SPECIAL FEATURE – ESSAY REVIEW
PLANT–SOIL FEEDBACKS IN A CHANGING WORLD

Plant–soil feedbacks: the past, the present and future challenges

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Summary

1. Plant–soil feedbacks is becoming an important concept for explaining vegetation dynamics, the invasiveness of introduced exotic species in new habitats and how terrestrial ecosystems respond to global land use and climate change. Using a new conceptual model, we show how critical alterations in plant–soil feedback interactions can change the assemblage of plant communities. We highlight recent advances, define terms and identify future challenges in this area of research and discuss how variations in strengths and directions of plant–soil feedbacks can explain succession, invasion, response to climate warming and diversity-productivity relationships.

2. While there has been a rapid increase in understanding the biological, chemical and physical mechanisms and their interdependencies underlying plant–soil feedback interactions, further progress is to be expected from applying new experimental techniques and technologies, linking empirical studies to modelling and field-based studies that can include plant–soil feedback interactions on longer time scales that also include long-term processes such as litter decomposition and mineralization.

3. Significant progress has also been made in analysing consequences of plant–soil feedbacks for biodiversity-functioning relationships, plant fitness and selection.

4. To further integrate plant–soil feedbacks into ecological theory, it will be important to determine where and how observed patterns may be generalized, and how they may influence evolution.

5. *Synthesis.* Gaining a greater understanding of plant–soil feedbacks and underlying mechanisms is improving our ability to predict consequences of these interactions for plant community composition and productivity under a variety of conditions. Future research will enable better prediction and mitigation of the consequences of human-induced global changes, improve efforts of restoration and conservation and promote sustainable provision of ecosystem services in a rapidly changing world.

Key-words: abundance, biodiversity-ecosystem functioning, density dependence, historical contingency, invasiveness, mycorrhizal fungi, plant–soil (below-ground) interactions, priority effect, rarity, succession

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Introduction

The nature of soil, shaped by its chemical, physical and biological properties, plays a key role in determining the growth, productivity and reproductive success of individual plants, the relative performance of coexisting plant species, and plant community composition and productivity. Plants can influence soil properties through inputs of chemical compounds and organic matter, by impacting upon hydrological processes and surface soil temperatures, as well as by providing habitats and/or resources for microscopic and macroscopic organisms (van Dam 2009; Bardgett & Wardle 2010). Plant influences on biotic and abiotic soil properties may alter the soil's ability to support these same individuals, other individuals of the same species or other plant species. Changes to soil properties that are caused by plants, which in turn influence the performance of plants are termed 'plant–soil feedbacks' (Bever, Westover & Antonovics 1997; Wardle 2002; Ehrenfeld, Ravit & Elgersma 2005; Kulmatiski & Kardol 2008).

Plant–soil feedbacks from a plant of a given species, which affect the individual itself or other individuals of the same species are referred to as direct, intraspecific or conspecific. Inversely, those that operate between species are referred to as indirect, interspecific or heterospecific (see Box 1 and Fig. 1) (McCarthy-Neumann & Kobe 2010; Van de Voorde, Van der Putten & Bezemer 2011). Plant–soil feedbacks is considered positive when it improves the performance of conspecifics and enhances the probability of that

species monopolizing its local habitat. Conversely, plant–soil feedbacks is considered negative when it makes soil less suitable for conspecifics by controlling dominance and decreasing vigour, as well as increasing the probability of that species being replaced by other species that are better suited to the new soil conditions. Because a single species may influence the soil through a variety of biotic and abiotic mechanisms, it is the sum of these effects, or the net plant–soil feedbacks, that determines whether plant performance is enhanced or depressed. The extent to which either plant-induced changes in soils or the responses to those changes are species-specific, will determine how much plant–soil feedbacks influences the composition of the plant community, with potential ramifications for ecosystem functioning, including interactions between plants and other above-ground biota (Bardgett & Wardle 2010). Interest in plant–soil feedbacks has increased in the past 10 years. The aim of this review is to synthesize our current knowledge on plant–soil feedbacks. We will begin by providing a historical overview showing that early agronomists and horticulturists were aware of plant–soil feedbacks and its specificity. We will then review knowledge of plant–soil feedbacks in plant population dynamics, community organisation and ecosystem functioning. Finally, we will discuss avenues for future research, before challenging the ecological community to incorporate the concept of plant–soil feedbacks into existing theories relating to the organisation and functioning of natural systems.

Box 1. Definitions

Here, we provide definitions for use in the field of plant–soil feedbacks.

Direct plant–soil feedback is used for *intraspecific*, or *conspecific* feedback effects and can be considered as the modification by roots and/or plant litter of a plant species on its biotic and abiotic soil environment and how that modification influences it or its offspring (free after Bever, Westover & Antonovics 1997) (Fig. 1, central panel). This type of feedback can be negative (resulting in a net growth-reducing effect from changes in the soil community, chemical and physical soil conditions to individuals of the same species), neutral (the net effect is that all influences of the soil community are zero), or positive (growth of the plants or subsequent individuals of the same species is promoted by the net soil effect). The direction of the effect and its impact on plant community dynamics follows the convention of theoretical ecology with negative feedback-stabilizing diverse plant communities and positive feedback-destabilizing diverse communities (Levins 1974; Bever 1994).

Thus far, the majority of direct/intraspecific/conspecific plant–soil feedback effects reported are negative (Bever 2003; Kulmatiski *et al.* 2008; Petermann *et al.* 2008), which is consistent with soil feedbacks contributing to plant species coexistence (Bever, Westover & Antonovics 1997; Bever 2003). Negative intraspecific plant–soil feedback effects may result in the degeneration of a plant, or part of a clone (Van der Putten, Van Dijk & Troelstra 1988), or it may lead to mortality of seedlings close to the parent (Packer & Clay 2000; Mangan *et al.* 2010). However, there may be more positive plant–soil feedbacks interactions in nature, which might be revealed when testing the concept in the field and over a longer period, for example as resulting from plant species-specific effects on decomposition, the so-called home field advantage effect that has been shown for some plant species. Other examples of positive feedback often involve changes in density of symbiotic mutualists, such as nitrogen-fixing rhizobacteria and mycorrhizal fungi. Positive plant–soil feedbacks may promote dominance (Klironomos 2002).

To understand how plant–soil feedback effects influence plant community dynamics, direct feedback effects need to be compared to *indirect feedback effects* (Bever, Westover & Antonovics 1997). *Indirect feedback effects* are *interspecific*, or *heterospecific* feedback effects from one plant species to another. These effects can also be negative, neutral or positive. Examples of negative indirect plant–soil feedbacks are mostly known from work on invasive exotic plant species. For example, invasive exotic plants that produce secondary metabolites unknown to the invaded community (Callaway & Ridenour 2004), and exotics that promote soil pathogens

that have a more negative effect on the surrounding native plant species than on the exotics themselves (Mangla, Inderjit & Callaway 2008), or that reduce local mycorrhizal fungi (Stinson *et al.* 2006) are causing indirect net negative feedback effects to native plant species. Indirect positive plant–soil feedbacks has been reported for many native plant species in mixed plant communities in *own* (conditioned by conspecifics) vs. *foreign* (conditioned by heterospecifics) soil comparisons (Kulmatiski *et al.* 2008). Indirect positive feedback effects have also been reported for early primary and secondary successional to later successional species.

Instead of determining the role of plant–soil feedback effects on plant community composition by combining all direct and indirect feedback effects contributed by individual plant species, *plant-soil community feedback*, or *weighted feedback* effects (Van de Voorde, Van der Putten & Bezemer 2011) may be analysed by having soil influenced by mixtures of plant species and testing the growth responses on a newly planted mixture of the same plant species. This approach has been used to determine the contribution of plant–soil feedbacks to secondary succession. Plant-soil community feedback effects can also be compared against direct feedback effects by growing species in mixtures vs. monocultures. An example of positive plant-soil community feedback effects is the overyielding in species-rich plant communities compared to monocultures (de Kroon *et al.* 2012), which has been proposed to explain plant diversity-productivity relationships (Maron *et al.* 2011; Schnitzer *et al.* 2011).

The past: a brief history

For more than 1000 years, humans have been aware of, and managed, plant–soil feedbacks in agriculture and horticulture. In agricultural settings, plant–soil feedbacks most often involves soil nutrient depletion or the build-up of species-specific, soil-borne pathogens. More than 2000 years ago in both Europe and Asia, it was known that fruit trees were subject to replanting failures when young trees were planted where conspecifics or congeners had grown. Rotational cropping systems were developed to reduce failures of crop establishment and to increase productivity. Fields were left fallow for a year or more, but as early as 814 AD, under Charles the Great, cropping and fallow rotations were altered in Europe to include leguminous species (Butt 2002), suggesting awareness of their ability to boost productivity of other crops.

That some biotic agents were responsible for declines in crop productivity was not revealed until the 19th century. The realization that soil sickness or soil fatigue, could be avoided by sterilizing soils, suggesting that biota play a role, has generated wide interest in replant diseases (Hoestra 1968). Soils becoming less able to support particular crops became more common during the second half of the 20th century, especially when the then global economy drove farmers to focus on high-yielding crops grown in short rotations. Ecologists have benefited greatly from insights into agricultural practices and the early knowledge about plant-pest and pathogen interactions. This relationship between agriculture and ecology has come a full circle as advances in plant–soil feedbacks research in natural systems are now used to develop and test methods of more sustainable crop production.

Ecologists have long known that wild plant species can affect decomposition and nutrient mineralization, and that these effects can feed back to plant growth, but empirical tests are scarce. For example, the mull and mor theory of Müller (1884) explicitly recognizes that variation both between and within plant species in litter decomposition can influence soil biota and other soil properties in a manner that feeds back to plant growth. Colonization by plant species with different litter characteristics can change plant commu-

nity composition by altering litter decomposition and nutrient mineralization. For example, enhancement of decomposition following the establishment of *Molinia caerulea* leads to *Erica tetralix* being out-competed, and heathland being changed into grasslands (Van Vuuren & Berendse 1993; Berendse, Schmitz & de Visser 1994).

There is evidence that some plant species show a so-called 'home field advantage' of litter breakdown in their own soil compared with soil obtained from the vicinity of other plant species (Ayres *et al.* 2009; Miki 2012), although there may also be other explanations for this phenomenon (Freschet, Aerts & Cornelissen 2012). For example, in the Pygmy forest in western California, there is evidence that some plant species, such as *Pinus muricata*, use mycorrhizal fungi to short-circuit the N cycle. This tree species can take up organically bound N through its ectomycorrhizal fungi, which is advantageous to the trees themselves, but not to other species (Northup *et al.* 1995). Handley's (1954) work on *Calluna vulgaris* in the UK and work on Swedish islands reported by Wardle *et al.* (2012) shows that plant species can impede rates of N mineralization by producing litter with high levels of polyphenols, which adversely affects earlier-successional plant species (Hättenschwiler & Vitousek 2000).

Whether plant–soil feedbacks influences plant community composition depends on how the feedback agents affect co-occurring plant species. Soil-borne plant pathogens have long been assumed to be less species-specific than above-ground pathogens but more specific than mycorrhizal fungi. However, studies are increasingly pointing to considerable specificity of soil biotic components (Klironomos 2003; Van der Putten 2003). When teasing apart the various components of plant–soil feedbacks, it needs to be considered that arbuscular mycorrhizal fungi can differ strongly in their resource exchange with plant individuals (Kiers *et al.* 2011), and that they may also act as pathogens (Johnson, Graham & Smith 1997), potentially generating negative feedbacks on plant growth (Castelli & Casper 2003).

When root-feeding insects (Brown & Gange 1990; Schädler *et al.* 2004), nematodes (Van der Putten & Van der Stoel 1998), and detrital food web organisms (Coleman 1985; Hättenschwiler, Tiunov & Scheu 2005) accumulate on certain
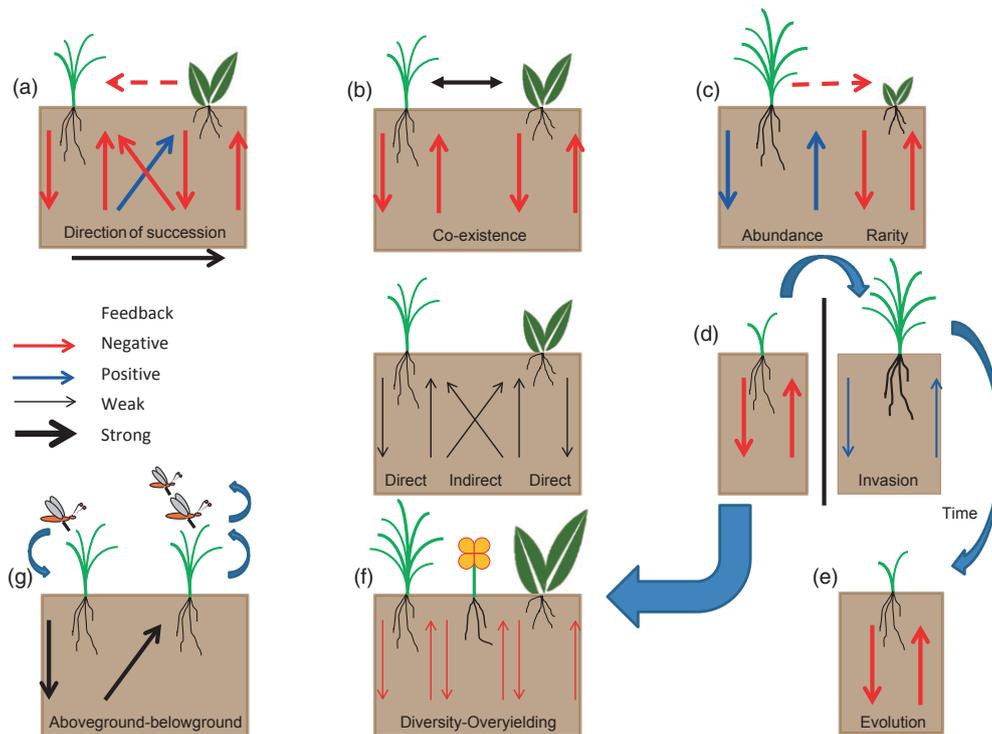
Fig. 1. Conceptualized contribution of plant–soil feedbacks to plant community organization. Red arrows: negative feedback effects, blue arrows: positive feedback effects and dashed arrows: indirect consequences for plant–plant interactions. Arrow thickness implies the effect strength. The central panel shows how plant species can exert direct feedback effects to themselves and indirect feedback effects to neighbours. Panel (a) shows how a change of one indirect feedback effect may result in species replacement that may contribute to species replacement and, subsequently, (primary or secondary) succession. Panel (b) illustrates how negative feedback effects operate when plant species coexist, whereas in panel (c) it is shown how combinations of positive and negative soil feedback may result in abundance of the (left) plant species with positive feedback and rarity of the (right) plant species with negative feedback. Panel (d) conceptualizes that rare species might become invasive when changing from negative plant–soil feedbacks in the native range to neutral or positive feedback in the introduced range, when having left behind the specialized enemies and, therefore, negative soil feedback. Panel (e) illustrates that over time, plant–soil feedbacks in the introduced range may become increasingly negative. This feedback might turn negative when local pathogens become specialized, evolve increased virulence or when soil pathogens from the original range become co-introduced. Both panels (d) and (e) may apply to cross-continental invasions, as well as climate warming-related range shifting. Panel (f) conceptualizes plant–soil feedbacks in mixed plant communities: individual plant species may have mild negative feedback in mixed plant communities opposite to when they are grown in monocultures because the density of specialized soil pathogens is diluted, so that in mixtures, plant species might produce more biomass than each individually in monospecific stands (as in panel d). This has been proposed to lead to overyielding in mixed vs. monospecific plant communities. Panel (g) illustrates an example of above-ground–below-ground–above-ground feedback through herbivory-induced changes in the soil that might influence not only the subsequent plants, their above-ground herbivores, but also the enemies of those herbivores.

plant species, feedback effects may influence the performance of the same or other plant species, thus influencing vegetation composition (Eisenhauer *et al.* 2011; Vandegehuchte, de la Pena & Bonte 2011). Although extensive research on soil-borne pathogens and root herbivores has taken place in agricultural systems, similar studies in natural systems are scarce. On the other hand, the role of plant–soil feedbacks through decomposition has been widely studied in natural ecosystems (Wardle 2002). However, little is known about how the role of detrital food webs, nutrient cycling and stability in soil food webs, as modelled by De Ruiter, Neutel & Moore (1995), may link to root feeders and soil pathogens.

Species-specific exudation of toxic chemical compounds from roots is another mechanism of plant–soil feedbacks (Inderjit *et al.* 2011). Direct evidence for these plant chemical effects is mixed, largely because of difficulties in demonstrating their effects independent of other factors, such as production of toxic compounds by soil microbes during

their decomposing activity (Lau *et al.* 2008). Nevertheless, some studies provide evidence that allelopathic compounds can be produced directly by plants without interference from soil biota (Bais *et al.* 2003; Vivanco *et al.* 2004). Work on allelopathy in natural systems is outweighed by that in agriculture (Bonanomi *et al.* 2005), but the suggestion that allelochemicals produced by some exotic plant species contribute to invasiveness (Callaway & Ridenour 2004) has increased interest in the role of these chemicals in plant–soil feedback interactions in natural systems.

The present: recent developments and advances

Changes in the strength and direction of interactions in a conceptual plant–soil feedbacks model (Bever, Westover & Antonovics 1997) suggest that plant community dynamics can change from a state in which different species coexist to

successional, in which there is ultimately domination by single species, or invasion by exotic species (Fig. 1). Specificity of plant–soil feedback interactions can result in succession and reduction of negative feedback effects in mixed plant communities might explain why monocultures produce less biomass than mixtures (Fig. 1). Using this conceptualized overview of interactions, we show how plant–soil feedbacks is currently believed to influence plant community dynamics.

PRIMARY AND SECONDARY SUCCESSION

During early successional stages, facilitation processes, operating either directly between plants or via soil organisms, are pivotal to ecosystem development (Brooker *et al.* 2008). Early successional stages are often associated with positive plant–soil feedbacks (Reynolds *et al.* 2003), for example, due to symbiotic nitrogen (N) fixation and plant associations with mycorrhizal fungi. A classic example of positive plant–soil feedbacks in primary succession involves the symbiosis between plants and nitrogen-fixing bacteria, which increases soil N (Chapin *et al.* 1994). The success of this symbiosis during primary succession is due to the fact that most parent material is devoid of N. Nitrogen-fixing legumes, such as *Lupinus lepidus*, which have colonized Mount St. Helens after the most recent eruption, can form 'islands of fertility' that promote conditions for growth of later successional plant species (Titus & del Moral 1998; Corti *et al.* 2002).

The initial benefit of symbioses may become a disadvantage when early successional plant species develop negative soil feedback, which reduces their competitive ability against later successional plant species that are tolerant of the pathogens accumulated by earlier successional species. Such processes may also occur without early successional plant species with symbiotic nitrogen fixation. A classic example of such negative plant–soil feedbacks is that of the foredune grass *Ammophila arenaria* (marram grass). This grass is most vigorous in mobile dunes, because the colonization of wind-deposited beach sand enables it to temporarily escape from soil-borne enemies. When dunes become stabilized, *A. arenaria* degenerates because its roots are continuously exposed to soil pathogens (Van der Putten, Van Dijk & Troelstra 1988). This is an example of negative direct plant–soil feedbacks (see Box 1). However, this soil feedback effect has an indirect positive effect on later successional plant species, because they are tolerant to the pathogens of their predecessor (Van der Putten, Van Dijk & Peters 1993) (Fig. 1a). Negative direct plant–soil feedbacks may also occur with the later successional nitrogen-fixing dune shrub *Hippophaë rhamnoides* (Oremus & Otten 1981). In this case, decreased symbiosis and increased pathogenicity have both been identified, but most evidence points towards increased pathogenicity (Oremus & Otten 1981).

Plant community composition in early stages of secondary succession can also change rapidly due to negative plant–soil feedbacks. In a series of old fields that differed in time since abandonment, early successional (weedy) plant species dem-

onstrated negative feedback effects, whereas later successional species had positive plant–soil feedbacks effects (Kardol, Bezemer & Van der Putten 2006). This suggests that during early secondary succession, effects of symbiotic mutualists (such as arbuscular mycorrhizal fungi) may have a smaller effect than soil-borne pathogens, but this is reversed in later successional stages (Janos 1980). Interestingly, similar effects have been observed in experiments where the soil biota consisted mainly of microbial pathogens and root-feeding nematodes (Van der Putten, Van Dijk & Peters 1993; Kardol, Bezemer & Van der Putten 2006), as well as in experiments where composition and numbers of larger soil organisms, such as microarthropods and insects were manipulated (Brown & Gange 1992; De Deyn *et al.* 2003; Schädler *et al.* 2004). While the proportional contribution of these different soil biota to the overall net plant–soil feedbacks effect is still unclear, they are considered to have substantial potential in ecological restoration (Eviner & Hawkes 2008; Harris 2009; Kardol & Wardle 2010).

HISTORICAL CONTINGENCY, LEGACIES AND PRIORITY EFFECTS

Every plant species causes changes in soil conditions, which can remain as 'soil carry-over effects' (Bartelt-Ryser *et al.* 2005), often referred to 'legacy effects', or 'historical contingencies'. These effects can persist in the soil for a period of time after a plant species has disappeared. The length of this legacy depends on the nature of the change in soil conditions (Van der Putten 2003). Legacy effects potentially have long-term consequences for plant community diversity and productivity (Grman & Suding 2010; Kulmatiski & Beard 2011). Microcosm studies, for example, have shown that microbial soil legacies left by early-successional grasses have more pronounced effects on mid-successional grasses than on mid-successional forbs (Kardol *et al.* 2007). Priority effects have also been demonstrated in microcosm studies where introducing certain plant species, or species groups, earlier than others can modify plant species composition; these effects can last for several years (Ejrnæs, Bruun & Graae 2006; Körner *et al.* 2008).

Priority effects have been suggested to be critical to the long-term dynamics of California grasslands, where initial dominance of exotic species with low dependence on mycorrhizal fungi leads to their sustained dominance. On the other hand, initial dominance of native species with high dependencies on mycorrhizal fungi will result in high densities of fungi and sustained dominance of native species (Vogelsang & Bever 2009). Some studies have related greenhouse-based legacy effects to priority changes under field conditions. For example, in abandoned arable fields, the weighted feedback effect of the early successional forb *Jacobaea vulgaris* on later successional plant species becomes increasingly positive with time since abandonment, suggesting that feedback of this forb influences which plant species may become dominant through priority effects and, consequently, the course of secondary succession (Van de Voorde, Van der Putten &

Bezemer 2011). If weeds or invasive exotic species have created soil legacies, then mere removal of these species will not be sufficient for successful restoration of pre-invasion plant communities (Suding, Gross & Houseman 2004; Suding & Hobbs 2009; Yelenik & Levine 2010).

PLANT ABUNDANCE AND RARITY: JANZEN-CONNELL PROCESSES

The Janzen-Connell pattern of reduced success of conspecifics in proximity to adults can be a dominant force, which structures tropical forests (Terborgh 2012). While originally thought to result from seed predators and above-ground pathogens, the pattern of reduced success of conspecifics near adult trees may also result from localized negative soil feedbacks (Fig. 1b). The first test of this possibility was carried out by Augspurger & Kelly (1984), who examined whether mature trees accumulate soil-borne pathogens that may prevent conspecific seedling establishment. Recent work has confirmed that reduced success of conspecific seedlings near adults (conspecific negative density dependence) in the tropics can be attributed to local scale plant–soil feedbacks (Mangan *et al.* 2010). Clear evidence of soil feedbacks driving the Janzen-Connell pattern in temperate forest was shown by Packer & Clay (2000). Failed establishment of black cherry (*Prunus serotina*) seedlings under conspecific adults was due to pathogenic soil microbes (*Pythium* sp.). Subsequent work has suggested that the decline in performance and abundance of seedlings near conspecific adult trees is common in both tropical and temperate forests (Comita *et al.* 2010; Johnson *et al.* 2012; Terborgh 2012). As the strength of negative density dependence of conspecific tree species in temperate forests was found to correlate with regional species richness and to increase towards the tropics, it has been suggested that plant–soil feedbacks may also contribute to latitudinal gradients in plant species richness (Johnson *et al.* 2012).

Within forested systems, the strength and direction of the soil feedback correlates with the relative abundance of tree species (Mangan *et al.* 2010). Dominant tree species had less negative plant–soil feedbacks than less-abundant species. A similar strong correlation was observed in a Canadian old field where frequently occurring plant species exhibited neutral to positive direct soil feedback, whereas less-abundant species had negative soil feedbacks (Klironomos 2002) (Fig. 1c). The consistency of this pattern in both forests and grasslands suggests that plant–soil feedbacks may provide an explanation for plant rarity. However, in a semi-arid grassland study, no such relationship between species abundance and soil feedback was found (Reinhart 2012).

BIOLOGICAL INVASIONS

One of the main reasons why exotic species can become so invasive in their new range is that they have become released from specialist natural enemies that control abundance in the native range (Fig. 1d). In a study in a Canadian old field, introduced exotic plant species had neutral to positive plant–soil feedbacks comparable to dominant native plant species (Klironomos 2002). This finding was taken to suggest that exotic plant species could become invasive by not being exposed to negative plant–soil feedbacks, but it does not exclude the possibility that the exotic species were dominants in their native range where they may have had neutral plant–soil feedbacks as well. Nevertheless, subsequent studies have shown that invasive exotic plant species can indeed switch from negative plant–soil feedbacks in their native range to neutral, or even positive feedback in the range where they have become introduced (Reinhart *et al.* 2003; Callaway *et al.* 2004).

Positive plant–soil feedbacks effects may result from enhanced effectiveness of symbiotic mutualists (Fitter 2005) and decomposer organisms and/or reduced exposure to specialized soil pathogens. Most invasive exotic species are early successionals (Blumenthal 2005), indicating that they may benefit more from soil-borne enemy release than from exposure to generalist symbionts (Kardol, Bezemer & Van der Putten 2006). In North America for example, introduced species appear to have less dependence on mycorrhizal fungi than native species (Pringle *et al.* 2009). However, there are also a variety of other mechanisms involving plant-soil feedback explaining why exotic plant species can become so invasive. For example, some exotic species show negative plant–soil feedbacks in the new range while still being invasive. This phenomenon could be explained by accumulation of local pathogens to which the exotic species are less susceptible than natives (Eppinga *et al.* 2006). Support for this 'accumulation of local pathogens' mechanism has been provided by research on *Chromolaena odorata* in India (Mangla, Inderjit & Callaway 2008). Other possible mechanisms may relate to plants altering soil physico-chemical properties in the invaded range, which might provide direct positive plant–soil feedbacks to the exotics and negative feedback to natives.

It has been proposed that exotic plant species can lose invasiveness (Simberloff & Gibbons 2004; Hawkes 2007), and some recent studies have shown that this may result from altered plant–soil feedbacks with time since introduction (Fig. 1e). For example, in a study from New Zealand, the soil feedback of 12 introduced exotic species was negatively correlated with their residence time (Diez *et al.* 2010). The cause of increased negative plant–soil feedbacks has not yet been elucidated. In another example, the soil-mediated effects of the glucosinolates produced by the introduced forb *Alliaria petiolata* in the USA were found to decrease with time since introduction (Lankau *et al.* 2009). Most exotics, however, do not become invasive at all. Little is known about plant–soil feedbacks patterns of these non-invasive exotics.

CLIMATE CHANGE: DIRECT IMPACTS AND RANGE SHIFTS

Both temperature increases and altered precipitation patterns are likely to influence plant–soil feedbacks, with potentially far-reaching consequences for ecosystem functioning. Climate change is likely to impact the soil organisms directly because warming of the soil can stimulate microbial activity, the

breakdown of organic matter and hence the loss of carbon from soil (Dorrepaal *et al.* 2009). Extreme weather events, such as drought and heavy rainfall, can have substantial effects on microbial physiology and the composition of soil microbial communities, with consequences for ecosystem-level carbon dynamics (Schimel, Balser & Wallenstein 2007). However, there is now increasing evidence that some of the most significant effects of climate change on ecosystem carbon and nutrient dynamics are mediated via plants and their interactions with soil organisms (De Vries *et al.* 2012). Moreover, multi-trophic interactions between plant and soil communities might become decoupled by climate change as plants, herbivores and predators may respond differently to climate changes, and this will almost certainly affect ecosystem functioning (Wardle *et al.* 2011).

The numerous routes by which climate change can impact plant–soil interactions and ecosystem functioning can operate at a variety of spatial and temporal scales. At the individual plant level, and over intra- and inter-annual timescales, changes in temperature, water availability and rising atmospheric carbon dioxide (CO_2) concentration, all impact plant photosynthesis and the transfer of photosynthetic carbon to soil, with cascading effects on soil organisms and ecosystem functioning. An example of this is a study on pine forest showing that elevated atmospheric CO_2 concentrations increased the flux of C to roots, which in turn stimulated microbial activity and the mineralization of organic matter, and hence C loss from soil (Drake *et al.* 2011). However, this process also stimulated the release and turnover of N and its uptake by the trees, which triggered a positive feedback that sustained enhanced rates of tree production and hence C gain under elevated CO_2. Changes in temperature and precipitation regimes and elevated CO_2 can also change the productivity and composition of plant communities over decadal timescales, which in turn impacts soil organisms and C cycling by altering the amount or quality of organic matter entering the soil.

Shifts in vegetation composition due to altered rainfall patterns, as found in tropical rainforest (Engelbrecht *et al.* 2007) and African savanna (Good & Caylor 2011), not only influence photosynthesis (Ward *et al.* 2009) and hence the exudation of photosynthate in the soil, but also the amount and quality of organic matter entering the soil as plant litter (roots and shoots). Moreover, such shifts can modify the soil physical, chemical and biological environment by changing root architecture and rooting depth (Jackson *et al.* 1996). These effects may influence composition of soil microbial communities and functioning. Finally, over hundreds of years, climate-mediated expansion of plant species from lower latitude and altitude, and its impact on organic matter supply to soil and soil physical conditions could potentially have consequences for soil food webs and the biogeochemical cycles at local and, potentially, global scales (Chapin *et al.* 2009; Ostle *et al.* 2009).

The current climate-mediated range expansion of many species (Walther *et al.* 2002) is expected to disrupt current communities when species differ in dispersal capacity: plants disperse faster than many soil organisms (Berg *et al.* 2010). Plant species with rapidly shifting ranges can potentially out-

run their natural soil-borne enemies, symbionts and decomposer organisms (Fig. 1d). For example, range shifting of *Tragopogon dubius* in Europe has resulted in release from growth-reducing soil biota (Van Grunsven *et al.* 2010). Thus, range shifting can expose plants to soils with a more positive balance between enemy and mutualist effects, which has also been shown for invasive exotic plant species from other continents. Two phylogenetically controlled experiments showed that range-shifting plant species can indeed have neutral soil feedback comparable in magnitude to cross-continental exotics and different from the negative direct soil feedbacks of natives (Engelkes *et al.* 2008). On the other hand, the range-shifting species had little effect on ecosystem processes such as litter decomposition (Meisner *et al.* 2012), so that their plant–soil feedbacks benefits were more due to altered pathogen/symbiont balances than to enhanced nutrient availability. These studies have all focused on the effects of range expansion, whereas little is known about legacy effects in soils and the resulting priority effects in plant–soil feedback interactions of the remaining plant species following range contractions.

BIODIVERSITY AND ECOSYSTEM FUNCTIONING

Until recently, there has been little work on plant–soil feedbacks in relation to plant species diversity influences on productivity. Recent work suggests that effects of plant species diversity on productivity may be due to combined community level responses to soil-borne pathogens and nutrition aspects (de Kroon *et al.* 2012). In 2011, two studies by Maron *et al.* (2011) and Schnitzer *et al.* (2011) showed that the proportionally low productivity in plant monocultures, compared to that in plant mixtures, could be increased by (partial) soil sterilization. Their studies suggested that pathogenic soil fungi may have been causing the negative effects on productivity in monocultures, thus explaining the typical positive relationship between plant species diversity and productivity.

These results provide a new perspective on plant diversity-functioning studies as they suggest that the phenomenon of overyielding in mixed plant communities may not be caused by resource complementarity alone, but also by dilution of negative plant–soil feedbacks effects in mixed plant communities (Fig 1f). Kulmatiski, Beard & Heavilin (2012) placed these findings in the context of a biomass-explicit, multi-species plant–soil feedbacks model to demonstrate that across a full range of plant–soil feedbacks effects, negative feedbacks should result in overyielding while positive feedbacks should result in underyielding. This and related work (Kulmatiski, Heavilin & Beard 2011; Hendriks *et al.* 2013) has highlighted the need for combined experimental studies and model comparisons between plant-soil community feedback effects (Box 1) and individual feedback effects.

ROLE IN ABOVE-GROUND–BELOW-GROUND MULTITROPHIC INTERACTIONS

Soil organisms in the rhizosphere, such as root-feeding insects, root pathogens or mycorrhizal fungi, as well as soil

organisms that do not directly interact with the plant such as decomposers or predators, can affect the performance of above-ground herbivorous insects and their natural enemies (Bardgett & Wardle 2010). Interactions between plant roots and soil organisms can result in altered growth and nutritional quality of above-ground plant parts. Many studies have shown, for example, that root feeding by insects or nematodes, or infections with soil pathogenic or mycorrhizal fungi can lead to changes in the concentration of primary or secondary plant compounds in leaf tissues. Such changes in the nutritional quality of above-ground plant parts can subsequently affect the performance of foliar herbivores and the natural enemies of these herbivores, such as parasitoids or predators (Pineda *et al.* 2010; Soler *et al.* 2012).

Both above-ground and below-ground herbivory can lead to changes in the composition of the soil biota (Bardgett & Wardle 2010). Above-ground grazing, for example, typically leads to short-term increases in C excretion from roots and this affects the functioning and composition of the soil microbial community (Hamilton & Frank 2001). Moreover, herbivory can lead to changes in the concentration of primary and secondary plant compounds in root tissues and this can affect direct interactions between roots and soil organisms, as well as the decomposition of root tissues, and hence affect the composition of soil communities (Van Dam *et al.* 2010). Via these influences on the soil community, herbivory can affect plant–soil feedbacks responses (Fig. 1g). Even though very few studies have examined such effects so far, the available evidence suggests that multi-trophic interactions including foliar herbivores or fungal endophytes can indeed affect plant–soil feedbacks responses (Matthews & Clay 2001; Mikola *et al.* 2005; Sørensen, Mikola & Kytöviita 2008). It is also possible that plant–soil feedbacks can influence the nutritional quality of plants, thereby modifying above-ground or below-ground multitrophic interactions.

While most research has focused on the joint effects of a shared host plant, above-ground–below-ground interactions can also occur when above-ground and below-ground organisms do not share the same plant. Kostenko *et al.* (2012) showed that herbivory, by affecting the soil community, can alter the composition of secondary compounds in plants that grow later in the soil, as well as the performance of above-ground herbivores and parasitoids on those plants. Clearly, multitrophic interactions between plants and herbivores above-ground and below-ground can influence plant–soil feedback interactions. Moreover, plant–soil feedbacks can affect the interactions between plants and consumers. Therefore, future studies should place plant–soil feedbacks in a multitrophic context and examine in more detail how top-down effects become bottom-up and vice versa (Moore *et al.* 2003).

EVOLUTIONARY PERSPECTIVES, FOUNDATION
SPECIES AND COMMUNITY GENETICS

Plant–soil feedbacks in natural systems are an emerging, but little studied, area of research linking ecological and evolu-

tionary processes. Whether directly or indirectly, plant functional traits, such as the C to N content of leaves, can create conditions that affect soil biota (i.e. their composition or activity) and decomposition processes that soil biota at least partly regulate (i.e. nutrient depolymerization or mineralization). Such niche construction, in the context of strong environmental gradients in soil, can create selective gradients that may affect the evolution of both plants and soil biota. The data so far demonstrate that genetically controlled variation in functional plant traits can influence soil communities and the processes they mediate in soil (i.e. create an 'extended phenotype'; Whitham *et al.* 2003, 2006; Schweitzer *et al.* 2008). The literature based upon above-ground systems has commonly found that herbivores and tri-trophic interactions serve as important selection pressures for plants (Fritz & Simms 1992; Hunter & Price 1992). However, the soil biota is also emerging as an important factor in mediating the evolutionary dynamics of plant functional traits (Lau & Lennon 2011). Recent studies show the importance of within-species genetic variance on plant–soil feedbacks that is mediated by aspects of the soil biota (Pregitzer *et al.* 2010; Felker-Quinn, Bailey & Schweitzer 2011; Lankau *et al.* 2011). These data are some of the first in natural systems to show that genetically based functional variation in plant traits can influence soil communities and that soil biota shaped by functional plant traits can then act as agents of selection for above-ground traits through feedbacks. As such, they implicate the soil biota as an important regulator of both below-ground processes as well as genetic variation in these systems. Plant–soil feedbacks has the potential to impact selection and evolutionary processes, from plant trait divergence to speciation, but examination of this possibility has only just begun.

Future challenges

To further integrate plant–soil feedbacks in ecological theory, it will be important to determine where and how the observed patterns may be generalized and how they may influence species evolution. One of the general findings to emerge from the literature to date is that most reported direct, intraspecific, plant–soil feedback effects are negative (Bever 2003; Kulmatiski *et al.* 2008; Petermann *et al.* 2008). This might depend on the methodologies used and the ecosystems focused upon. Moreover, the variation in strength of the negative feedback over time, as well as indirect, interspecific feedback effects on neighbouring plant species, may differ (Van de Voorde, Van der Putten & Bezemer 2011). These issues need to be further explored under more realistic conditions and time scales, to determine the extent to which plant-soil community feedback interactions explain the spatio-temporal patterns and processes in vegetation. Feedback experiments in the field (De Rooij-van der Goes, Peters & Van der Putten 1998; Casper & Castelli 2007) are needed to complement and verify feedback experiments under more controlled indoor conditions.

To assist generalization, future studies also need to compare plant–soil feedbacks across ecosystems and successional stages

within these ecosystems. Plant–soil feedbacks are likely to differ across ecosystems, so that there is a need to determine the factors that control this variation. For example, while there has been considerable recent interest in how plant functional traits may determine community and ecosystem properties (de Bello *et al.* 2010), there have been few attempts to evaluate the extent to which these traits can predict the magnitude or direction of plant–soil feedbacks. Although plants with traits associated with enhanced nutrient acquisition support soil communities that differ functionally from plants with traits associated with resource conservation, direct empirical tests to determine how these differences in turn feedback to plant growth are scarce (Bardgett & Wardle 2010).

Conceptual and mathematical models have provided valuable insight into the potential effects of plant–soil feedbacks on plant community development. These models predict that negative plant–soil feedbacks promotes diversity or depresses diversity through positive plant–soil feedbacks. However, plant–soil feedbacks models, rely primarily on simple two-plant-species systems (Bever, Westover & Antonovics 1997; Bonanomi, Giannino & Mazzoleni 2005; Eppstein & Molofsky 2007). Because several important advances have been made recently, there is now a great potential and need to combine and test these models in multi-species plant communities to begin to understand the role of plant–soil feedbacks relative to other factors such as herbivory, propagule pressure, life history strategy, environmental stochasticity and evolutionary interactions.

Ultimately, the challenge for the future will be to use insights into how plant–soil feedback interactions affect the above-ground biodiversity to manage terrestrial ecosystems and the services that they provide under human-induced global environmental changes. Also, a key challenge is to use current knowledge and new insights to mediate effects of climate warming, conserve endangered plant species, control invasive exotic plant species and to enhance food, feed and bioenergy sustainability. The rapidly accumulating knowledge about plant–soil feedback interactions might be used, for example, to enhance pathogen and pest resistance in crops, so this field of research could be used to maintain the quality of production systems for future generations.

Conclusion

Plant–soil feedbacks has become an important concept of relevance when trying to understand plant population dynamics, community composition and functioning of terrestrial ecosystems. In addition to testing this concept through experimental studies under controlled conditions and modelling approaches, it also needs testing in the field, and the underlying mechanisms need to be elucidated. The contributions of the various abiotic and biotic soil components to plant–soil feedbacks relative to other factors that influence ecosystem composition and functioning need to be quantified, and the role in species evolution needs to be determined. This will lead to enhanced understanding of ecological-evolutionary consequences of plant–soil feedbacks, which may allow better prediction and

mitigation of consequences of human-induced global changes, such as climate warming, invasions and land use change for sustainable provisioning of ecosystem services in a rapidly changing world.

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