ECOSYSTEMS, EVOLUTION AND PLANT–SOIL FEEDBACKS
Eco-evolutionary dynamics in plant–soil feedbacks

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Summary

1. In the past decade, ecologists have begun to more fully appreciate the role of evolution in explaining contemporary ecological processes. Evolution is most likely to affect ecological patterns when selection pressure is particularly strong, or when the generation time of at least one interacting species is relatively short.

2. Interactions between plants and soil microbes are an excellent candidate for examining eco–evo interactions because interactions between organisms are tightly knit with the potential for species with relatively short generation times to impose strong selection on one another. Here, we examine the potential for eco–evolutionary dynamics in plant–soil feedbacks (PSFs).

3. Genetic variation in plant traits and subsequent evolution of those traits can affect traits and species composition of soil microbial communities. Soil microbial communities can, in turn, alter the evolutionary trajectory of plant traits. Further, the direction and magnitude of PSFs can affect the plant community, which may alter the selection on plant traits via intra- and interspecific interactions.

4. Finally, we consider how eco-evolutionary feedbacks might enhance or mitigate the effects of PSFs in driving the structure of natural plant communities.

Key-words: community ecology, competition, eco–evo feedback, genetic variation mycorrhizae, natural selection, rhizobia, soil microbes, succession

Introduction

Biologists have long recognized that ecological processes drive trait evolution. For decades, Hutchinson's (1965) description of the 'ecological theatre and the evolutionary play' has served as a metaphor for understanding the effects of ecology on evolution. The implication of the metaphor is that while ecology drives evolution, evolution that occurs over hundreds to thousands of generations is unlikely to affect contemporary ecological processes (Slobodkin 1961; Pianka 2000), just as an actor in a theatre is unlikely to alter the scenery. In contrast, Pimentel (1961) suggested that population density could drive genetic changes, but these genetic changes altered population growth rates and population density, which affected selection further. This implies a dynamic feedback between the actor and the scenery, in which each alters the actions of the other.

Ecologists have increasingly recognized the importance of contemporary evolution for understanding ecological processes (reviewed in Thompson 1998; Fussmann, Loreau

& Abrams 2007; Johnson & Stinchcombe 2007; Schoener 2011). Organisms with very short generation times have the potential to evolve on much shorter time-scales, but rapid evolutionary rates need not be limited to short-lived organisms. Strong selection, such as that which results from global change or biological invasions, can also increase rates of evolutionary change (Reznick & Ghalambor 2001; Visser 2008; Lavergne *et al.* 2010; Moran & Alexander 2014; Colautti & Lau 2015). With increasing global change, we have seen a bevy of both empirical and theoretical studies demonstrating that contemporary evolution can affect population demography (Reznick *et al.* 2012), the outcome of species interactions (Yoshida *et al.* 2003; terHorst, Miller & Levitan 2010), species diversity (Schreiber, Buerger & Bolnick 2011; Pantel, Duvivier & Meester 2015) and ecosystem function (Bassar *et al.* 2012; terHorst, Lennon & Lau 2014). This body of work has demonstrated that, in many cases, it is impossible to understand the ecology of a community without accounting for concurrent evolutionary change.

Feedbacks between plants and soil microbes (Fig. 1) can have important consequences for the ecology of both plant and microbial communities. PSFs can maintain species

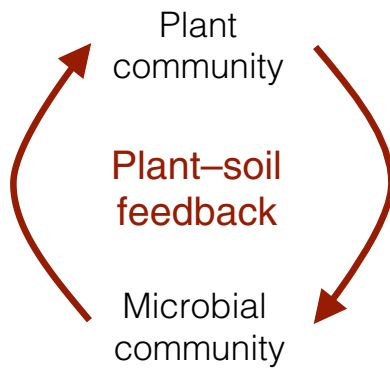*Correspondence author. E-mail: casey.terhorst@csun.edu

Fig. 1. Plant–soil feedbacks occur when the plant community affects the composition of the microbial community and these changes feedback to alter the composition of the plant community.

and genetic diversity (Van Nuland *et al.* 2016). PSFs also affect the success of colonization by invading species (Nijjer, Rogers & Siemann 2007; Lee, Flory & Phillips 2012). Changes in the strength or direction of PSF affect species dominance and drive community assembly and successional trajectories (Kardol *et al.* 2013, Herrera Paredes & Lebeis 2016).

Interactions between plants and soil microbes are likely to be affected by contemporary evolution (Schweitzer *et al.* 2014; Evans *et al.* 2016, Fig. 2). Soil microbes typically have short generation times, giving them the potential to evolve rapidly. While many plants, especially annuals, have relatively short generation times and can evolve rapidly, strong selection can change genotype frequencies over short time-scales, even in long-lived species. The ecology of soil microbes is greatly influenced by plant traits and plant community composition (Van Nuland *et al.* 2016, in

Fig. 2. Eco–evo feedbacks occur when plant traits affect the function of the microbial community, either through changes in species composition or evolution of microbial traits (a). These changes in function feedback to change the evolutionary trajectory of plant traits (b).

review, van der Putten *et al.* 2016 Fig. 2a). Similarly, plant fitness is tightly coupled with the soil microbial community, creating the potential for microbes to impose strong selection on plant traits (Lau & Lennon 2012; Fig. 2b). Interactions between ecological and evolutionary dynamics in PSF are likely because the plant and microbial traits under selection are also the traits that strongly influence the reciprocal ecological dynamics. Yet, eco-evolutionary dynamics between plants and soil microbes have only recently gained theoretical and empirical attention (Van Nuland *et al.* 2016).

Here, we review different mechanisms by which eco-evolutionary dynamics can affect PSFs and vice versa. Primarily, we address previous work that suggests that (i) evolution of plant traits can affect soil microbial communities and (ii) microbial communities can affect the evolution of plant traits (Fig. 2). In addition to the eco–evo interactions between plant traits and soil microbes, we also address (iii) how the strength and direction of ecological PSFs can affect the evolution of plant traits. Finally, we consider (iv) how interactions between PSFs and eco-evolutionary dynamics could affect both plant and microbial communities.

How do plant traits affect soil microbial communities?

As illustrated in this Special Issue, many studies have examined the effects of plants on the soil microbial community. Here, we examine how specific plant traits can affect the soil microbial community (Fig. 2a). We then address the evidence for whether genetic variation in traits within a plant species has the potential to affect soil microbes and, finally, whether evolution of those plant traits can affect properties of the soil microbial community.

Many studies have addressed the role of plant diversity in driving microbial community composition (e.g. Zak *et al.* 2003; Rodriguez-Loinaz *et al.* 2008). A portion of this diversity effect is likely caused by variation in plant traits. Studies that have used trait-based approaches have found variation among plant species in functional traits (e.g. plant productivity, root porosity and carbon exudation) that affect microbial species composition and biomass (McGill, Sutton-Grier & Wright 2010; Sutton-Grier & Megonigal 2011). It is also important to note that the effects of plant traits on soil microbial communities may be context dependent; plants can have different effects on soil microbes across seasons, depending on whether or not the plants are photosynthetically active (Thoms & Gleixner 2013).

To better understand eco-evolutionary interactions, we need to understand how specific plant traits affect the microbial community. Changes in leaf chemistry, such as condensed tannins, can slow rates of leaf litter decomposition and alter the soil microbial community (Schweitzer *et al.* 2008). Increased relative growth rates or
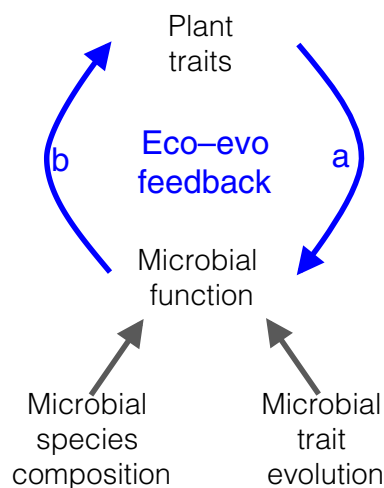
above-ground biomass can lead to increased soil nutrient inputs via leaf litter (Orwin *et al.* 2010; Cantarel *et al.* 2015), which is likely to affect soil microbial communities. Below-ground traits are also relevant for predicting the abundance and species composition of bacteria and fungi in the soil (Legay *et al.* 2014; Fig. 2). Plant traits, such as root length, root surface area, nitrogen concentration and affinity for ammonium, are good predictors of the abundance and composition of soil microbes, microbial diversity and denitrification in soils (Maul & Drinkwater 2010; Cantarel *et al.* 2015). Plant carbon-to-nitrogen ratio affects decomposition rates of plant matter, a result that is likely driven by different abundances of microbes or composition of the soil microbial community (Cornwell *et al.* 2008).

The rise of metagenomics has allowed for greater characterization of microbial communities and how particular microbial taxa respond to plant traits. For example, Blagodatskaya *et al.* (2014) examined how plant competitive ability affected different taxa within the soil microbial community. In two strawberry species growing at low nutrient levels, competitive plants grew larger roots and depleted nutrient levels in the soil, thus benefiting the microbes that use resources more efficiently, but grow more slowly (Blagodatskaya *et al.* 2014). Similarly, de Vries *et al.* (2012) examined how plant traits affected different microbial taxa. Exploitative plant traits, such as high nitrogen content, were associated with bacterial-dominated communities, while traits that conserve resources, such as low specific leaf area, were associated with fungal-dominated communities (de Vries *et al.* 2012).

EFFECTS OF TRAIT VARIATION WITHIN PLANT SPECIES

The majority of these trait-based studies examined traits across plant species and are thus unable to distinguish between the effect of a trait and that of species identity. Species with different trait combinations can affect microbes differently (Eviner 2004). One way to avoid this confounding effect is to examine trait variation within species. To understand eco-evolutionary dynamics, it is critical to examine intraspecific trait variation to understand the potential for traits to evolve (Bolnick *et al.* 2011).

Both plant phenotype and genotype can affect soil microbial communities. *Baccharis pilularis* (coyote brush) is a dominant shrub that produces two distinct morphologies: a prostrate and an erect morph. Prostrate morphs produce more biomass and leaf litter and maintain a more humid environment underneath the shrub; consequently, the prostrate morphs support a different soil microbial community from erect morphs (Crutsinger *et al.* 2014). Soils underneath prostrate morphs had higher bacterial species richness, although fungal species richness was similar between morphs. Similarly, *Senecio inaequidens* (narrow-leafed ragwort) produces different genotypes, or cytotypes, as a result of polyploidy. Cytotype affects flowering phenology and the ratio of resource allocation to

reproduction vs. below-ground growth, which alters bacterial diversity and abundance in the soil (Thébault *et al.* 2010). However, these effects of genotype are species dependent, as different cytotypes of *Centaurea maculosa* (spotted knapweed) had no effect on soil microbial communities (Thébault *et al.* 2010).

Dozens of studies have investigated the 'extended phenotype' of other community members that tend to be associated with specific plant genotypes (e.g., Whitham *et al.* 2006; Genung *et al.* 2011). Recent work has examined the soil microbial community as an extended phenotype, finding strong associations between plant genotype, litter decomposition and soil community structure, particularly in cottonwood trees (*Populus* spp.) (Schweitzer *et al.* 2008; Lamit *et al.* 2015). Agricultural research has found effects of plant genotype on the communities of bacteria and fungi in the soil, including effects of different cultivars of chickpeas (Ellouze *et al.* 2013) and maize (Peiffer *et al.* 2013; Cotta *et al.* 2014; Ondreickova *et al.* 2014).

Interactions between plant genotypes and soil microbes may also include other community members that interact with plants. Genetically based susceptibility to herbivory by moths in *Pinus edulis* affected the composition of the ectomycorrhizal fungal community (Sthultz *et al.* 2009). Trees that were genetically susceptible to moth herbivory tended to be associated with drought-tolerant fungal species (Sthultz *et al.* 2009). Garlic mustard (*Allaria petiolata*) produces allelochemicals that reduce the abundance of mycorrhizal fungi in the soil, which reduced the growth and competitive ability of other plants in the community that largely depend on mycorrhizae for nutrient acquisition (Lankau 2011; Evans *et al.* 2016). In goldenrods (*Solidago* spp.), the amount of nutrients supplied to soil microbial communities through leaf litter and decomposition depends on the genetic identity of the plant competitor (Genung, Bailey & Schweitzer 2013). Effects of plant genotype on the soil microbial community may also feedback to improve the fitness of the plant genotype, as the microbial community becomes more beneficial to particular plant genotypes (Madritch & Lindroth 2011).

EFFECTS OF PLANT TRAIT EVOLUTION

Overall, there is widespread evidence that variation in plants traits can affect the soil microbial community, suggesting a potential for plant trait evolution to affect soil microbes. Fewer studies have directly tested how plant trait evolution may influence soil microbes. Plants with short generation times or Long-Term Ecological Research (LTER) sites may be useful systems for exploiting multigenerational exposure of plants to various ecological conditions to gain a better understanding of how the evolution of specific plant traits may affect microbes.

In a 5-year study of *Oenothera biennis* (evening primrose), Fitzpatrick *et al.* (2015) found that suppression of insect herbivores drove the evolution of earlier flowering phenology, increased competitive ability and reduced tissue

phenol content. These evolutionary changes also resulted in reduced soil respiration rates, presumably as a result of changes in the soil microbial community (Fitzpatrick *et al.* 2015). In another study, terHorst and colleagues manipulated the evolutionary environment of rapidly cycling *Brassica rapa* (terHorst, Lennon & Lau 2014). Plants were exposed to wet or dry soil conditions for three generations and then reciprocally transplanted to wet or dry soils. Plants that evolved in drought treatments caused increased bacteria : fungi ratios in the soil. Plant evolutionary history explained nearly as much variation in the soil microbial community (29 ± 3%) as contemporary soil moisture (37 ± 6%). However, the strong effects of plant evolution were dependent on ecological context, as plant evolutionary responses to drought were most important when plants and microbes were grown in contemporary drought conditions (terHorst, Lennon & Lau 2014).

More studies that manipulate evolutionary environments, or take advantage of long-term manipulations or natural variation in evolutionary environments, would help to directly test whether plant trait evolution affects the soil microbial community. Additionally, as more studies take advantage of next-generation sequencing technologies and metagenomics, we expect that more specific information about which microbial taxa are favoured by certain plant traits will become more readily available. In terms of eco-evolutionary dynamics, we are ultimately interested in whether ecological or evolutionary changes in microbial species or communities due to changes in plant traits feedback to further affect selection on plant traits.

How do soil microbes affect the evolution of plant traits?

Soil microbes can alter the evolution of plant traits directly through species interactions, or indirectly through changes in abiotic or biotic factors. Here, we do not attempt to distinguish between direct and indirect effects of microbes, but focus on how these interactions impose selection on plant traits (Fig. 2b). We describe several mechanisms by which microbes could impose selection on plant traits and review the empirical evidence of these effects. We then consider how the evolution of microbial species might impose selection on plant traits, potentially resulting in co-evolutionary dynamics.

MECHANISMS OF SELECTION ON PLANT TRAITS BY SOIL MICROBES

The most well-studied interactions between plants and soil microbes involve the trading of resources with mycorrhizal fungi or rhizobia bacteria. These interactions can range from mutualism to parasitism (Johnson, Graham & Smith 1997). Mutualistic microbes may select for plant traits that increase investment in mutualism, such as carbon allocation. Alternatively, parasitic or less beneficial 'cheater' strains of microbes may experience selection to take advantage of plant resources without a return benefit (Sachs *et al.* 2004). Cheater strains of microbes may impose selection for plant traits that sanction cheaters by diverting more resources to cooperative microbes (Bull & Rice 1991; Kiers *et al.* 2003; Kiers & Denison 2008; Weyl *et al.* 2010) or plants that preferentially allocate resources to beneficial strains (Bever *et al.* 2009). Experimental evidence indicates that there is genetic variation within some legume species for forming associations with different rhizobia strains (Robinson *et al.* 2000; Simonsen & Stinchcombe 2014). This sets the stage for selection on plant traits that stabilize mutualisms with beneficial rhizobia. Empirically, there is some evidence that the evolution of plant investment in mutualism depends on the soil microbial community (Kiers, Hutton & Denison 2007; Simonsen & Stinchcombe 2014). However, in one of the only studies to measure selection on plant investment in mutualism, rhizobia were found to not impose strong selection on a legume to sanction their bacterial partners (Porter & Simms 2014). Further empirical tests are required to determine generally whether or not soil microbes can impose selection as a result of their interactions with plants.

Plant pathogens have important fitness consequences for plants (Burdon, Thrall & Ericson 2006). Pathogenic soil microbes might impose selection for plant traits that aid in resistance or recovery from infection (Frank 1993; Laine 2006; Springer 2007). However, resistance can be costly (Roy & Kirchner 2000), so the predicted evolutionary trajectory of plant resistance traits is not always straightforward (Kniskern & Rausher 2007).

Microbes can affect nutrient supply to plants, or reduce levels of toxins that might otherwise impose selection on plants (Adriaensen *et al.* 2005; Mortensen, Strobel & Hansen 2006; Rodriguez & Redman 2008; Lankau 2010). Thus, microbes can affect selection on plant traits by changing the way that plants interact with other selective agents. Competition, herbivory and disease are important selective agents on plant traits, and changes in the strengths of those interactions are likely to affect how plant traits evolve. Soil microbes can affect the competitive ability of plants or mitigate competitive interactions (reviewed in Hodge & Fitter 2013). Associations with arbuscular mycorrhizal fungi tend to increase plant tolerance of negative biotic interactions, including herbivory and pathogens (Yang *et al.* 2014). Increased investment in below-ground biomass by legumes that associate more strongly with rhizobia may affect their ability to tolerate herbivores (Heath & Lau 2011; Heath & McGhee 2012). Rhizobia may also affect the attractiveness of plant nectar, potentially affecting interactions with pollinators and other mutualists (Godschalx *et al.* 2015). Nonadditive selection from multiple species in a community can arise from indirect ecological effects, but more empirical studies are required to quantify the prevalence of nonadditive selection in natural communities (terHorst *et al.* 2015).

The evolutionary effects of microbes can also act through complex pathways, as a result of interactions with

multiple biotic and abiotic factors. For example, when soil microbes affect the ecological response of a plant to drought (Ruiz-Lozano 2003; Figueiredo *et al.* 2008), and when plant competitive interactions are drought dependent (Liancourt, Callaway & Michalet 2005), interactions with soil microbes may affect selection by plant competitors more so during drought conditions. Indirect genetic effects occur when the expression of genes in one individual affects the phenotype of other individuals (Moore, Brodie & Wolf 1997; Wolf *et al.* 1998; Bailey *et al.* 2014), and may alter interactions between plant genotypes and soil microbes. Just as the genetic identity of plant neighbours can affect interactions with pollinators (Genung, Bailey & Schweitzer 2012), indirect genetic effects between plants may affect the extent to which plants experience selection by the soil microbial community.

Finally, microbes may alter the evolutionary trajectory of plant traits by altering the expression of genetic variation, heritability, or the opportunity for selection. For example, genetic variation in traits that confer drought tolerance is unlikely to be expressed in wet conditions. When microbes confer drought tolerance to plants, it could change the level of soil moisture at which plants perceive drought, and thus alter the point at which genetic variation in drought tolerance is expressed. Heritabilities of traits, such as leaf number and leaf length in cottonwoods, tended to be lower in soils with higher soil microbial biomass (Pregitzer *et al.* 2010). By changing the biotic or abiotic environment that plants experience, soil microbes may enhance or limit the evolutionary potential, or evolvability (Wagner & Altenberg 1996), of plant populations.

Despite these many potential pathways by which microbes could affect selection on plant traits, there are few empirical estimates of selection imposed on plant traits or evolutionary responses of plant traits in response to microbes. To some extent, this is due to the length of time needed to observe evolutionary changes in many longer-lived species, although it is relatively easy to measure selection on traits in most plant species when reliable proxies for fitness are available. Lau & Lennon (2011) used *Brassica rapa*, with generation times approaching 30 days, to impose drought stress over multiple plant generations in soils with simple or complex microbial communities. In soils with simple microbial communities, plants experienced strong selection on plant growth and flowering phenology in response to drought, but much weaker selection in the presence of complex soil microbial communities (Lau & Lennon 2011). Similar approaches that manipulate the selection environment imposed by microbes, using plants with short generation times, or imposing strong selection pressure, will help to elucidate the potential for soil microbes to alter evolutionary trajectories of plant traits. Such studies might be most feasible using annual plants with short generation times, but these may not be an accurate representation of all plant species. LongTerm Ecological Research sites, designed to manipulate ecological variables over long periods, may prove to be a valuable resource for evolutionary biologists studying evolution in longer-lived species.

EVOLUTION OF MICROBES MAY ALTER PLANT TRAIT EVOLUTION

Given their short generation times, as well as potentially strong selection pressure, microbes may evolve on timescales short enough to affect plant ecological dynamics (Adriaensen *et al.* 2005; Rodriguez & Redman 2008). For example, *Stemphylium* is a dominant foliar fungus that causes leaf necrosis. Over the course of months, *S. solani* evolved increased rates of infection on clover host species (Gilbert & Parker 2010). Pathogens of common crop species are expected to rapidly evolve in response to climate change and altered land use (Pangga, Hanan & Chakraborty 2011; Papaix *et al.* 2015). The increasingly negative effects of such plant pathogens should impose selection on plant traits that confer resistance or tolerance of these pathogens.

While microbes can impose selection on plant traits, plants that interact strongly with a particular species of soil microbe may impose selection on soil microbe populations. This sets the stage for reciprocal co-evolutionary dynamics that affect both plants and microbes. Mutualisms between plants and microbes likely arose from ancestral host–parasite interactions, where each of the partner species is under selection to maximize their own benefit while minimizing costs (Bull & Rice 1991; Neuhauser & Fargione 2004; Sachs *et al.* 2004). For example, theory suggests that plants grown at high resource levels should allocate less energy towards acquiring resources from beneficial microbes (Sachs & Simms 2006; Thrall *et al.* 2007; Kiers *et al.* 2010). Similarly, microbes should provide fewer benefits to plants from which they receive fewer resources.

Weese *et al.* (2015) studied legume–rhizobia interactions at a LTER site that manipulated nitrogen addition over the course of 30 years. They isolated rhizobia from replicate high- and low-nitrogen plots and then measured the effect of these strains on three species of clover (*Trifolium* spp.). Rhizobia that evolved in high-nitrogen environments provided less growth benefits to the plants (Weese *et al.* 2015). Presumably, this was an evolutionary response to plant trait evolution in the high-nitrogen plots that experienced selection in response to less cooperative rhizobia. Similar experiments are needed to fully evaluate the extent to which changes in microbial community composition or evolutionary changes within microbial species can alter selection pressure and evolutionary trajectories of plant traits.

Effects of PSF on the evolution of plant traits

In the previous section, we addressed the many ways in which soil microbes might affect the evolution of plant

traits. Now we ask whether the strength or direction of PSFs as a whole could also alter plant trait evolution. Ecological feedbacks between plants and their soil microbes have been shown to be important in the maintenance of diversity (Van Nuland *et al.* 2016), the spread of invasive species (Nijjer, Rogers & Siemann 2007; Lee, Flory & Phillips 2012), and community assembly and successional trajectories (reviewed in Paredes & Lebeis in review, this issue). In this section, we discuss how ecological feedbacks between plants and soil microbes (Fig. 1) affect plant community diversity and how this ultimately could cascade to affect plant trait evolution (Fig. 2b).

Plant–soil feedbacks can vary in both strength and direction (Bever, Platt & Morton 2012). The nature of PSFs can have important consequences for the ecology and evolution of plant communities. The direction of PSF (negative or positive) indicates how a plant's interaction with the soil microbial community results in subsequent growth of conspecific and heterospecific plant species (Bever, Westover & Antonovics 1997). Under negative PSFs, the interaction between a focal plant species and soil microbes leads to a relative increase in the growth rate of other plant species (van der Putten *et al.* 2013). Negative PSFs increase plant community diversity and can be an important mechanism of coexistence (van der Putten *et al.* 2013). In contrast, a positive PSF increases the fitness of the focal plant species relative to heterospecifics. Positive PSFs can lead to competitive dominance and the exclusion of other plant species (van der Putten *et al.* 2013).

The resulting effects of PSFs on plant community structure have the potential to affect plant trait evolution. Traits governing competitive ability in plants are of huge importance to plant fitness (Aarssen & Keogh 2002). However, plants must simultaneously cope with competition from both conspecifics (intraspecific competition) and heterospecifics (interspecific competition). Traits that confer a benefit in intraspecific competition may not always confer a benefit in interspecific competition (Miller 1995; Lankau 2008; Lankau & Strauss 2008). As PSFs shift from positive to negative and shift plant communities from those dominated by conspecifics to those dominated by heterospecifics, selection pressure may also shift from traits favouring intraspecific competitive ability to those that enhance interspecific competitive ability. In some cases, one trait, such as growth rate or water uptake rate, may increase both intra- and interspecific competitive ability. Yet, in many cases, there may be a trade-off between intra- and interspecific competitive traits. For example, the production of the allelochemical sinigrin by *Brassica nigra* decreases the abundance of heterospecifics, but sinigrin is costly to produce, has no effect on conspecifics, and decreases intraspecific competitive ability (Lankau 2008).

In addition to these indirect evolutionary consequences on plant competitive traits, PSFs may also generate selection pressure on plant reproductive mode. For example, in addition to considering the direction of PSF among plant species, we can also consider PSFs among plant genotypes

within species. Negative PSF should generate more genetically diverse populations and positive PSF should lead to dominance by one or a few genotypes. Bever, Westover & Antonovics (1997) argue that negative feedbacks favour sexual reproduction because outcrossing is beneficial if there are neighbouring plants with different genetic composition. Conversely, positive feedbacks should favour asexual reproduction, which is presumably less energetically expensive and produces similar results to outcrossing with genetically similar neighbours.

Alternatively, if we consider PSF among, rather than within species, we would make different predictions about the evolution of plant mating systems. In the case where negative PSFs generate species-diverse communities, outcrossing could be deleterious if shared pollinators cause pollen interference by heterospecifics (Petit 2011; Fang & Huang 2013; de Waal, Anderson & Ellis 2015). Therefore, selfing could be favoured by selection in diverse communities maintained through negative PSF. Conversely, in a low-diversity community with high abundances of conspecifics, plants are more likely to receive pollen from the appropriate species, and selection should favour outcrossing.

These examples show the potential for how ecological PSF could change selection pressures on plant species by changing the plant community surrounding a focal plant species. However, few empirical tests of these ideas exist. A widely used protocol for testing for positive or negative PSF compares plant fitness in 'home' soil (soil that has been conditioned by the same plant species or genotype) and 'away' soil (soil that has been conditioned by different plant species or genotypes) (reviewed in van der Putten *et al.* 2013). Measuring plant traits, as well as plant fitness, in such experiments would allow for estimates of selection on plant traits (Lande & Arnold 1983) in response to positive or negative PSF. The potential for a dynamic ecological feedback to alter the evolution of functional plant traits that are important for fitness indicates that PSFs are a useful system for investigating eco–evo feedbacks (EEFs).

Interactions between PSFs and EEFs

Until now, we have focused largely on the evolutionary consequences of feedbacks between plants and soil microbe communities (PSFs). We now turn to examine how PSFs (Fig. 1) interact with EEFs (Fig. 2, Fussmann, Loreau & Abrams 2007; Post & Palkovacs 2009; Schoener 2011). EEFs occur when an organism modifies some feature of its biotic or abiotic environment and changes the nature of selection it experiences from the environment (Travis *et al.* 2014). By this definition, if plant traits affect soil microbial communities (Fig. 2a), and soil microbial communities affect the evolution of plant traits (Fig. 2b), an EEF occurs. EEFs are difficult to demonstrate in a reasonable amount of time, but the tightly coupled interactions between plants and soil microbes and rapid eco-

evolutionary dynamics in such communities make PSF a strong contender for where EEF may be common.

The simplest EEF occurs when evolutionary changes in one plant trait affect some property of the soil microbial community, which feeds back to cause subsequent changes in the same plant trait and microbial community property. However, more complex EEFs can occur among multiple traits and community properties, and even include genetically based traits in other species (Palkovacs & Post 2008; Bailey *et al.* 2009, 2014). Particularly in these more complex scenarios, evolutionary changes in plant traits or ecological changes in soil community properties are likely to alter the strength or direction of the PSF, which may have cascading effects on further EEF, involving either the same or different plant traits and soil community properties. To our knowledge, there has been no empirical demonstration of an EEF involving plants and soil microbes, although this is not surprising considering that there few empirical examples of EEF in any system (but see Post & Palkovacs 2009; Becks *et al.* 2012; Agrawal *et al.* 2013; Turcotte, Reznick & Hare 2013). Demonstration of effects of plant traits on soil microbial communities and demonstration of effects of soil microbes on the evolution of plant traits (Fig. 2) are strong evidence for the potential for EEF, but have not yet been linked together in the same study system.

EFFECTS ON SUCCESSIONAL TRAJECTORIES

Many mechanisms could lead to interactions between PSF and EEF, but there is little research on this topic, making it ripe for future exploration. Here, we describe one hypothetical example of how PSF and EEF might interact. Much previous work has described how PSF can drive plant successional patterns in one direction (Kardol *et al.* 2013), but here we hypothesize how EEF could continuously interact with PSF to affect plant successional trajectories.

In general, early successional plant species tend to be involved in negative PSF (Fig. 3); in other words, these early successional plant species tend to support soil microbial species that benefit heterospecifics (Reynolds *et al.* 2003; De Deyn, Raaijmakers & Van der Putten 2004; Kardol, Bezemer & van der Putten 2006; Kardol *et al.* 2007; van de Voorde, van der Putten & Bezemer 2011; van der Putten *et al.* 2013). This negative PSF breaks the dominance of early successional plant species and facilitates recruitment by later successional species that eventually replace the early species (Kardol *et al.* 2007). As the plant community ages, PSFs shift from negative to positive, allowing later successional species to exist in a stable climax community (Fig. 3, Reynolds *et al.* 2003; Kardol, Bezemer & van der Putten 2006; van der Putten *et al.* 2013). Through this process, PSF can drive a plant community through successional stages.

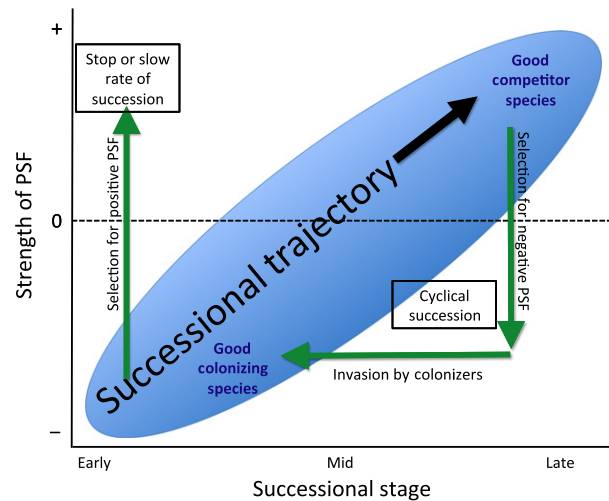However, in this scenario of PSF-driven plant succession, the plant traits are assumed to be fixed and cannot

Fig. 3. Potential interactive effects of plant–soil feedbacks (PSFs) and eco–evo feedbacks (EEF) on plant succession. The blue bubble represents the domain of attraction of ecological succession that is driven by PSF. Early successional communities are dominated by negative PSFs which benefit heterospecifics, allowing later successional species to invade. Late successional communities are dominated by positive PSF, in which plant species are associated with microbes that benefit conspecific plants, maintaining a stable community. Green arrows represent evolutionary pathways that move communities outside of the ecological successional trajectory. During early succession, if early colonizing species evolve to create positive PSF, ecological succession will slow or stop (left). Later in succession (right), if colonizing species evolve to create negative PSF, invasion by colonizers can occur, moving the community back to an earlier successional state, where it re-enters the domain of ecological succession. The latter could result in cyclical succession as a result of both PSF and EEF.

evolve, despite strong selection pressure from both PSF and plant community (described above in Effects of PSF on the evolution of plant traits). In diverse communities, selection may result from both direct and indirect effects to favour genotypes that employ the best strategy to reduce negative direct effects and maximize positive indirect effects (Miller & Travis 1996). If genotypes within species vary in their response to PSF or in their ability to alter PSF, then plant trait evolution could alter the ecological effects of PSF (Schweitzer *et al.* 2014). If plant trait evolution alters the strength or direction of PSF, it may mitigate the effects of PSF in driving plant succession, potentially even reversing community successional trajectories (Fig. 3). The extent to which EEF may reverse or slow the effects of PSF in driving plant succession deserves more attention in predictive quantitative models, but here we describe two simple qualitative scenarios.

Early successional species tend to be ruderal or pioneer species that are susceptible to pathogens in the soil, making them particularly subject to negative PSF, as pathogens reduce the fitness of these plants. This effect on fitness should impose strong selection pressure. Plant populations can vary in their susceptibility to pathogens, which may allow traits, such as pathogen resistance, to evolve and reduce the severity of PSF. Further, plant traits, such as

growth rates or carbon allocation, could evolve to take advantage of mutualistic microbes in the soil, potentially leading to positive PSF. A reduction in the strength of negative PSF would slow the demise of early successional species and the rate of succession, while a switch to positive PSF could stop succession altogether, resulting in a stable community of early successional species that maintain their dominance and resist invasion by other plant species (Fig. 3).

Consider another scenario that could occur later in succession. Presumably early successional species, which tend to be good colonizing species, continually try to invade late successional communities. However, these communities are dominated by competitive species with strong mutualistic interactions with soil microbes that create positive PSF that benefit late successional plant species. Selection on the colonizing species should favour plant genotypes that have negative effects on the mutualistic microbes of late successional species, leading to less positive PSF. Additionally, if microbes evolve a better ability to cheat their mutualistic partners, this would result in more negative PSF with late successional plant species. A shift towards more negative PSF could break the dominance by late successional species and allow 'early' colonizing species to reinvade a community (Fig. 3). This would shift the community back towards an earlier successional stage, where PSF-driven successional dynamics may drive the community back towards dominance by late successional species. Through the interaction of EEF and PSF, communities may experience cyclical successional patterns, even in the absence of disturbance (Fig. 3).

At this point, these consequences of interactions between EEF and PSF are speculative and relatively simple. However, the ecological and evolutionary dynamics of soil microbial communities can alter soil properties quickly, on the order of months to years (van der Putten, Vandijk & Peters 1993; Bever, Westover & Antonovics 1997), relative to slow changes in abiotic conditions in the soil that are typically thought to drive succession, which can take centuries to millennia (Wardle, Walker & Bardgett 2004). This suggests that interactions between EEF and PSF may play a large role in explaining temporal dynamics in plant communities on time-scales of interest to most researchers.

Future models and experiments should incorporate more complexity to understand community dynamics. For example, our hypothetical examples have failed to include evolution of late successional species, which may experience selection in response to potential invaders, intraspecific competition, or soil microbes, which could result in even stronger positive PSF during late succession and counteract some of the evolutionary trajectories in Fig. 3. Nor have we accounted for indirect genetic effects, whereby an individual's phenotype is strongly determined by the expression of genes in its neighbour (Shuster *et al.* 2006; Bailey *et al.* 2014), whether conspecific or heterospecific. These indirect genetic effects could occur within either plant or microbial communities, as well as between

them, or between other members of the community (consumers, pathogens, etc.), creating even greater potential for interactions between PSF and EEF. Further, plant generation times are likely to change with successional age, which could affect potential rates of evolution; annual grasses in early successional stages may be able to evolve faster than long-lived late successional trees. The effects of both PSF and EEF may be difficult to detect when both act simultaneously; future theoretical work should strive to partition the effects of each of these processes and generate predictions that could be tested empirically. Testing these ideas will require moving beyond relatively simple greenhouse studies to examine interactions among multiple species that incorporate greater complexity over temporal and spatial scales.

Conclusion

In this review, we have explored mechanisms by which eco-evolutionary dynamics can affect PSFs. We argue that PSFs are an exciting area of research for eco-evolutionary studies because of the strong interdependence of plants and soil communities and relatively short generation times of these species. Both of these can result in strong selection pressures, co-evolutionary dynamics and evolution on ecological time-scales. Based on previous research, there is strong evidence that plant traits affect the soil microbial community and that soil microbes can impose selection on plant traits. Further, the direction of PSFs can alter plant community structure, which can impose further selection on plant traits. All of this evidence suggests that there is the potential for eco-evolutionary feedbacks between plants and soil microbes, although there is not yet direct empirical evidence of such feedbacks. If eco-evolutionary feedbacks occur, and are important for explaining both plant and microbial community structure, then plant–soil and eco-evolutionary feedbacks may interact with each other and further explain variation in plant–soil interactions across spatial and temporal scales. Experiments in this area are not simple, but the rise of metagenomics and metabolomics has allowed researchers unprecedented access into the dynamics of microbial community structure and function. We urge others to take advantage of long-term manipulations of selection pressure or relatively short-lived plant species as a first step to exploring how PSFs and EEFs may affect natural communities.

Acknowledgements

Data accessibility

This manuscript does not use data.

References

Aarssen, L.W. & Keogh, T. (2002) Conundrums of competitive ability in plants: what to measure? *Oikos*, **96**, 531–542.

Adriaensen, K., Vralstad, T., Noben, J.P., Vangronsveld, J. & Colpaert, J.V. (2005) Copper-adapted *Suillus luteus*, a symbiotic solution for pines colonizing Cu mine spoils. *Applied and Environmental Microbiology*, **71**, 7279–7284.

Agrawal, A.A., Johnson, M.T.J., Hastings, A.P. & Maron, J.L. (2013) A field experiment demonstrating plant life-history evolution and its eco-evolutionary feedback to seed predator populations. *American Naturalist*, **181**, S35–S45.

Bailey, J.K., Hendry, A.P., Kinnison, M.T., Post, D.M., Palkovacs, E.P., Pelletier, F. *et al.* (2009) From genes to ecosystems: an emerging synthesis of eco-evolutionary dynamics. *New Phytologist*, **184**, 746–749.

Bailey, J.K., Genung, M.A., Ware, I., Gorman, C., Van Nuland, M.E., Long, H. *et al.* (2014) Indirect genetic effects: an evolutionary mechanism linking feedbacks, genotypic diversity and coadaptation in a climate change context. *Functional Ecology*, **28**, 87–95.

Bassar, R.D., Ferriere, R., Lopez-Sepulcre, A., Marshall, M.C., Travis, J., Pringle, C.M. *et al.* (2012) Direct and indirect ecosystem effects of evolutionary adaptation in the Trinidadian Guppy (*Poecilia reticulata*). *American Naturalist*, **180**, 167–185.

Becks, L., Ellner, S.P., Jones, L.E. & Hairston, N.G. (2012) The functional genomics of an eco-evolutionary feedback loop: linking gene expression, trait evolution, and community dynamics. *Ecology Letters*, **15**, 492–501.

Bever, J.D., Platt, T.G. & Morton, E.R. (2012) Microbial population and community dynamics on plant roots and their feedbacks on plant communities. *Annual Review of Microbiology*, **66**, 265–283.

Bever, J.D., Westover, K.M. & Antonovics, J. (1997) Incorporating the soil community into plant population dynamics: the utility of the feedback approach. *Journal of Ecology*, **85**, 561–573.

Bever, J.D., Richardson, S.C., Lawrence, B.M., Holmes, J. & Watson, M. (2009) Preferential allocation to beneficial symbiont with spatial structure maintains mycorrhizal mutualism. *Ecology Letters*, **12**, 13–21.

Blagodatskaya, E., Littschwager, J., Lauerer, M. & Kuzyakov, Y. (2014) Plant traits regulating N capture define microbial competition in the rhizosphere. *European Journal of Soil Biology*, **61**, 41–48.

Bolnick, D.I., Amarasekare, P., Araujo, M.S., Buerger, R., Levine, J.M., Novak, M. *et al.* (2011) Why intraspecific trait variation matters in community ecology. *Trends in Ecology & Evolution*, **26**, 183–192.

Bull, J. & Rice, W. (1991) Distinguishing mechanisms for the evolution of cooperation. *Journal of Theoretical Biology*, **149**, 63–74.

Burdon, J.J., Thrall, P.H. & Ericson, L. (2006) The current and future dynamics of disease in plant communities. *Annual Review of Phytopathology*, **44**, 19–39.

Cantarel, A.A.M., Pommier, T., Desclos-Theveniau, M., Diquelou, S., Dumont, M., Grassein, F. *et al.* (2015) Using plant traits to explain plant-microbe relationships involved in nitrogen acquisition. *Ecology*, **96**, 788–799.

Colautti, R.I. & Lau, J.A. (2015) Contemporary evolution during invasion: evidence for differentiation, natural selection, and local adaptation. *Molecular Ecology*, **24**, 1999–2017.

Cornwell, W.K., Cornelissen, J.H.C., Amatangelo, K., Dorrepaal, E., Eviner, V.T., Godoy, O. *et al.* (2008) Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecology Letters*, **11**, 1065–1071.

Cotta, S.R., Franco Dias, A.C., Marriel, I.E., Andreote, F.D., Seldin, L. & van Elsas, J.D. (2014) Different effects of transgenic maize and nontransgenic maize on nitrogen-transforming archaea and bacteria in tropical soils. *Applied and Environmental Microbiology*, **80**, 6437–6445.

Crutsinger, G.M., Rodriguez-Cabal, M.A., Roddy, A.B., Peay, K.G., Bastow, J.L., Kidder, A.G. *et al.* (2014) Genetic variation within a dominant shrub structures green and brown community assemblages. *Ecology*, **95**, 387–398.

De Deyn, G.B., Raaijmakers, C.E. & Van der Putten, W.H. (2004) Plant community development is affected by nutrients and soil biota. *Journal of Ecology*, **92**, 824–834.

Ellouze, W., Hamel, C., Vujanovic, V., Gan, Y., Bouzid, S. & St-Arnaud, M. (2013) Chickpea genotypes shape the soil microbiome and affect the establishment of the subsequent durum wheat crop in the semiarid North American Great Plains. *Soil Biology & Biochemistry*, **63**, 129–141.

Evans, J.A., Lankau, R.A., Davis, A.S., Raghu, S. & Landis, D.A. (2016) Eco-evolutionary feedbacks in the invasive plant *Alliaria petiolata*. *Functional Ecology,* **30**, 1053–1061.

Eviner, V.T. (2004) Plant traits that influence ecosystem processes vary independently among species. *Ecology*, **85**, 2215–2229.

Fang, Q. & Huang, S.-Q. (2013) A directed network analysis of heterospecific pollen transfer in a biodiverse community. *Ecology*, **94**, 1176–1185.

Figueiredo, M.V.B., Burity, H.A., Martinez, C.R. & Chanway, C.P. (2008) Alleviation of drought stress in the common bean (*Phaseolus vulgaris* L.) by co-inoculation with *Paenibacillus polymyxa* and *Rhizobium tropici*. *Applied Soil Ecology*, **40**, 182–188.

Fitzpatrick, C.R., Agrawal, A.A., Basiliko, N., Hastings, A.P., Isaac, M.E., Preston, M. *et al.* (2015) The importance of plant genotype and contemporary evolution for terrestrial ecosystem processes. *Ecology*, **96**, 2632–2642.

Frank, S. (1993) Coevolutionary genetics of plants and pathogens. *Evolutionary Ecology*, **7**, 45–75.

Fussmann, G.F., Loreau, M. & Abrams, P.A. (2007) Eco-evolutionary dynamics of communities and ecosystems. *Functional Ecology*, **21**, 465–477.

Genung, M.A., Bailey, J.K. & Schweitzer, J.A. (2012) Welcome to the neighbourhood: interspecific genotype by genotype interactions in Solidago influence above- and belowground biomass and associated communities. *Ecology Letters*, **15**, 65–73.

Genung, M.A., Bailey, J.K. & Schweitzer, J.A. (2013) The afterlife of interspecific indirect genetic effects: genotype interactions alter litter quality with consequences for decomposition and nutrient dynamics. *PLoS One*, **8**, e53718.

Genung, M.A., Schweitzer, J.A., Ubeda, F., Fitzpatrick, B.M., Pregitzer, C.C., Felker-Quinn, E. *et al.* (2011) Genetic variation and community change - selection, evolution, and feedbacks. *Functional Ecology*, **25**, 408–419.

Gilbert, G.S. & Parker, I.M. (2010) Rapid evolution in a plant-pathogen interaction and the consequences for introduced host species. *Evolutionary Applications*, **3**, 144–156.

Godschalx, A.L., Schaedler, M., Trisel, J.A., Balkan, M.A. & Ballhorn, D.J. (2015) Ants are less attracted to the extrafloral nectar of plants with symbiotic, nitrogen-fixing rhizobia. *Ecology*, **96**, 348–354.

Heath, K.D. & Lau, J.A. (2011) Herbivores alter the fitness benefits of a plant-rhizobium mutualism. *Acta Oecologica-International Journal of Ecology*, **37**, 87–92.

Heath, K.D. & McGhee, K.E. (2012) Coevolutionary constraints? The environment alters tripartite interaction traits in a legume. *PLoS One*, **7**, e41567.

Herrera Paredes, S., & Lebeis, S.L. (2016) Giving back to the community: microbial mechanisms of plant–soil feedback. *Functional Ecology*, **30**, 1043–1052.

Hodge, A. & Fitter, A.H. (2013) Microbial mediation of plant competition and community structure. *Functional Ecology*, **27**, 865–875.

terHorst, C.P., Lennon, J.T. & Lau, J.A. (2014) The relative importance of rapid evolution for plant-microbe interactions depends on ecological context. *Proceedings of the Royal Society B-Biological Sciences*, **281**, 20140028.

terHorst, C.P., Miller, T.E. & Levitan, D.R. (2010) Evolution of prey in ecological time reduces the effect size of predators in experimental microcosms. *Ecology*, **91**, 629–636.

terHorst, C.P., Lau, J.A., Cooper, I.A., Keller, K.R., La Rosa, R.J., Royer, A.M. *et al.* (2015) Quantifying nonadditive selection caused by indirect ecological effects. *Ecology*, **96**, 2360–2369.

Hutchinson, G. E. (1965) *The Ecological Theater and the Evolutionary Play*. Yale University Press, New Haven, CT, USA.

Johnson, N.C., Graham, J.H. & Smith, F.A. (1997) Functioning of mycorrhizal associations along the mutualism-parasitism continuum. *New Phytologist*, **135**, 575–586.

Johnson, M.T.J. & Stinchcombe, J.R. (2007) An emerging synthesis between community ecology and evolutionary biology. *Trends in Ecology & Evolution*, **22**, 250–257.

Kardol, P., Bezemer, T.M. & van der Putten, W.H. (2006) Temporal variation in plant-soil feedback controls succession. *Ecology Letters*, **9**, 1080–1088.

Kardol, P., Cornips, N.J., van Kempen, M.M.L., Bakx-Schotman, J.M.T. & van der Putten, W.H. (2007) Microbe-mediated plant-soil feedback causes historical contingency effects in plant community assembly. *Ecological Monographs*, **77**, 147–162.

Kardol, P., De Deyn, G.B., Laliberte, E., Mariotte, P. & Hawkes, C.V. (2013) Biotic plant-soil feedbacks across temporal scales. *Journal of Ecology*, **101**, 309–315.

Kiers, E.T. & Denison, R.F. (2008) Sanctions, cooperation, and the stability of plant-rhizosphere mutualisms. *Annual Review of Ecology Evolution and Systematics*, **39**, 215–236.

Kiers, E.T., Hutton, M.G. & Denison, R.F. (2007) Human selection and the relaxation of legume defences against ineffective rhizobia. *Proceedings of the Royal Society B-Biological Sciences*, **274**, 3119–3126.

Kiers, E.T., Rousseau, R.A., West, S.A. & Denison, R.F. (2003) Host sanctions and the legume-rhizobium mutualism. *Nature*, **425**, 78–81.

Kiers, E.T., Palmer, T.M., Ives, A.R., Bruno, J.F. & Bronstein, J.L. (2010) Mutualisms in a changing world: an evolutionary perspective. *Ecology Letters*, **13**, 1459–1474.

Kniskern, J.M. & Rausher, M.D. (2007) Natural selection on a polymorphic disease-resistance locus in *Ipomoea purpurea*. *Evolution*, **61**, 377–387.

Laine, A.L. (2006) Evolution of host resistance: looking for coevolutionary hotspots at small spatial scales. *Proceedings of the Royal Society B-Biological Sciences*, **273**, 267–273.

Lamit, L.J., Busby, P.E., Lau, M.K., Compson, Z.G., Wojtowicz, T., Keith, A.R. *et al.* (2015) Tree genotype mediates covariance among communities from microbes to lichens and arthropods. *Journal of Ecology*, **103**, 840–850.

Lande, R. & Arnold, S. (1983) The measurement of selection on correlated characters. *Evolution*, **37**, 1210–1226.

Lankau, R. (2008) A chemical trait creates a genetic trade-off between intra- and interspecific competitive ability. *Ecology*, **89**, 1181–1187.

Lankau, R. (2010) Soil microbial communities alter allelopathic competition between *Alliaria petiolata* and a native species. *Biological Invasions*, **12**, 2059–2068.

Lankau, R.A. (2011) Intraspecific variation in allelochemistry determines an invasive species' impact on soil microbial communities. *Oecologia*, **165**, 453–463.

Lankau, R.A. & Strauss, S.Y. (2008) Community complexity drives patterns of natural selection on a chemical defense of *Brassica nigra*. *American Naturalist*, **171**, 150–161.

Lau, J.A. & Lennon, J.T. (2011) Evolutionary ecology of plant-microbe interactions: soil microbial structure alters selection on plant traits. *New Phytologist*, **192**, 215–224.

Lau, J.A. & Lennon, J.T. (2012) Rapid responses of soil microorganisms improve plant fitness in novel environments. *Proceedings of the National Academy of Sciences of the United States of America*, **109**, 14058–14062.

Lavergne, S., Mouquet, N., Thuiller, W. & Ronce, O. (2010) Biodiversity and climate change: integrating evolutionary and ecological responses of species and communities. *Annual Review of Ecology, Evolution, and Systematics*, **41**, 321–350.

Lee, M.R., Flory, S.L. & Phillips, R.P. (2012) Positive feedbacks to growth of an invasive grass through alteration of nitrogen cycling. *Oecologia*, **170**, 457–465.

Legay, N., Baxendale, C., Grigulis, K., Krainer, U., Kastl, E., Schloter, M. *et al.* (2014) Contribution of above- and below-ground plant traits to the structure and function of grassland soil microbial communities. *Annals of Botany*, **114**, 1011–1021.

Liancourt, P., Callaway, R.M. & Michalet, R. (2005) Stress tolerance and competitive-response ability determine the outcome of biotic interactions. *Ecology*, **86**, 1611–1618.

Madritch, M.D. & Lindroth, R.L. (2011) Soil microbial communities adapt to genetic variation in leaf litter inputs. *Oikos*, **120**, 1696–1704.

Maul, J. & Drinkwater, L. (2010) Short-term plant species impact on microbial community structure in soils with long-term agricultural history. *Plant and Soil*, **330**, 369–382.

McGill, B.M., Sutton-Grier, A.E. & Wright, J.P. (2010) Plant trait diversity buffers variability in denitrification potential over changes in season and soil conditions. *PLoS One*, **5**, e11618.

Miller, T.E. (1995) Evolution of *Brassica rapa* L. (Cruciferae) populations in intra- and interspecific competition. *Evolution*, **49**, 1125–1133.

Miller, T.E. & Travis, J. (1996) The evolutionary role of indirect effects in communities. *Ecology*, **77**, 1329–1335.

Moore, A.J., Brodie, E.D. & Wolf, J.B. (1997) Interacting phenotypes and the evolutionary process.1. Direct and indirect genetic effects of social interactions. *Evolution*, **51**, 1352–1362.

Moran, E.V. & Alexander, J.M. (2014) Evolutionary responses to global change: lessons from invasive species. *Ecology Letters*, **17**, 637–649.

Mortensen, G.K., Strobel, B.W. & Hansen, H.C.B. (2006) Degradation of zearalenone and ochratoxin A in three Danish agricultural soils. *Chemosphere*, **62**, 1673–1680.

Neuhauser, C. & Fargione, J.E. (2004) A mutualism-parasitism continuum model and its application to plant-mycorrhizae interactions. *Ecological Modelling*, **177**, 337–352.

Nijjer, S., Rogers, W.E. & Siemann, E. (2007) Negative plant-soil feedbacks may limit persistence of an invasive tree due to rapid accumulation of soil pathogens. *Proceedings of the Royal Society B-Biological Sciences*, **274**, 2621–2627.

Ondreickova, K., Mihalik, D., Ficek, A., Hudcovicova, M., Kraic, J. & Drahovska, H. (2014) Impact of genetically modified maize on the genetic diversity of rhizosphere bacteria: a two-year study in Slovakia. *Polish Journal of Ecology*, **62**, 67–76.

Orwin, K.H., Buckland, S.M., Johnson, D., Turner, B.L., Smart, S., Oakley, S. *et al.* (2010) Linkages of plant traits to soil properties and the functioning of temperate grassland. *Journal of Ecology*, **98**, 1074–1083.

Palkovacs, E.P. & Post, D.M. (2008) Eco-evolutionary interactions between predators and prey: can predator-induced changes to prey communities feed back to shape predator foraging traits? *Evolutionary Ecology Research*, **10**, 699–720.

Pangga, I.B., Hanan, J. & Chakraborty, S. (2011) Pathogen dynamics in a crop canopy and their evolution under changing climate. *Plant Pathology*, **60**, 70–81.

Pantel, J.H., Duvivier, C. & Meester, L.D. (2015) Rapid local adaptation mediates zooplankton community assembly in experimental mesocosms. *Ecology Letters*, **18**, 992–1000.

Papaix, J., Burdon, J.J., Zhan, J. & Thrall, P.H. (2015) Crop pathogen emergence and evolution in agro-ecological landscapes. *Evolutionary Applications*, **8**, 385–402.

Peiffer, J.A., Spor, A., Koren, O., Jin, Z., Tringe, S.G., Dangl, J.L. *et al.* (2013) Diversity and heritability of the maize rhizosphere microbiome under field conditions. *Proceedings of the National Academy of Sciences of the United States of America*, **110**, 6548–6553.

Petit, S. (2011) Effects of mixed-species pollen load on fruits, seeds, and seedlings of two sympatric columnar cactus species. *Ecological Research*, **26**, 461–469.

Pianka, E.R. (2000) *Evolutionary Ecology*, 6th edn. Benjamin Cummings, San Francisco, CA, USA.

Pimentel, D. (1961) Animal population regulation by genetic feedback mechanism. *American Naturalist*, **95**, 65–79.

Porter, S.S. & Simms, E.L. (2014) Selection for cheating across disparate environments in the legume-rhizobium mutualism. *Ecology Letters*, **17**, 1121–1129.

Post, D.M. & Palkovacs, E.P. (2009) Eco-evolutionary feedbacks in community and ecosystem ecology: interactions between the ecological theatre and the evolutionary play. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **364**, 1629–1640.

Pregitzer, C.C., Bailey, J.K., Hart, S.C. & Schweitzer, J.A. (2010) Soils as agents of selection: feedbacks between plants and soils alter seedling survival and performance. *Evolutionary Ecology*, **24**, 1045–1059.

van der Putten, W.H., Vandijk, C. & Peters, B. (1993) Plant-specific soil-borne diseases contribute to succession in foredune vegetation. *Nature*, **362**, 53–56.

van der Putten, W.H., Bardgett, R.D., Bever, J.D., Bezemer, T.M., Casper, B.B., Fukami, T. *et al.* (2013) Plant-soil feedbacks: the past, the present and future challenges. *Journal of Ecology*, **101**, 265–276.

van der Putten, W.H., Bradford, M.A., Brinkman, E.P., van der Voorde, T.F.J. & Veen, G.F. (2016) Where, when and how plant–soil feedback matters in a changing world. *Functional Ecology*, **30**, 1109–1121.

Reynolds, H.L., Packer, A., Bever, J.D. & Clay, K. (2003) Grassroots ecology: plant-microbe-soil interactions as drivers of plant community structure and dynamics. *Ecology*, **84**, 2281–2291.

Reznick, D.N. & Ghalambor, C.K. (2001) The population ecology of contemporary adaptations: what empirical studies reveal about the conditions that promote adaptive evolution. *Genetica*, **112**, 183–198.

Reznick, D.N., Bassar, R.D., Travis, J. & Rodd, F.H. (2012) Life-history evolution in guppies VIII: the demographics of density regulation in guppies (*Poecilia reticulata*). *Evolution*, **66**, 2903–2915.

Robinson, K.O., Beyene, D.A., van Berkum, P., Knight-Mason, R. & Bhardwaj, H.L. (2000) Variability in plant-microbe interaction between *Lupinus* lines and *Bradyrhizobium* strains. *Plant Science*, **159**, 257–264.

Rodriguez, R. & Redman, R. (2008) More than 400 million years of evolution and some plants still can't make it on their own: plant stress tolerance via fungal symbiosis. *Journal of Experimental Botany*, **59**, 1109–1114.

Rodriguez-Loinaz, G., Onaindia, M., Amezaga, I., Mijangos, I. & Garbisu, C. (2008) Relationship between vegetation diversity and soil functional diversity in native mixed-oak forests. *Soil Biology & Biochemistry*, **40**, 49–60.

Roy, B.A. & Kirchner, J.W. (2000) Evolutionary dynamics of pathogen resistance and tolerance. *Evolution*, **54**, 51–63.

Ruiz-Lozano, J.M. (2003) Arbuscular mycorrhizal symbiosis and alleviation of osmotic stress. New perspectives for molecular studies. *Mycorrhiza*, **13**, 309–317.

Sachs, J.L. & Simms, E.L. (2006) Pathways to mutualism breakdown. *Trends in Ecology & Evolution*, **21**, 585–592.

Sachs, J.L., Mueller, U.G., Wilcox, T.P. & Bull, J.J. (2004) The evolution of cooperation. *Quarterly Review of Biology*, **79**, 135–160.

Schoener, T.W. (2011) The newest synthesis: understanding the interplay of evolutionary and ecological dynamics. *Science*, **331**, 426–429.

Schreiber, S.J., Buerger, R. & Bolnick, D.I. (2011) The community effects of phenotypic and genetic variation within a predator population. *Ecology*, **92**, 1582–1593.

Schweitzer, J.A., Madritch, M.D., Bailey, J.K., LeRoy, C.J., Fischer, D.G., Rehill, B.J. *et al.* (2008) From genes to ecosystems: the genetic basis of condensed tannins and their role in nutrient regulation in a *Populus* model system. *Ecosystems*, **11**, 1005–1020.

Schweitzer, J.A., Juric, I., van de Voorde, T.F.J., Clay, K., van der Putten, W.H. & Bailey, J.K. (2014) Are there evolutionary consequences of plant-soil feedbacks along soil gradients? *Functional Ecology*, **28**, 55–64.

Shuster, S.M., Lonsdorf, E.V., Wimp, G.M., Bailey, J.K. & Whitham, T.G. (2006) Community heritability measures the evolutionary consequences of indirect genetic effects on community structure. *Evolution*, **60**, 991–1003.

Simonsen, A.K. & Stinchcombe, J.R. (2014) Standing genetic variation in host preference for mutualist microbial symbionts. *Proceedings of the Royal Society B-Biological Sciences*, **281**, 20142036.

Slobodkin, L.B. (1961) *Growth and Regulation of Animal Populations*. Holt, Rinehart and Winston, New York, NY, USA.

Springer, Y.P. (2007) Clinal resistance structure and pathogen local adaptation in a serpentine flax-flax rust interaction. *Evolution*, **61**, 1812–1822.

Sthultz, C.M., Whitham, T.G., Kennedy, K., Deckert, R. & Gehring, C.A. (2009) Genetically based susceptibility to herbivory influences the ectomycorrhizal fungal communities of a foundation tree species. *New Phytologist*, **184**, 657–667.

Sutton-Grier, A.E. & Megonigal, J.P. (2011) Plant species traits regulate methane production in freshwater wetland soils. *Soil Biology & Biochemistry*, **43**, 413–420.

Thébault, A., Frey, B., Mitchell, E.A.D. & Buttler, A. (2010) Species-specific effects of polyploidisation and plant traits of *Centaurea maculosa* and *Senecio inaequidens* on rhizosphere microorganisms. *Oecologia*, **163**, 1011–1020.

Thompson, J.N. (1998) Rapid evolution as an ecological process. *Trends in Ecology & Evolution*, **13**, 329–332.

Thoms, C. & Gleixner, G. (2013) Seasonal differences in tree species' influence on soil microbial communities. *Soil Biology & Biochemistry*, **66**, 239–248.

Thrall, P.H., Hochberg, M.E., Burdon, J.J. & Bever, J.D. (2007) Coevolution of symbiotic mutualists and parasites in a community context. *Trends in Ecology & Evolution*, **22**, 120–126.

Travis, J., Reznick, D., Bassar, R.D., Lopez-Sepulcre, A., Ferriere, R. & Coulson, T. (2014) Do eco-evo feedbacks help us understand nature? Answers from studies of the Trinidadian guppy. *Advances in Ecological Research*, **50**, 1–40.

Turcotte, M.M., Reznick, D.N. & Hare, J.D. (2013) Experimental test of an eco-evolutionary dynamic feedback loop between evolution and population density in the green peach aphid. *American Naturalist*, **181**, S46–S57.

Van Nuland, M.E., Wooliver, R.C., Pfennigwerth, A.A., Read, Q.D., Ware, I.M., Mueller, L., Fordyce, J.A., Schweitzer, J.A. & Bailey, J.K. (2016) Plant–soil feedbacks: connecting ecosystem ecology and evolution. *Functional Ecology*, **30**, 1032–1042.

Visser, M.E. (2008) Keeping up with a warming world; assessing the rate of adaptation to climate change. *Proceedings of the Royal Society B-Biological Sciences*, **275**, 649–659.

van de Voorde, T.F.J., van der Putten, W.H. & Bezemer, T.M. (2011) Intra- and interspecific plant-soil interactions, soil legacies and priority effects during old-field succession. *Journal of Ecology*, **99**, 945–953.

de Vries, F.T., Manning, P., Tallowin, J.R.B., Mortimer, S.R., Pilgrim, E.S., Harrison, K.A. *et al.* (2012) Abiotic drivers and plant traits explain landscape-scale patterns in soil microbial communities. *Ecology Letters*, **15**, 1230–1239.

de Waal, C., Anderson, B. & Ellis, A.G. (2015) Relative density and dispersion pattern of two southern African Asteraceae affect fecundity through heterospecific interference and mate availability, not pollinator visitation rate. *Journal of Ecology*, **103**, 513–525.

Wagner, G.P. & Altenberg, L. (1996) Perspective: complex adaptations and the evolution of evolvability. *Evolution*, **50**, 967–976.

Wardle, D.A., Walker, L.R. & Bardgett, R.D. (2004) Ecosystem properties and forest decline in contrasting long-term chronosequences. *Science*, **305**, 509–513.

Weese, D.J., Heath, K.D., Dentinger, B.T.M. & Lau, J.A. (2015) Long-term nitrogen addition causes the evolution of less-cooperative mutualists. *Evolution*, **69**, 631–642.

Weyl, E.G., Frederickson, M.E., Yu, D.W. & Pierce, N.E. (2010) Economic contract theory tests models of mutualism. *Proceedings of the National Academy of Sciences of the United States of America*, **107**, 15712–15716.

Whitham, T.G., Bailey, J.K., Schweitzer, J.A., Shuster, S.M., Bangert, R.K., LeRoy, C.J. *et al.* (2006) A framework for community and ecosystem genetics: from genes to ecosystems. *Nature Reviews Genetics*, **7**, 510–523.

Wolf, J.B., Brodie, E.D., Cheverud, J.M., Moore, A.J. & Wade, M.J. (1998) Evolutionary consequences of indirect genetic effects. *Trends in Ecology & Evolution*, **13**, 64–69.

Yang, H., Dai, Y., Wang, X., Zhang, Q., Zhu, L. & Bian, X. (2014) Meta-analysis of interactions between arbuscular mycorrhizal fungi and biotic stressors of plants. *Scientific World Journal*, 746506.

Yoshida, T., Jones, L.E., Ellner, S.P., Fussmann, G.F. & Hairston, N.G. (2003) Rapid evolution drives ecological dynamics in a predator-prey system. *Nature*, **424**, 303–306.

Zak, D.R., Holmes, W.E., White, D.C., Peacock, A.D. & Tilman, D. (2003) Plant diversity, soil microbial communities, and ecosystem function: are there any links? *Ecology*, **84**, 2042–2050.