

## ECOSYSTEMS, EVOLUTION AND PLANT–SOIL FEEDBACKS

# Where, when and how plant–soil feedback matters in a changing world

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### Summary

1. It is increasingly acknowledged that plant–soil feedbacks may play an important role in driving the composition of plant communities and functioning of terrestrial ecosystems. However, the mechanistic understanding of plant–soil feedbacks, as well as their roles in natural ecosystems in proportion to other possible drivers, is still in its infancy. Such knowledge will enhance our capacity to determine the contribution of plant–soil feedback to community and ecosystem responses under global environmental change.

2. Here, we review how plant–soil feedbacks may develop under extreme drought and precipitation events, CO<sub>2</sub> and nitrogen enrichment, temperature increase, land use change and plant species loss vs. gain. We present a framework for opening the ‘black box of soil’ considering the responses of the various biotic components (enemies, symbionts and decomposers) of plant–soil feedback to the global environmental changes, and we discuss how to integrate these components to understand and predict the net effects of plant–soil feedbacks under the various scenarios of change.

3. To gain an understanding of how plant–soil feedback plays out in realistic settings, we also use the framework to discuss its interaction with other drivers of plant community composition, including competition, facilitation, herbivory, and soil physical and chemical properties.

4. We conclude that understanding the role that plant–soil feedback plays in shaping the responses of plant community composition and ecosystem processes to global environmental changes requires unravelling the individual contributions of enemies, symbionts and decomposers. These biotic factors may show different response rates and strengths, thereby resulting in different net magnitudes and directions of plant–soil feedbacks under various scenarios of global change. We also need tests of plant–soil feedback under more realistic conditions to determine its contribution to changes in patterns and processes in the field, both at ecologically and evolutionary relevant time-scales.

**Key-words:** biodiversity loss, carbon and nutrient cycling, climate change, community composition, invasive plants, land use, plant–soil feedback triangle, range expansion

### Introduction

There is increasing awareness that interactions between plants and the biotic and abiotic properties of soil may play an important role in structuring plant and above-ground communities, and also ecosystem responses to environmental change (Ehrenfeld, Ravit & Elgersma 2005;

Bardgett & Wardle 2010). These plant–soil feedbacks (PSFs; Bever 1994) may contribute to succession in plant communities, invasiveness and coexistence (Van der Putten, van Dijk & Peters 1993; Klironomos 2002; Bever 2003), with consequences for carbon and nutrient cycling (Ehrenfeld, Ravit & Elgersma 2005; Lee, Flory & Phillips 2012). Experimental evidence of PSFs is accumulating rapidly for a wide range of biomes (Van der Putten *et al.* 2013). However, we lack an explicit understanding of the

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mechanisms that determine the PSFs, especially in the context of global environmental change, and how in more realistic field settings PSFs could interact with other factors that are known to shape plant community composition and function. Resolving these issues will improve predictions of the contribution of biotic PSFs to phenomena observed *in situ*.

The three main categories of soil biota that shape PSF are enemies (microbial soil pathogens, herbivorous nematodes, insect larvae and other invertebrates), symbionts (mycorrhizal fungi, non-mycorrhizal endophytic fungi, endophytic bacteria, nitrogen-fixing microbes and plant growth-promoting micro-organisms in the rhizosphere) and decomposers (organisms involved in carbon and nutrient cycles that break down litter, root exudates and soil organic matter) (Wardle 2002). Each can influence plant growth directly, and indirectly through their influence on soil physico-chemical properties, such as pH, organic matter content, water holding capacity, temperature and soil structure (Ehrenfeld, Ravit & Elgersma 2005). Although the net effects of soil biota on plants are increasingly understood, their individual contributions to a 'black box' of soil effects are not well resolved. The contribution of PSF to processes in the field is often deduced, with some exceptions (Casper & Castelli 2007), from short-term experiments under highly controlled conditions. For example, there is little direct evidence for the role played by soil-borne pathogens in plant coexistence (Mordecai 2011). In actuality, the role of PSF is probably only one of several components that contribute to the temporal dynamics of dominant plant species in secondary vegetation succession (Van de Voorde, van der Putten & Bezemer 2012), and the strength of PSF is not constant across environmental gradients (Kardol *et al.* 2013), including those induced by global changes.

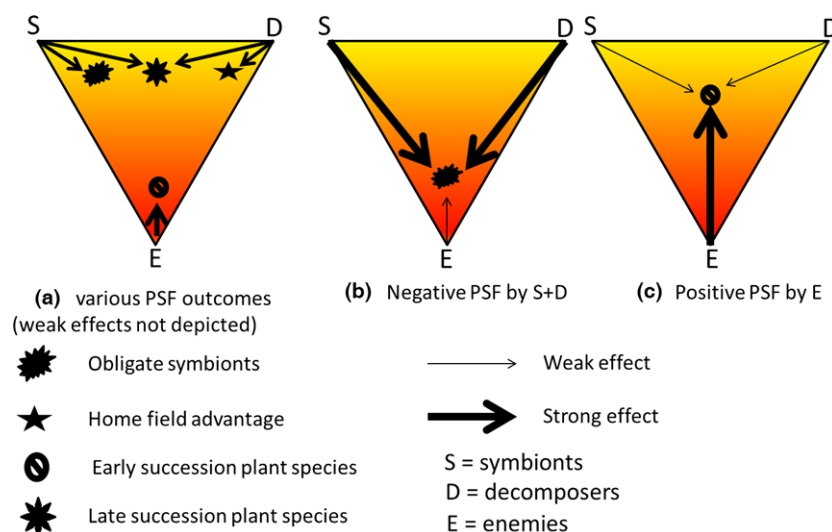
A number of recent overview studies have discussed PSF in relation to climate change (Van der Putten 2012; Bardgett *et al.* 2013; Classen *et al.* 2015), ecological restoration following land use change (Kardol & Wardle 2010) and invasions (Reinhart & Callaway 2006; Bever *et al.* 2010). To predict how PSFs develop under these environmental changes, the underlying components need to be dissected and studied separately, because the various soil organisms might show individual response rates to the global change factors (Bardgett *et al.* 2013; Classen *et al.* 2015). These individual responses need to be understood to predict the temporal and spatial dependence of global change effects on the composition and functioning of ecosystems as mediated by PSF. It follows that predicting how PSF contributes to community and ecosystem responses in the real world also requires understanding its effect relative to other factors that can also drive plant community composition, for example grazing (Veen *et al.* 2014), pollination (Bronstein 2009), above-ground endophytes (Rudgers & Orr 2009), soil fertility (Wardle, Walker & Bardgett 2004), soil type and water availability (Wardle 2002; Yelenik & Levine 2011).

Here, we discuss how to further open the black box of soil biota contributions to PSF and how to assess the proportional role of PSF in shaping the composition of communities and the functioning of ecosystems. We explore how PSF may influence changes in community composition and ecosystem processes in a world that is rapidly changing as a consequence of human activities. Our first aim is to propose a framework that integrates the contributions of the three categories of soil biota (enemies, symbionts and decomposers) to PSF, and to use that framework to evaluate possible shifts in net PSF effects under the various types of environmental change. Our second aim is to place PSF into context with other drivers that may structure plant community composition and functioning. We focus on extreme drought and precipitation events, CO<sub>2</sub> and nitrogen enrichment, temperature increase, land use change and plant species loss vs. gain, because these are among the major world-wide environmental drivers of changes in terrestrial ecosystems. We do not include abiotic PSFs, as these are subject of another contribution in the present volume (de la Peña *et al.* 2016).

### The plant–soil feedback triangle

We present a triangular framework inspired by the plant disease triangle (Francel 2001), combined with Grime's concept of plant strategies (Grime 1979). In our PSF triangle, net effects are the result of plant interactions with soil-borne enemies, symbionts and decomposers that are represented by the three corners of the triangle (Fig. 1a). The triangle points down with the bottom corner representing enemies, which corresponds to their contribution to negative PSF. Symbionts and decomposers generally result in positive PSF (Ehrenfeld, Ravit & Elgersma 2005) and occupy the top two opposing corners. Plant species positioned in the downward side of the triangle are strongly controlled by soil-borne pathogens, or negative effects of symbionts and decomposers (Johnson, Graham & Smith 1997; Laliberté *et al.* 2015; Mazzoleni *et al.* 2015) (Fig. 1b). Enemies may cause less negative PSF effects when, for example, root herbivores promote root exudation and mineralization (Bardgett, Denton & Cook 1999), which could result in increased nutrient uptake. In that case, plant species move up the triangle (Fig. 1c). Finally, the strength of the contribution of symbionts, decomposers and enemies to PSF may be visualized by arrow thickness (Fig. 1b,c).

The PSF of plant species with a life cycle strongly dominated by soil pathogens and root herbivores, such as early succession weed species (Kardol, Bezemer & van der Putten 2006), early succession forest trees (e.g. *Prunus serotina*; Packer & Clay 2000), low-abundance grassland plants (Klironomos 2002) and low-abundance trees (Mangan *et al.* 2010; Johnson *et al.* 2012) all have been shown to be negative, so these are positioned in the bottom section of the triangle. Strength of PSF can vary among plant species, which will be visualized by arrow thickness. Mycor-



**Fig. 1.** The plant–soil feedback (PSF) triangle as inspired by plant disease triangle (Francel 2001) and plant strategies (Grime 1979) approaches. Positions at the PSF triangle may represent individual plant species, or entire plant community feedback values, which can vary from positive (top) to negative (bottom). The contributions from symbionts, decomposers and enemies to the PSF values are indicated by arrows of which the length and thickness indicates their proportional contribution to the PSF effect: short and thick arrows represent strong effects, whereas long and thin arrows represent weak effects. Horizontally, PSF values do not differ in sign and strength, but the contribution of symbionts, decomposers and enemies to the PSF effect differs. (a) Positive and negative PSF values caused by dominant enemy, symbiont and decomposer effects, or by a combination of symbionts and decomposers. (b) Negative PSF values may be caused by parasitic symbionts or toxic decomposer effects, which can reduce growth and fitness of the host plants. (c) Positive PSF values may be caused by low levels of root enemies, which could stimulate compensatory growth of the host plants.

rhizal-dependent, or nitrogen fixation-dependent plant species are situated in the section close to the symbiont corner. Examples of highly mycorrhizal-dependent plant species are coniferous trees from the pygmy forest that short-circuit the nitrogen cycle by ectomycorrhizal fungi (Northup *et al.* 1995), plant species from calcareous grasslands that depend on arbuscular mycorrhizal fungi (AMF) for phosphorous uptake (Van der Heijden *et al.* 1998), as well as plant species from serpentine soils (Casper & Castelli 2007), drylands, and other extreme environments. Plant species that experience so-called home-field advantage of decomposing litter (Ayres *et al.* 2009), such as some tree species (Veen *et al.* 2015), or species that produce litter more similar to the average litter quality (Freschet, Aerts & Cornelissen 2012) will also be nearer the top of the PSF triangle, but close to the decomposition corner. Again, arrow thickness will visualize the strength of the contribution of each group of soil biota to the PSF effect.

## Plant–soil feedbacks and global changes

### INCREASED EXTREME DROUGHT AND PRECIPITATION EVENTS

One of the expected consequences of global environmental change is that extreme drought and precipitation events increase in frequency and intensity in most areas around the globe (Jentsch, Kreyling & Beierkuhnlein 2007; IPCC 2013). Such changes in precipitation will not only affect

plant growth and plant community composition directly (Kardol *et al.* 2010a; Wu *et al.* 2011; Yang *et al.* 2011; Hoepfner & Dukes 2012), but will also alter the activity and community composition of soil organisms (Fierer, Schimel & Holden 2003; Eisenhauer *et al.* 2012; Barnard, Osborne & Firestone 2013). Drought generally reduces the rate at which soil processes occur, as well as the abundances of soil biota (e.g. Kardol *et al.* 2010b). Fast-growing soil organisms, and those from higher trophic levels, are more susceptible to drought than slow-growing soil organisms and those from lower trophic levels (Van Gestel, Merckx & Vlassak 1993; Lindberg & Bengtsson 2006). Moreover, drought reduces the role of fungi and increases the role of bacteria in the soil food web. As fungi usually are more conservative in their resource use, drought will result in more C and N losses from the soil (De Vries *et al.* 2012a).

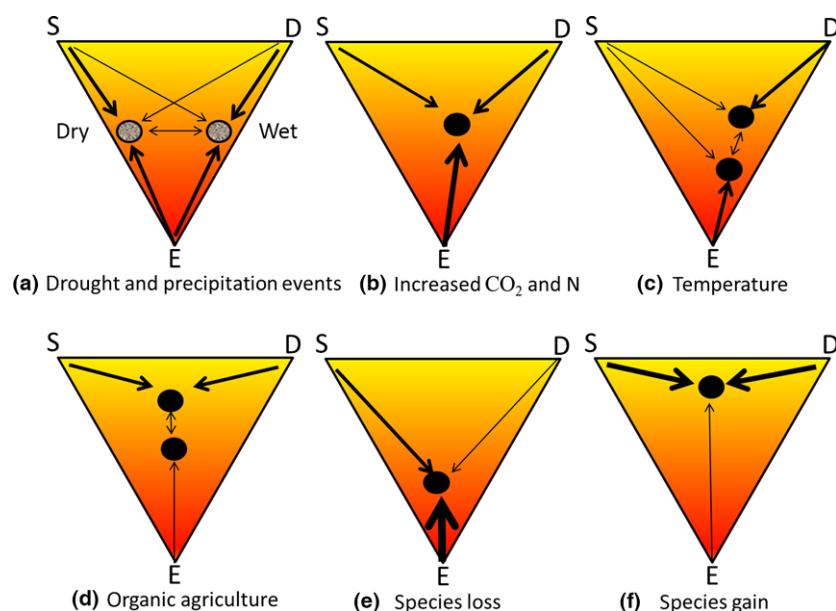
Microbial pathogens can adapt quickly to drought (Newton, Johnson & Gregory 2011) and break out of specific pathogens may be favoured by changes in moisture conditions (Desprez-Loustau *et al.* 2006; Olofsson *et al.* 2011). For example, increased snow cover in the Swedish tundra has been shown to favour outbreaks of the host-specific parasitic fungus *Arwidssonia empetri*, which had a detrimental impact on the dominant plant species, *Empetrum hermaphroditum* (Olofsson *et al.* 2011). Mycorrhizal associations may reduce plant water stress under drought, but the response of mycorrhizal fungi to drought is variable (Mohan *et al.* 2014). Decomposition processes are generally hampered by drought (e.g. Vogel *et al.* 2013;

Santonja *et al.* 2015) and may result in an increase in antagonistic interactions between litter types in litter mixture (Santonja *et al.* 2015), potentially due to a loss of complementarity among decomposers (Tiunov & Scheu 2005). However, the adaptation of soil decomposer communities to community-specific litter material may reduce the impact of drought on decomposition processes (Vogel *et al.* 2013).

Rewetting of soils generally has a positive effect on the abundance of soil organisms and soil microbial activity (Birch 1958; Xiang *et al.* 2008). Often this effect is stronger in forest than in grassland soils, probably because frequent exposure of grassland soils to drying and rewetting events may have resulted in exclusion of stress-intolerant microbes (Fierer & Schimel 2002; Fierer, Schimel & Holden 2003). The response of soil organisms to rewetting depends on the moisture conditions before drought and on the length of the drought period; prolonged drying results in a slower response of the microbial community (Meisner, Rousk & Bååth 2015). Increased activity after a rainfall event is due to re-activation of the indigenous bacterial community, with clear differential responses among

bacterial taxa: fast responders (e.g. Actinobacteria, Spirochaetes and Verrucomicrobia), intermediate responders (e.g. Firmicutes) and slow responders (e.g. Sphingomonadales and Xanthamonadales) potentially depend on how well these bacteria can use the substrate that becomes available upon rewetting (Placella, Brodie & Firestone 2012). Drying–rewetting cycles generally reduce fungal biomass (Bapiri, Bååth & Rousk 2010), but increase microbial activity and change soil community composition (Fierer, Schimel & Holden 2003). These drying–rewetting-induced changes in soil biota may create soil legacy effects that can alter the growth of plants in a species-specific way, thereby changing the outcome of competitive and facilitative interactions among plant species and hence plant community composition (Meisner *et al.* 2013).

It is hard to extrapolate from these previous studies into enemy, symbiont and decomposer responses as to how PSF will change under altered drought or precipitation regimes (Fig. 2a). The limited amount of research that has been published is inconclusive. For example, recent experiments indicate that drought may make PSF of plant species grown in monoculture more positive (De Vries *et al.*



**Fig. 2.** Six representations of plant–soil feedback (PSF) under human-induced global changes, assuming that the original state was centred at the triangle. Explanations of the schemes are provided in Fig. 1, whereas published evidence and theoretical considerations underpinning the length and thickness of the arrows is provided in the main text of the article under the related sections. Two symbols in one panel mean that different states are possible, depending on the responses of symbionts, decomposers and enemies to the global change event. (a) Extreme drought and precipitation events may change the proportional contribution of symbionts and decomposers to the PSF effects: symbionts contribute more under dry than wet conditions, whereas decomposers contribute more under conditions of high precipitation rate. (b) In case of  $\text{CO}_2$  and N enrichment, PSF becomes increasingly negative, due to strong enemy effects and weak symbiont effects; effects of decomposers are intermediate. (c) Temperature may cause increasing negative PSF effects when enemies start multiplying faster. However, PSF effects can become more positive when enhanced decomposition predominates. Contributions of symbionts to PSF are expected to be less substantial when temperature increases. (d) Organic agriculture promotes the role of symbionts and decomposers, so that PSF effects become more positive, except when soil pathogens break out, which will not be combatted by chemicals, resulting in a more negative PSF. (e) species loss decreases the dilution of soil-borne enemies, so that PSF effects to individual plant species become increasingly negative. Symbionts, for example arbuscular mycorrhizal fungi, are less specific than pathogens, so that they may still contribute to the PSF effects. Decomposers have relatively little influence on PSF effects. (f) Species that are gained usually originate from other continents (intercontinental exotics) or from the same continent (intracontinental range shifts). Both types of species benefit from enemy release, while still making use of the relatively non-specific symbionts, resulting into positive PSF.



2012b; Lau & Lennon 2012), meaning that performance of new individuals of that species is promoted in those environments where the monoculture has been growing. However, the outcome of PSF effects measured in multi-species communities seems instead dependent on the relative effect of altered soil moisture on the different species (Meisner *et al.* 2013), meaning that a positive PSF in monoculture may not translate to better performance in a mixture.

To complicate prediction further, the impact of altered drought and precipitation regimes on PSFs depends on the type of extreme weather event (drought or rainfall), the timing (before or during plant growth) and the frequency (Meisner *et al.* 2013). Soil communities may adapt quickly to drought conditions, which can enhance water availability for plants and increase plant fitness (Lau & Lennon 2012; Fischer *et al.* 2014). However, in the longer term plant and soil communities may re-organize. Although it is not yet clear how this will affect PSF-related processes (Bardgett *et al.* 2013) and plant evolutionary dynamics (terHorst & Zee 2016), it has been shown that community reordering (new genotypes or species) may have a large impact on carbon cycling and soil nutrient availability, because drought-adapted plant species often have very different nutrient acquisition strategies (Sthultz, Gehring & Whitham 2009; Fischer *et al.* 2014).

#### CO<sub>2</sub> AND NUTRIENT ENRICHMENT

The response of soil pathogens to elevated CO<sub>2</sub> and changing nutrient availability, such as might occur through aerial nitrogen deposition, seems to have received relatively little research attention (Pritchard 2011; Grover *et al.* 2015). This gap makes conjecture about how negative PSFs might respond to these environmental changes highly uncertain. Although not tested directly, increasing concentrations of atmospheric CO<sub>2</sub> seem likely to shape the nature of PSFs. Even where plant growth is not stimulated by elevated CO<sub>2</sub>, a consistent response appears to be greater carbon allocation to roots and rhizodeposition, potentially fuelling root-associated mutualisms, enemies and the activity of decomposer food webs (Fig 2b). Although there is little information to assess enemy responses to these enhanced below-ground inputs, there is evidence that stimulation of positive PSFs by enhanced root inputs can maintain nitrogen supply to plants (Drake *et al.* 2011; Brzostek *et al.* 2012; Yin *et al.* 2013). However, in other systems a progressive decrease in nitrogen availability occurs (Luo, Field & Jackson 2006; Reich *et al.* 2006), apparently because nitrogen is locked up in additional biomass growth (the so-called CO<sub>2</sub>-fertilization effect), potentially enhancing plant reliance on root symbionts despite the fact they may become increasingly costly as soil nitrogen availability declines. The substantial uncertainty over whether the CO<sub>2</sub>-fertilization effect will be strongly limited by soil nitrogen availability (Wieder *et al.* 2015), as well as whether nitrogen deposition causes a release of sequestered carbon or not (Janssens *et al.* 2010), highlights the need to

understand PSF to predict with confidence the carbon sink strength of the terrestrial biosphere in a changing world. Yet the net response of PSFs to elevated CO<sub>2</sub> and nitrogen deposition remains unanswered for any one system.

Above-ground and theoretical work on pathogens, such as plant viruses, suggests the potential that increasing nutrient availability will increase pathogen loads of individual plants and that mutualists may be required for pathogens to persist at low nutrient availabilities (Rua & Umbanhowar 2015; Whitaker, Rua & Mitchell 2015). Such dynamics may mean that positive and negative PSFs counteract one another at low nutrient availabilities and shift towards increasingly negative PSFs as nutrient availability increases, favouring pathogens but disfavouring mutualists such as mycorrhizae that plants rely on for nutrient acquisition at low availabilities (Johnson *et al.* 2008; Fig. 2b).

In contrast to soil pathogens, the wealth of studies on mutualistic and saprotrophic soil organisms, as well as on direct and indirect effects of nitrogen enrichments on soil food webs (Meunier *et al.* 2016), highlights how environmental context will likely be a key determinant of net PSFs. For example, nitrogen enrichment of soils is expected to reduce the saprotrophic microbial biomass and shift the communities towards more *r*-selected taxa that decompose more labile substrates (Treseder 2004; Fierer *et al.* 2012). Such shifts may reduce positive PSFs for plant species that rely on rapid nutrient cycling through decomposer activity, albeit still favour them over plant species adapted to more oligotrophic conditions, because nutrient availability is elevated by the exogenous nitrogen addition. Arable systems may be an exception because mounting evidence suggests that nitrogen fertilization increases both soil microbial biomass and also its catabolic capacity, potentially by promoting plant matter inputs to soils in systems where they are otherwise very low (Geisseler & Scow 2014; Wood *et al.* 2015). As a result, this 'boost' to the decomposer subsystem may enhance positive PSFs mediated through nutrient resupply to plants. Whether these components that contribute to positive PSFs translate to a net positive PSF in arable systems may depend on management practices, as, for example, Hol *et al.* (2013) showed that a cereal crop was much more sensitive to weed competition when soil pathogens were present.

The few studies directly investigating how PSFs are affected by soil nutrient availabilities suggest that the outcomes are likely to be strongly species specific and depending on the proportional levels of various nutrients, changing individual plant performance and consequently community composition (Corkidi *et al.* 2002; Manning *et al.* 2008; Larios & Suding 2015). For example, high nutrient supply counteracted the negative effects of soil pathogens on grasses, retarding development of the plant community towards one that was more forb-dominated (De Deyn, Raaijmakers & Van der Putten 2004). Differing plant dependence on mycorrhizal fungi might also alter community trajectories under shifting nutrient availabilities. These 'mutualists' seem to represent a net cost to

plant performance under conditions of very low nutrient supply (Laliberté *et al.* 2015) but in temperate deciduous forest and grassland mycorrhizae are assumed to provide a competitive advantage by facilitating nutrient acquisition (Hodge & Storer 2015). It seems highly likely that as nutrient availability is increased, the initial conditions will determine how PSFs mediated by mycorrhizae will shift. For example, across space mycorrhizal symbioses appear to shift from ericoid to ectomycorrhizal to arbuscular mycorrhizal as soil nitrogen availability increases (Averill, Turner & Finzi 2013; Phillips, Brzostek & Midgkey 2013). If the same pattern holds temporally for increasing nutrient availability, then we would expect shifts in plant community composition consistent with species that associate with different mycorrhizal functional groups and an accompanying weakening of the strength of positive PSFs through the mutualism. The reality of such possibilities occurring, however, will depend on processes such as dispersal to supply the new host species required for such successional dynamics to occur. Furthermore, such expectations are shaped from a strong system bias in mycorrhizal research, with research concentrated on temperate systems leaving much less certain the manner in which PSFs will respond to eutrophication in tropical, boreal and arctic systems (Mohan *et al.* 2014).

#### TEMPERATURE INCREASE

The increase in average ambient temperature as a consequence of changed global atmospheric composition will influence both plants and soil (micro-)organisms (Bardgett *et al.* 1999; Frey *et al.* 2008). In the short term, temperature increase will directly stimulate metabolic rates and increase soil microbial activity. This stimulated activity may lead, for example, to increased decomposition of organic matter and release of CO<sub>2</sub> (Denman *et al.* 2007; Dorrepaal *et al.* 2009). However, as with drought and rainfall, the response to temperature changes differs between organisms (Blankinship, Niklaus & Hungate 2011; Yin, Chen & Liu 2012) and sites (Cregger *et al.* 2014) and is generally strongest in colder regions (Blankinship, Niklaus & Hungate 2011). In general, bacteria respond more positively to higher temperatures than fungi (Pietikäinen, Pettersson & Bååth 2005), which will lead to higher bacterial: fungal ratios in soil (Cregger *et al.* 2014). One potential result is that simple carbon compounds will be decomposed faster than the more recalcitrant compounds, at least in terms of absolute decomposition rates (Davidson & Janssens 2006). These changes would promote fast-growing plants, which may benefit from positive plant–soil feedback by enhanced decomposition and nutrient mineralization.

The activity and abundance of soil pathogens is expected to increase with rising temperatures directly because life cycles will be shortened, and indirectly due to extra root activity and decomposition (Bragazza *et al.* 2013). At the same time, the activity of mycorrhizal fungi

may decrease with warming (Mohan *et al.* 2014). These responses would result in more negative PSF effects, which could especially suppress early successional fast-growing plant species that are highly pathogen sensitive (Kardol, Bezemer & van der Putten 2006). However, these responses may be counteracted, at least in part, by the enhanced nutrient release through decomposition. Therefore, predicting the overall effect of temperature increases on PSF will require examples from various biomes on different positions along climate gradients. At the moment, we have very few controlled empirical studies to test predictions against. One study focussing on PSF of range-expanding and native species found that an increase of 5 °C did not change the direction or strength of the feedback, neither for native, nor for range-expanding plant species (Van Grunsven *et al.* 2010b). The influence of soil temperature on pathogens, symbionts and decomposers was not resolved in this study, but the net effect of temperature on PSF was clearly neutral.

One challenge is to generalize shorter-term results on effects of abiotic and biotic changes in the environment to predict the net outcome of long-term changes in PSF. For example, decomposer responses that were initially positive may slow with the duration of warming because soil carbon pools are depleted and soil microbes adapt or acclimate (Bradford *et al.* 2008; Bradford 2013), but see Blankinship, Niklaus & Hungate (2011). However, if plant productivity does increase with warming as is often projected because the initial stimulation of decomposition makes more nutrients available, then greater root growth and hence rhizodeposition may further stimulate the activities of microbial decomposers (Bragazza *et al.* 2013). Furthermore, warming may directly stimulate the activity of invertebrate decomposers, enhancing litter decomposition and hence nitrogen availability for plants (Makoto, Arai & Kaneko 2014). Certainly, plants have been shown to respond to such temperature-induced biotic and abiotic changes in the soil (De Long *et al.* 2015), but the net outcome of PSF under warming is far from certain (Fig. 2c).

#### LAND USE CHANGE

The growing world population requires increased amounts of products derived from agriculture and forests (Foley *et al.* 2005), which requires an increased area that is more intensively managed by man. However, there are also attempts to counteract the influence of human disturbance by changing high-intensity conventional agricultural practices into more sustainable organic agriculture, or by restoration of agricultural land into (semi-)natural areas. When changing land use, legacies of past land use can last for decades to centuries and include physical, chemical and biological changes to the soil (Foster *et al.* 2003; McKey *et al.* 2010). Therefore, managing land use change requires knowledge on how to manage PSF effects. Comparing conventional and organic agriculture shows that PSF in these systems plays a contrasting role with strong

implications for management. Conventional agriculture strongly suffers from soil-borne pathogens, which cause negative PSF that can only be managed by crop rotation or agrochemical biocides, whereas organic agriculture depends on positive PSF from symbionts and decomposers.

Avoidance of the use of agrochemicals increases numbers of bacteria and species richness of both bacteria and nematodes (Van Diepeningen *et al.* 2006) and the diversity of arbuscular mycorrhizal fungi (Oehl *et al.* 2004; Verbruggen *et al.* 2010). Further, cessation of agrochemical use increases the abundance of meso- and macrofauna (including earthworms) and accelerates litter decomposition rates (Attwood *et al.* 2008; Dominguez *et al.* 2014). Organic agriculture refrains from the use of artificial fertilizers and pesticides that are commonly applied in conventional agriculture. Organic and conventional agriculture also differ in a number of system aspects, such as the use of higher amounts of organic matter returns to soil, reduced tillage and a more diverse crop rotation. The use of organic matter and manure may suppress soil-borne diseases for various reasons; however, results on the suppression of soil-borne diseases are inconsistent (Larkin 2015). Crop rotation limits the build-up of specific pathogen populations, and in some cases may even decrease pathogen inoculum density (Raaijmakers *et al.* 2009). Crop rotation also may increase the diversity of arbuscular mycorrhizal fungi (Verbruggen & Kiers 2010) and accelerate decomposition rates (McDaniel *et al.* 2014). As a result, PSF effects in organic agriculture may be more positive than in conventional agriculture, but when pathogens and diseases break out incidentally they are not controlled by chemicals, which results in occasional more negative PSF effects in organic agriculture (Fig. 2d).

Land management is expected to have a profound influence on PSF effects; especially soil tillage, which increases decomposition rates and changes the decomposer community composition, results in lower amounts of soil organic matter and litter residues that differ in chemical composition from no-till fields (Wickings *et al.* 2011). Tillage reduces the density and richness of arbuscular mycorrhizal fungi (Helgason *et al.* 1998; Sale *et al.* 2015). Conservation tillage may restore mycorrhizal abundance due to reduced soil disturbance and plant debris in the top layer provides a habitat for other micro-organisms that may compete with the pathogens or act as antagonists (Sturz, Carter & Johnston 1997). However, plant debris can also act as a source for pathogens, so that increased pathogen outbreak is a major threat of conservation tillage. The effect of soil tillage on PSF is expected to depend on the specific pathogen–soil–crop–environment system (Raaijmakers *et al.* 2009) and may vary from positive to negative. Still, the production in no-till systems (Pittelkow *et al.* 2015) and in organic agriculture (De Ponti, Rijk & van Ittersum 2012; Ponisio *et al.* 2015) is generally, but not always, lower than in tillage-based agriculture. The latter is probably due to lower amounts of available nutrients and

difficulties in the control of pests and diseases. This leaves the impression that reducing both soil tillage and the use of agrochemicals increases the effects of decomposers and mycorrhiza, but more so of pathogens, potentially resulting in a net negative PSF effect (Fig. 2d). On the other hand, reduced soil tillage may increase the resilience to drought that is expected to occur more frequently in a changing climate (Van Diepeningen *et al.* 2006).

#### PLANT SPECIES LOSS VS. SPECIES GAIN

Loss and gain of plant species both can have substantial impacts on PSF, but loss and gain can also be influenced by PSF. The relation of PSF with plant species loss has received less attention than with species gain, but interest is rapidly growing. Work focusing on primary production under declining plant species diversity (Maron *et al.* 2011; Schnitzer *et al.* 2011) suggests that with decreasing plant diversity negative PSF effects on individual plant species increase, resulting in reduced primary productivity. These studies point out that not only does PSF control plant species diversity (Bever 2003), but in turn plant species diversity also may control the PSF effect to individual plant species and that these effects may influence ecosystem functions, such as biomass production (Maron *et al.* 2011; Schnitzer *et al.* 2011). If diverse plant communities contain many species with predominantly negative host species-specific PSF, plant species loss will result in enhanced negative PSF of the remaining plant species, because pathogens will be able to accumulate and, therefore, PSF becomes more negative. In biodiversity–ecosystem functioning studies, decomposition usually decreases with decreasing plant diversity (Eisenhauer *et al.* 2010), so that with plant species loss the contribution of decomposition to PSF might decrease as well. It has been suggested that arbuscular mycorrhizal fungi have lower host specificity than pathogens (Klironomos 2003). In that case, species loss may result in increasingly negative PSF because of enhanced pathogen influence and decreased decomposer influence (Fig. 2e). Most work on plant species loss hitherto has been focussed on loss of biodiversity, but an area open for further studies concerns the question how PSF is influenced by the loss of species with specific traits or roles in a certain ecosystem (Van Nuland *et al.* 2016).

The relationship of PSF with plant species gain has been more intensively studied than with species loss, and a large number of possible relationships have been suggested. Species gain may occur both through intercontinental introductions and intracontinental climate warming-induced range shifts (Walther *et al.* 2009). A number of studies have shown that exotic plant species have a less negative, or even a positive PSF in the new compared to the native range (Callaway *et al.* 2004; Van Grunsven *et al.* 2010a). In most of these studies, the precise origin of the introduced exotics was not known; however, in one study where the origin of introduced trees was well documented, seedlings of *Pinus contorta* produced 62% more biomass in

sterilized soil inoculated with new range rather than native range soil (Gundale *et al.* 2014). Although not specifically tested, the result suggests that introduction in the new range enabled *P. contorta* to escape from native soil pathogens. Introduced exotic plant species may also have a more positive PSF by acquiring mutualists in the novel range, which could lead to double benefits of enemy release and mutualistic benefits (Callaway *et al.* 2011).

Exotic plant species may also influence PSF in other, more indirect ways. For example, they may reduce local symbionts (Stinson *et al.* 2006; Vogelsang & Bever 2009), which results in indirect negative PSF to native plant species that depend on these symbionts (Wilson, Hickman & Williamson 2012). Introduced exotics may also increase local pathogens without suffering from them, leading to negative spill-over effects on natives (Mangla, Inderjit & Callaway 2008). Other indirect negative effects are when introduced exotics produce toxic secondary metabolites to which native plant species are not well adapted (Callaway & Ridenour 2004), or when exotics increase site fertility by producing readily decomposable litter (Kourtev, Ehrenfeld & Huang 1998). Such changes in nutrient dynamics following species introductions have been reported quite often (Fraterrigo *et al.* 2011), and it has been proposed that many invasive exotics, which also happen to originate from nutrient rich environments, benefit by escaping enemies, as well as by changing nutrient dynamics of the invaded environment (Blumenthal *et al.* 2009).

As a result, species gain by introduced exotics, both from inter and intracontinental origin, can result in escape from negative PSF and a transition, in the new range, to a positive PSF by enhanced decomposition and newly acquired symbionts (Fig. 2f). Underlying this transition seems to be shifts in interaction strength with all three of the biotic groups involved in PSF, with those shifts involving both direct (to conspecifics) and indirect (to natives) PSF effects. Direct effects may be based on decreased pathogen exposure and increased benefits from symbioses and decomposition, whereas indirect effects may act in the reverse direction by enhancing pathogen exposure to natives, reducing their benefits from symbionts and decomposers, or by introducing novel chemical compounds in the invaded environment. There is no general pattern as to whether these specific mechanisms operate simultaneously or alone in any one system; instead, the exact combination and their relative influence appear highly species and context specific.

### Role of PSF in the field

The majority of PSF studies have been carried out under controlled greenhouse conditions, usually lasting 2–3 months, up to maximally a year. Studies under controlled conditions are highly instrumental for producing proof of principle, and results may be correlated to observations in the field. However, to determine the role of PSF in the field, additional studies need to be carried out under

realistic environmental conditions. Numerous studies have already measured effects of individual plant species, plant populations or experimentally manipulated conditions, such as grazing, fire or nutrient supply on abiotic and biotic soil properties in the field (McLaren, Wilson & Peltzer 2004; Eisenhauer 2012; Mariotte *et al.* 2013), but only few such studies have considered feedback effects of those induced changes in soil properties. As a result, little is known about the actual role of PSF in driving changes in plant community composition and ecosystem functioning, both in current and future environmental conditions.

Comparing PSF effects between greenhouse and the field is a real challenge, because in the field conditions are so much more complex than in most greenhouse experiments (Cortois & De Deyn 2012). The local scale effects of PSF in the field will be influenced by regional differences in climate, soil type, hydrology and the available species pool. For example, studies with the same plant species showed that the strengths of PSF effects differed between slightly acid sandy loam and calcareous soils (Bezemer *et al.* 2006). These differences may be explained by variation in soil biology, as well as by differences in soil texture and soil chemistry (Ehrenfeld, Ravit & Elgersma 2005). In other cases, however, PSF effects appeared independent of soil physico-chemical conditions (Harrison & Bardgett 2010). It is also possible that physico-chemical and PSF effects both have their share in the observed responses in the field. For example, the coastal sand dune grass *Ammophila arenaria* is known to benefit from burial by wind-blown sand from the beach as that enables escape from negative PSF, but the emergence from sand burial turned out to be a primary response to burial, irrespective of whether soil enemies were present in the soil or not (De Rooij-van der Goes, Peters & van der Putten 1998).

Biotic interactions may also interfere with each other. For example, plant competition that was experimentally varied in the field, suppressed PSF effects (Casper & Castelli 2007). This confirms findings under controlled conditions that PSF may be influenced by plant competition, however, in some greenhouse studies competition enhanced, rather than counteracted PSF effects. For example, competition by weeds increased sensitivity of cereals to negative PSF effects (Hol *et al.* 2013). Whereas plant competition may be influenced more by direct or indirect interactions with soil-borne enemies, symbionts and decomposer organisms might be more involved in inter-specific plant facilitation (Valiente-Banuet & Verdu 2007). For example, two neighbouring alpine plant species had positive PSF to each other through facilitating each other's ammonium uptake (Ashton *et al.* 2008). The roles of competition and facilitation may also change along environmental, for example altitudinal, gradients (Michalet *et al.* 2014), so that the role of PSF can be expected to covary correspondingly.

Feedback effects from above-ground herbivores through stimulation of the soil decomposer subsystem have been thoroughly investigated in the field (McNaughton,



Banyikwa & McNaughton 1997; Hamilton & Frank 2001). Herbivory tends to promote positive feedback from the soil decomposer subsystem (Bardgett & Wardle 2003) and can overrule the negative feedback effects (Veen *et al.* 2014). Effects of grazing may also change PSF effects by altering soil organic matter (Burke *et al.* 1998), whereas above-ground endophytes may alter PSF through changing root exudation (Casas *et al.* 2011). It has been well-established that plants can integrate physiological responses and biomass allocation to heterogeneity in soil, as well as heterogeneity in light availability (del Pino, Brandt & Burns 2015). These examples all suggest that in the field PSF effects may influence, as well as be influenced by, abiotic and biotic environmental factors that co-influence the composition and functioning of plant communities. Therefore, besides understanding the relative contribution of enemies, symbionts and decomposers to net PSF effects, a major challenge is to obtain information about the relative role of PSF – in the light of these other factors – in shaping patterns and processes in the field.

## Ways forward

Plant–soil feedback clearly has become an integral component of plant population and community ecology with important consequences for understanding the functioning of terrestrial ecosystems. The rich body of research on PSFs demonstrates convincingly that positive and negative PSFs have the potential to shape individual plant performance and consequently plant community composition and productivity. There is also direct experimental evidence that the net effects of PSFs are determined by environmental context, such as competition, nutrient availability and above-ground biotic interactions, such as herbivory. However, there is still little understanding of the role of PSF in shaping the structure and function of natural communities in the real world. Critical to such assessments will be identification of the factors that determine when, where and to what extent PSFs must be considered to predict community and ecosystem change. This requires further elucidation of the contribution of the various components (enemies, symbionts and decomposers) to net PSF effects and how PSF depends on environmental context.

The highly controlled nature of most PSF work means that the internal validity (mechanistic knowledge) aspect of the research has been generated under rather unnatural conditions. Manly (1992) stated that ‘Internal validity concerns whether the apparent effects or lack of effects shown by the experimental results are due to the factor being studied, rather than some alternative factor’. The common trade-off is that high internal validity translates to low external validity: that is, we do not know the extent to which PSF results can be generalized – or extrapolated – to nature (Cortois & De Deyn 2012). Other research themes, such as biodiversity and ecosystem functioning research, have had to go through a similar progression

from more microcosm and mesocosm-based study systems to field experiments that much better approximate the natural system (Naeem 2001). The challenge for PSF research moving forward is to ask what understanding we can confidently extrapolate from PSFs to facilitate temporally and/or spatially predictive science.

Robust prediction may not always demand field research but rather the ability to show that results from simple experimental systems can at least be scaled to more realistic, complex scenarios. For example, Navas *et al.* (1999) demonstrated that plant community responses to elevated CO<sub>2</sub> and nitrogen enrichment could be approximated from monocultures but not from individual plant responses. To make further progress with PSF research, it is now critical to focus on a number of key findings and determine how results from experiments under controlled conditions may explain the patterns that can be observed in the field. For example, if exotics, or climate warming-induced range-expanding plant species, have less negative PSF in their new range (Reinhart & Callaway 2006; Engelkes *et al.* 2008), how much does this explain their invasiveness in the newly colonized habitats? Empirical tests are needed to translate PSFs effects under controlled greenhouse conditions to ‘real-world’ situations.

New experiments are also needed to test *a priori* predictions, such as those based on predicted contributions of net outcomes of enemy–symbiont–decomposer interactions, to validate whether indeed the three components play the role as predicted by the current evidence. This approach requires that the biota are experimentally manipulated such that the three components of PSF may be tested alone and in the various combinations, without and with the other environmental variables that influence community composition and ecosystem functioning. Without *a priori* hypotheses and measuring all components, rather than one or two of them, it will be difficult to find other causal mechanisms beyond the ones studied. In this approach, short-term effects of enemies and symbionts will need to be compared with long-term effects of decomposer organisms to understand the relative role of each component at the temporal scale across which they cumulatively operate and evolve.

Our suggestion of a triangular framework for PSF is intended to emphasize the necessity of placing results from individual studies into the broader context of enemy–symbiont–decomposer interactions, thereby facilitating the development of a mechanistic understanding of PSF complete enough to make projections of net PSF effects in which we have medium-to-high confidence. This understanding must therefore be applied in the context of multiple other factors that shape plant communities and ecosystem processes under current and changing conditions, if PSF research is to contribute effectively to a predictive global change science. Plant–soil feedback research is at a critical juncture: the potential for PSF effects to shape community and ecosystem response has been convincingly demonstrated through highly controlled experi-

ments. The challenge for the field now is to show where, when and how PSF matters in the real world for explaining and predicting community and ecosystem responses to a changing world.

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## Data accessibility

This manuscript does not use data.

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