

Why are plant–soil feedbacks so unpredictable, and what to do about it?

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Abstract

1. The study of feedbacks between plants and soils (plant–soil feedbacks; PSFs) is receiving increased attention. However, PSFs have been mostly studied in isolation of abiotic and biotic drivers that could affect their strength and direction. This is problematic because it has led to limited predictive power of PSFs in “the real world,” leaving large knowledge gaps in our ability to predict how PSFs contribute to ecosystem processes and functions.
2. Here, we present a synthetic framework to elucidate how abiotic and biotic drivers affect PSFs. We focus on two key abiotic drivers (temperature and soil moisture) and two key biotic drivers (above-ground plant consumers and below-ground top-down control of pathogens and mutualists). We focus on these factors because they are known drivers of plants and soil organisms and the ecosystem processes they control, and hence would be expected to strongly influence PSFs.
3. Our framework describes the proposed mechanisms behind these drivers and explores their effects on PSFs. We demonstrate the impacts of these drivers using the fast- to slow-growing plant economics spectrum. We use this well-established paradigm because plants on opposite ends of this spectrum differ in their relationships with soil biota and have developed contrasting strategies to cope with abiotic and biotic environmental conditions.
4. Finally, we present suggestions for improved experimental designs and scientific inference that will capture and elucidate the influence of above- and belowground drivers on PSFs. By establishing the role of abiotic and biotic drivers of PSFs, we will be able to make more robust predictions of how PSFs impact on ecosystem function.

KEYWORDS

climate, herbivory, litter, plant traits, soil food web, trophic interactions and cascades

1 | THE IMPORTANCE OF PLANT–SOIL FEEDBACKS AND CRITICAL KNOWLEDGE GAPS

Throughout their life spans, plants alter the biotic (e.g., litter decomposers, root herbivores and pathogens, symbionts) and abiotic (e.g.,

nutrient availability, dead organic matter, microclimate) properties of the soil, which alter the performance of plants that subsequently grow in the soil. Such processes are called plant–soil feedbacks (PSFs) (van der Putten et al., 2013). Plant–soil feedbacks may play a critical role in understanding ecosystem functioning, and research efforts in a number of fields are increasingly targeting PSF as a key driver of

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observed processes (Bennett et al., 2017; Mariotte et al., 2018; Teste et al., 2017; van der Putten, Bradford, Brinkman, Voorde, & Veen, 2016). There have been recent calls to investigate how PSFs are contingent on external drivers that either affect plants, soil biota or both (Smith-Ramesh & Reynolds, 2017; van der Putten et al., 2013; Whitaker, Bauer, Bever, & Clay, 2017). This is important because understanding how the strength and direction of PSFs vary according to above- and belowground drivers is critical to predicting ecosystem function, particularly under global change scenarios (van der Putten et al., 2016). However, the impacts of such drivers on PSFs have not been formally integrated into PSF experimental design.

Here, we propose a framework that identifies the impacts of multiple drivers on the major components of PSF; that is, plant roots and shoots, belowground mutualists, root pathogens and herbivores, and litter decomposers. Calls have been made previously to consider the impacts of external factors on PSFs (Smith-Ramesh & Reynolds, 2017; van der Putten et al., 2016) because failure to consider such

factors is likely why so many PSF experiments yield results that are either unpredictable or inconsistent between the glasshouse and the field (Heinze & Joshi, 2018; Heinze, Sitte, Schindhelm, Wright, & Joshi, 2016; Kulmatiski & Kardol, 2008; Kulmatiski, Beard, Stevens, & Cobbold, 2008; Veen, de Vries, Bakker, van der Putten, & Olf, 2014). Here, we make specific predictions about how such drivers might alter the strength and direction of PSFs, including potential interactive effects. Such predictions will assist in the design of better experiments and help to unravel the mechanisms behind how these factors shift PSFs. We focus on two key abiotic drivers (temperature and soil moisture) and two key biotic drivers (aboveground plant consumers and belowground top-down control of root-associated soil biota and litter decomposers) (Figure 1). There are numerous additional external drivers of PSF that are beyond the scope of this paper (Box 1). However, the factors examined in detail here are known drivers of plant and soil organism performance and the ecosystem processes (e.g., nutrient cycling, productivity, carbon sequestration)

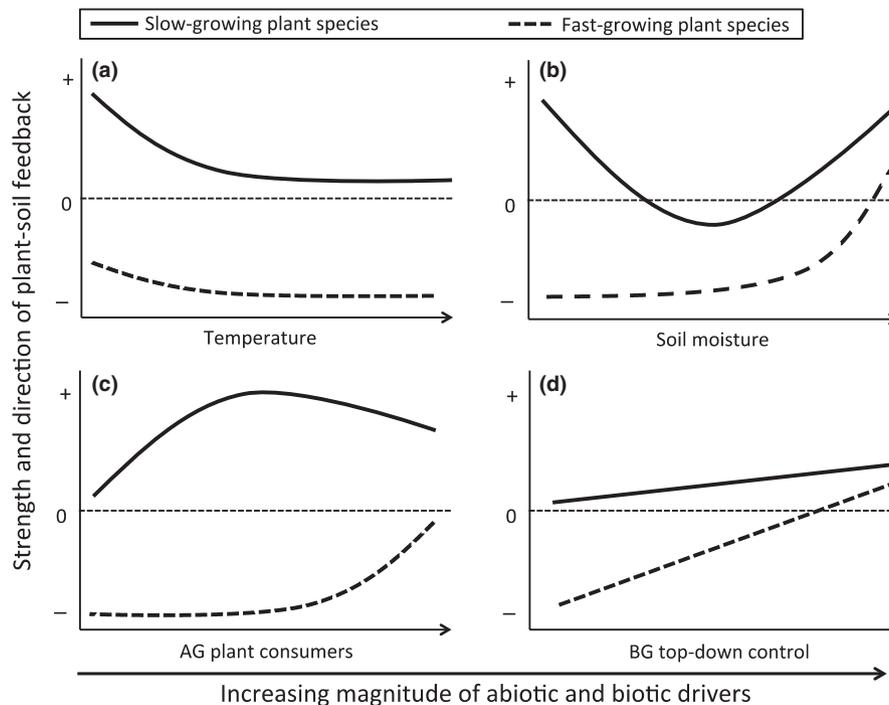


FIGURE 1 Abiotic and biotic drivers of plant–soil feedbacks (PSFs). Diagrams showing how net PSFs might be altered by abiotic (panels a, b) and biotic (panels c, d) drivers. The x-axis shows increases of each driver from left to right (i.e., increasing temperature, moisture, herbivory pressure, belowground top-down control), while the y-axis shows how the *net* PSF is expected to shift (i.e., become more positive, negative, or neutral). Plant species with fast versus slow growth strategies can be expected to show contrasting responses as the influence of a driver increases. (a) Increasing temperatures will result in more negative PSFs to fast-growing plants due to increased pathogen pressure (Burns et al., 2013; Mohan et al., 2014), while slow-growing plants will also experience increasingly negative PSFs due to the loss of mutualists under higher temperatures (Mohan et al., 2014). (b) Increasing soil moisture will lead to less negative PSFs that eventually become positive for fast-growing plants because of increased decomposition and nutrient cycling (Reich, 2014). Slow-growing plants will experience shifts towards positive PSFs as moisture increases because they are adapted to cope with stressful conditions (i.e., too much water) (Fischer et al., 2016). (c) High aboveground plant consumer pressure will decrease negative PSFs for fast-growing plants due to increased nutrient cycling (Sitters & Olde Venterink, 2015). On the other hand, slow-growing plants will experience more positive feedbacks at high rates of herbivory because they are better defended and able to cope with increasing pathogen pressure and inhibited decomposition associated with moderate levels of herbivory (Agrawal & Weber, 2015; Reich, 2014); these benefits will eventually decrease as herbivory pressure becomes too intense. (d) High belowground top-down control will lead to more positive PSFs for both fast- and slow-growing plants due to enhanced nutrient cycling caused by the consumption of root herbivores, pathogens and decomposers (Kulmatiski et al., 2014). However, we expect fast-growing plants to benefit slightly more than slow-growing plants because they are more dependent on high nutrient availability (Reich, 2014). See text for further details on these predictions.

BOX 1 A broader context: additional drivers

The abiotic and biotic factors examined in depth here are not the only potential drivers of PSFs that should be considered in future experiments. Site-specific soil characteristics such as pH and texture will likely affect PSFs. For example, plant-induced shifts in soil pH could drive changes in soil microbial community composition (Fierer & Jackson, 2006), and may result in host-specific microbial pathogen accumulation, thereby increasing negative PSFs (Merges, Balint, Schmitt, Bohning-Gaese, & Neuschulz, 2018). Soil texture can also shape PSFs, with plants showing contrasting feedbacks depending on sand content (Meijer, Holmgren, & Van der Putten, 2011). In addition to soil factors, both natural and anthropogenic disturbances can play a role in shaping PSFs. For example, in many ecosystems fire disturbance is a key driver of plant community composition and abiotic and biotic soil properties. Fire can selectively kill soil organisms such as plant pathogens or mutualists (Bergner, Johnstone, & Treseder, 2004). Therefore, it could take years to millennia for the pre-fire soil communities to recover (Bokhorst, Berg, & Wardle, 2017), resulting in a strong potential for fire to interact with PSFs. However, the effect of fire on PSFs remains untested. Further, changes in land-use that result in increased or decreased disturbance could also shift PSFs. For example, through the intensification of agriculture, organic matter is often lost from the soil (Foster et al., 2003), thereby changing nutrient supplies. Further, shifts from conventional to organic agriculture can have positive effects on soil organisms (Bengtsson, Ahnstrom, & Weibull, 2005) that could affect the capacity of soil communities to alter the strength and direction of PSFs. The discussion above and in the main text highlights that it is important to consider drivers of PSFs and their interactions when designing experiments. However, the selection of drivers must be carefully considered depending on the ecosystem under investigation and the types of questions and spatial and temporal scales addressed. Photo credit: Paul Kardol.

they drive and hence would be expected to be important drivers of PSFs (Andriuzzi & Wall, 2017; Blankinship, Niklaus, & Hungate, 2011; Smith-Ramesh & Reynolds, 2017). We selected these drivers because they are ubiquitous across ecosystems and are strongly associated with pressing ecological concerns (e.g., climate change, sustainable management of soils, trophic cascades), and the substantial research conducted to date allowed us to make robust predictions about how they might drive PSFs under different scenarios.

We explore the impacts of these drivers using the fast- to slow-growing plant economics spectrum. We chose this well-established paradigm because plants on opposite ends of this spectrum differ in their relationships with soil biota and have developed contrasting strategies to cope with abiotic and biotic environmental conditions (Reich, 2014; Wright et al., 2004). Specifically, fast-growing plants generally have more exploitative traits (i.e., higher specific leaf area and specific root length), higher tissue nutrient concentrations and are poorly defended, thereby making them more susceptible to accumulation of pathogens. This runs in contrast to slow-growing plants, which typically are more conservative in their resource acquisition and growth, have lower tissue nutrient concentrations, better tissue defences and invest more in mutualistic relationships with other organisms. As a result, fast-growing plants are typically associated with increased ecosystem productivity, fast nutrient cycling rates, greater and higher rates of nutrient loss and turnover, while slow-growing plants are generally the opposite. Evidence for the plant economics spectrum has been found in both above- and belowground plant organs, and these general patterns can be observed across ecosystems (Díaz et al., 2016; Reich, 2014). Therefore, fast-versus slow-growing plants likely differ in their feedbacks with soil abiotic and biotic factors and will consequently respond differently to drivers that impact on the components of PSF (Cortois, Schröder-Georgi, Weigelt, van der Putten, & De Deyn, 2016) and the resultant effects will likely have contrasting impacts on ecosystem function. Together, our framework assists to better understand the mechanisms behind these above- and belowground drivers, highlights the critical knowledge gaps regarding their contributions to PSFs and proposes a stepwise procedure by which to test the importance of these drivers under both glasshouse and field conditions.

2 | ABIOTIC DRIVERS

2.1 | Temperature

Plants and soil organisms respond differently to changes in temperature, either along latitudinal (De Frenne et al., 2013) or elevational gradients (Sundqvist, Sanders, & Wardle, 2013), as well as due to climate change (Classen et al., 2015). Abiotic stressors such as temperature have been shown to strengthen the effects of both pathogens and mutualists on plant performance (Pineda, Dicke, Pieterse, & Pozo, 2013), which will alter the strength and direction of PSFs. For example, under cold conditions with slow recycling of nutrients, plants may be more dependent on symbiotic soil biota for acquisition of nutrients. This might lead slow-growing plants to allocate

more resources to soil mutualists via higher root exudation (van der Heijden, Bardgett, & van Straalen, 2008). Under warmer conditions, the activity of arbuscular mycorrhizal fungi (AMF) is expected to decrease (Mohan et al., 2014). This may weaken positive PSFs, particularly for slow-growing species that are most dependent on mycorrhizae (Figure 1a). Increased temperatures are also expected to increase prevalence of soil pathogens because pathogen life cycles will be shortened (Chakraborty, 2013). This could promote the build-up of root pathogens, leading to more negative PSFs, particularly in fast-growing plant species that are typically less well-defended than slow-growing species (Agrawal & Weber, 2015). However, the direct effects of temperature on PSFs might be context-dependent (van Grunsven, van der Putten, Bezemer, & Veenendaal, 2010), and more research is needed to determine whether or not general patterns exist concerning the effects of temperature on PSFs.

Temperature can also affect soil organism activity, and thereby nutrient cycling and decomposition rates. High temperatures generally increase bacterial, but decrease fungal, activity, leading to lower fungal to bacterial ratios (Cregger, Sanders, Dunn, & Classen, 2014) and increased rates of nutrient cycling (Burns et al., 2013). This can result in positive plant–litter feedbacks (plant above- and belowground litter can feedback to impact on plant performance after it senesces), generating greater nutrient uptake by plants and resultantly higher quality litter, especially for fast-growing species that prefer high nutrient levels (Reich, 2014). Consequently, high-quality litter may strengthen “home field advantage effects” (i.e., accelerated breakdown of a plant’s litter in the vicinity of where a plant originates (vs. away from where it originates) due to the presence of specialised decomposers) by increasing the competition between decomposer organisms. This may lead to specialisation in decomposer communities, which may selectively benefit fast-growing plants that typically produce high-quality litter (Austin, Vivanco, González-Arzac, & Pérez, 2014). Under global warming, positive PSF effects through increased nutrient cycling may decrease when organisms adapt to warmer soils or undergo community shifts (Cregger et al., 2014).

Overall, increasing temperature should have a positive impact on nutrient cycling and pathogen build-up, but a negative impact on the activity of mutualists. As a result, slow-growing plants could experience reduced positive PSF under higher temperatures, while fast-growing species may experience increased negative PSF, but this might be compensated by increased nutrient availability provided via the plant–litter feedback pathway (Figure 1a).

2.2 | Moisture

Plants and soil organisms are strongly affected by changes in soil moisture. Generally, AMF favour plant growth under drier conditions because of their ability to assist in water uptake (Mohan et al., 2014) and similar effects have been found for rhizobacteria, which may assist with water retention and water usage efficiency (Rubin, van Groenigen, & Hungate, 2017). If changes in soil moisture affect how plants interact with mutualists and pathogens, this could

affect the soil biota they leave in the soil, thereby affecting future PSFs. For example, more positive PSFs might occur under drought, particularly for slow-growing plants that heavily rely on and invest in soil mutualists (Reich, 2014) (Figure 1b). Further, soil pathogens are generally more diverse and abundant in moist than dry ecosystems (Tedersoo et al., 2014). This may generate increasingly negative PSFs with higher soil moisture. Changes in soil moisture that affect pathogens may be short-lived because pathogens can adapt quickly to moisture conditions (Chakraborty, 2013). Yet, plants may become increasingly susceptible to soil pathogens under moisture extremes (Suzuki, Rivero, Shulaev, Blumwald, & Mittler, 2014), resulting in increased negative PSFs (Kaisermann, de Vries, Griffiths, & Bardgett, 2017; van der Putten et al., 2016).

Moisture also has the potential to affect litter decomposition and nutrient cycling rates. Decomposition is usually slow under very wet (Wiedermann, Kane, Potvin, & Lilleskov, 2017) or dry conditions (Vogel, Eisenhauer, Weigelt, & Scherer-Lorenzen, 2013), which could result in lower soil nutrient availability to plants and hence the production of lower-quality root and shoot litter at the extreme ends of the moisture gradient (Reich, 2014). This could result in more negative plant–litter feedbacks for fast-growing plants that are more dependent on high nutrient inputs and less able to tolerate harsh conditions (Figure 1b). Further, droughts are usually followed by a nutrient pulse upon rewetting (Bloor & Bardgett, 2012), which can neutralise negative PSFs due to increased nutrient availability (Fry et al., 2018). However, in soils that are adapted to long periods of drought, PSFs may be unaffected (Meijer et al., 2011). In addition, flooding could disrupt plant–litter feedbacks. Slow-growing plants tend to be more resistant to flooding than fast-growing plants (Fischer et al., 2016). If slow-growing species thrive post-flood, more recalcitrant root and shoot litter inputs to the soil could generate PSFs that further favour these species (Figure 1b).

Overall, fast-growing plants should experience negative feedbacks under drought conditions that become more positive with increasing moisture levels due to faster decomposition rates and increased nutrient availability (Figure 1b). On the other hand, slow-growing plants could experience the most positive feedbacks under moisture extremes because they profit more from relationships with mutualists under drought and they have traits that could allow them to better cope with flooding (Figure 1b).

3 | BIOTIC DRIVERS

3.1 | Aboveground consumers

Increasing pressure of aboveground consumers such as herbivores and foliar pathogens could further drive PSFs. Aboveground consumers can induce plant species-specific shifts to soil microbial communities through changes in root exudation (Jones et al., 2015), which may lead to suppression of root herbivores and pathogens through root defence compounds (Agrawal & Weber, 2015). This may result in overall positive PSFs for fast-growing

plant species that are typically less well-defended against belowground consumers (Chen, Christensen, Nan, & Hou, 2017). In contrast, aboveground consumers can also decrease root defence compounds and allow for the proliferation of root pathogens (Kostenko, van de Voorde, Mulder, Putten, & Bezemer, 2012). Under this scenario, slow-growing plants might be better able to cope with this increased pathogen load due to their inherently higher chemical and structural defences, thereby neutralising potential negative PSFs (Figure 1c). Long-term moderate grazing by vertebrate herbivores can change plant community composition and nutrient availability, which could benefit mutualists like AMF (Ren et al., 2018). Legacies of increased AMF in the soil could benefit the next generation of plants, particularly obligate mycorrhizal species, as is often the case with slow-growing plants. However, increases in plant defence compounds as the result of aboveground pathogens may also inhibit mutualists (Ballhorn, Younginger, & Kautz, 2014).

Aboveground consumers may speed up soil nutrient cycling by consuming recalcitrant plant biomass, and returning more labile dung and frass to the soil (Sitters & Olde Venterink, 2015). Foliar pathogens may also increase plant root and shoot litter quality (due in part to premature abscission of leaves or nutrient-rich fungal tissue in infected leaves) (Butenschoen & Scheu, 2014), leading to more nutrients released during decomposition and more positive PSFs through the plant-litter feedback pathway (Figure 1c). Both scenarios could favour plant nutrient uptake and thereby improve litter quality, particularly of fast-growing plants, resulting in accelerated nutrient cycling and positive plant-litter feedbacks (Chen et al., 2017) (Figure 1c). However, overgrazing or selective grazing can remove nutritious plants from the system, leaving plants of poorer quality, thereby inhibiting decomposition rates (Sitters & Olde Venterink, 2015) and leading to less positive PSFs. Both herbivores and foliar pathogens can also affect PSFs by inducing plant defence, resulting in increased levels of secondary compounds in plant root and shoot litter. This makes the litter unattractive to saprotrophic microbes and soil fauna (Chomel et al., 2016) and reduces positive PSF effects via the plant-litter feedback pathway. Recent research also showed that plants can experience negative plant-litter feedbacks due to leaf litter harbouring a pathogenic phyllosphere (Whitaker et al., 2017). Finally, changes induced by aboveground herbivores to root exudation patterns (Olsen et al., 2011) could change the strength and direction of PSFs.

Overall, we expect that PSFs for fast-growing plants should become less negative with increasing aboveground consumer pressure due to increased nutrient cycling rates and induced defence. These combined effects may help them cope with increased root pathogen pressure (Figure 1c). In contrast, slow growers might experience neutral feedbacks at low aboveground consumption and increasingly positive feedbacks at moderate consumption rates, with a decrease in feedbacks eventually occurring as grazing pressure becomes too high (Figure 1c). This is because slow-growing plants are typically able to cope with increased soil pathogen pressure that occurs with grazing, while simultaneously able to take

advantage of increases in AMF usually associated with moderate grazing.

3.2 | Belowground top-down control

Finally, evidence is accumulating that predation of rhizosphere organisms integral to PSFs can play an important role in plant performance (Schuldt et al., 2017). In many experiments, the soil food web has been treated as a black box, thereby hindering our ability to determine the role of belowground trophic interactions on PSFs. However, top-down control of soil organisms could shift the strength and direction of PSFs. For example, top-down control may occur when predators directly consume soil pathogens (Kulmatiski et al., 2014), or when higher trophic-level organisms, such as earthworms, consume the litter where pathogens lie dormant in the soil (Meyer-Wolfarth, Schrader, Oldenburg, Weinert, & Brunotte, 2017). Top-down control of soil mutualists such as mycorrhizae (Jonas, Wilson, White, & Joern, 2007) could also dampen positive PSFs. Conversely, consumption of soil pathogens (Löbmann et al., 2016) could reduce negative PSFs, as pathogens would not be allowed to build up in the soil over time. The elimination of pathogens via top-down control would be more beneficial to fast-growing plants that are typically more susceptible to pathogen attack (Agrawal & Weber, 2015) (Figure 1d). However, a recent meta-analysis revealed that the impact of belowground predators on plant performance tended to be positive, irrespective of whether the predators consumed soil pathogens or mutualists (Kulmatiski et al., 2014). This unexpected finding was explained by predator-mediated nutrient release in the vicinity of the root system, which benefited the plants. Such top-down control would disproportionately favour fast-growing plants, which could rapidly exploit these resources, thereby generating a positive feedback of faster nutrient cycling (Figure 1d).

The plant-litter feedback pathway can also be affected by belowground top-down control. Predatory arthropods that prey on root and shoot litter consumers have been shown to negatively impact on decomposition (Liu, Chen, He, Hu, & Yang, 2014). In contrast, top-down control of certain fungi by isopods allows for the competitive release of other litter-decomposing fungi and bacteria, which may lead to increased decomposition rates (Crowther et al., 2013). Furthermore, if predators selectively consume decomposers that target certain litter types (García-Palacios, Maestre, Kattge, & Wall, 2013), this might nullify home field advantage effects.

Overall, increasing top-down control on soil biota should result in positive feedbacks for both fast- and slow-growing plants (Figure 1d). This is because both types of species will probably benefit from enhanced nutrient cycling, which would speed up the plant-litter feedback pathway, and the consumption of pathogens (Figure 1d). However, we expect that fast-growing plants might benefit more from belowground top-down control than slow-growing plants (i.e., the slope of the line in Figure 1d is steeper for fast- than for slow-growing plants).

4 | INTERACTIONS AND THE RELATIVE IMPORTANCE OF SCALE

To make robust predictions about how PSFs affect ecosystem function in natural systems, the net impact of above- and belowground drivers on PSFs and the effect of each driver and their interactions should be considered together (Figure 2). For example, climate change could alter temperature and precipitation patterns in ways that might affect biotic interactions and reorder the relative importance of the drivers of PSFs (van der Putten et al., 2016). Increased temperature could result in greater importance of top-down control of soil organisms (Crowther et al., 2015), thereby suppressing soil pathogens and mutualists and affecting PSFs. Additionally, temperature and precipitation increases could benefit aboveground pathogens (Chakraborty, 2013), which could affect how this driver affects PSFs. Collectively, interactions between the abiotic and biotic drivers could have synergistic, additive or antagonistic effects on the net outcome of PSFs. Therefore, disentangling how such interactions manifest under natural conditions, and thereby translate to impacts on ecosystem function, is an important research frontier, which so far has received little attention (Heinze & Joshi, 2018). Here, our a priori model (Figure 2) and our stepwise research procedure (Figure 3) provide a starting point for the design of future experiments that seek to disentangle the role of above- and belowground drivers of PSFs.

Further, the relative importance of single and interactive effects of abiotic and biotic drivers on PSFs depends on the spatial and temporal scales. Drivers that operate at larger spatial scales have the potential to change the components of PSF at the ecosystem level, but how these drivers interact with other drivers across scales might vary. For example, vertebrate herbivores will likely influence PSFs at larger spatial scales (Egelkraut, Kardol, De Long, & Olofsson, 2018) than aboveground insect consumers (Heinze & Joshi, 2018) when considered individually, but competition between vertebrate and invertebrate herbivores might interact to influence PSFs (Branson & Haferkamp, 2014). Plant–plant interactions, such as competition and facilitation, should also be taken into account (Box 2). Therefore, the spatial context under which drivers are considered would determine their relative importance for shaping PSFs. Furthermore, the temporal scale considered could affect the strength and direction of above- and belowground drivers and their impacts on PSFs. For example, the duration of drought events could have differential effects on decomposer organisms versus pathogens (van der Putten et al., 2016). Finally, temporal changes (i.e., seasonal fluxes) that reorder the relative importance of the drivers of PSFs are bound to occur. Nonetheless, how different spatial and temporal scales affect the drivers of PSFs has rarely been tested and hence should be considered alongside the above- and belowground drivers proposed here.

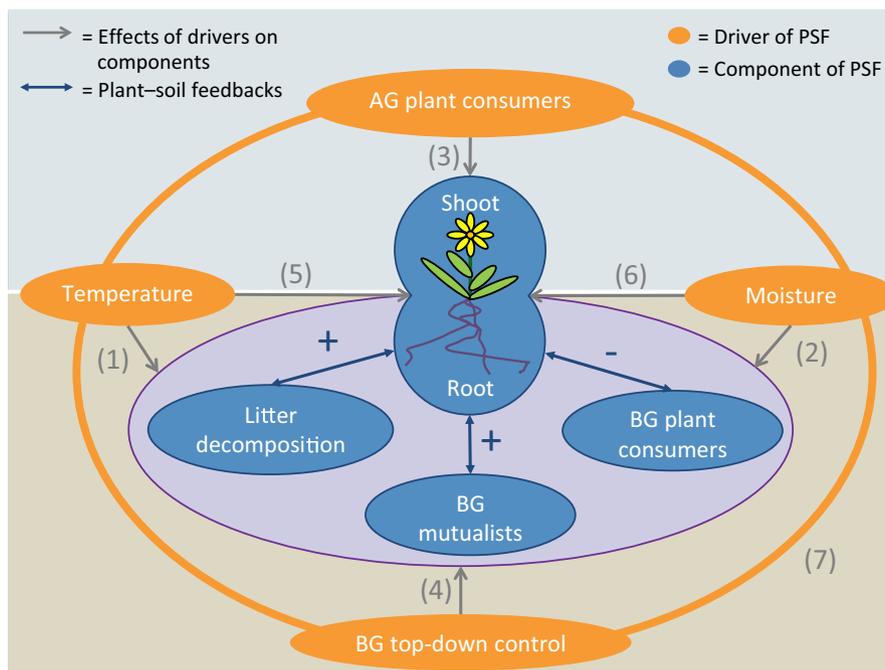


FIGURE 2 A priori model of how abiotic and biotic drivers affect plant–soil feedbacks (PSFs). Drivers such as temperature (1), moisture (2), aboveground (AG) plant consumers (3), belowground (BG) top-down control (4) impact on components of plant–soil feedbacks, for instance, BG mutualists, BG plant consumers, litter decomposition. The orange ovals show the abiotic and biotic drivers of the components of PSFs, which are shown in blue ovals. Subsequently, the components of PSFs control whether or not the feedback response is positive or negative. Temperature, moisture and aboveground plant consumers could also impact directly on plant performance (5, 6, 7). Importantly, all of the abiotic and biotic drivers could interact with one another (8; circle connecting the drivers), which could affect the way each driver impacts on the components of PSFs. This a priori model provides a starting point for new experimental designs that seek to disentangle the relative importance and interactions between these drivers for controlling PSFs

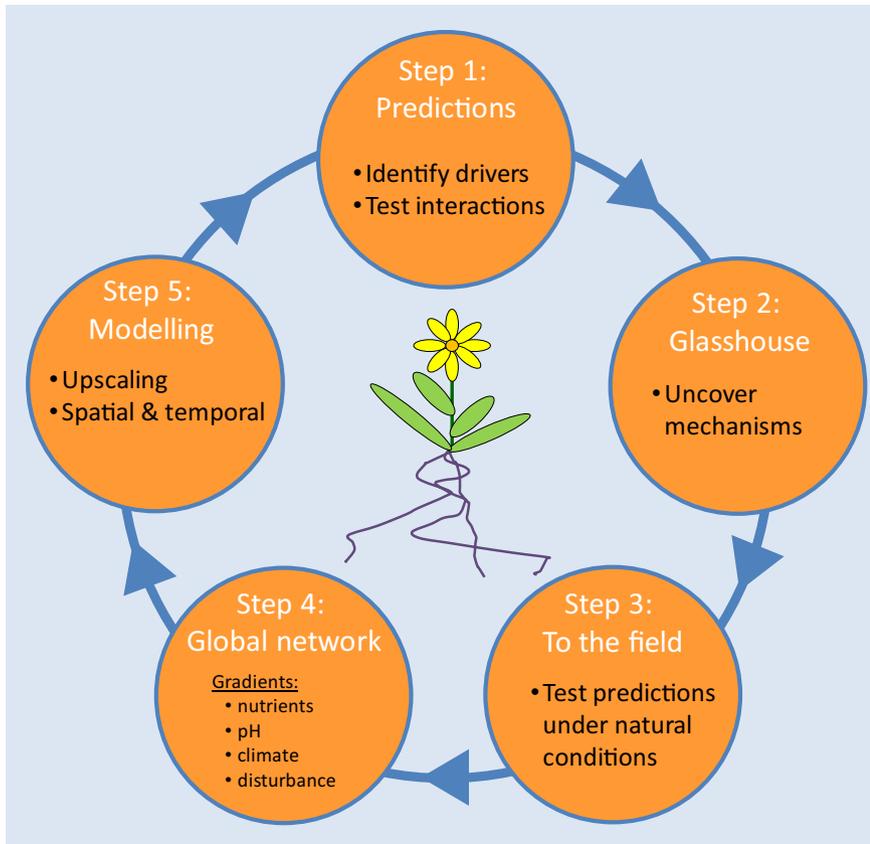


FIGURE 3 Schematic showing how our framework could be applied to the design of experiments to better predict plant–soil feedbacks (PSFs). In the first step, predictions will be made as to how the drivers of PSF and their interactions will influence PSFs. In the second step, under controlled, glasshouse conditions, the strongest drivers will be determined and their mechanisms identified. In the third step, predictions will be tested under natural field conditions. In the fourth step, global networks will be established that seek to understand how the drivers of PSFs operate across environmental gradients. Finally, in the fifth step, global data on PSFs can be used to develop and test models, allowing for the upscaling and better predictive power, thereby initiating the stepwise research procedure anew

5 | THE WAY FORWARD

Application of our framework of above- and belowground drivers of PSFs will allow us to obtain a better understanding of how each individual driver, as well as their interactions, alters PSFs. Here, we showed several abiotic and biotic drivers that are important in controlling the components of PSF. Although recent conceptual advances to understanding these drivers have been made, we now need to test the framework presented here with new experimental designs incorporating the multiple drivers of PSFs. Inclusion of drivers that have hereto largely been ignored in PSF research will ensure that a complete, “real world” picture of PSFs is generated and will likely help explain why so many PSF experiments yield unexplainable or irreproducible results.

Specifically, using our a priori model as a guide (Figure 2), we make a call for the following stepwise research procedure, that can be applied to PSF research in order to formally integrate the drivers of PSF into experimental designs and thereby increase our predictive capacity (Figure 3): (1) Test which of the drivers induce the strongest individual or interactive impacts on PSFs. Controlled experiments that seek to identify important drivers and then disentangle interactions between multiple drivers of PSF simultaneously need to be developed based on our current knowledge; (2) Unravelling the mechanisms behind the drivers of PSFs under controlled, glasshouse conditions. For example, using a trait-based approach in PSF research in the context of external drivers would be a good starting point (Cortois et al., 2016; Ke, Miki, & Ding, 2015).

Experiments that involve explicitly identifying and potentially manipulating the soil organisms responsible for PSFs alongside external drivers will generate a better understanding of how the soil community drives PSFs (Kardol, Veen, Teste, & Perring, 2015); (3) Once the strongest drivers and their mechanisms are identified, the next step is to examine these drivers in the field. PSFs detected in the glasshouse often do not manifest under natural conditions (Heinze et al., 2016; Kulmatiski & Kardol, 2008; Kulmatiski et al., 2008). This is because glasshouse studies typically do not account for external drivers of PSFs (but, see Kaisermann et al., 2017; Fry et al., 2018). Therefore, taking above- and belowground drivers that affect PSFs in the glasshouse and then setting them to interact with other drivers in the field is the only way to fully understand their importance in driving PSFs in natural ecosystems; (4) Conduct PSF experiments across large-scale nutrient, pH, climate and disturbance gradients by setting up global networks across ecosystems that investigate how above- and belowground drivers affect PSFs. The power of existing long-term global experimental networks, such as NutNet (Borer et al., 2014) or ITEX (Arft et al., 1999), should be harnessed and incorporated into future PSF research. For example, combining new experimental work alongside data that have already been collected on plant community composition across these networks could allow us to follow back plant species’ abundance over time, thereby potentially identifying key drivers of PSFs retroactively, once the mechanisms are better understood. Executing PSF experiments across gradients has been proposed previously (Smith-Ramesh & Reynolds, 2017), but not with explicit exploration

BOX 2 Plant–plant competition



There is accumulating evidence that plant–plant competitive interactions can result in changes to patterns of plant dominance and diversity (Klironomos, 2002; Teste et al., 2017). Therefore, competitive interactions with neighbouring species are probably important drivers of PSFs. Despite this, the importance of neighbouring species in driving PSFs is rarely included in PSF experiments (Bezemer, Jing, Bakx-Schotman, & Bijleveld, 2018; Kaisermann et al., 2017; Kardol, Cornips, van Kempen, Bakx-Schotman, & van der Putten, 2007). A recent meta-analysis demonstrated that competitive interactions can eclipse the direct effects of PSFs and that the identity (i.e., intra- vs. interspecific) and density of the neighbouring plants need to be considered (Lekberg et al., 2018). This is surprising because negative PSFs could be enhanced if interspecific competitors were more affected by the build-up of root pathogens or herbivores than the focal species (Shannon, Flory, & Reynolds, 2012). Further, in mixed plant communities where functionally different species tightly coexist, the identity of neighbouring species may not only determine the strength of PSFs through resource competition, but also indirectly through their respective effects on soil biota (Teste et al., 2017). Conversely, plant–plant interactions might also take on a facilitative effect due to increased colonisation of mycorrhizae when a species is grown in the vicinity of more conspecifics (Casper & Castelli, 2007). Such interactions could have far-reaching consequences for plant community assembly by accelerating successional development if negative intraspecific feedbacks and positive interspecific feedbacks occur concurrently (van de Voorde, van der Putten, & Bezemer, 2011). Hence, the strength of feedbacks may be overestimated when plants are grown in isolation from interspecific competitors, as moderating influences of neighbours are ignored. This leads to incorrect conclusions about how PSFs might change plant community assembly and ecosystem function. Photo credit: Paul Kardol.

of external drivers; and (5) Finally, using the global data collected to develop ecological mathematical models (e.g., biogeochemical models) will allow us to scale up our findings and make robust, comprehensive predictions about how the drivers of PSF will influence ecosystem processes (e.g., plant community composition shifts, decomposition, formation of soil organic matter, nutrient cycling) at larger, ecologically meaningful spatial and temporal scales. The stepwise procedure highlighted here can be systematically and continuously applied to design more predictive PSF experiments (Figure 3).

AUTHORS' CONTRIBUTIONS

J.R.D.L., E.L.F., G.F.V. and P.K. conceived the idea. J.R.D.L. led the writing of the manuscript, and all authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

This manuscript does not use data.

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SUPPORTING INFORMATION

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