et al.*, 2019). These properties are well aligned with the conservation gradient, which reflects a trade-off between the production of nutrient-rich tissues supporting fast growth and defended tissues that increase tissue lifespan (Wright *et al.*, 2004; Diaz *et al.*, 2016; Weigelt *et al.*, 2021). The input of high-quality litter from fast-growing plants selects for distinct decomposer communities dominated by copiotrophic bacteria that ensure fast N mineralization (Wardle *et al.*, 2004; Fierer *et al.*, 2007; Baxendale *et al.*, 2014) and can hence generate positive feedback to plant growth (i.e. total PSF, Box 1). However, low-quality litter from slow-growing plants results in dominance of fungal decomposers, slow rates of N mineralization and microbial immobilization (Wardle *et al.*, 2004; de Vries *et al.*, 2012), which may lead to negative total PSF.

In addition to variation in litter properties, root exudation plays a key role in regulating the composition and activity of decomposer communities (Zhalnina *et al.*, 2018). Plants can enhance nutrient mineralization by altering the quality and quantity of root exudation, for example during stages of exponential growth (Zhao *et al.*, 2021), in response to defoliation (Hamilton *et al.*, 2008), and when recovering from drought (de Vries *et al.*, 2019). Higher

exudation of sugars can increase microbial activity, which in turn may result in higher rates of N mineralization, and thus feed back positively to plant growth (Zwetsloot *et al.*, 2018; Williams *et al.*, 2022). Conversely, exudation of phenolic compounds can suppress microbial activity (Zwetsloot *et al.*, 2018) or have allelopathic effects on neighbouring plants through microbial degradation of these compounds (Bains *et al.*, 2009). In addition, plants can directly regulate N cycling by exuding nitrification inhibitors (Coskun *et al.*, 2017).

Recent studies suggest that root exudation rate is associated with both the conservation and collaboration gradients of the plant economic spectrum (Henneron *et al.*, 2020a; Williams *et al.*, 2022). Within a range of common grassland species, thicker roots were linked to higher exudation rates, which may attract mycorrhizal symbionts (Williams *et al.*, 2022). Fast-growing species with high photosynthetic capacity are also characterized by high root exudation rates (Williams *et al.*, 2022), which stimulate microbial activity and prime the decomposition of soil organic matter (Henneron *et al.*, 2020b). It is therefore likely that variation in PSF across the conservation gradient is not only driven by interactions with soil pathogens and mycorrhizal fungi, but also the stimulatory and inhibitory effects on nutrient cycling mediated by root exudates of fast-growing and slow-growing plant species, respectively.

2. Specificity in litter-decomposer associations

Decomposer communities often exhibit an affinity towards specific litter. In a phenomenon known as home field advantage, decomposition rates are enhanced when litter is placed back in 'home' soil previously occupied by the same plant species or genotype compared to in an 'away' soil conditioned by a different species or genotype (Austin *et al.*, 2014; Veen *et al.*, 2015). The microbial drivers of home field advantage are still poorly understood but seem to be related to the abundance of certain fungal taxa in litter and the colonization of live tissues by endophytes that switch to a saprotrophic lifestyle upon tissue senescence (Veen *et al.*, 2019; Fanin *et al.*, 2021; Francioli *et al.*, 2021). The latter may be particularly important for generating specificity in litter decomposition, as home field advantage was significantly reduced in studies using sterilized litter (Veen *et al.*, 2019). Leaf endophytes may enhance decomposition via priority effects by being in the litter before the arrival of other saprotrophs, initiating fast decomposition of labile compounds and thereby making recalcitrant compounds more accessible to later-arriving decomposers (Fanin *et al.*, 2021). Home field advantage is commonly observed when comparing highly contrasting litters in terms of quality or dominant plant species identity (Veen *et al.*, 2015), suggesting that plant traits and plant community context play an important role in mediating variation in litter-decomposer interactions.

3. From specific decomposer associations to specific effects on plants

The existence of specific decomposer associations does not automatically lead to specific PSFs that either preferentially

enhance or suppress the growth of the species that produced the litter or root exudates. For example, seedlings of any species can benefit from establishing in soil enriched in high-quality litter. However, positive specific PSFs can arise if plant traits modulate competition for nutrients derived from litter or soil organic matter. Fast-growing species can gain a competitive advantage by producing abundant litter or exudates that enhance soil N cycling, and thus outcompete slow-growing species that do not have the capacity for fast uptake of mineralized nutrients (Hofland-Zijlstra & Berendse, 2010; Baxendale *et al.*, 2014). Alternatively, slow-growing plants produce litter with high C : N ratio, causing microbial communities to be strongly limited by N. This leads to an increase in N-use efficiency in decomposer communities, which in turn results in microbial N immobilization, reinforcing plant N limitation (Bråthen *et al.*, 2010; Averill *et al.*, 2014). While the growth of all plant species will be limited, slow-growing species can gain dominance over species with high competitive ability but also high demand for nutrients (de Vries *et al.*, 2015). Further, the simultaneous availability of root exudates and litter modulates microbial succession and creates an additional niche for decomposers specializing on the combination of root exudates and decaying roots (Nuccio *et al.*, 2020). Such interactive effects may cause specific PSFs where the match between the species identity of living roots and litter can modify decomposition and feed back to plant nutrition.

VII. Synthesis: mapping plant–microbial interactions and resulting PSFs onto major axes of variation in plant form and function

If each plant species were to possess and be equally impacted by a host-specific pathogen, the resulting negative specific PSFs would enable co-existence in a clear and consistent way. However, strict host-specificity seems to be uncommon (as shown in Fig. 1), and a wide range of possible PSF outcomes is possible as a result of effective specialization in plant-associated microbiota and as a function of variation in plant traits and community structure.

Our exploration of existing theoretical knowledge and limited empirical examples indicates that soil pathogens, mycorrhizal fungi and decomposers may affect total and specific PSFs via three axes of variation in plant functional traits (Fig. 3). Total PSFs driven by pathogenic interactions should most closely relate to the tissue conservation gradient, with fast-growing species exhibiting higher susceptibility to generalist pathogens and hence more negative total PSF than slow-growing but well-defended species (Lemmermeyer *et al.*, 2015; Semchenko *et al.*, 2018). Decomposer activity is also strongly related to the conservation gradient but is expected to make total PSF more positive for species producing litter and exudates that are richer in nutrients and labile C (Henneron *et al.*, 2020b). Total PSF also varies as a function of root diameter – species with thicker roots are more dependent on fungal collaboration for nutrient uptake (Bergmann *et al.*, 2020) and hence experience more positive total PSF (Cortois *et al.*, 2016; Semchenko *et al.*, 2018).

Dispersal ability may represent a third axis of plant trait variation that could be an important evolutionary driver of PSF (Fig. 3). Efficient dispersal allows pathogen escape and hence releases plants

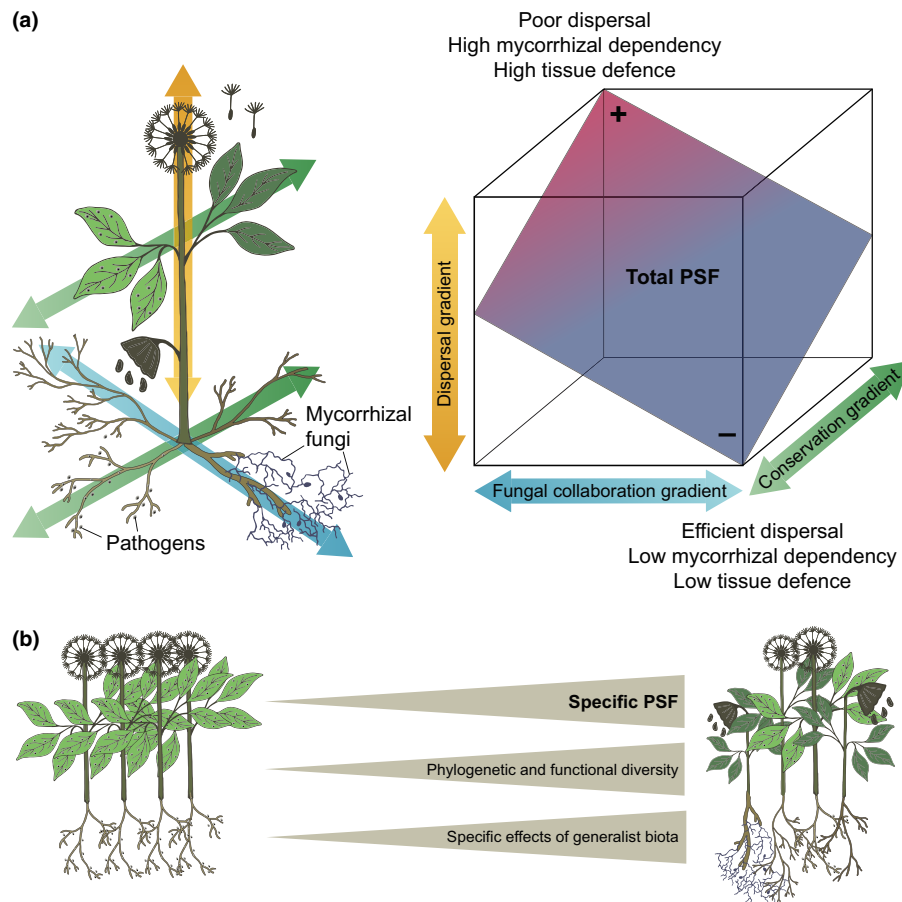


Fig. 3 Mapping plant–soil feedback (PSF) driven by generalist soil microbiota onto major axes of variation in plant form and function. (a) Total PSF should vary along the tissue conservation gradient (green arrow), with species characterized by fast growth but high susceptibility to pathogen attack experiencing more negative PSF than slow-growing species that invest in pathogen defence. However, the ability of fast-growing species to tolerate pathogen damage, and the positive impact on decomposer activity and nutrient cycling via nutrient-rich litter, can make PSF more positive for such species. Total PSF will also vary along the fungal collaboration gradient reflecting the ability of the species to either acquire nutrients independently via an extensive system of fine roots or by outsourcing nutrient uptake to mycorrhizal fungi (blue arrow). Species with high dependence on mycorrhizal symbiosis will experience more positive total PSF than species with low dependence. Lastly, total PSF is expected to vary with dispersal ability (yellow arrow) as efficient dispersal should reduce selection for pathogen defence resulting in negative PSF, while locally dispersed offspring can benefit from the litter decomposition and mycorrhizal network of the mother plant and should experience strong selection for pathogen defence, resulting in more positive PSF. The depiction of a plant with major gradients of trait variation is adopted from Weigelt *et al.* (2021). (b) The potential of the three trait gradients to drive specific PSF is fundamentally dependent on the phylogenetic and functional diversity of biotic communities, with more diverse communities presenting the greatest potential to generate specific feedback effects on plant performance.

from selective pressure for investment into defence, resulting in negative total PSF (Stump & Comita, 2020). By contrast, species with poor dispersal are easy targets for pathogen spread and specialization, and hence will be under selection to invest into tissue protection (Bennett & Klironomos, 2018). Such species also benefit from mycorrhizal networks and litter saprotrophs accumulated underneath mother plants, which counteracts pathogen effects and can shift total PSF in a positive direction (Bergmann *et al.*, 2017; Liang *et al.*, 2021). Clonal dispersal and persistence strategies may also play an important role in shaping PSF, but such relationships remain largely unexplored (D’Hertefeldt & van der Putten, 1998; Klimešová *et al.*, 2021).

Based on these predictions, total PSF will be most negative for fast-growing species with efficient seed dispersal and low dependence on mutualistic associations, while the most positive PSFs will

occur in slow-growing species with poor dispersal and strong reliance on mutualistic associations (Fig. 3). Total PSF may be less negative for fast-growing species due to the beneficial effects of decomposers on nutrient mineralization (Henneron *et al.*, 2020b), and potentially higher tolerance of pathogen attack in this species group (Parker & Gilbert, 2018).

We predict that specific PSFs will change along the same axes of variation in plant traits, but the strength of specific PSFs will be tightly linked to variance in defence levels, mycorrhizal dependency, dispersal ability and litter and exudate properties of co-existing species (Fig. 3). Species susceptible to pathogen attack will experience more negative specific PSF when inhabiting soils of species with high pathogen resistance, but more positive specific PSF will occur if heterospecific neighbours are more susceptible to pathogen attack than conspecifics. The modification of nutrient

cycling by decomposers will make specific PSFs more positive for both fast- and slow-growing species when competing with the opposing resource economic strategy.

The ability to regulate investment into different mycorrhizal partners will further modify specific PSFs. We propose that this ability is inversely related to root diameter. We expect to find a strong ability to control colonization by different fungal partners in plants with thin roots, which allow efficient nutrient uptake in the absence of optimal mutualistic partners. However, strong dependence on mycorrhizal fungi for nutrient provision in species with thick roots is likely to preclude differentiation between fungi and lead to the accumulation of less beneficial fungal partners. As a result, in a community with plants of mixed strategies, thick-rooted species will experience strong positive total PSFs but negative specific PSFs due to more mutualistic mycorrhizal fungi in the rhizosphere of heterospecifics with finer roots than conspecifics.

Plant–soil feedback outcomes are likely to be further modified by interactions between microbial guilds and nonindependent evolution of traits related to tissue conservation and fungal collaboration. For example, EcM fungi are known to not only enhance plant nutrition but also protect plants from pathogen attack, leading to more positive PSF (Bennett *et al.*, 2017; Liang *et al.*, 2021). In addition, plants associating with EcM fungi also tend to invest more into tissue defence than arbuscular mycorrhizal plants, making them even less susceptible to pathogens (Averill *et al.*, 2019). Among plant species associating with AMF, there may be a trade-off between allocation to defensive compounds and investment into mycorrhizal symbiosis (Xia *et al.*, 2021), which may equalize PSFs across the gradient of mycorrhizal dependency. Mycorrhizal fungi can also interfere with saprotroph activity by modifying belowground C transfer and litter decomposition (Kaiser *et al.*, 2015; Smith & Wan, 2019) and competing for nutrients (Averill *et al.*, 2014; Franklin *et al.*, 2014).

Our review highlights that PSF outcomes not only depend on the traits of individual host plants but also on the phylogenetic and functional diversity of co-existing plant species. The extent of pathogen dilution and spillover, the analogous process of accumulation of less beneficial mutualists in the rhizosphere of some hosts, and competitive advantages conveyed by modified nutrient cycling, are all fundamentally dependent on plant community composition (Parker *et al.*, 2015; Cappelli *et al.*, 2020). The net outcome of these interactions will also depend on the overall level of diversity in both plant and microbial communities (Jokela *et al.*, 2000; Thrall *et al.*, 2007; Semchenko *et al.*, 2018). Hence, the role of PSF in local plant community dynamics is likely dependent on the size and composition of plant and microbial species pools, which are in turn shaped by dispersal and environmental filtering, as well as by evolutionary and biogeographical processes (Zobel, 2016; Delavaux *et al.*, 2019). Several global change factors affect ecosystems by causing biodiversity loss and shifts in functional trait composition (Newbold *et al.*, 2015; Bjorkman *et al.*, 2018). Our synthesis of potential drivers of PSF opens up new hypotheses as to how global change may modulate PSF. A reduction in plant functional diversity may lead to reduced potential for generalist-

driven PSFs and their role in equalizing species fitness along major life history trade-offs. However, the wide spread of a few species benefiting from human activity may foster the evolution of pathogen specialization, as has been shown for domesticated crops (Stukenbrock *et al.*, 2007), which can restrict further spread of such plant species and associated biodiversity loss.

VIII. Future directions

1. Knowledge gaps in understanding where and how specialist and generalist interactions drive PSF

Because generalist and specialist plant microbiota potentially affect PSF in distinct ways, identifying the factors that favour one type of association over the other across plant lineages and communities will improve our understanding of how microorganisms modulate plant community dynamics. In communities where generalist interactions prove to be the main driver of PSF dynamics, the focus should shift from properties of individual hosts to the structure and diversity of interacting communities, and thereby to landscape and regional processes that shape these ecosystems.

We also require a deeper understanding of the lifestyles of individual microbial taxa, as well as of their effects on plant performance. A large body of research has already been devoted to identifying factors that drive the distribution and assembly of plant-associated microbiota (e.g. Davison *et al.*, 2015, 2020; Leff *et al.*, 2018; Wang *et al.*, 2019; Maciá-Vicente & Popa, 2021). We still need to integrate this knowledge with the functions that microorganisms play within plant hosts. While achieving this may involve considerable efforts to cultivate, characterize and test individual microorganisms in experimental settings, substantial research is underway to identify microbial traits that can serve as proxies to predict different types of interactions in a more nuanced way than classification into broad ecological guilds (Kia *et al.*, 2017; Levy *et al.*, 2018; Mesny *et al.*, 2021).

2. Predicting PSF from plant traits

While a significant proportion of variation in PSF can be explained with commonly measured traits reflecting investments in mycorrhizal symbiosis and tissue structural defence, it is likely that several critical aspects of plant–microbial interactions are not captured by these traits. Importantly, there appears to be a mismatch between the traits that are commonly measured to predict PSF and the assumption that PSF is driven by host-specific microbiota. Namely, the widely measured plant functional traits (such as tissue density and nutrient content, specific leaf area and root length) are likely to drive interactions with generalist microbiota but may not affect host-specific or specialized interactions. For example, plants have evolved a diverse arsenal of chemical defences and induced responses to natural enemy attack, and the inclusion of these defence mechanisms could result in better predictive models of PSF as a function of host traits (e.g. Marden *et al.*, 2017). Similarly, morphological root traits are unlikely to fully explain variation in partner selectivity in mycorrhizal symbiosis or capture alternative mutualistic interactions with free-living organisms.

Root exudation may be a key process that coordinates plant interactions with antagonistic as well as mutualistic and saprotrophic organisms. It is receiving increasing attention in ecological research, but we still lack a comprehensive understanding of which aspects of exudation may be important in driving PSF. Evidence is accumulating that high root exudation rates are related to the strategy of fast returns on investment (Henneron *et al.*, 2020b; Williams *et al.*, 2022). Exudation is also related to the collaboration axis and may serve as a signalling pathway to establish mycorrhiza or as an alternative strategy to mycorrhizal symbiosis for acquisition of phosphorus (Lambers & Teste, 2013; Williams *et al.*, 2022). Root exudates are also key in host detection by pathogens and rhizobia, as well as in recruitment of free-living mutualistic organisms (Sasse *et al.*, 2018). These complex signalling and nutritional interactions certainly present plants with allocational and evolutionary dilemmas leading to diverse strategies that we are only beginning to disentangle. How such chemical interactions cascade to PSF is a challenging but exciting avenue of future research.







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Author contributions

MS conceived the idea for the review. JGM-V analysed the empirical data on host specificity. KEB performed a literature search on PSF-trait relationships. The manuscript content was developed and written collaboratively by MS, KEB, FTdV, LM, MM and JGM-V.

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Data availability

All data and code are available online at <https://doi.org/10.6084/m9.figshare.19169609>.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Phylogenetic distance among the host plant genera included in the case studies shown in Fig. 1(b).

Fig. S2 Host-specificity of plant-associated fungal guilds estimated by the standardized Kullback–Leibler distance (d).

Methods S1 Analysis of likely host range breadths of plant-associated fungal guilds.

Table S1 Information on the case studies used in the analysis of likely host ranges of plant-associated fungi.

Table S2 Overview of the studies examining the effect of plant traits on plant–soil feedback.

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