Plant–soil feedbacks: connecting ecosystem ecology and evolution

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Summary

1. While an appreciation of plant–soil feedbacks (PSF) continues to expand for community and ecosystem ecology, the eco-evolutionary mechanisms and consequences of such feedbacks remain largely unknown or untested.

2. Determining the cause and effect of plant phenotypes is central for understanding these eco-evolutionary dynamics since phenotypes respond to soil selective gradients that are, in turn, modified by plant traits. Genetic variation in plant phenotypes can change soil processes and biotic communities; oppositely, soil gradients and microbial communities can influence the expression and evolution of plant phenotypes.

3. Although these processes represent the two halves of genetic based PSF, research in these areas has developed independently from one another. Greater connectivity between research on ecosystem consequences of plant genetic variation and soil selective gradients that drive plant phenotypic evolution will create novel and important opportunities to link ecology and evolution in natural systems.

4. Papers in this special feature build on the inherent ecological and evolutionary processes involved in PSF, outlining many ways to identify and test mechanisms that connect ecosystem ecology and evolution.

Key-words: above-ground–below-ground relationships, eco-evolutionary dynamics, ecosystem ecology, G × G interactions, plant–soil feedback, selection, soil gradients, soil microbes

Introduction

Plant–soil feedbacks (PSF) have important evolutionary implications because they are associated with changes in plant fitness (van der Putten 1997), which might ultimately affect genetic divergence among populations, adaptive or contemporary evolution, and diversification (Bailey et al. 2014; Schweitzer et al. 2014). Plants alter the soils in which they grow and evidence that these modifications can feed back to influence the same or different plants represents a rich and growing mechanism for a variety of ecological phenomena. By exuding root compounds such as hormones, phenolics, sugars and organic acids (reviewed in Bais et al. 2006), and contributing organic matter such as leaf and root litter (Vivanco & Austin 2008), plants shape soil biotic communities that use these plant products as energy sources. Plant interactions with soil biota (bacteria, fungi, archaea, viruses and macro- and microarthropods) in turn alter the physical and chemical properties of soils that, together with soil biota, positively or negatively affect the fitness and phenotype of the same or different plants (Ehrenfeld, Ravit & Elgersma 2005; Kulmatiski et al. 2008; Miki 2012). These effects of past soil changes that influence plant performance and fitness are known as PSF (Bever 1994). Such feedbacks have been shown to facilitate or slow the spread of invasive species (Kourtev et al. 2002; Wolfe & Kironomos 2005; Levine et al. 2006; Reinhart & Callaway 2006; Nijjer, Rogers & Siemann 2007; Batten, Scow & Espeland 2008), direct plant community succession (Kardol, Bezem & van der Putten 2006) and underlie abundance and coexistence patterns within plant communities (Kironomos 2002; Kulmatiski et al. 2008; Mangan et al. 2010; van der Putten et al. 2013). While an appreciation of PSF continues to expand for community and ecosystem ecology, much less work has focused on the evolutionary mechanisms and consequences of PSF.

Understanding the evolutionary dynamics of PSF relies on identifying the cause and effect of plant phenotypes...
since (i) they are the material upon which natural selection acts and (ii) they largely control plant–soil relationships. For instance, soil metal toxicity is an important selective agent for plants on abandoned mine sites or harsh serpentine soils that leads to locally adapted populations with phenotypes of increased tolerance of aluminium (Al) and magnesium (Mg) (Whitaker 1954; Shaw 1989; Brady, Kruckenberg & Bradshaw 2005; Anacker 2014). However, soils are hyper-diverse with living organisms, and biotic interactions with soil microbes create genetic environments that also impact phenotypes. Such is the case when plant growth-promoting rhizobacteria in the soil environment produce phytohormones that direct plant root growth, mycorrhizal development of roots or root nodule formation for symbiotic nitrogen (N) fixation (Dighton 2014). These interactions can result in phenotypic shifts due to plasticity and may not always result in relatively fast reciprocal selection (Agrawal 2001; Fordyce 2006), but here we focus on the selective consequences of plant–microbe interactions. While soils and microbes can shape the underlying genetic variation and expression of plant phenotypes, plants actively change below-ground processes and determine the nature of above-ground–below-ground relationships (Kardol et al. 2015). For example, Ke, Miki & Ding (2015) modelled how the effect of plant traits (e.g. litter decomposability) on PSF direction and strength depend on the relative abundance of certain soil biota groups (e.g. decomposers, mutualists, pathogens). As a broader example, litter decomposability is an important phenotype determining soil nutrient status through plant–litter–nutrient feedbacks (Hobbie 1992, 2015). With the potential for feedback loops to exist between plants, microbial communities and soil environments, understanding the genetic basis of these interactions is essential for PSF research to begin incorporating and demonstrating evolutionary concepts.

Genetic variation in plants can affect soil microbial communities, and in turn, these communities affect genetically based plant traits. For example, when seedlings from 20 randomly collected Populus angustifolia genetic families were planted into soils that were conditioned by various Populus species, P. angustifolia seedlings grown in their own soils were twice as likely to survive and had the highest genetic variation in performance traits, even though P. angustifolia soils were less fertile overall (Pregitzer et al. 2010). A related study using P. angustifolia genotypes found that positive feedback effects on plant performance traits were related to conditioned soil communities (Smith et al. 2012). If PSF comprise genetic interactions between plants and soil communities, then not only could these feedbacks drive genetic changes in plants and alter biodiversity patterns (Vitousek 2004; Bailey et al. 2014), but the feedbacks themselves might evolve across different environments (Schweitzer et al. 2014). Because (i) soil microbial communities respond to plant phenotypes, (ii) plants respond to variation in soil microbial communities, (iii) plant–microbial interactions drive nutrient cycling, and (iv) these interactions vary and evolve along environmental gradients that are critical to ecosystem function and evolutionary processes, the field of PSF is an excellent opportunity for placing ecosystem ecology into an evolutionary framework and vice versa.

Building upon a growing literature and a previous special feature highlighting the ecological mechanisms and consequences of PSF (van der Putten et al. 2013), papers in this special feature demonstrate or suggest many of the evolutionary mechanisms and consequences of PSF at a broad scale. Topics in this special feature include the evolutionary role of PSF in biodiversity and ecosystem function (Evans et al. 2016; terHorst & Zee 2016), local adaptation of soil microbial communities and their reciprocal effects on plant phenotypes (Herrera Paredes & Lebeis 2016; Revillini, Gehring & Johnson 2016), phylogenetic responses of plants to soil N, demonstrating large-scale evolutionary effects of plant–soil linkages (Wooliver et al. 2016), and finally, the applications and frontiers of PSF under land use and environmental change (de la Pena et al. 2016; van der Putten et al. 2016). Using the geneto-ecosystems concepts expressed throughout the special feature, the goal of this paper is to highlight how PSF research bridges ecological and evolutionary concepts to place ecosystem ecology into an evolutionary framework.

Mechanisms that link ecosystems and evolution via PSF

Genetic variation and ecosystem functions are linked in terrestrial systems (Schweitzer et al. 2004; Crutsinger, Souza & Sanders 2008; Hughes et al. 2008; Bailey et al. 2009; Fitzpatrick et al. 2015; terHorst & Zee 2016). The link between genes and ecosystems is fundamentally related to genetically based species interactions and the energy flow or nutrient cycling that emerges from these interactions (Whitham et al. 2003, 2006; Shuster et al. 2006; Bailey et al. 2014; Schweitzer et al. 2014). Here, we define genetically based interactions between plants and soil microbial communities as Genotype × Genotype interactions (G × G), where genetically based plant phenotypes interact with phylogenetically diverse soil microbial communities. Although soil communities harbour an immense level of diversity, conceptually referring to them as a single genetic unit is a first step for our purposes of exploring genetic links above- and below-ground. Below, we outline how PSF research provides an important platform to identify and test mechanisms that connect ecology and evolution through these plant–soil genetic linkages.

Below-Ground Consequences of Above-Ground Genetic Variation

The effect of plant genes can reach to higher levels of communities and ecosystems (Dawkins 1982; Whitham et al. 2003, 2006). This is a critical element to the evolutionary mechanisms of PSF, whereby G × G interactions change

the soil environment, and those changes ultimately affect plant fitness and phenotypes. In this way, \( G \times G \) interactions structure communities (Goodnight 1990a,b; Brodie 2005; Shuster et al. 2006; Allan et al. 2012) and drive ecosystem-level change (Whitham et al. 2003, 2006; Lojewski et al. 2009, 2012; Genung et al. 2011; Miki 2012; Genung, Bailey & Schweitzer 2013; Schweitzer et al. 2014). This has been shown repeatedly for plants across many terrestrial (and aquatic) systems (reviewed in Bailey et al. 2009; Schweitzer et al. 2012; Bailey et al. 2014; Matthews et al. 2014). Genetically based phenotypic variation in plant chemistry, morphology and physiology structures below-ground communities and regulates soil processes (reviewed in Schweitzer et al. 2012; Table 1). Plants vary in soil nutrient uptake and use (Wooliver et al. 2016), affecting the quantity and quality of root and leaf litter (e.g. lignin content and foliar C to N ratio). These differences lead to well-documented effects on litter arthropod assemblages, soil fungal and bacterial community composition, and ultimately carbon (C) and N mineralization (Zinke 1962; Hobbie 1992; Bardgett 2005; Chapman et al. 2006; Bardgett & Wardle 2010; Gorman et al. 2013). At finer scales, species modify local soil conditions in the vicinity of their highly variable root environments through the exudation of hormones, sugars, phenolics and amino acids (Bardgett & van der Putten 2014). Root exudates structure rhizosphere communities by providing carbohydrate sources and functioning as signalling molecules (Chaparro et al. 2013; Dighton 2014; Herrera Paredes & Lebeis 2016). Plant control on soil and root microbiota has been observed under highly controlled greenhouse, common garden and agricultural settings (Marschner et al. 2001; Schweitzer et al. 2008a; Lundberg et al. 2012), and recently in wild plant species growing in close proximity in the field (Alekket et al. 2015). Even in diverse tropical forests, taxonomic and phylogenetic metrics of tree composition are correlated with soil bacterial and fungal composition (Barberán et al. 2015). Below-ground microbial activity (e.g. decomposition, nutrient cycling, predator-prey dynamics) changes soil physico-chemical properties such as the type and concentration of inorganic nutrients, pH or water holding capacity (Bardgett 2005; Ehrenfeld, Ravit & Elgersma 2005; van der Putten et al. 2016), all of which can feedback to impact plant performance. Since the expression of genes determine plant phenotypes, and the effects of plants on soil biotic and abiotic environments are the result of phenotypic variation, soils modified by plants create a link between genes, soil communities and ecosystem function that generate PSF with evolutionary consequences (Whitham et al. 2006; Schweitzer et al. 2008b, 2014; Genung, Bailey & Schweitzer 2013; Bailey et al. 2014).

### Table 1. Evidence that plant genetic effects influence abiotic and biotic soil properties

<table>
<thead>
<tr>
<th>Plant genetic effect</th>
<th>Soil response</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Abiotic</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Genotype, genotypic diversity, population, provenance</td>
<td>Nitrogen availability</td>
<td>Fischer et al. (2010), Schweitzer et al. (2011b)</td>
</tr>
<tr>
<td><strong>Biotic</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Genotype, species</td>
<td>Microbial nutrient pools</td>
<td>Schweitzer et al. (2008a,b), Pregitzer et al. (2010)</td>
</tr>
<tr>
<td>Genotype, population</td>
<td>Extracellular enzyme activity</td>
<td>Schweitzer et al. (2008a,b), Madritch, Greene &amp; Lindroth (2009)</td>
</tr>
<tr>
<td>Genotype</td>
<td>Net nitrogen mineralization</td>
<td>Schweitzer et al. (2011a)</td>
</tr>
<tr>
<td>Genotype</td>
<td>Soil C respiration and efflux</td>
<td>Fischer et al. (2007), Lojewski et al. (2012), Fitzpatrick et al. (2015)</td>
</tr>
<tr>
<td>Genotype, population, species</td>
<td>Microbial community composition</td>
<td>Schweitzer et al. (2008a,b), Alekket et al. (2015)</td>
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</table>

evolution on the landscape is specific to the microbial context. Similarly, soil microbes affect the strength and direction of selection on plant phenology by altering plasticity in flowering time and impacting fecundity (Wagner et al. 2014). Moreover, the reciprocal interactions that drive ecological changes to soil microbes can drive plant evolution in novel environments (Lau & Lennon 2011, 2012), and logical changes to soil microbes can drive plant evolution under varying selective pressures from soil microbes or nutrients (Table 2). Perhaps the earliest and clearest example of plant evolutionary responses to soils comes from decades of work studying serpentine plant populations (re-reviewed in Anacker 2014). Soil-mediated selection has repeatedly been shown to result in plant evolution under these harsh conditions using reciprocal transplants (Brady, Kruckeberg & Bradshaw 2005) and gene sequencing approaches (Turner et al. 2010) to examine local adaptation. In these studies, plant populations evolve increased resilience to soil toxicity by adapting to high metal concentrations that are characteristic of serpentine soils (e.g. phenotypes with an enhanced ability to sequester, transport, or selectively uptake Mg and Al). Plant phenotypes that condition the soil microbial community to suppress pathogen activity or to facilitate resource uptake may also be favoured (Kinkel, Bakker & Schlatter 2011; Revillini, Gehring & Johnson 2016). For example, when Andropogon gerardii ecotypes collected from phosphorus (P)-limited and N-limited grasslands were grown with all possible 'home' and 'away' combinations of soils and mycorrhizal communities, soil fertility was a key driver of locally adapted symbioses such that mycorrhizal exchange of the most limiting soil nutrient resource for each ecotype was maximized (Johnson et al. 2010). Reciprocal transplant experiments such as those used in Johnson et al. (2010) consistently indicate that varying selective pressures from soil microbes or nutrients lead to patterns of local adaptation and geographic mosaics of plant–microbe interactions that vary in strength (Pregitzer et al. 2010; Andonian et al. 2012; Smith et al. 2012). Such variation in plant–microbe interactions have the potential to create PSF differences along environmental gradients that may lead to genetic divergence on the landscape through the evolution of feedbacks (Schweitzer et al. 2014; Evans et al. 2016). Because plant–microbial interactions also modify soils, the selective gradients that underlie plant–microbial interactions may be reinforced, ultimately affecting the direction and pace of evolution.


<table>
<thead>
<tr>
<th>Soil Factor</th>
<th>Plant phenotype response (species)</th>
<th>Evo implication</th>
<th>Method</th>
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</thead>
<tbody>
<tr>
<td>Abiotic</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Serpentine</td>
<td>Flowering time (Collinsia sparsiflora)</td>
<td>Local adaptation</td>
<td>Wright, Stanton &amp; Scherson (2006)</td>
</tr>
<tr>
<td>Serpentine</td>
<td>Growth (Achillea borealis)</td>
<td>Local adaptation</td>
<td>Kruckeberg (1954)</td>
</tr>
<tr>
<td>Serpentine</td>
<td>Metal detox a transport (Arabidopsis lyrata)</td>
<td>Local adaptation</td>
<td>Turner et al. (2010)</td>
</tr>
<tr>
<td>Aluminin</td>
<td>Al tolerance</td>
<td>Local adaptation</td>
<td>Gould, McCouch &amp; Geber (2014)</td>
</tr>
<tr>
<td>Nutrients</td>
<td>Growth (Populus angustifolia)</td>
<td>Local adaptation</td>
<td>M.E. Van Nuland, J.K. Bailey &amp; J.A. Schweitzer (unpublished data)</td>
</tr>
<tr>
<td>Biotic</td>
<td>Productivity (Allantus altissima)</td>
<td>Divergence</td>
<td>Felker-Quinn, Bailey &amp; Schweitzer (2011)</td>
</tr>
<tr>
<td>Bacteria and fungi</td>
<td>Flowering time (Arabidopsis spp.)</td>
<td>Selection intensity</td>
<td>Wagner et al. (2014)</td>
</tr>
<tr>
<td>Microbes</td>
<td>Growth and Phenology (Brassica rapa)</td>
<td>Selection intensity</td>
<td>Lau &amp; Lennon (2011)</td>
</tr>
<tr>
<td>Fungi</td>
<td>Survival, Growth (Pseudotsuga menziesii)</td>
<td>Local adaptation</td>
<td>Pickles et al. (2015)</td>
</tr>
<tr>
<td>Microbes</td>
<td>Biomass (P. angustifolia)</td>
<td>Local adaptation</td>
<td>Pregitzer et al. (2010), Smith et al. (2012)</td>
</tr>
<tr>
<td>Rhizobia</td>
<td>Specific Leaf Area (Glycine max)</td>
<td>N/A</td>
<td>Harris, Pacovsky &amp; Paul (1985)</td>
</tr>
<tr>
<td>AM fungi</td>
<td>Clonality (Prunella vulgaris)</td>
<td>N/A</td>
<td>Streitwolf-Engel et al. (2001)</td>
</tr>
<tr>
<td>Rhizobia</td>
<td>Leaf frost sensitivity (Medicago sativa)</td>
<td>N/A</td>
<td>Bertrand et al. (2007)</td>
</tr>
<tr>
<td>Rhizobia</td>
<td>Height (Oryza sativa)</td>
<td>N/A</td>
<td>Perrine-Walker et al. (2007)</td>
</tr>
<tr>
<td>AM fungi</td>
<td>Specific root length (Zea mays)</td>
<td>N/A</td>
<td>Kothari, Marschner &amp; George (1990)</td>
</tr>
<tr>
<td>EM fungi</td>
<td>Fine root diameter (Pinus taeda)</td>
<td>N/A</td>
<td>Rousseau, Sylvia &amp; Fox (1994)</td>
</tr>
<tr>
<td>Rhizobia</td>
<td>Root distribution (Trifolium subterraneum)</td>
<td>N/A</td>
<td>Morris &amp; Djordjevic (2006)</td>
</tr>
<tr>
<td>AM fungi</td>
<td>95% rooting depth (Triticum aestribum)</td>
<td>N/A</td>
<td>Ellis, Larsen &amp; Boosalis (1985)</td>
</tr>
<tr>
<td>Bacteria</td>
<td>Stress recovery (Capsicum annum)</td>
<td>N/A</td>
<td>Marasco et al. (2012)</td>
</tr>
</tbody>
</table>

Microbes: non-specified collection of bacteria, fungi, archae and viruses; EM fungi: ectomycorrhizae; AM fungi: arbuscular mycorrhiza. N/A implies no direct test of plant evolutionary response or implication to the soil factor in the respective study.
The ability of plants to alter their surrounding soil creates environmental variation that can lead to and maintain genetic divergence. This occurs when soil gradients drive phenotypic evolution, thus changing the distribution of plant traits that control ecosystem processes and structure soil communities (Vitousek 2004; Felker-Quinn, Bailey & Schweitzer 2011; Smith et al. 2012; Pregitzer, Bailey & Schweitzer 2013). Variation in soil parent materials and underlying chemistry may result in fitness differences among individual as plants differ in their ability to tolerate specific soil conditions (Ellis & Weis 2006; Alvarez et al. 2009). These soil gradients influence plant phenotypes indirectly by affecting soil microbial communities and altering \( G \times G \) interactions. For example, natural gradients in soil pH have been shown to influence the community composition of bacteria, fungi and arbuscular mycorrhizal communities (Fierer & Jackson 2006; Dumbrell et al. 2010). A classic example for understanding how soils may impact plant phenotypic evolution is the long-term soil age gradient of Hawai’i. Gradients of substrate age and soil development influence nutrient availability (Vitousek 2004). With low soil nutrient availability, symbiotic mutualists and a slow cycling microbial community generally occur. Low nutrient availability may also select for small leaves, high nutrient use efficiency, slow growth rates, long foliar life span, high nutrient resorption and recalcitrant plant tissues that decay slowly. Such recalcitrant plant tissues may lead to continued low soil nutrient availability and thus a consistent selective pressure on plant traits that convey fitness advantages under these environmental conditions. With high nutrient availability, the opposite patterns have been demonstrated. Reinforcement of these patterns may ultimately lead to local adaptation due to variation in soil nutrient availability and divergence in functional phenotypes (sensa Bertness & Callaway 1994; Wooliver et al. 2016).

Synthesis and conclusions

The relative importance and extent of reciprocal interactions between the ecology of populations, communities and ecosystems, and their evolutionary dynamics remains an open issue (Fussmann, Loreau & Abrams 2007; Post & Palkovacs 2009; Schoener 2011; Matthews et al. 2014). While other examples in aquatic and plant–herbivore realms are emerging (Reznick 2013; Fitzpatrick et al. 2015), recent empirical and theoretical work suggests that genetically based plant–soil–microbe interactions are a model arena to demonstrate these eco-eco linkages (Lau & Lennon 2011, 2012; terHorst, Lennon & Lau 2014; Schweitzer et al. 2014; Evans et al. 2016; terHorst & Zee 2016; Revillini, Gehring & Johnson 2016). Here, we outlined how plant genetic effects can change soil communities and nutrient cycling (Table 1), and how soil biotic and abiotic selective pressures drive plant phenotypic evolution (Table 2). Although both are key components of eco-evolutionary feedbacks that emerge from PSF, such research has developed largely independent of one another. Below, we outline a conceptual synthesis of these ideas using a genes-to-ecosystems approach, highlighting the opportunity of PSF research to address the links between evolution, community dynamics and ecosystem function.

THREE LEVELS OF ECO-EVOLUTIONARY FEEDBACK IN PLANT–SOIL SYSTEMS

Feedbacks shape the strength and direction of natural selection on the landscape. To date, feedbacks have generally been regarded as a population or co-evolutionary phenomenon (Thompson 2005). However, ecosystem-level feedbacks can affect evolutionary dynamics in at least three ways (Fig. 1). First, feedbacks can be co-evolutionary and driven by \( G \times G \) interactions (FB1). Here, they are largely a localized phenomenon within populations and communities (Thompson 1994). Depending upon the geographic distribution and underlying differences in phenotypic variation of the interacting species, these interactions may drive among-population level patterns of genetic divergence on the landscape, irrespective of other abiotic environmental factors (Thompson 2005, 2013). Secondly, feedbacks can result from ecosystem-level effects of past \( G \times G \) interactions that vary independently of geographic variation in abiotic selective gradients (FB2). These are ecosystem-level feedbacks that are a consequence of local plant–microbe interactions. Similar to co-evolutionary feedbacks, ecosystem-level feedbacks may vary based upon the geographic distribution and phenotypic variation of the interacting species. This holds evolutionary significance because ecosystem-level feedbacks may interact with co-evolutionary feedbacks to reinforce or disrupt among-population patterns of genetic divergence. Thirdly, feedbacks can result from ecosystem-level effects of past plant–microbe interactions that covary with geographic variation in abiotic selective gradients (FB3). Abiotic selective gradients such as climate, parent material and mineral nutrient availability commonly impact plant phenotypes that are expressed by organisms and drive evolutionary dynamics of those species (Read et al. 2014; Wooliver et al. 2016). The energy and nutrients that emerge from plant–microbe interactions reinforcing selective gradients, as is the case with PSF (Kylafis & Loreau 2008; Schweitzer et al. 2014), are the drivers of ecosystem-level evolutionary dynamics. While these types of eco-evolutionary feedbacks remain difficult to identify and test in nature (Reznick 2013), terHorst & Zee (2016) describe how \( G \times G \) interactions between plants and soil microbes offer a promising direction for future research because of short generation times that allow for rapid evolution, strong selection pressures and tight co-evolutionary dynamics. As an empirical test, Evans et al. (2016) identify components of an eco-evolutionary feedback operating in the invasive garlic mustard,
where heritable phenotypic variation of an allelopathic compound drives plant–soil interactions that feedback to alter demographic rates. If eco-evolutionary feedbacks are common and explain both above- and below-ground community structure, then the interaction of plant–soil and eco-evolutionary dynamics could be important for generating spatial and temporal variation in PSF.

**RESEARCH FRONTIERS**

As highlighted in this and other papers throughout the special feature, understanding how the strength and direction of PSF relates to genetic interactions between plants, soils and microbes is an important new step for identifying how systems respond to increasing stress caused by human activity. As a result, the eco-evolutionary dynamics of PSF could offer a unique and underused resource to empirically test the response of populations, communities and ecosystems to environmental change. To achieve this, we have identified research frontiers covering local and landscape scales that form an integrated set of challenges critical to advance PSF research across disciplines and tackle serious global change issues.

A major frontier for ecological research is a more precise understanding of how plants and microbes interact (a significant component of the ‘black box’; Kardol et al. 2015; Fig. 2). For instance, there has been a great deal of work on the genetic and molecular mechanisms that underlie plant–pathogen signalling in crops (Baker et al. 1997) and the signal exchanges between plants and *Rhizobium* that form root nodules (Long 1996). However, this level of detail has been largely absent from PSF studies despite its obvious importance for understanding the basis and consequences of plant–microbe interactions on the landscape. As Herrera Paredes & Lebeis (2016, this issue) review, new methods and statistical approaches are making it easier to test the microbial mechanisms of PSF, such as sequencing and bioinformatic tools that link plant and microbial phenotypes with functional gene content. In addition, Revillini, Gehring & Johnson (2016) use a novel approach with optimal resource allocation models to characterize these interactions and predict PSF outcomes across resource gradients. Characterizing plant-microbe and microbe-microbe signalling pathways alongside plant and soil manipulation experiments will allow for a more mechanistic understanding of how plants condition different soil microbial communities and microbes that mediate plant phenotypic expression. Importantly, this frontier can only be addressed through greater collaboration between ecologists and cellular and molecular biologists working to understand plant–soil linkages from molecular to ecosystem scales (Herrera Paredes & Lebeis 2016).

A significant goal for eco-evolutionary PSF studies is to examine how abiotic stress gradients influence plant genetics, soil microbial structure and function, and $G \times G$ interactions between plants and microbes that alter ecosystem processes (Fig. 2). Evans et al. (2016, this issue) provide one of the first empirical examples of an eco-evolutionary feedback that is driven by plant–soil linkages and could be important for understanding garlic mustard invasion in the south-eastern USA. Moreover, terHorst & Zee (2016, this issue) outline why feedbacks between ecological and evolution dynamics might be common and interact with PSF as soil microbes influence ecosystem processes and the expression of specific plant phenotypes that
may be critical to plant responses and resilience to global change through feedbacks. Using a meta-analysis, Wooliver et al. (2016, this issue) examine how phylogenetic relationships relate to plant strategic responses to elevated N, demonstrating that past evolution towards greater plant growth responses to N is associated with certain plant functional types and suggesting that N enrichment could lower functional diversity. There was no evidence, however, for divergent selection across biomes and along climatic gradients, indicating that evolutionary consequences of PSF vary independently of environment. Future studies that examine how environmental selection pressures alter plant-soil G × G interactions and their ecosystem consequences will generate important information for predicting if populations can adapt, respond plasticly or migrate towards more favourable sites under environmental change. 

Feedbacks may interact at different levels, but it remains unclear what conditions cause local-scale feedbacks to disrupt or accelerate ecosystem-level feedbacks and vice versa (Fig. 2). However, recent mathematical models indicate the possibility of an overarching link between heritable plant traits, selection and plant-soil microbial feedbacks (Kylafis & Loreau 2008; Jiang & DeAngelis 2013; Schweitzer et al. 2014). For instance, Schweitzer et al. (2014) used a spatially explicit individual-based model that incorporated genetically based plant-microbe interactions, below-ground consequences of above-ground plant genetic variation and abiotic selective pressures to examine the links between PSF and plant evolution. Their findings demonstrate that feedbacks from the ecosystem-level drive phenotypic trait change as well as the evolution of the feedback itself through plant-soil conditioning. Moreover, both positive and negative feedbacks evolved along a gradient of gene flow, highlighting how processes at broader spatial scales influence local-scale feedbacks.

Highly controlled experiments unequivocally show the importance of PSF for structuring biodiversity and ecosystem processes (van der Putten et al. 2013), as well as the possibility of reciprocal dynamics between ecological and evolutionary processes (Post & Palkovacs 2009; Turcotte, Reznick & Hare 2013). The next great challenge will be testing real-world scenarios of where, when and how such feedbacks occur in natural settings and dictate plant and soil responses to ongoing environmental change. To help in this effort, van der Putten et al. (2016, this issue) present a PSF triangle that balances symbiont, decomposer and enemy contributions to net PSF values under human-induced global changes. In general, they indicate that climate change (i.e. CO₂, temperature and precipitation changes) might lead to increasingly negative PSF based on strong enemy effects, although the proportional contribution of symbionts and decomposers would become more important under certain conditions. Beyond changing climates, land-use transformation is one of the most dramatic and devastating ways that human activity affects Earth’s systems by destroying or homogenizing habitat and reducing biodiversity both above- and below-ground (Zuppinger-Dingley et al. 2014; Veresoglou, Halley & Rillig 2015). Conversion of agricultural land back to semi-

Fig. 2. Research frontiers for eco-evolutionary dynamics of plant-soil feedback (PSF). Based on papers in this special feature, we emphasize a suite of integrated challenges spanning local to landscape scales that represent the frontiers of eco-evolutionary PSF research. First, a deeper examination of plant-microbe and microbe-microbe signalling pathways will improve our mechanistic understanding of how plants condition soil communities (coloured ovals), the role of soil microbes in plant phenotypic expression and how plant--microbe interactions change ecosystem processes that reciprocally influence plant traits. Secondly, as the scope and severity of global change increases, investigating how abiotic stress gradients impact plant genetic diversity and selection on functional traits, soil microbial community structure and function, and genetically based plant-microbe interactions that control ecosystem processes will offer novel insights towards population responses (e.g., adaptation, plasticity, and/or migration). Thirdly, it is critical to study how feedbacks interact across scales, such as with models that investigate conditions where local, co-evolutionary feedbacks (FB1) disrupt or enhance community-and ecosystem-level feedbacks (FB2 and FB3). Finally, a significant challenge remains in moving eco-evolutionary and plant-soil feedback experiments from highly controlled settings to field environments where we can begin to determine their effects in natural systems.
natural ecosystems continues and de la Pena et al. (2016, this issue) show how the legacy of soil changes due to plant–soil interactions impacts plant community assembly and could be considered to improve the success of restoration efforts.

Conclusions

Ecosystems provide the energy and nutrient constraints – the environmental context – within which species evolve, while genetically based species interactions drive many ecosystem processes. Despite the fact that phenotypic variation is at the heart of both ecology and evolution, there has been little effort or success to date in bridging ecosystem ecology and evolutionary biology (but see Schoener 2011; Schweitzer et al. 2014; Matthews et al. 2014). Theoretical and empirical advances have revolutionized our view of how phenotypes are determined based on the causes and consequences of G × G interactions, whereby individuals make up the biotic environment of other individuals. In the field of PSF, this provides an opportunity to unify ecosystem ecology in an evolutionary framework at local and landscape scales. Such an effort is important as feedbacks from the ecosystem level can reinforce or disrupt genetically based species interactions that affect the strength of natural selection and the rate of evolutionary change. Examining the role of genetic interactions at the ecosystem level could begin a paradigm shift that places ecosystems within an evolutionary framework and evolution within an ecosystems framework, transforming our understanding of factors that affect the strength and direction of natural selection and population divergence. The papers in this special feature represent the frontier of PSF research, linking ecosystems and evolution like never before which will open many novel empirical and theoretical research directions for years to come.

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Data accessibility

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References


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