

SPECIAL FEATURE – FORUM

PLANT–SOIL FEEDBACKS IN A CHANGING WORLD

Biotic plant–soil feedbacks across temporal scales

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Summary

1. Plant effects on soil biota can result in feedbacks affecting plant performance, with consequences for plant community and ecosystem dynamics on short and long time-scales. In addition, the strength and direction of plant–soil feedbacks depend on temporal shifts in abiotic environmental conditions.

2. We synthesize current knowledge on temporal aspects of plant–soil feedbacks and present new ideas to better understand and predict the effects of plant–soil feedbacks on community and ecosystem properties across temporal scales.

3. Explaining short-term temporal feedback dynamics requires us to better understand mechanistic linkages between plants, soil organisms and locally available resources. On the other hand, we need to refine our understanding of the context-dependency of plant–soil feedbacks, as the strength and direction of feedback interactions are influenced by ‘external’ temporal ecosystem dynamics, such as variation in soil resource availability after disturbance or during succession.

4. *Synthesis.* Based on our synthesis of temporal aspects of plant–soil feedbacks, we suggest three main avenues for future research: (i) how plant–soil feedbacks changes with ontogeny, (ii) how plant and soil organism traits drive temporal variation in plant–soil feedbacks and (iii) how environmental changes across temporal scales alter the strength and direction of plant–soil feedbacks.

Key-words: competition, disturbance, life history, mycorrhizas, plant traits, population and community dynamics, primary and secondary succession, soil legacy

Introduction

Interactions and feedbacks between plants and soil organisms are increasingly recognized as important in driving and maintaining key ecosystem properties such as productivity and diversity (e.g. De Deyn *et al.* 2003). Plant species vary greatly in their influence on herbivorous, pathogenic and mutualistic soil organisms, and such plant species-specific impacts on soil biota can in turn affect plant performance, resulting in ‘biotic’ plant–soil feedback (Van der Putten, Van Dijk & Peters 1993). However, predicting how these feedbacks change through time and how they contribute to temporal ecosystem dynamics is one of the most challenging tasks

in ecology because of the complexity of interactions among the component organisms and their environment.

So far, many aspects of temporal plant–soil feedback dynamics therefore remain poorly tested and little understood. First, despite the recognition that feedbacks can play a role in long-term ecosystem dynamics, most plant–soil feedback studies have only been short-term (Kulmatiski & Kardol 2008), often much shorter than a plant’s life span (Fig. 1a). Short-term feedback studies will therefore only partly capture the true consequences for plant population and larger scale community dynamics. Secondly, it is often assumed that shifts in soil communities result in linear effects on plant growth rates, and that plant and soil communities vary over similar time-scales (e.g. Bever, Westover & Antonovics 1997), yet nonlinear relationships are also possible (Hawkes *et al.* 2012). Thirdly, and probably most overlooked, the strength of feed-

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backs may vary due to fluctuating abiotic environmental conditions that directly or indirectly affect the balance of plant–microbe interactions.

We propose that plant–soil feedbacks should not be treated as a fixed parameter, but one that may vary strongly over time due to both direct plant–soil organism interactions and external environmental factors. We synthesize current knowledge on temporal aspects of plant–soil feedback and present new ideas to better understand and predict feedback effects on community and ecosystem properties across temporal scales. We focus on how plant–soil feedback (i) controls pop-

ulation, community and ecosystem temporal dynamics and (ii) is influenced by temporal shifts in external environmental conditions.

Plant-soil feedback drives temporal community and ecosystem dynamics

In the short term, temporal feedback dynamics are best explained in terms of direct feedback interactions, i.e. dynamics resulting directly from interactions between plants and soil organisms.

Direct interactions have been the focus of most plant–soil feedback studies to date, with the assumption that temporal changes in response to environmental conditions are minimal. However, environmental changes could potentially modify or overwhelm direct feedbacks (e.g. Yelenik & Levine 2011) (see ‘Environmental effects on temporal variation in plant–soil feedback’). Direct feedback interactions include the build-up of pathogens in the rhizosphere, establishment of mycorrhizal networks and other interactions that can affect plant growth and are mediated via soil biota (e.g. Klironomos 2002). Direct feedbacks generally develop over shorter periods than the lifespan of an individual plant, although in some cases the feedback effects only become apparent after multiple generations of plant growth.

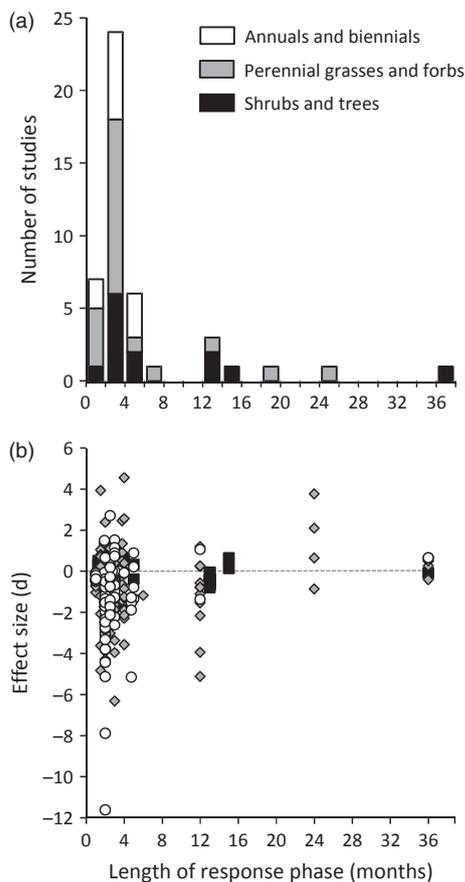


Fig. 1. (a) Number of plant–soil feedback studies by the duration of the response phase, binned in 2-month intervals. Data from Kulmatiski *et al.* (2008). (b) Effect size d is plotted as a function of the length of the response phase. Results are based on a re-analysis of studies that compared plant growth on soils conditioned by conspecifics with soils conditioned by heterospecifics reported by Kulmatiski *et al.* (2008). Negative and positive effect sizes indicate negative and positive plant–soil feedback, respectively. Each point represents a single experimental test. Different colours and symbols indicate plant life form: annual and biennials (white, circles), perennial grasses and forbs (grey, diamonds) and shrubs and trees (black, squares). Effect sizes tended to correlate positively with the length of the response phase ($R^2 = 0.32$), but the relationship was not statistically significant ($F_{1,267} = 1.49$, $P = 0.22$) based on meta-regression analysis. There also was no interaction between length of the response phase and plant life form ($F_{2,267} = 0.21$, $P = 0.81$). Meta-regression was run in R version 2.12.1 using the `lme` function with response phase and plant life form as fixed factors, study as random factor and the inverse of the variance as weighing factor.

PLANT LIFE STAGE AND POPULATION DYNAMICS

Species-specific feedback with populations of soil organisms affects plant growth rates and temporal plant population dynamics. Plant–soil feedbacks depend on the growth and population dynamics of the component species, and hence are inherently time-dependent. Plants can experience different feedbacks during ontogeny, but it is not clear whether the magnitude of feedback to an individual plant increases (or decreases) linearly through time as a result of these changes (Fig. 2). Different plant–soil feedbacks in response to the same microbial community may occur during ontogeny, if the plants in each life stage respond differently, or if they associate with different microbial communities. Variability in feedback with plant life stage has been observed due to changes in vulnerability to pathogens or in the relative benefits derived from mutualists such as mycorrhizal fungi (Bardgett *et al.* 2005). Seedling stages, which are the focus of most feedback experiments, may be particularly susceptible to mortality caused by pathogens (e.g. Packer & Clay 2000; Hersh, Vilgalys & Clark 2012) or to growth promotion or suppression governed by the presence of an established mycorrhizal network (Van der Heijden & Horton 2009). Stronger negative plant–soil feedbacks have been observed in shorter-term studies than in longer-term studies (Fig. 1b), which could suggest that the short duration of most feedback experiments creates a bias towards detection of negative plant–soil feedbacks. However, feedback studies carried out beyond 12 months are scarce (Fig. 1) and more work is needed to substantiate this idea.

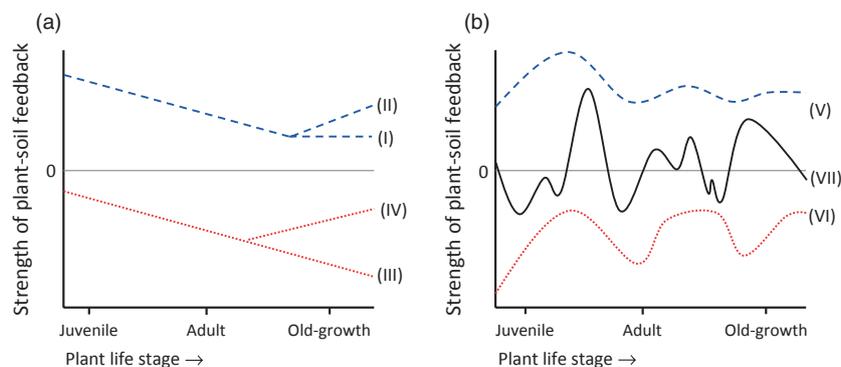


Fig. 2. Hypothetical shifts in the relative strength and direction of biotic plant-soil feedbacks with plant life stage. (a) Linear declines over time in plant dependence on soil mutualists (eventually leveling off) would be expected for perennial plants in a temporally stable environment where nutrients are stable (I), but if nutrients are depleted a slight increase over time would be expected (II). Linear increases in pathogen susceptibility over time would be expected if pathogens accumulate as plants age and plants do not change in susceptibility (III); if plants do become less susceptible with age, less negative plant-soil feedbacks over time can develop (IV). (b) Nonlinear responses might be expected when plant physiology shifts dramatically with life stage, in a temporally fluctuating environment, or when novel microbial strains appear through immigration or evolution. Initial dependence on soil mutualists at the seedling stage declines as plants transition to juvenile and adult stages and then equilibrates (V). Initial seedling susceptibility to pathogens declines, except for periods of pathogen evolution, introduction of new strains, or other external influences on pathogen abundance (VI). Idiosyncratic changes in the strength of plant-soil feedbacks can also occur due to environmental effects, microbial immigration or a lack of evolutionary interactions (as in the case of exotic species) (VII).

Little is known about how quickly plants can alter soil communities or vice-versa, and how the strength and direction of plant–soil feedbacks changes with plant life stage (Fig. 2). Species-specific temporal variation has been observed in the direction and magnitude of feedbacks over 19 months in perennial grasses, with both linear, directional and nonlinear, non-directional patterns and sign switching at different time points (Hawkes *et al.* 2012). Such temporal variation in plant–soil feedback limits the potential for extrapolating results from single-endpoint studies. A lag in plant population responses may be observed if plants respond via altered growth rather than survival or mortality. For example, *Jacobaea vulgaris* populations appear to develop strong negative feedbacks immediately after establishment in old fields, but populations do not decline for at least 5 years as seedling recruitment slows (Van de Voorde, Van der Putten & Bezemer 2011). Furthermore, when considering invasions occurring throughout a 210-year time span, feedback for non-native plant species became more negative with time since establishment in New Zealand (Diez *et al.* 2010). Evolutionary change in both non-native plants and native soil microorganisms may contribute to nonlinear feedback patterns, particularly over such long time-scales. Clearly, there are various mechanisms that can affect feedbacks across different temporal scales, but we do not have a working framework for predicting their occurrence or understanding their generality.

A trait-based approach or a ‘functional matrix’ approach (*sensu* Eviner & Chapin 2003) may prove useful for understanding temporal plant–soil feedback if traits can be related to mechanisms underlying plant–soil interactions. Plant effects on populations of soil organisms and the resulting feedback may depend on key plant traits relating to resource acquisition, allocation (e.g. specific root length) or defense that vary among both plant genotypes and species. For example, some plants defend against below-ground herbivore and pathogen

attacks with secondary chemicals, others respond positively to attacks by compensatory growth, whereas others experience negative growth when eaten or infected (Rasmann *et al.* 2011). Each of these mechanisms can differentially affect soil biota, potentially resulting in characteristic effects on the rate of build-up of soil organisms that cause feedback to plant growth and population dynamics. The net outcome will depend on how both populations of growth-suppressing and growth-enhancing rhizosphere organisms respond over time. Below-ground plant traits may be particularly useful in predicting feedback outcomes, but so far they have been poorly studied. Notably, it has been shown that root and leaf lifespan are not always correlated, limiting the use of ‘above-ground proxies’ (Withington *et al.* 2006). Although equally important to temporal plant–soil feedback dynamics, even less is known about specific traits of the soil organisms involved, and what role they play in the build-up of feedbacks.

COMPETITIVE INTERACTIONS AND COMMUNITY DYNAMICS

Soil feedbacks to individual plants and population dynamics may scale up to the level of plant communities by influencing the competitive hierarchies of coexisting species, and hence, affecting plant community composition and the rate of species turnover through time. Furthermore, feedback effects on temporal plant species turnover and more complex plant community dynamics can only be understood when simultaneously considering both intra-specific (as described above) and interspecific feedbacks (Bever, Westover & Antonovics 1997). Illustratively, interspecific competition may enhance (Kardol *et al.* 2007) or eliminate (Casper & Castelli 2007) the expression of feedbacks, suggesting that the extent to which competing species differ in their effects on and response to soil community composition (trait dissimilarity)

through time may partly control feedback effects on plant community dynamics.

Plant effects on soil biota can also result in soil legacies affecting other species, with consequences for temporal plant community dynamics (Kardol *et al.* 2007; Hamman & Hawkes 2013). Soil legacies are not always equated with feedbacks, but are essentially feedbacks considered on longer time-scales and may play an integral role in effects of plant–soil feedbacks on temporal plant community dynamics. Feedbacks in one generation can become soil legacies for the next, potentially altering the rate and direction of plant species turnover. In both field and greenhouse studies, plant competitive interactions have been affected by biotic soil legacies from preceding plant species; such soil legacies may be specific to plant species or functional groups, such as grasses and forbs (Bezemer *et al.* 2006; Kardol *et al.* 2007) or have similar effects on all species within a plant community, which would be more likely to occur when these legacies involve changes in nutrient availability. Soil legacies can persist from a few years to several centuries (e.g. Hamman & Hawkes 2013) and their decay rate should depend on the temporal dynamics of plant and soil communities as affected by environmental context. However, the persistence of direct feedback interactions in shaping plant population and community dynamics is largely unknown and should be among the priorities for future research (Fig. 4).

The role of plant–soil feedbacks in temporal plant community dynamics has been most extensively studied in the context of succession (e.g. Van der Putten, Van Dijk & Peters 1993; Kardol, Bezemer & Van der Putten 2006). Primary succession represents the early stages of ecosystem development, during which organisms colonize a recently exposed and ‘biologically empty’ geological substrate. Here, facilitation is thought to be pivotal, given the typically harsh conditions of low soil nutrient and water availability. The classic case of a positive plant–soil feedbacks during primary succession involves the symbiosis between plants and N₂-fixing bacteria on N-poor substrates (Walker 1993). For example, following the eruption of Mount St-Helens in 1980, the N₂-fixing legume *Lupinus lepidus* rapidly formed mono-dominant patches on pyroclastic flows, leading to ‘islands of fertility’ that promoted the growth of later colonists (Morris & Wood 1989). Opportunities for positive plant–soil feedbacks during primary succession are not limited to N₂ fixation. As the first colonists in the earliest stages of primary succession are frequently non-mycorrhizal, AM fungi rapidly become important (Brankatschk *et al.* 2011).

Secondary succession starts from a situation where a resident soil community is present and this community contributes to the development of plant communities (Carbajo *et al.* 2011). The first colonizers in secondary succession are typically fast-growing plant species with little defense against root pathogens, whereas the plant species from later successional stages are slow-growing and typically associate with mutualistic soil organisms such as mycorrhizal fungi (Kardol, Bezemer & Van der Putten 2006). Hence, in secondary succession, negative feedback in early stages can increase the rate of species

turnover and positive feedbacks in later stages can promote temporal community stability relative to a situation with no plant–soil feedbacks. However, temporal changes in plant communities do not always translate directly to changes in soil biota (Hedlund *et al.* 2003), suggesting that plant–soil feedbacks are driven more by the plants than by the soil communities or that soil organisms respond more to external factors than to plants. It has also been argued that changes in vegetation occur faster than changes in soil, perhaps due to the buffered soil environment where dead plant remains can persist as soil organic matter long after the living plant community has shifted. The rate of change, however, may strongly differ among groups of soil organisms and depend on their interactions with soil abiotic properties (Cortois & De Deyn 2012).

Environmental effects on temporal variation in plant–soil feedbacks

Plant–soil feedbacks depends on direct interactions between plants and soil organisms, but the nature of these interactions may be modified by shifts in external environmental conditions. Temporal variation may add ‘noise’ to feedbacks (Fig. 2b). For example, seasonal and annual changes in the environment, such as resource or stress levels, can directly affect factors relevant to feedbacks including plant and microbial physiology, and soil resource pools (e.g. Eviner, Chapin & Vaughn 2006). Anthropogenic forcing, including climate change and nitrogen deposition, can play a similar role in modifying feedbacks (see also Bardgett *et al.* 2013). Observed feedbacks at any given time may therefore reflect the interaction of the plant with both soil biotic effects and environmental conditions (Fig. 3).

Changes in limiting soil resources over time are expected to modify feedback relationships, for example through altered plant reliance on mutualistic associations, susceptibility to root pathogens (De Deyn, Raaijmakers & Van der Putten 2004) or altered decomposer activity (Manning *et al.* 2008). It has been shown that nitrogen (N) enrichment weakens the strength of negative plant–soil feedbacks in grasslands, although the underlying mechanism was not identified (Gustafson & Casper 2004). Such decoupling of biotic plant–soil interactions may be an important ecological consequence of anthropogenic nutrient enrichment. Importantly, plants and soil organisms may not respond in tandem to temporal shifts in soil resources (or other environmental conditions). For example, plants and mycorrhizal fungi may differ in their thresholds for N and phosphorus (P) limitation (Treseder 2004), suggesting that feedbacks between plants and mycorrhizal fungi would shift when nutrient availability changes. The strongest feedbacks would be expected to occur at N and P levels where plant growth remains resource-limited whereas fungal growth is not.

Over broader temporal scales, environmental control of feedbacks cannot simply be considered at the plant species level as shifts in environmental conditions result in plant species turnover. Instead, the importance of plant–soil feedback in driving plant community dynamics is better considered at

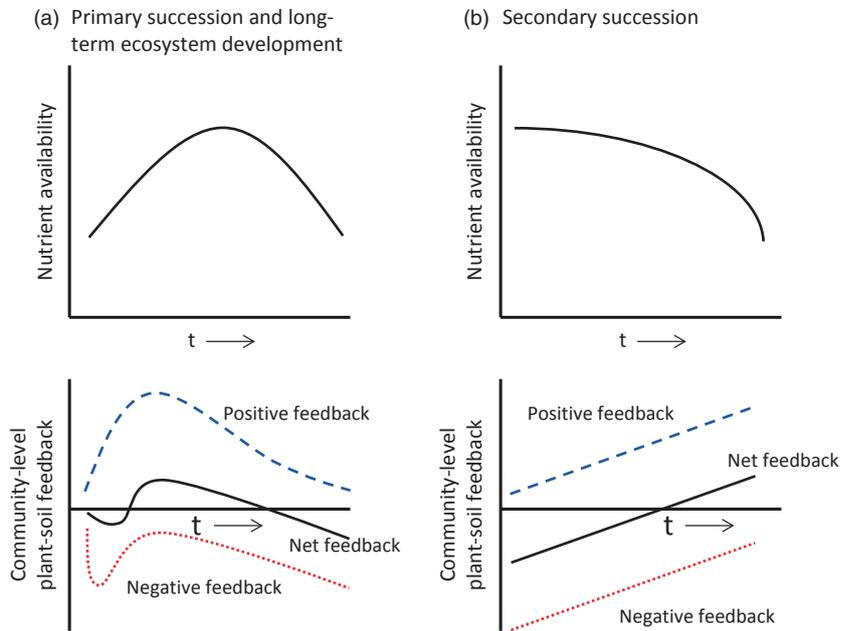


Fig. 3. (a) The strength of plant-soil feedbacks may shift with temporal changes in the abiotic environment such as soil nutrient availability. (a) During primary succession and long-term ecosystem development occurring across decades to millennia, net feedbacks can track the rise and fall of nutrient availability. (b) Secondary succession occurs on shorter time scales, typically from years to decades, and allows us to directly assess whether feedback tracks nutrient declines. Note that the net feedback here is based on the assumption that positive and negative feedbacks are additive.

the community level, i.e. the abundance-weighted average of the positive and negative feedbacks of the component species. Despite little evidence for tracking community-level feedback to temporal variability in resources, we might expect feedbacks to be affected by changing resource levels (or variation in other aspects of the environment). Importantly, the scales at which shifts in environmental conditions affect direct feedback interactions depend on the nature of the control. For example, in the case of disturbances, external control may occur stochastically, or pulse-wise with regular or irregular time intervals, could occur across scales of time and could affect feedback both at the individual and at the community level. In the case of long-term ecosystem development and succession, environmental control may be more directional and predictable, and would mainly act at the plant community level.

DISTURBANCES

Environmental control of plant-soil feedbacks can result from sudden changes in the abiotic environment. Disturbances that alter plant-soil interactions, such as tillage, animal activity, fire and extreme weather events (heat waves, droughts, intense rainfall) can play an important role in subsequent ecosystem recovery. Soil disturbance, for example, can decrease the activity of both pathogens and mutualists, and hence, slow-down or 'reset' the development of negative and positive plant-soil feedbacks (Kulmatiski & Kardol 2008). Importantly, soil disturbances may trump the effects of plant species on soil communities. Soil community responses to disturbance will largely depend on the disturbance tolerance and intrinsic population growth rates of component taxa, which can determine the trajectory of post-disturbance plant-soil feedbacks. Thus, disturbance effects on feedbacks may partly act as a mechanism for observed plant community pat-

terns in a manner consistent with Grime's CSR theory (Grime 1977). More frequent and intense disturbances over time should reduce negative feedback and favour ruderal plant species that are likely to realize rapid growth with decreased pathogen activity, increased nutrient availability and competitive release. With infrequent and mild disturbance, both negative feedbacks and competition are likely to be more important, such that plant communities are dominated by more pathogen-tolerant, competitive species that are typical of late succession (Kardol, Bezemer & Van der Putten 2006). Despite our emphasis here on local community responses, the role of plant-soil feedbacks after disturbance also depends on spatio-temporal processes such as dispersal. The same is true for succession and other assembly processes. Dispersal is inherently different for plants and soil organisms and also varies among functional groups of soil organisms, which together will create the local feedback response. Differences in immigration rates among taxa may be crucial to the development of plant-soil feedbacks at a given time and place as well as across larger spatial scales and meta-communities (e.g. Packer & Clay 2000; see also van der Putten *et al.* 2013).

ECOSYSTEM DEVELOPMENT AND SUCCESSION

Ecosystems tend to peak in productivity and resource availability within decades to centuries after the start of their development, but can then enter a 'retrogressive' phase where these properties decline over thousands of years in the absence of major soil-rejuvenating processes (Peltzer *et al.* 2010). Long-term ecosystem development is linked to changes in soil nutrient availability, as plant productivity shifts from being N-limited to P-limited (e.g. Laliberté *et al.* 2012). Changes in N and P availability, in turn, favour plants of contrasting nutrient-acquisition strategies (Lambers *et al.* 2008). We hypothesize that resource changes during ecosystem development

influences the strength and direction of biotic plant–soil feedbacks, with community-level implications (Fig. 3a). During the very early stages of primary succession, soil nutrient levels are low, and positive effects of mutualists (e.g. N₂-fixing microorganisms) may therefore initially be strong and promote dominance. However, these positive effects are likely to be rapidly outweighed by negative effects of pathogens as host densities increase. As N pools build up and P becomes increasingly limiting in intermediate-aged soils, mycorrhizal fungi can promote P uptake and provide pathogen protection, creating the potential for positive feedback and promoting plant dominance. However, in some ancient and strongly weathered soils where the little remaining P is poorly available (e.g. south-western Australia), species-rich communities can be found that are characterized by a high proportion of non-mycorrhizal plant species that develop dense, short-lived specialized roots that mobilise P (Lambers *et al.* 2008). Such short-lived roots may show poor structural defenses against pathogens, potentially leading to negative feedbacks that promote species coexistence, and high plant species diversity, during late stages of ecosystem development.

As our hypothesis remains speculative, initial tests are possible using plants and soils collected along well-defined long-term soil chronosequences, similar to what was done for secondary succession. In secondary succession, shifts in external environmental conditions have been shown to control community-level plant–soil feedbacks (Kardol, Bezemer & Van der Putten 2006). During the early stages of secondary succession, high soil fertility promotes fast-growing, poorly-defended pioneer species, which typically show negative plant–soil feedbacks, promoting high rates of species turnover. Over time soil nutrient availability decreases, and during late stages of secondary succession positive plant–soil feedbacks of slow-growing, mycorrhizal-dependent plant species dominates the community and promotes species coexistence (Fig. 3b).

Conclusions

Recognition of the potential importance of temporal variation in plant–soil feedbacks, either resulting from organismal development and intrinsic population dynamics or from changing environmental context, should help us to move beyond ‘snapshot’ and ‘black box’ studies and focus more on the mechanisms that underlie plant–soil feedbacks. Analogous to the ‘disease triangle’ model commonly used in phytopathology (Stevens 1960), the development of plant–soil feedbacks results from the interaction of a susceptible host plant and an active soil community within an environmental context; to advance our understanding of the temporal dynamics of plants and soil organisms requires consideration of each component and their interactions over time. A trait-based approach can help to tackle this challenge. For example, we know reasonably well how plant physiological and nutrient-acquisition traits determine plant responses to temporal changes in environmental conditions, and we have some understanding of how soil community composition shifts with environmental change. However, we know little about plant traits involved in interactions with soil organisms, and about traits of soil organisms involved in interactions with plants, and how those traits drive temporal plant–soil feedbacks dynamics.

To better predict how short-term plant–soil feedbacks could scale up from species-level to longer-term ecosystem dynamics, and in turn how plant–soil feedbacks is driven by temporal shifts in environmental context, we need plant–soil feedbacks experiments across environmental gradients, either using natural gradients (such as soil chronosequences) or using multi-level experimental manipulations in the field or greenhouse (Kardol, De Long & Sundqvist 2012). These experiments should explicitly account for the functional traits of both the plants and the soil organisms, as related to biotic and environmental interactions. For soil organisms this would first require opening the ‘black box’ (Cortois & De Deyn 2012),

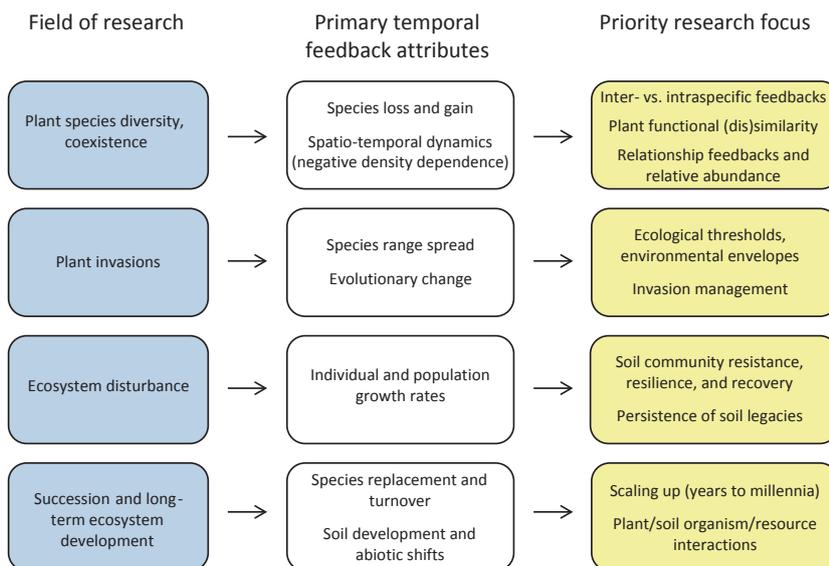


Fig. 4. The way forward: directions for future research in four core fields of ecology where temporal aspects of plant–soil feedbacks are likely to play a role.

i.e. identifying the relevant species, and their traits, where new molecular methods allowing rapid identification of soil organisms may open new windows of opportunities. The next step then would be to manipulate plant and soil organism traits in factorial combinations, for example, through inoculation experiments (e.g. Klironomos 2002; Kardol *et al.* 2007), and follow their responses over time. Such experiments would be a way forward and could be informative to a wide variety of research areas where temporal aspects are important (Fig. 4).

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