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Application and Theory of Plant–Soil Feedbacks on Aboveground Herbivores

Kaplan, Ian; Pineda, Ana; Bezemer, T.M.

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# Chapter 14

## Application and Theory of Plant–Soil Feedbacks on Aboveground Herbivores



Ian Kaplan, Ana Pineda, and Martijn Bezemer

### 14.1 Introduction

The soil is an essential component of all terrestrial ecosystems. It serves as a medium in which plants root, but also houses an overwhelming abundance of living organisms such as bacteria, fungi, protozoa, viruses, nematodes, and arthropods that interact in complex networks (Wall 2004). Soil organisms consume organic compounds, other soil organisms, or plant roots and recycle and mineralize nutrients or interact with living plants. As primary producers, plants provide the basic resources to the soil food web (Bardgett and Wardle 2010). They contribute litter originating from dead shoots or roots, and living plant roots release compounds such as sugars, organic acids, hormones, and secondary metabolites. Via these inputs, plants shape soil biotic communities that use these resources or are influenced by them and alter the physical and chemical properties of soils (Van der Putten et al. 2009, 2013).

Evidence is rapidly accumulating that these plant-mediated soil changes influence the performance of other plants that grow later in the same soil (Klironomos 2002;

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I. Kaplan (✉)

Department of Entomology, Purdue University, West Lafayette, IN, USA

e-mail: [ikaplan@purdue.edu](mailto:ikaplan@purdue.edu)

A. Pineda

Department of Terrestrial Ecology, Netherlands Institute of Ecology, Wageningen, The Netherlands

e-mail: [A.Pineda@nioo.knaw.nl](mailto:A.Pineda@nioo.knaw.nl)

M. Bezemer

Department of Terrestrial Ecology, Netherlands Institute of Ecology, Wageningen, The Netherlands

Institute of Biology, Section Plant Ecology and Phytochemistry, Leiden University, Leiden, The Netherlands

e-mail: [M.Bezemer@nioo.knaw.nl](mailto:M.Bezemer@nioo.knaw.nl)

Kulmatiski et al. 2008). This phenomenon is called plant–soil feedback, and it is now receiving considerable attention in the ecological literature (Bever et al. 1997; Ehrenfeld et al. 2005; Van der Putten et al. 2013). Many studies argue that plant–soil feedbacks can aid in the understanding of invasiveness of exotic plants, succession of natural plant communities, plant coexistence and plant competition, and even plant–herbivore interactions (Klironomos 2002; Van der Putten et al. 2009, 2013). Much of the work on plant–soil feedback is carried out with wild species and within the context of natural plant communities. However, these legacy effects play a central role in agriculture where the concept of soil sickness—which, by definition, is a form of plant–soil feedback—has been recognized for centuries among those cultivating crops (Huang et al. 2013).

In this chapter, we first briefly introduce the terminology and concepts used in plant–soil feedback research. We then review the effect of plant–soil feedbacks on aboveground phytophagous insects, a topic that is only beginning to develop but clearly illustrates how soil properties cascade to influence relationships with foliar herbivores. Next, we focus on the mechanisms by which soil microbiota induce changes in plant growth and resistance and the consequences for plant-feeding insects and their natural enemies. Finally, we discuss how knowledge about plant–soil feedbacks can be used to steer soil communities in agricultural systems so that the current or succeeding crops become more resistant to aboveground and belowground insect pests and diseases.

## 14.2 Plant–Soil Feedback: Concepts and Definitions

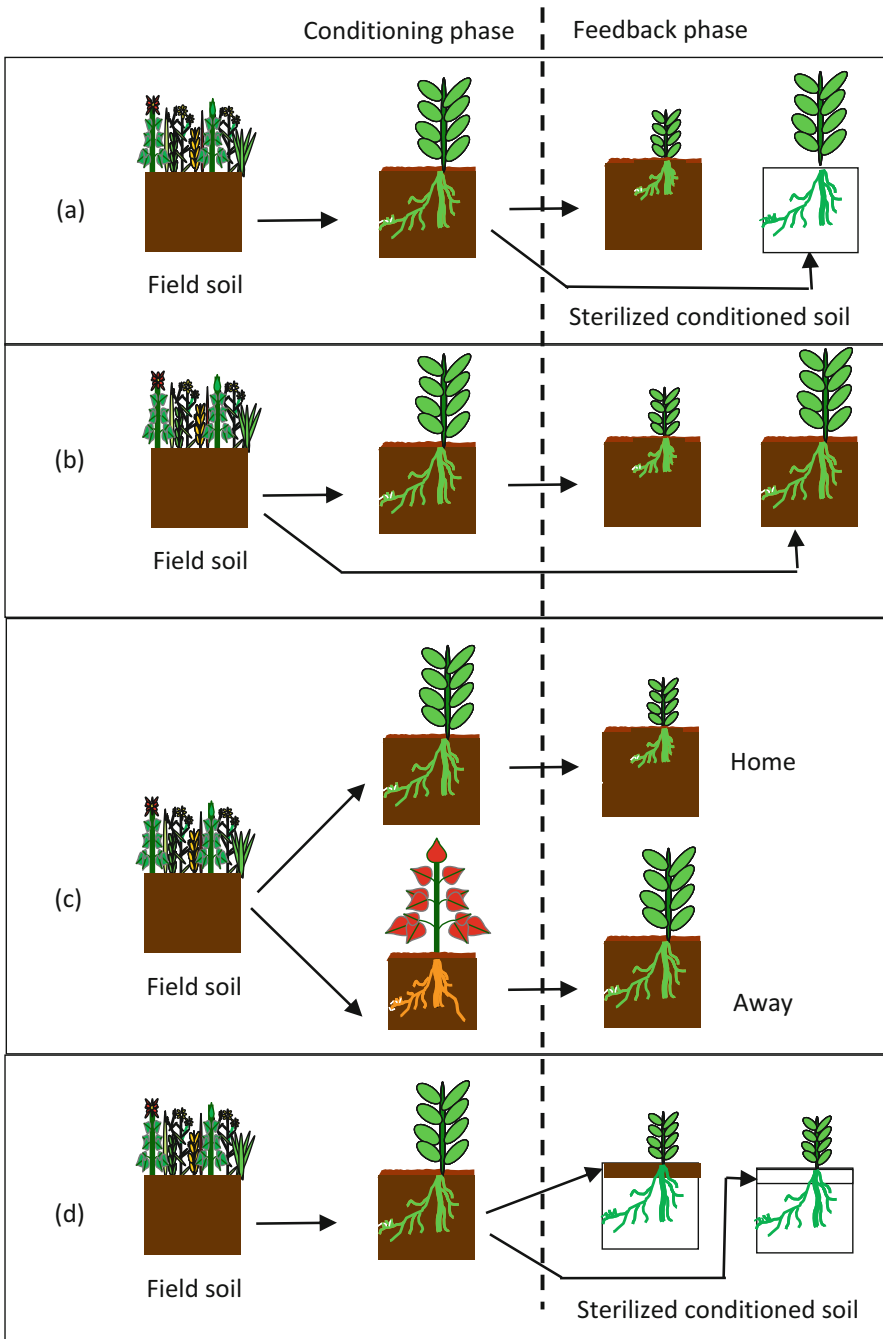
Plant–soil feedback is the effect of a plant on the soil, that subsequently influences the performance of another plant that grows later in the soil. If the initial plant causing changes in the soil and the plant responding to these changes belong to the same species, this is called conspecific or direct plant–soil feedback. When the species that cause and respond to the effect differ, the feedback is called heterospecific or indirect (Van der Putten et al. 2013). Conspecific feedbacks are usually negative, whereas heterospecific feedbacks are variable and can be negative, neutral, or positive (Kulmatiski et al. 2008; Van de Voorde et al. 2011).

Plant–soil feedback studies typically consist of two stages. During the *first phase*, the plant influences the soil it grows in. This is called the “conditioning phase.” In the majority of studies, “live” soil (i.e., non-sterilized, presumably rich with microbial life) is collected from the field, and plants are then grown in pots filled with this soil for a fixed period of time, often between 2 and 4 months. Alternatively, soil can be collected from beneath specific plant species in the field or from monocultures. In this case, the soil is naturally conditioned in the field rather than experimentally assigned to plant species in controlled environments, but this approach is less common (Bezemer et al. 2005; Badri et al. 2013; Pendergast et al. 2013; Kos et al. 2015a). The underlying assumption is that during the conditioning phase, plants shape the soil microbial community in a specific manner via their input of organic

compounds. The structure of the microbial community will change depending on the amount and composition of root exudates and sloughed root tissue that is deposited in the soil, and plant pathogens and symbionts will increase in the presence of their host. Although often ignored, abiotic soil conditions such as nutrient availability, moisture, and physical structure also change depending on the plant species that was previously growing in the soil. These changes could either impact subsequent plant growth directly (e.g., a nitrogen-fixing legume may provide excess nutrients for plants sharing the same soil) or indirectly by modifying the microbial community that also responds strongly to abiotic factors (Fierer et al. 2012; Ramirez et al. 2012).

At the end of the conditioning phase, the plant is removed and the remaining soil is then used for the *second phase*. This is called the “feedback phase” or “test phase,” in which the growth of a focal plant in the conditioned soil—also called “home soil”—is compared to a control soil. As both abiotic and biotic soil properties change during the conditioning phase, selecting the appropriate control is not trivial. Several studies compare plant growth in conditioned soil with growth in the same soil that was sterilized (Fig. 14.1a; e.g., Cortois et al. 2016). However, this comparison can be misleading. Sterilization often increases nutrient availability and hence the feedback effect is confounded by nutritional differences among the two soil groups, namely, artificially lower nutrient levels in the conditioned treatment. Thus, negative effects of conditioned soil on plant growth tend to be overestimated, particularly in low fertility soils (Troelstra et al. 2001).

Three other types of controls are commonly used in plant–soil feedback studies. *First*, feedback effects can be determined by comparing the growth in conditioned “home” soil to live field soil that was not conditioned (Fig. 14.1b). A potential caveat with this approach is that the “unconditioned” field soil is used during the conditioning phase and as control soil during the feedback phase. As the conditioning phase can take several months, the “unconditioned” field soil should be stored and during storage the microbial composition can change. Alternatively, fresh “unconditioned” soil can be collected later at the beginning of the feedback phase. However, because microbial communities vary over time and change depending on season, climatic conditions, and plant age or phenology (Lauber et al. 2013), the later collected soil may fundamentally differ from the soil originally used during the conditioning phase. *Second*, growth of a focal plant in “home” soil conditioned by the same species can be compared with “away” soil conditioned by another species. This can be accomplished using several “away” soils, providing a quantitative measure of the soil-mediated influence of a plant on conspecifics relative to other species (Fig. 14.1c; e.g., Van de Voorde et al. 2011; Wubs and Bezemer 2016). When a series of soils are used, the home soil can also be compared to a mixture of all away soils (Engelkes et al. 2008; Brinkman et al. 2010). A *third* way of testing plant–soil feedback effects is to inoculate sterilized soil with a small amount—ca. 10%—of conditioned soil. This can then be compared to inoculation using the same amount of sterilized conditioned soil (Fig. 14.1d; e.g., Bever et al. 1997; Van der Putten et al. 2013). A benefit of this approach is that the complicating effect of nutritional differences from using pure conditioned soil, as shown in Fig. 14.1a, is minimized since both treatments contain primarily sterile soil with relatively minor



**Fig. 14.1** Schematic view of several approaches that are used to examine plant–soil feedback effects. Live soil is collected from a field site (“Field soil”). During the conditioning phase, the focal plant grows in this soil. At the end of the conditioning phase, the plant is removed from the soil and the soil is used in the feedback phase. The plant–soil feedback effect of a focal species can be

differences in total volume due to the addition of small quantities of inoculum in the conditioning treatment. The drawback here is that adding low inoculum volumes may underestimate the feedback if microbial factors are density dependent (i.e., adding 50% soil inoculum generates a relatively stronger impact compared with only 10% inoculum). To our knowledge, this is not well known or documented.

An important question that is still highly debated is whether and to what extent plant–soil feedbacks are predictable. It is hypothesized that the phylogenetic relatedness between the plant that conditions the soil and the species that responds to this soil predicts the magnitude of the feedback (Dostal and Paleckova 2011; Mehrabi and Tuck 2015). The assumption is that closely related species share soil pathogens or symbionts and, as most conspecific feedbacks are negative (Kulmatiski et al. 2008), the prediction is that there should be a negative relationship between relatedness and feedback. However, most studies, so far, indicate that relatedness is a poor predictor (Dostal and Paleckova 2011; Mehrabi and Tuck 2015; Fitzpatrick et al. 2017; but see Anacker et al. 2014). Other studies show that the strength of feedbacks is better explained by proximate plant traits such as growth rate or specific root length. Fast growing species generally exhibit stronger negative conspecific feedbacks than slower growing ones (Cortois et al. 2016). Differences between conditioning and response species in trait values also appear to be predictive, but increases in trait differences can lead to both stronger and weaker feedbacks (Fitzpatrick et al. 2017). Hence, to what extent plant traits can explain plant–soil feedbacks remains an open question. Some plant–soil feedback effects may also be predictable according to plant functional group with, for instance, grasses, legumes, and forbs modifying the soil microbiome in fundamentally different ways (Cortois et al. 2016). In this context, it is important to note that the effect of a plant species on its soil community depends in large part on the microbial composition prior to conditioning and that unconditioned soils already have a legacy. Thus, true unconditioned soils do not technically exist. This may partly explain why plant–soil feedback studies that are carried out with the same species can show highly variable outcomes and why it is so difficult to make general predictions.

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**Fig. 14.1** (continued) determined by (a) comparing growth in home soil with that in sterilized home soil; (b) comparing growth in conditioned soil versus unconditioned soil (field soil); (c) comparing growth in soil conditioned by the focal species (home) with growth in soil conditioned by another species (away); or (d) comparing growth in sterile soil inoculated with a small amount of home soil with growth in sterile soil inoculated with a small amount of sterile home soil or live away soil

### 14.3 Plant–Soil Feedbacks and Aboveground Plant–Insect Interactions

The majority of plant–soil feedback studies examine how changes in soil microbes impact plant growth; however, changes in the amount or quality of the host plant due to changes in the soil community can also influence aboveground herbivorous insects (Wurst and Ohgushi 2015). Many studies show that the addition of specific soil biota such as root herbivores (Johnson et al. 2012; Soler et al. 2012), mycorrhizal fungi (Koricheva et al. 2009), rhizobacteria (Hol et al. 2010; Pineda et al. 2010; Pangesti et al. 2013), or nematodes (Wondafraash et al. 2013) influence aboveground plant-feeding insects. These prior investigations clearly illustrate the *potential* for individual groups of soil organisms to shape aboveground interactions. Because plant–soil feedbacks simultaneously change the full soil community, including all taxonomic and functional groups, we expect feedbacks to have major consequences for foliar insect herbivory. Yet, unlike plants, for which there is a clear prediction of negative conspecific feedbacks, the insect response is far more difficult to anticipate.

The few studies that integrate leaf-feeding insects into plant–soil feedback dynamics show that their interactions with host–plants are considerably altered. In a study where ragwort (*Senecio jacobaea*) plants were grown in soils conditioned by 10 different plant species, abundance of the specialized aphid *Aphis jacobaea* varied almost 10-fold between the worst and best soils in terms of *A. jacobaea* population growth. These effects could be explained by plant–soil feedback-related changes in amino acid concentration in the phloem (Kos et al. 2015a, b). In the same experiment using the same host plant species, however, the generalist aphid *Brachycaudus cardui* was far less sensitive to soils from the ten plant species, indicating that these effects depend greatly on the combination of plants, soils, and insects used (Kos et al. 2015a, b). Herbivory by generalist snails (*Cepaea species*) was also unaffected by plant–soil feedback in a study with *Solidago canadensis* and *Tanacetum vulgare*, even though *T. vulgare* exhibited a negative conspecific feedback (Schittko and Wurst 2014). More studies are needed to determine whether generalist herbivores are less sensitive to plant–soil feedback and broadly to changes in the composition of soil microbial communities. However, it is known that generalists and specialists, or insects in different feeding guilds, vary in their response to qualitative or quantitative changes in their host plants (Bezemer and Jones 1998; Awmack and Leather 2002; Ali and Agrawal 2012). Root damage, for instance, often increases the performance of aboveground sapsuckers while reducing the performance of leaf-chewers (Johnson et al. 2008, 2012).

Not only are aboveground insects sensitive to plant–soil feedback, several studies also show that foliar herbivory or grazing during the conditioning phase influences the feedback effect (Medina-Roldan et al. 2012; Veen et al. 2014). Leaf damage by the caterpillar *Mamestra brassicae* on *S. jacobaea* increased the negative conspecific plant–soil feedback, possibly due to herbivore-induced changes in soil fungi (Kostenko et al. 2012; Bezemer et al. 2013). Remarkably, herbivory during the conditioning phase also increased the tolerance of *S. jacobaea* to aboveground

herbivory during the feedback phase and increased insect performance on the later growing plants. The emergence rate of *Microplitis mediator* parasitoids from caterpillar hosts was higher when plants were growing in soil in which conspecific plants had been grown that were exposed to aboveground herbivory (Kostenko et al. 2012). These studies suggest that aboveground multi-trophic interactions are influenced by plant-mediated changes in soil microbiota and that aboveground higher trophic levels alter plant–soil feedbacks.

Perhaps one of the best demonstrations of how plant–soil feedbacks affect aboveground insect interactions comes from a study that used an elegant design to isolate the microbial mechanism responsible for the effect (Badri et al. 2013). These authors used field soil collected from *Arabidopsis*, pine, corn, and potato plantings; then, created soil slurry amendments from these soils to dissect the microbial component. To do so, they mixed the soil in liquid and collected the supernatant to apply as an unfiltered microbial consortium to sterilized soil containing *Arabidopsis thaliana* plants. This was compared with control plants receiving the same slurry that was centrifuged and filter-sterilized (0.45  $\mu\text{m}$  filters). The authors report that larval weights of the leaf-feeding caterpillar *Trichoplusia ni* were reduced on most microbe-inoculated plants compared with the control, regardless of which feedback species was tested. A combination of 454 pyrosequencing of the soil community and GC-MS to quantify the leaf metabolome further demonstrated that these microbe-induced changes were mechanistically linked to foliar amino acid content. Overall, this approach is similar to those described earlier in Fig. 14.1, but offers several advantages, namely, isolating the microbial mechanism while experimentally accounting for nutritional or allelopathic effects. The technique could be further refined by using a series of nested sieves to assess which of several broad microbial groups are responsible for eliciting effects on insects, as employed in recent studies testing the role of soil biota in plant health (Wagg et al. 2014; Bender and van der Heijden 2015).

#### 14.4 Mechanisms of Plant–Soil Feedbacks on Plants and Insects

Feedbacks can be caused by plant-mediated effects on multiple aspects of the soil environment, including the biotic community, nutrient availability, and allelochemical residues. Numerous phytochemicals, for example, have been identified that are released by roots into the rhizosphere (Bais et al. 2004), affecting the growth or physiology of other plants (Hierro and Callaway 2003; Glinwood et al. 2011). In addition to the high amount of organic carbon released into the rhizosphere, secondary metabolites are exuded such as phenolics, glucosinolates, and even phytohormones (van Dam and Bouwmeester 2016). Secondary metabolites, in particular, are considered the most important compounds involved in chemical communication between plants and soil organisms (van Dam and Bouwmeester 2016). Root exudates

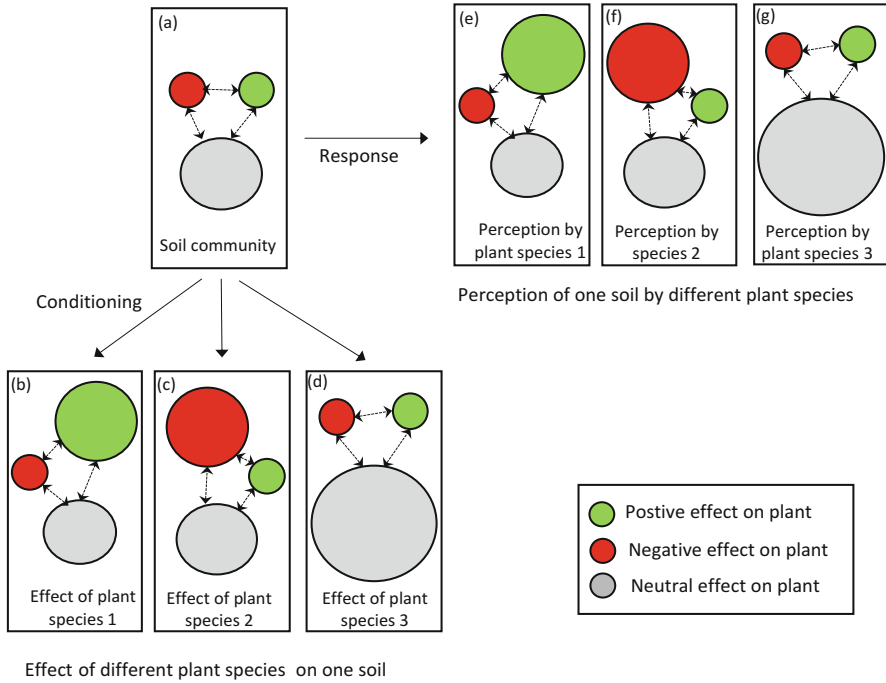


have been studied for decades because of their allelopathic effects on other plants. And, whereas most of these compounds inhibit other plants as a means to avoid competition, some compounds stimulate germination or growth of certain plants (Inderjit et al. 2011).

A major challenge in allelopathy is to disentangle the contribution of direct and indirect effects in plant–plant interactions (Cipollini et al. 2012; Zeng 2014). Root exudates are key elements at shaping the rhizosphere microbiome, and many plant-secreted chemicals are rapidly metabolized by soil microbes. Compounds such as malic acid and benzoxazinoids enhance or recruit beneficial soil microbes into the rhizosphere (Rudrappa et al. 2008; Neal et al. 2012). Similarly, strigolactones are a recently discovered group of phytohormones that stimulate the germination of parasitic plants, but at the same time elicit mycorrhizal colonization (Bouwmeester et al. 2007), showing how plants can be directly and indirectly affected by root exudates from a different plant. In the context of plant–soil feedbacks, exudates have recently been shown to be a mechanism underlying plant–plant interactions through microbial changes (Li et al. 2016a).

While allelopathy is mostly studied in the context of plant–plant competition, the effects could also cascade to impact insects aboveground. For example, barley plants exposed to root exudates of the weed grass *Elytrigia repens* became less acceptable for the aphid *Rhopalosiphum padi*, and this could be reproduced by applying a mixture of four chemicals previously identified in the root exudates from the weed (Glinwood et al. 2003). Similarly, tobacco roots exude high amounts of nicotine into the soil that later accumulate in rice leaf tissue aboveground, potentially reducing insect herbivory (Zhang et al. 2015). If true, this would represent a novel mechanism by which a plant can hijack the defensive metabolites of an unrelated plant via the soil. Altering the levels of soil minerals involved in leaf defense by one plant, which influences uptake in another plant, is another mechanism by which plants can interact via soil feedbacks. Silicon, the most abundant mineral in the soil, can prime plants for enhanced aboveground resistance to insect herbivores mediated by jasmonic acid (Ye et al. 2013). It is yet unknown whether this mechanism operates in plant–soil feedbacks but it warrants attention, i.e., silicon levels change after the conditioning phase to affect subsequent plant–insect interactions.

Despite the fact that allelopathic interactions and nutritional changes are recognized as potentially important drivers of plant–soil feedbacks, the vast majority of published work tends to focus on effects mediated by soil biota. Thus, we focus the discussion below largely on the biotic community. While we primarily emphasize soil microbes, invertebrates can also be important and may be underappreciated in feedbacks. It is well documented that belowground insect herbivores and detritivores affect aboveground insects up to the fourth trophic level (Soler et al. 2005, 2012; Rasmann and Turlings 2007; Wurst 2013). Another possible invertebrate mechanism affecting foliar herbivory is feedbacks influencing soil-dwelling predators that prey on aboveground herbivores, either by moving to the aerial tissues or preying on developmental stages that occur in the soil (Muñoz-Cárdenas et al. 2017). These hypothetical mechanisms are not yet covered in the literature on plant–soil feedbacks.



**Fig. 14.2** Conceptual view of how plants can differ in how they condition a standard soil community (a) and how they respond or perceive this standard soil community. The soil microbial community can have positive (green circles), negative (red circles), or neutral (grey circles) effects on a plant. The size of the circle indicates the importance in the soil. Plant species 1 promotes microbes that have a positive effect on plant growth (b) such as, e.g., plant-growth promoting rhizobacteria or mycorrhizae, plant species 2 promotes plant microbes with negative effects such as pathogens (c), and plant species 3 stimulates microbes that do not influence plant growth (d). Plant species also differ in how they perceive a single soil. In the example, plant species 1 overall perceives a soil as “positive” (e), plant species 2 perceives the same soil as “negative” (f) while the soil is perceived as “neutral” by plant species 3 (g). The groups of soil microbes that have positive, negative, or neutral effects also interact with each other in the soil food web, indicated by the dashed arrows

#### 14.4.1 How Plants Modify the Soil Biotic Environment

Plants influence the soil biotic community in a species-specific manner, and the responses of a plant to changes in the composition or abundance of soil biota can also differ greatly depending on the plant species being investigated (Fig. 14.2). This bidirectional dependency leads to highly species-specific plant–soil feedbacks. These results are usually attributed to the build-up of specialized soil pathogens; however, the vast majority of plant–soil feedback studies only report the effects of one plant on the growth of another without reporting the mechanisms involved. In most instances, the specific soil organisms or groups of soil organisms responsible for causing these effects are totally unknown. While many studies point at the

important effects of soil pathogens in plant–soil feedbacks, the soil biotic community consists of a wide array of microorganisms. These microorganisms can negatively influence plant performance, such as pathogens, but others have positive effects (e.g., plant growth promoting rhizobacteria, nitrogen-fixing rhizobia, mycorrhizal fungi). It is also important to realize that the abundance of the majority of soil microbes do not appear to influence plant growth directly. Hence, the soil consists of a consortium of microbes that have positive, negative, and neutral effects and the net effects of all these interactions determine the soil feedback effect (Fig. 14.2).

Plants are a major driver at determining the soil and rhizosphere microbiome (Fig. 14.2). Interestingly, this is not only at the species level, which is the focus of plant–soil feedback studies, but even genotypes/cultivars of the same species or plants at varying developmental stages can mold unique microbiomes (Bulgarelli et al. 2013; Peiffer et al. 2013; Chaparro et al. 2014; Li et al. 2016b). For example, natural accessions of *Arabidopsis thaliana* have completely different plant–soil feedbacks, with some positive, some negative, and others neutral (Bukowski and Petermann 2014).

#### ***14.4.2 How Plants and Insects Respond to Microbial Changes in the Soil***

Recent evidence suggests that plants initially perceive mutualistic microbes as potential invaders and trigger an immune response (Zamioudis and Pieterse 2012). Later, a dialogue between plant and microbe leads to mutualistic interactions and to changes in plant physiology. At higher trophic levels, two main mechanisms are thought to be responsible for the effects of soil microbes on herbivores. On one hand, beneficial soil microbes often improve plant performance, by means of growth or nutritional quality, which, in turn, leads to improved herbivore performance. On the other hand, certain soil microbes induce resistance in systemic tissues against pathogens and insects (Zehnder et al. 1997; Pangesti et al. 2014; Pieterse et al. 2014). The balance of these opposing forces—plant growth promotion and induced systemic resistance—determines the final effect of soil microbes on insect herbivores and is probably the main determinant of variable outcomes observed for microbe–plant–insect relationships. It is important to note that soils with an identical community can be perceived entirely different by two plants (i.e., positive by one species and negative by the other one), even if these two plants are phylogenetically closely related (Fig. 14.2). This explains why such a broad range of plant–soil feedback effects are typically reported, even when the origin of soil is the same.

Induced systemic resistance is mainly studied in the context of microbial pathogens, but it is also activated in response to herbivory. Some of the characteristics of induced systemic resistance, compared with other types of induced resistance, are: (1) it is triggered by colonization with nonpathogenic microbes; (2) it involves priming of plant defense; (3) it is regulated by the plant immune system, mostly

through the signaling pathways controlled by the hormones jasmonic acid, salicylic acid, and ethylene (Soler et al. 2013; Martinez-Medina et al. 2016). The priming concept implies that in the absence of an attacker, no major defensive changes occur in the plant, but upon attack the plant responds faster and/or stronger than it otherwise would. This renders the plant more resistant when colonized by appropriate rhizosphere microbes. Independent of priming, however, soil microbes also directly enhance the levels of defensive metabolites with negative consequences for herbivores and pathogens (van de Mortel et al. 2012; Sanchez-Bel et al. 2016). In either case, the effect that microbes have on insects depends on which pathway each group triggers. Because hormones such as JA and SA can display negative cross-talk, microbes could trigger induced systemic susceptibility when SA-inducing microbes co-occur with JA-inducing insects, or vice versa (Soler et al. 2013).

Another mechanism includes the direct effects of endophytic microbes on insects aboveground. During the germination and seedling stage, plants can acquire microbes from the soil that act as foliar endophytes. Some of these leaf endophytes, such as those from certain grasses, produce alkaloids that are toxic for the herbivores (although these are frequently seed-transmitted). Recent studies have shown that several entomopathogenic microbes can also have an endophytic stage (Ownley et al. 2010). Fungi such as *Metarrhizium* and *Beauveria* are common in soils and can colonize plants and promote growth (Jaber and Enkerli 2016).

Mycorrhizal fungi have perhaps been the dominant microbial group investigated for interactions involving insects (Gehring and Bennett 2009; Koricheva et al. 2009; Pineda et al. 2010). However, recent work has shown that soil microbe–plant–aboveground insect interactions also occur in non-mycorrhizal plants. An example is crucifers that do not form symbioses with mycorrhizal fungi. In this system, plant growth promoting rhizobacteria induce analogous effects, with the outcome potentially being determined by insect diet breadth. Generalist caterpillars such as *Mamestra brassicae* and *Spodoptera exigua* are negatively affected by *Pseudomonas* bacteria, but specialists such as *Pieris brassicae* and *P. rapae* are unaffected, and aphids such as *Myzus persicae* and *Brevicoryne brassicae* are positively and not affected, respectively (van Oosten et al. 2008; Pineda et al. 2012; Pangesti et al. 2014).

The above-mentioned studies were carried out using a single bacterial strain of *Pseudomonas*. However, several studies have argued that microbial complexity matters in microbe–plant–insect interactions and that the effects on plants, herbivores and natural enemies vary depending on the combination of microbial strains present (Gange et al. 2003, 2005). Although most studies show that combinations have detrimental effects for plants in terms of herbivory compared to single strain inoculations (Gadhavé et al. 2016), the opposite effect is also sometimes the case (Saravanakumar et al. 2008). Unfortunately, many isolated microbial strains that seem promising in laboratory experiments fail in the field even when applied as mixtures, probably due to competition with the established soil microbiome (Gadhavé et al. 2016; Raaijmakers and Mazzola 2016). In this context, it is important to realize that in real soils that encompass a wide array of microbes, plants are exposed simultaneously to positive and negative microbe interactions (Fig. 14.2) that can all induce plant defense and growth responses.

## 14.5 Opportunities and Challenges for Manipulating Plant–Soil Feedbacks in Agriculture

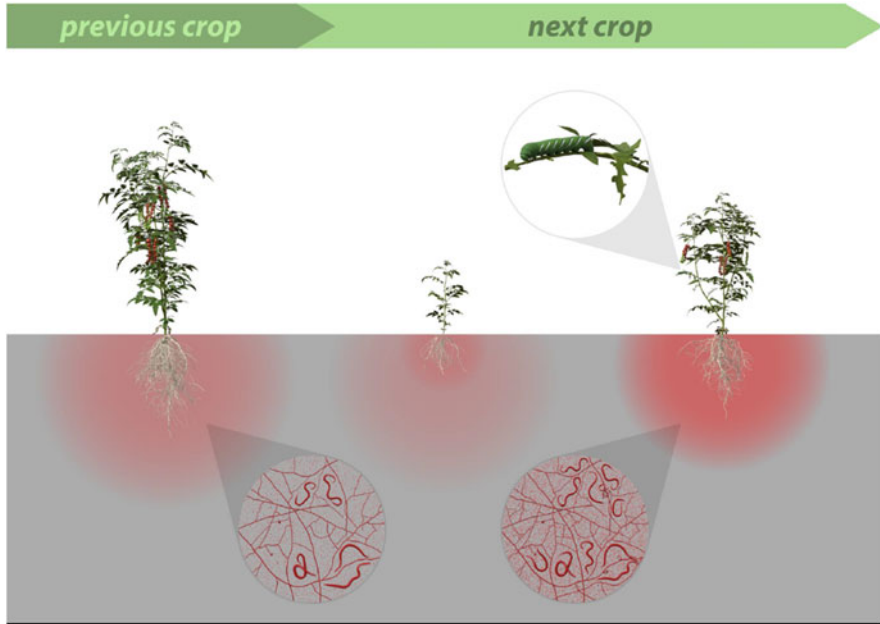
The emergence of microbes as beneficial partners in crop production is apparent as many large companies, even those historically focused on pesticides, now maintain microbial development groups. Some consider this the final frontier as plant breeding and synthetic fertilizers appear close to maximizing their impacts on yield (Mayer 2014). Early microbial products include inocula, mostly focused on a small number of strains and genera of fungi (e.g., *Trichoderma*) and bacteria (e.g., *Bacillus*) as a soil amendment. Only a fraction of soil microbes can be cultured, however, and many of those that can be isolated and reapplied elsewhere do not persist in their new environment. Thus, the microbial commercialization pipeline creates an enormous taxonomic bottleneck with the vast majority of microbes bypassed due to methodological constraints. In addition, a prevailing school of thought in the scientific community maintains that the reductionist approach taken by microbial strain isolation will ultimately fail because the whole is the greater than the sum of its parts (Vandenkoornhuysen et al. 2015; Raaijmakers and Mazzola 2016). In other words, microbes are best studied as whole microbiomes where emergent properties among thousands of taxa clustered by interaction networks are responsible for observed benefits to plant health (Berendsen et al. 2012; Mendes et al. 2013; Philippot et al. 2013; van der Heijden and Hartmann 2016). While the reductionist versus holistic debate is far from resolved in plant health research, interestingly, a parallel debate is occurring in human health studies where probiotic supplements, once touted as a cure for numerous ailments, are being replaced by community-level fecal transplants (Borody and Khoruts 2012). Methodological advances in next generation sequencing platforms continually allow scientists to provide increasing taxonomic resolution on the microbiome. Even if this increased knowledge of microbial community structure and composition cannot result in the isolation of specific microbial strains for inoculation in new soils, these improved analyses will at the very least point to taxa that should be targeted in microbiome manipulations. We now know, for example, that even rare microbes impact foliar insect herbivory (Hol et al. 2010). These rare species could be favored or discouraged by changing any number of agricultural management practices.

The question then becomes how to steer microbial communities in agricultural soils to benefit crop growth, yield, and/or protection against pests (see Pineda et al. 2017). This bypasses the aforementioned problems associated with maintaining single-strain cultures and persistence in foreign soils, but introduces a new set of unique challenges. For instance, manipulation of complete microbiomes is likely to result in variable outcomes and it is unclear how to consistently mold complex communities in the field. This is not for lack of thought. A number of recent reviews discuss ways to harness agricultural microbiomes for crop production (Bakker et al. 2012; Lakshmanan et al. 2014; Barea 2015; Schlaeppi and Bulgarelli 2015; Bender et al. 2016; Dessaux et al. 2016; Busby et al. 2017; Pineda et al. 2017). Although the impacts of specific agricultural practices on soil life are well described, these

practices tend to be coarse tools that either enhance (e.g., compost amendments) or disrupt (e.g., tillage) soil biota. Similarly, differences in soil properties between organic versus conventional cropping systems are well characterized (Drinkwater et al. 1995; Williams et al. 2014; van der Heijden and Hartmann 2016). Notably, organic growers have long claimed that their crops are more resistant to insect pests due to enhanced microbial activity in the soil (although experimental evidence to support this anecdotal claim remains elusive); yet, aside from building organic matter, harnessing this effect has not been feasible.

We argue that the conceptual framework provided by plant–soil feedbacks provides a novel means to shape the phytobiome (*sensu* Leach et al. 2017) to enhance crop performance and protection. Plant–soil feedbacks differ from existing soil engineering approaches in a few key ways. Perhaps most importantly, their impact is species-specific, i.e., each plant conditions the soil to create a unique microbiome compared with that of other species. While some of the core concepts of plant–soil feedbacks are inherently woven into the fabric of agricultural management strategies such as crop rotation, surprisingly, the term is almost never used in applied studies (but see Hol et al. 2013; Huang et al. 2013; Dias et al. 2015; Miller and Menalled 2015). Further, the two ideas—i.e., plant–soil feedback versus crop rotation or diversity, in general—are not the same. Most consider increasing plant diversity, from monoculture to polyculture, as beneficial for sustainable agriculture (Ratnadass et al. 2012); however, the rationale is largely based on disrupting life cycles for host-specific pests and pathogens (Borneman and Becker 2007). Under this scenario, incorporating virtually any non-self plant will suffice. Plant–soil feedback similarly recognizes that “self” or “home” soil generally has detrimental impacts on focal plants, but also acknowledges that heterospecific plants usually have vastly different legacy effects (van der Putten et al. 2013). This subtle, but significant, shift in perspective has important consequences for management. Polycultures are not simply about breaking disease cycles; ideally, they are engineered to identify and exploit synergistic plant pairings. We suspect that most farmers, as well as agricultural scientists, are aware that rotations are desirable because single species cultivation leads to disease build-up over time, but far fewer appreciate that the identity of the preceding crop or non-crop plant matters.

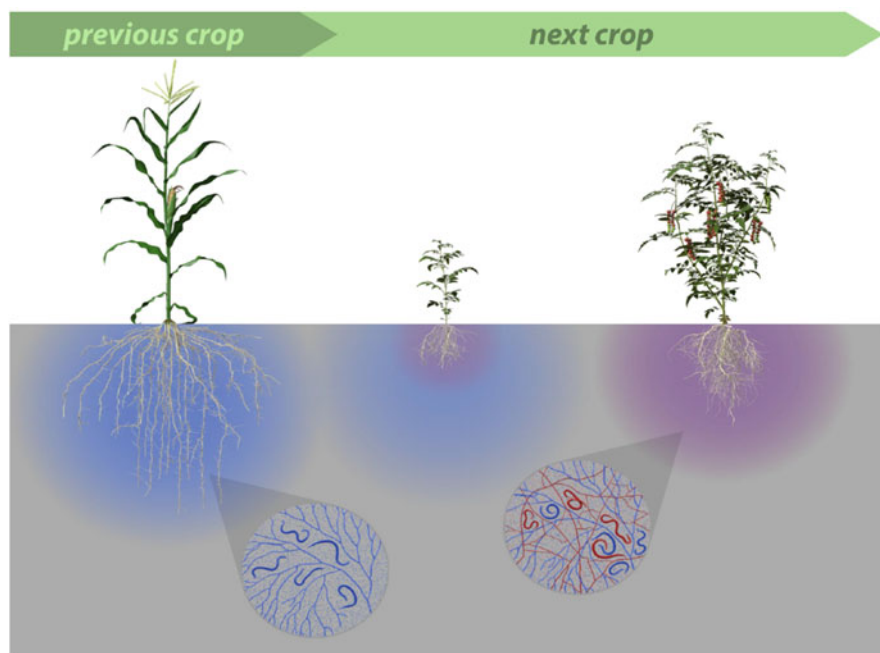
An agricultural plant–soil feedback perspective is unique for a few additional reasons. First, the mechanism capitalizes on the varied benefits from a diverse microbiome, including beneficial associations, rather than merely focusing on the suppression of one or a few phytopathogens (compare Figs. 14.3 and 14.4). Second, the approach explicitly accounts for microbe–crop–insect interactions that combat aboveground pests via induced systemic resistance. Crop rotations can also reduce insect pest populations but through an entirely different route that is analogous to pathogen suppression. The corn rootworm (*Diabrotica virgifera*), for example, is controlled by rotating corn and soybean across years. This rotation is effective because soybean is a non-host for rootworms and thus disrupts their life cycle (Vidal et al. 2005), not because soybean creates a more desirable microbiome for subsequent corn plantings.



**Fig. 14.3** Consequences of *conspecific* plant–soil feedback and microbial mechanisms responsible for the effect. Tomato cultivates host-specific pathogens that become increasingly prevalent—indicated by gradually darker shade of red halo surrounding tomato roots and soil inset showing growth of nematodes, fungal hyphae, and bacteria—when a second tomato plant is preceded by tomato in the same soil over time. Note that the second tomato plant (on the right) attains a smaller final size compared to the initial tomato plant (on the left) and has consequences for foliar-feeding insects such as the hornworm caterpillar, *Manduca sexta*, shown in the aboveground inset. Illustration created by Thomas Degen

Last, it is important to note that plant–soil feedbacks fit well in the context of existing agricultural management schemes. Spatial influences can occur through intercropping whereby one crop shapes the soil for a neighboring crop (Li et al. 2007; Brooker et al. 2015; Li et al. 2016a). This obviously necessitates close proximity as would occur when alternating rows host a different crop. However, plant–soil feedbacks are mostly studied in a temporal sequence with the two plants separated over time in the same location (Brinkman et al. 2010). This is also most relevant to modern crop management practices. While intercropping is relatively uncommon, at least in large-scale industrial agriculture used for most global food production, sequences such as rotations and cover crops are widely employed, even in high intensity systems. Also, it can be more complicated to isolate the soil mechanism at play in intercropping because of the confounding influence that leaf volatiles have on aboveground insect host-plant finding (Glinwood et al. 2011; Kos et al. 2015c). As a result, we focus our discussion and examples below on temporal relationships in agricultural fields.





**Fig. 14.4** Consequences of *heterospecific* plant–soil feedback and microbial mechanisms responsible for the effect. In this case, corn cultivates host-specific pathogens, indicated by the blue halo surrounding corn roots and soil inset showing nematodes, fungal hyphae, and bacteria. However, when corn is replaced over time by tomato, which cultivates a unique species-specific microbial assemblage indicated by the red halo in Fig. 14.3, the resulting “average” blue and red communities create a purple halo with a more diverse microbial inset and overall larger tomato plant compared with the conspecific feedback depicted in Fig. 14.3. Illustration created by Thomas Degen

### 14.5.1 Cover Crops as Plant–Soil Feedback Drivers

Cover crops are noncash crops used to manage soils—e.g., erosion, nutrients, organic matter—and pests such as weeds and soil-borne pathogens or nematodes (Schipanski et al. 2014; Wittwer et al. 2017). In temperate annual systems, covers are often fall-seeded after the summer crop is harvested and then put on biomass through the fall, after which the plant is either winter-killed or maintained through the subsequent spring. Thus, cover crops can be thought of as an “extra” non-crop species sandwiched between a single crop cycle. In the Midwestern USA, which has among the most intense agricultural systems in the world, the popularity of cover crops is increasing (Singer et al. 2007; Dunn et al. 2016), as is the case for other regions in the USA and beyond. Cover crops are a particularly interesting target for plant–soil feedbacks because of the larger variety of species available compared with rotations that are limited to economically viable crops.



Several legumes are popular covers such as vetch (*Vicia* sp.) and clover (*Trifolium* sp.) that are notable for adding nutrients to the soil as a green manure, which can reduce the nitrogen inputs needed for subsequent crops (Ebelhar et al. 1984). Insect pests respond differently to crops treated with organic versus synthetic fertilizers (Eigenbrode and Pimentel 1988; Altieri and Nicholls 2003; Staley et al. 2010). Therefore, we anticipate a strong nutritional legacy of a leguminous cover on crop–insect relationships by simply shifting the form of nitrogen metabolized by the later occurring plant. Yet, to our knowledge, this hypothetical scenario has not been experimentally demonstrated, despite the likelihood from what we know of pest responses to different fertilizer types.

Covers also generate allelopathic interactions that have both direct consequences for soil microbes and indirect effects on foliar insects via the crop (Farooq et al. 2011; Huang et al. 2013). Mustards (*Brassica* sp.), for example, are common cover crops that release isothiocyanates with antimicrobial properties into the soil. Although this is helpful when used to suppress plant-pathogenic nematodes (Hooks et al. 2010), it may also disrupt beneficial rhizosphere associations. Indian mustard (*Brassica juncea*) planted as a cover reduced mycorrhizal availability for corn plants that followed (Njeru et al. 2014). Similarly, *B. juncea* acts as a bio-fumigant for entomopathogenic nematodes, interfering with biocontrol of insect crop pests (Ramirez et al. 2009). These same covers simultaneously shift the community composition of free-living nematodes involved in decomposition and food web processes (Gruvera et al. 2010).

Another ubiquitous cover crop, rye (*Secale cereale*), dramatically reduced the abundance of the invasive soybean aphid (*Aphis glycines*), a major soybean pest in the Midwestern USA (Koch et al. 2012, 2015). This example is especially interesting because the pattern repeatedly occurred on large-scale commercial fields. Further, the authors sampled the natural enemy community to determine whether the pattern could be explained by higher predator density, which can occur with cover crops due to increased structural complexity and refuge (Blubaugh et al. 2016). Because there were no differences in any of the predator guilds, they can exclude this potential mechanism and concluded that: “Interactions between soybean and rye may affect host plant quality and deserve further investigation as potential mechanisms driving differences in aphid populations”. Rye is known to exude benzoxazinoids from their roots (Schulz et al. 2013), and this may be a mediating factor.

A key consideration of whether and how covers impact crops and their insect pests is the manner in which it is managed, which varies greatly. Sometimes crops are directly planted into living covers, while other times the cover is killed first. If it is killed, this can be accomplished in a few ways, namely with either herbicides or tillage. This decision has a major bearing on microbial life due to the disruptive capacity of tillage on the soil ecosystem. The residues of dead cover crops can also be left to decompose on the soil surface or it can be incorporated into the soil matrix, resulting in litter-mediated feedbacks. This not only affects microbial activity, but also the abundance of decomposing arthropods such as Collembola that serve as prey for spiders and other generalist predators that forage widely between the above- and below-ground systems (Miyashita et al. 2003; Birkhofer et al. 2008; Muñoz-

Cárdenas et al. 2017). These real management decisions undoubtedly mediate the mechanism, magnitude, and direction of plant–soil feedbacks of cover crops on later following cash crops, but in almost all cases these have not been directly quantified, especially as they relate to pest population dynamics.

### ***14.5.2 Crop Rotations as Plant–Soil Feedback Drivers***

Crop rotations are similar to cover crops, except that the feedback has a longer time lag with the soil legacy extending nearly one full year from the fall to the following spring. While crop residues can remain from the previous year’s planting, particularly in no-till or reduced till systems, this is less common than with cover crops. Thus, the mechanisms are likely different in rotations.

Because agricultural rotations have been employed for centuries to avoid “soil sickness” (Huang et al. 2013; van der Putten et al. 2013), it is frequently assumed that the feedback of one crop on the next is well documented. Shockingly, this is not the case. As outlined in a comprehensive review by Dias et al. (2015), upon surveying 149 publications on crop rotations they conclude: “after carefully reviewing all the papers obtained through our search we could not find a single one containing science-based criteria for crop rotations. . .there appears to be no consistent scientific basis to justify the use of a particular crop rotation over another.” This evidence seems to support the notion that crop rotations are decided more on nonscientific criteria such as social or economic factors.

The only “rule” that may be guided by plant–soil feedbacks is that growers are typically advised to avoid successive plantings with two crops in the same family. For instance, if you planted cucumbers in a given field, you would avoid planting cucumber again, or a close relative (i.e., any other crop in the Cucurbitaceae such as watermelon or pumpkin), for several years. In the interim, any non-cucurbitaceous crop is acceptable. Thus, there is an implicit phylogenetic underpinning to the lone crop rotation guideline, even though there is little scientific evidence to support this rule of thumb. As noted earlier, phylogeny is often a poor predictor of plant–soil feedbacks (Mehrabi and Tuck 2015). This was also true when evaluated in the only known test using an actual crop rotation (Miller and Menalled 2015), and our own work in tomato using a diversified vegetable rotation supports this assertion (Ingerslew and Kaplan 2018). Making the matter more complicated, crop cultivar choice can also affect the outcome of these interactions (Li et al. 2016b). This is not to say that crop rotational diversity does not matter, but rather that the type of diversity needed is unclear at this point. Indeed, diversity among rotation crops, compared to single-species cultivation, is functionally linked to microbial diversity and positively affects belowground ecosystem processes (Tiemann et al. 2015).

Despite the fact that plant–soil feedbacks in rotations are poorly studied and the one rule for their management appears to lack a strong scientific foundation, studies have clearly shown that crop identity shapes microbiomes (Garbeva et al. 2008; Navarro-Noya et al. 2013; Jiang et al. 2016). Moreover, these shifts have species-specific consequences for crops that follow (Yang et al. 2013). It is surprising that so

little is known about how rotations affect insects, aside from disrupting life cycles (e.g., Gallo and Pekár 2001; Chilcutt and Matocha 2007; but see Lundgren et al. 2017). Future studies should try to document the functional links between rotation identity, soil microbiome composition, and foliar insect pest pressure. A good model can be seen in the only study, to our knowledge, that explicitly makes these connections, provided by Schrama et al. (2016). This work examines the soil legacy effect of four bioenergy crops—maize, willow, *Miscanthus × giganteus*, switchgrass—on wheat as a follow-up food crop. In addition to having major consequences for the soil microbial community, species-specific legacy effects were observed for wheat growth and susceptibility to insects. Specifically, wheat grown in willow soil had a higher biomass, but also favored the aphid *Rhopalosiphum padi*, whose population growth was nearly twice as high on willow soil compared with the other bioenergy crops. It appears that the soil-mediated nutritional benefits passed on from willow to wheat extend aboveground to wheat consumers, although this mechanism needs to be verified by measuring phloem chemistry.

### 14.5.3 Future Opportunities and Implementation Challenges

Beyond the standard agricultural approaches such as cover crops and rotations, plant–soil feedbacks could be exploited in other new ways that have yet to be demonstrated. For example, in our own work in Chrysanthemum, growers cultivate flowers in monoculture with steam sterilization that severely disrupts soil microbiomes, leading to the spread of r-selected pathogens (van der Voort et al. 2016). Consequently, we have experimented with using the legacy from a wide variety of wild plant species to condition the soil for optimizing flower growth and resistance to foliar insect pests (Bezemer et al., unpublished data). Even using as little as 10% of feedback soil as an inoculum can transfer these effects across species and potentially much less than this amount could be used (0.1–10% of total soil volume according to Berendsen et al. 2012). However, this creates an interesting dilemma: how to best transplant microbiomes from one plant to another. A recent large-scale field study showed over a 6-year period how adding soil inoculum for ecosystem restoration results in different soil communities but also target plant communities, ranging from grassland to heathland vegetation depending on the inoculum source (Wubs et al. 2016). Should microbiomes be transferred in a soil matrix or can a complex microbial consortium be consolidated in liquid for direct targeted injection into the rhizosphere of focal crops (as in Badri et al. 2013)? How long can microbiomes be stored in these matrices while retaining their integrity? These, among other, questions are yet to be answered, but warrant attention.

Rather than moving microbiomes from other locations, another approach could be to select or engineer plants with optimized plant–soil feedbacks (Gopal and Gupta 2016). This could work especially well for high intensity systems where rotation or other forms of diversity are difficult or impossible to introduce. While plant–soil feedbacks are usually studied at an interspecific level, different plant genotypes

within a species vary widely in feedbacks at an intraspecific level (Bukowski and Petermann 2014; Li et al. 2016b). Perhaps crops could be selected to behave more like invasive plants (Klironomos 2002), with neutral or positive plant–soil feedbacks. This could be accomplished via traditional breeding, simple cultivar selection, or grafting onto rootstock with desirable feedback properties. An important consideration in all of these tactics is the ability of crops to steer microbiomes from the outset. Clearly, wild plants are selected to recruit an assemblage of beneficial rhizosphere microbes for their survival in nature (e.g., Santhanam et al. 2015), but accumulating evidence shows that domestication may have resulted in crops with impaired rhizosphere associations (Pérez-Jaramillo et al. 2016). This domestication syndrome should be considered, ideally by comparing crops with their progenitors to evaluate potential losses in these traits and exploring ways to reintroduce them using wild germplasm.

An overriding issue that ecologists are rarely forced to confront, but farmers, agronomists, and industry scientists are, is consistency. The unfortunate reality is that microbiome composition is highly variable over small spatial scales and turns over rapidly even in the same soil over short periods of time. Thus, is it reasonable to expect the same manipulations to work equally well in different fields that vary, for example, in soil type (e.g., clay vs. sandy soils) or across years where precipitation patterns fluctuate from wet to dry? While the degree of consistency is debatable (i.e., is achieving a particular outcome 80% of the time sufficient?), *some* amount of consistency is absolutely required for these to be reliable management tools and this issue must be addressed by applied ecologists. The basis for these manipulations are already implemented in crop rotation guidelines; however, employing a plant–soil feedback framework in agriculture will help account for the wider diversity of aboveground benefits afforded to plants by their belowground symbiotic partners.

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