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Microbial Root Mutualists Affect the Predators and Pathogens of Herbivores above Ground: Mechanisms, Magnitudes, and Missing Links

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Tri-trophic interactions among plants, herbivores, and natural enemies of herbivores are common in nature, and are crucial components of trophic cascades and the dynamics of community composition. Plant traits are key determinants of the interactions between herbivores and their natural enemies aboveground, which in turn are affected by soil organisms. Recent years have seen a surge in studies of the interactions between below- and aboveground biota, including descriptions of how microbial root mutualists influence plant traits and herbivore performance. However, concomitant effects on the natural enemies of herbivores remain relatively poorly understood. Here, we review the currently available literature to assess how and when mutualistic root microbes impose significant indirect effects on the performance of predators and pathogens of insect herbivores. We focus on how root microbes influence predator attraction, on-plant foraging efficiency, and the quality of prey tissues. We also consider the underappreciated effects of microbial root mutualists on the growth, transmission, and virulence of insect pathogens. We end by discussing missing links and important directions for future research.

Keywords: above- and below-ground interrelationships, tri-trophic interactions, soil ecology, disease dynamics, mycorrhizal fungi, soil biota, plant-herbivore interactions, microbial root mutualist

INTRODUCTION

Understanding the mechanisms that underlie species interactions remains a central theme in ecology. Tri-trophic interactions among primary producers, herbivores and natural enemies of herbivores (predators, parasitoids, and pathogens) are common in nature, and are crucial mediators of trophic cascades, which can subsequently determine community dynamics, biodiversity, and ecosystem productivity (Hunter and Price, 1992; Polis et al., 2000; Borer et al., 2005). Therefore, understanding the factors that affect tri-trophic interactions is not only important for ecological research, but also critical for agricultural applications and conservation activities (Agrawal, 2000; Hunter, 2016). For example, natural enemies of herbivores are used extensively as agents of biological control, and understanding the factors that affect their efficiency can potentially optimize pest management and crop yield (Symondson et al., 2002). Furthermore, human disruption of tri-trophic interactions can lead to substantial consequences for biodiversity management. In the southeastern United States for instance, over-harvesting of blue crabs, predators of plant-grazing snails, may result in extensive die-offs of plants in salt marshes, leading to substantial losses in biodiversity and primary production (Silliman and Bertness, 2002).

Plant traits, such as nutrient content, size, and secondary chemistry, are key determinants of the interactions between herbivores and their natural enemies (Price et al., 1980; Vet and Dicke, 1992; Cory and Hoover, 2006); these plant traits provide the mechanistic basis by which tri-trophic interactions occur. In turn, these same plant traits respond to the complex interactions that take place between plants and soil organisms belowground. Both root mutualists (e.g., rhizobia, mycorrhizal fungi, and detritivores) and root antagonists (e.g., herbivores, parasites) can strongly alter the fundamental plant traits that drive tri-trophic interactions above ground (Smith and Read, 2008; Chapin et al., 2011). As a consequence, recent work has begun to explore how belowground biota influence tri-trophic interactions aboveground through generating variation in plant traits (Hunter, 2016; Rasmann et al., 2017). Recent years have seen a surge in studies of the interactions between below- and aboveground biota, demonstrating that belowground organisms have major effects on aboveground ecological processes, including plant physical and chemical traits, plant performance, herbivore and pollinator performance, and their recruitment (Van der Putten et al., 2001; Wardle et al., 2004; Bezemer and van Dam, 2005; Schädler and Ballhorn, 2016). However, our understanding of the role of belowground interactions between plants and other organisms on aboveground tri-trophic interactions remains in its infancy (Rasmann et al., 2017). Most of the limited work to date has focused on microbial root mutualists, their impacts on plant traits, and how these traits generate tri-trophic interactions between plants, arthropod herbivores, and arthropod natural enemies. Here, we summarize this work, while adding in some recent studies of how the performance of the pathogens of herbivores responds to variation in plant traits introduced by microbial root mutualists. Our goals are (1) to summarize recent progress and identify the mechanisms by which belowground mutualists alter predation and pathogens pressure on herbivores aboveground; and (2) to point out missing links and important directions for future research. Under "mechanisms" we focus here on the plant traits that mediate the tri-trophic interactions. We also describe any associated changes that those plant traits engender in the behavior of herbivores or enemies that translate to modify herbivore mortality.

As we will show throughout the paper, this field is still in its infancy with a small number of published studies focusing on a handful of study systems. As a consequence, the mechanisms that we review here are by no means a complete accounting of the vast diversity and context-dependency of below-aboveground interactions. Rather, our main purpose is to demonstrate that belowground root mutualists can have major impacts on aboveground tri-trophic interactions through a variety of trait-based pathways, and that many exciting questions await future research.

FOCUS OF THE REVIEW

Our purpose here is not to review the myriad of ways in which microbial root mutualists influence plant traits and plant ecology. There are reviews, book chapters, and entire texts already available on these topics (Heath and Tiffin, 2007; Smith and Read, 2008; Hunter, 2016). Instead, we focus specifically on how root mutualists influence the tri-trophic interactions among plants, arthropod herbivores and their enemies (arthropod predators or parasitoids and agents of disease). Arthropod herbivores represent one of the largest and most diverse groups of metazoans on earth, and play essential roles in determining food web stability, community composition, diversity, and ecosystem functioning (Speight et al., 2008). Arthropod herbivores sustain a great diversity of enemies including predators, parasitoids and pathogens. At the same time, plants form associations with many organisms in the soil, from antagonistic organisms such as root herbivores and pathogens to mutualistic organisms including arbuscular mycorrhizal fungi (AMF), rhizobia, symbiotic bacteria, detritivores, and decomposers (Van der Putten et al., 2001; Wardle et al., 2004; Bezemer and van Dam, 2005; Pineda et al., 2013a; Schädler and Ballhorn, 2016). Here, we focus primarily on the beneficial microbes that associate with roots and summarize our current understanding of how they affect the impacts of predators and pathogens above ground. Again, the mechanistic basis underlying these tri-trophic interactions is generally the changes in plant traits mediated by plant associations with root microbes; we focus on the traits that dominate the literature on tri-trophic interactions, particularly primary and secondary metabolites and plant morphology. While we note briefly the simple but pervasive effects of mutualistic microbes on plant size and vigor, such effects have been reviewed recently (Rasmann et al., 2017) and are not a major focus here. Additionally, while belowground mutualists can affect the composition of enemy communities above ground (Schreck et al., 2013), we focus here on the performance and population dynamics of predators and pathogens because their links to chemical plant traits are much more firmly established. We first consider predators and parasitoids of arthropod herbivores, which belowground mutualists influence indirectly by changing the plant traits that determine long-distance plant attractiveness, on-plant foraging by enemies, and the nutritional quality of prey. Second, we consider how microbial root mutualists influence herbivore pathogens through their indirect effects on pathogen growth, transmission and virulence. We searched ISI Web of Science and Google Scholar using the keys words "belowground aboveground tri-trophic interactions" and their variants to find relevant publications. Subsequently, we read the literature cited by these papers to find and compile all other relevant studies. **Table 1** provides a full summary of existing studies and **Figure 1** provides three representative examples for a predator, parasitoid, and pathogen, respectively.

TABLE 1 | Published studies of the effects of belowground organisms on aboveground tri-trophic interactions.

Study	Type of belowground organism	Type of enemy	Response
PARASITOIDS AND PREDATORS: PREY LOCALIZATION			
Guerrieri et al., 2004	AMF	Parasitoid	(+) preference
Soler et al., 2007b	Root herbivore	Parasitoid	(–) avoidance
Hoffmann et al., 2011b	AMF	Predator	(+) preference
Schausberger et al., 2012	AMF	Predator	(+) preference
Battaglia et al., 2013	Non-AMF fungi	Parasitoid, Predator	(+) preference
Kruidhof et al., 2013	Root herbivore	Parasitoid	(–) avoidance in *C. glomerata;* (+) preference in *C. rubecula*
Pineda et al., 2013b	Rhizobia	Parasitoid	(–) avoidance
Godschalx et al., 2015	Rhizobia	Predator	(–) avoidance
Pangesti et al., 2015	Rhizobia	Parasitoid	(+) preference
PARASITOIDS AND PREDATORS: PREY QUALITY			
Masters et al., 2001	Root herbivore	Predator	(+) higher abundance
Gange et al., 2003	AMF	Parasitoid	(+, –, 0) on parasitism rate, depending on the fungal species
Bezemer et al., 2005	Soil microorganism and nematode	Parasitoid	(+) nematodes increase parasitoid survival, size and female ratio
Soler et al., 2005	Root herbivore	Parasitoid	(–) reduced size and increased development time
Hempel et al., 2009	AMF	Parasitoid	(+) increased parasitism rate and size, reduced development time
Megías and Müller, 2010	Detritivore and root herbivore	Parasitoid	(+) detritivores increased parasitism rate and abundance
Hoffmann et al., 2011c	AMF	Predator	(+) higher population growth rate
Johnson et al., 2011	Earthworm	Parasitoid	(+) higher abundance
Katayama et al., 2011	Rhizobia	Predator	(+) higher abundance and species richness
Wooley and Paine, 2011	AMF	Parasitoid	(+, 0) on abundance depending on AMF strain
Battaglia et al., 2013	Non-AMF fungi	Predator	(+) on development rate, (0) on birth rate
Moon et al., 2013	AMF	Parasitoid	(+, –) on percent parasitized depending on herbivore species
Kruidhof et al., 2013	Root herbivore	Parasitoid	(0) no effects on development time and adult weight
Pineda et al., 2013b	Rhizobia	Parasitoid	(–, 0) no effects on development time, survival or weight; negative effects on abundance
Schreck et al., 2013	AMF	Predator	(+) on predator density
Ueda et al., 2013	AMF	Predator	(+, –) on predator abundance depending on the sampling date
Pangesti et al., 2015	Rhizobia	Parasitoid	(0) on developmental time, survival, weight
PATHOGENS			
Tao et al., 2015	AMF	Pathogen	(+, –, 0) on parasite virulence and sporeload depending on plant species and AMF colonization level

(+), (–), and (0) signify positive, negative, and neutral effects of belowground organisms on traits of the enemies, respectively. AMF, arbuscular mycorrhizal fungi.

MUTUALISTIC MICROBES BELOW GROUND AFFECT PREDATORS AND PARASITOIDS OF HERBIVORES ABOVE GROUND

Here, we separate the interactions between herbivores and their parasitoids and predators into three stages: a prey localization stage, during which enemies actively forage for herbivores over long distances; an on-plant foraging stage, during which plant physical traits mediate enemy foraging efficiency; and an after-contact stage, when enemies consume and/or reproduce in herbivore tissues, the quality of which determines enemy performance. Critically, the mechanisms underlying all of these interactions are based on variable plant traits (morphology, chemistry, physiology), that are subject to modifications by microbial root mutualists. We encourage readers to explore a recent paper (Rasmann et al., 2017), which also considers how microbial traits (microbial volatiles) may influence tri-trophic interactions above ground, and (b) includes a review of indirect defenses below ground, which we do not consider here.

Prey Localization

Predators and parasitoids must locate their herbivorous prey before attacking those prey items. Prey location by invertebrate predators mainly occurs through visual and olfactory cues, which are strongly affected by plant morphology and chemical traits (the mechanisms). Plant size and architectural complexity are key determinants of foraging efficiencies of parasitoids, with increases in size and complexity reducing per capita foraging efficiency (Cloyd and Sadof, 2000; Gingras and Boivin, 2002), while increasing the diversity of alternative prey (Lawton, 1983; Fowler, 1985). Consequently, when oxeye daisies (*Leucanthemum vulgare*) grow larger through association with AMF, rates of parasitism of the leaf miner *Chromatomyia*

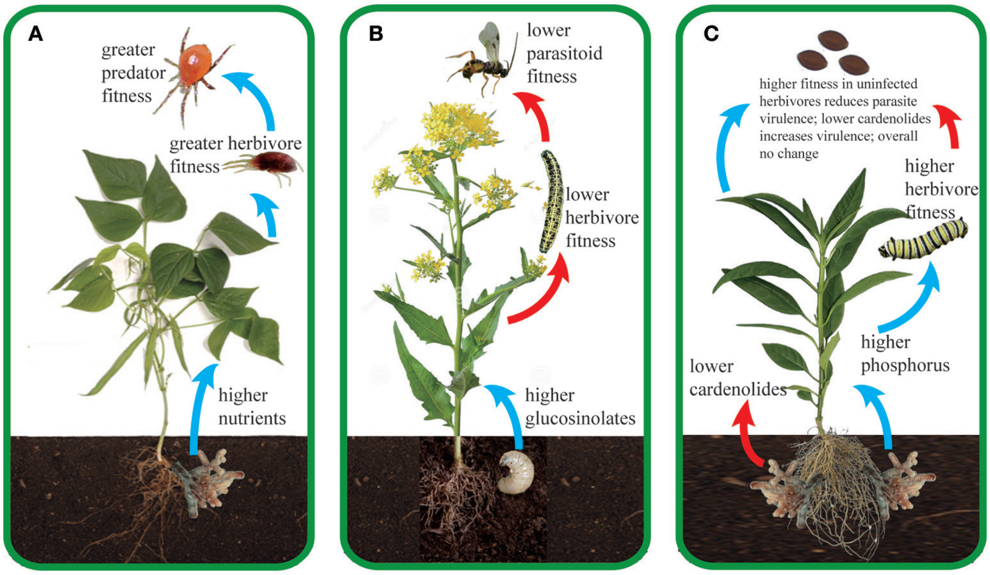

FIGURE 1 | Representative examples of how root mutualists **(A,C)** and root antagonists **(B)** can influence tri-trophic interactions aboveground. Blue and red arrows signify positive and negative effects on the next trophic level, respectively. **(A)** Associations with the arbuscular mycorrhizal fungus (AMF) *Glomus mosseae* can lead to higher macronutrient (phosphorus and potassium) content in bean plants (*Phaseolus vulgaris*), which subsequently results in greater oviposition rate, growth rate, and shorter doubling time of the herbivorous spider mite *Tetranychus urticae* (Hoffmann et al., 2009). Higher quantity and quality of *T. urticae* directly translate into higher fitness and population growth rate of the predatory mite *Phytoseiulus persimilis* (Hoffmann et al., 2011c). Female *P. persimilis* preferentially select eggs of *T. urticae* that are reared on AMF-associated bean plants due to their higher quality (Hoffmann et al., 2011b); additionally, they can “smell” AMF-associated plants because AMF increase the production of β-ocimene and β-caryophyllene in *T. urticae*-infested plants (Schausberger et al., 2012). Although AMF increase performance of the herbivore *T. urticae*, higher population growth of *P. persimilis* and higher plant tolerance compensate for the negative effects of the herbivores, leading to higher seed production in the bean plants (Hoffmann et al., 2011a). Additionally, *P. persimilis* increases root AMF colonization rates, which may create a positive feedback among AMF, plants and predators in this important agricultural system (Hoffmann et al., 2011a). **(B)** Infestation of black mustard (*Brassica nigra*) roots by cabbage fly larvae (*D. radicum*) increases sinigrin concentrations (a type of glucosinolate) in plant shoots, which negatively affects fitness of cabbage butterfly larvae (*P. brassicae*) and their parasitoid wasps *Cotesia glomerata* (Soler et al., 2005). As a result, both *P. brassicae* and *C. glomerata* have evolved to avoid plants with root herbivores (Soler et al., 2007a, 2010; Kruidhof et al., 2013), possibly through avoiding sulfur volatile compounds that are emitted by the plants after attack by the root herbivore (Soler et al., 2007a). Such avoidance behavior can increase foraging efficiency of *C. glomerata* on plants surrounded by root-infested plants, because the volatiles may provide a contrast within the background blends emitted by plants without root herbivory (Soler et al., 2007b). **(C)** AMF—milkweed *Asclepias* spp.—monarch butterfly *Danaus plexippus*—protozoan parasite *Ophryocystis elektroscirrha* For monarch butterflies (*Danaus plexippus*), milkweed (*Asclepias* spp.) secondary chemicals called cardenolides reduce growth of the protozoan parasite *Ophryocystis elektroscirrha* and increase the lifespan of infected butterflies (de Roode et al., 2008, 2011; Sternberg et al., 2012; Gowler et al., 2015). In both uninfected and infected butterflies, nutrients such as nitrogen and phosphorus positively affect monarch larval performance (Tao and Hunter, 2012; Tao et al., 2014, 2015). Since associations with AMF can significantly change cardenolide and nutrient concentrations across milkweed species (Vannette and Hunter, 2011; Vannette et al., 2013; Tao et al., 2015, 2016), they indirectly affect parasite virulence and monarch tolerance (Tao et al., 2015). For example, in *A. curassavica* (shown here), AMF increase foliar P concentrations while decreasing foliar cardenolide concentrations, yielding overall neutral effects on the lifespan of infected butterflies (Tao et al., 2015).

syngenesiae by the wasp *Diglyphus isaea* decline (Gange et al., 2003).

Plants recruit predators and parasitoids through indirect defense mechanisms, such as food rewards (e.g., extrafloral nectars), shelters (domatia), and volatile organic compounds (VOCs) (Dicke, 1999; Agrawal, 2000) that can attract predators and parasitoids over long distances. Because allocation to domatia and extra-floral nectaries depend on both nutrient status and plant size (Frederickson et al., 2012; Heil, 2015), microbial root mutualists are likely to influence the quality of such food and shelter rewards for predators and parasitoids (Heil et al., 2001; Radhika et al., 2008; Holland et al., 2009). Notably, microbial root mutualists receive sugar from their plant hosts, in exchange for mineral nutrients and water. The carbon costs associated with hosting microbial mutualists may explain why some plants reduce their rewards to enemies aboveground when associated with root microbes. For example, in *Vicia faba*, association with AMF reduces extrafloral nectaries, which may result in reduced protection by ants against herbivores (Laird and Addicott, 2007). Similarly, rhizobia reduce extrafloral nectar production by lima beans (*Phaseolus lunatus*), leading to fewer ants attracted to rhizobia associated plants (Godschalx et al., 2015). Here, the mechanistic basis underlying the tri-trophic interaction above ground appears to be a tradeoff in plant resource allocation between root mutualists and indirect defense rewards.

Compared to the other mechanisms described here, there is much more evidence in support of the hypothesis that microbial root mutualists alter the expression by plants of VOCs (Rasmann et al., 2017). For example, in sweet wormwood *Artemisia annua*, association with AMF increases emissions of the monoterpene limonene and artemisia ketone (Rapparini et al., 2008), which attract both herbivores and their natural enemies (Wei et al., 2008; Rodríguez et al., 2011). Similarly, the root fungal endophyte *Acremonium strictum* changes the terpene composition in volatiles of tomato *Lycopersicon esculentum* (Jallow et al., 2008). In *Plantago lanceolata*, AMF reduce herbivore-induced sesquiterpenes, chemicals that recruit parasitoids after herbivory (Fontana et al., 2009). In short, since the composition of volatile compounds is key to predator/parasitoid attraction, these mutualist-induced changes in VOC emission likely represent dominant mechanisms by which microbial root mutualists influence tri-trophic interactions aboveground.

We should note that belowground mutualists may affect the composition of plant VOCs aboveground through multiple mechanisms. First, mutualistic microbes may alter the production and emission of plant VOCs by modifying nutrient availability. For example, higher nutrient (nitrogen, phosphorus and potassium) concentrations in *Eucalyptus tereticornis* increase emission of the volatile terpene 1,8-cineole, which subsequently attracts more predators and parasitoids (Low et al., 2014). Similarly, supplementing *A. annua* with phosphorus (P) largely mimics the effects of AMF on VOC production (Rapparini et al., 2008).

In contrast, greater attraction of aphids to beans, *V. faba*, associated with AMF is not due to changes in P availability (Babikova et al., 2014). Rather, microbial mutualists may influence expression of the jasmonic acid (JA), salicylic acid (SA), cytokinin, and abscisic acid (ABA) pathways (Pineda et al., 2013a), all of which influence the production of VOCs (Ballhorn et al., 2013; Pineda et al., 2013b). For example, by interfering with the JA pathway in *Arabidopsis thaliana*, rhizobia change the induction of plant VOCs by the aphid *Myzus persicae*, thereby reducing attraction of the parasitoid wasp *Diaeretiella rapae* (Pineda et al., 2013b). Moreover, mycorrhizal mycelia often connect the roots of neighboring plants (Francis and Read, 1984), such that mycorrhizal fungi may transmit signals among plants and thereby affect enemy attraction by neighboring plants (Song et al., 2010). For example, bean plants (*V. faba*) detect aphid herbivory of their neighbors through mycorrhizal fungal connections and alter their own production of VOCs (specifically increasing methyl salicylate), so that parasitoids are more attracted to them compared to plants without belowground mycelial connections (Babikova et al., 2013).

While evidence is accumulating that microbial root mutualists play an important role in mediating the production of VOCs and subsequent enemy foraging behavior, their impact is system-specific. Sometimes the effects can be large; in the tomato *L. esculentum,* for instance, association with the AMF *Glomus mosseae* results in a two-fold increase in parasitoid attraction, even in the absence of herbivores (Guerrieri et al., 2004). In other circumstances, effects are harder to detect. For example, attraction of the predatory mite *Phytoseiulus persimilis* to bean plants (*Phaseolus vulgaris*) appears unaffected by association with AMF, at least during the first 3 days of spider mite (*Tetranychus urticae*) infestation (Schausberger et al., 2012). This variation in effect sizes may be due to differences in responses of plants to their root mutualists, and/or interspecific variation in responses of enemies to plant VOCs (Leitner et al., 2010; Kruidhof et al., 2013). We return to this challenge of variability in the section on Missing Links (below).

We emphasized above that changes to plant chemical and physical traits provide the mechanistic basis underlying the effects of microbial root mutualists on the enemies of herbivores above ground. Consequently, when microbial root mutualists change more than one physical or chemical trait simultaneously, predicting the net outcome for tri-trophic interactions can be a major challenge. For example, with regard to the oxeye daisy-leaf miner-parasitoid interaction described previously, association with AMF increases plant size, which reduces parasitism of the leaf miner by the parasitoid due to lower prey location efficiency (Gange et al., 2003). However, in bean plants (*P. vulgaris*), AMF increase the emission of VOCs that can attract enemies (Schausberger et al., 2012). Thus, if both of these processes were to operate in the same system, their relative strength would determine whether the net effect of AMF was an increase or a decrease in parasitism. At this time, there are almost no data describing effects of root mutualists on tri-trophic interactions under multiple changes in plant traits. As we note under Missing Links (below) future studies are urgently needed to help understand the species specificity of plant responses to belowground mutualists, and incorporate simultaneously their effects on multiple plant traits that mediate herbivore-enemy interactions.

On-Plant Foraging Efficiency

After a predator or parasitoid successfully locates a plant with prey, it needs to find its prey on the plant and attack it. This foraging process is also influenced strongly by physical and chemical plant traits that can be altered by microbial root mutualists. For instance, glandular trichomes, hairs with secretory cells, can directly intoxicate parasitoids (Kennedy, 2003) and/or impede enemy walking speed (Krips et al., 1999), resulting in lower foraging efficiency. However, for some specialist predators, sticky trichomes may trap insect cadavers, thereby attracting more predators (Krimmel and Pearse, 2013). Similarly, plant epicuticular waxes can decrease attachment of predatory insects and parasitoids to the plant surface and disrupt their feeding (Eigenbrode, 2004). Critically, belowground mutualists affect the expression of both glandular trichomes and epicuticular waxes (Goicoechea et al., 2004; Copetta et al., 2006), providing additional mechanistic pathways by which microbial root mutualists may influence tri-trophic interactions. Unfortunately, to our knowledge, no study has explored explicitly the links among root mutualists, plant trichomes/waxes, and the efficiency of enemy foraging aboveground. Again, such work is urgently needed.

Prey Quality

Microbial root mutualists alter the nutrient and toxin concentrations of herbivore tissues (Hunter, 2016), providing an additional mechanistic pathway by which root mutualists mediate tri-trophic interactions aboveground. Prey quality is important in determining the fitness of predators and parasitoids. Compared to herbivorous insects, predatory arthropods and parasitoids have higher body nitrogen (N) and P contents, so increases in plant nutrition can lead to greater performance of predators and parasitoids (Denno et al., 2002; Wurst and Jones, 2003; Maure et al., 2016). Therefore, by affecting plant nutritional status, root microbes belowground can indirectly affect predators and parasitoids aboveground. For example, in the presence of AMF, the predatory mite *P. persimilis* has a greater oviposition rate and shorter development time due to the higher quality of its prey, the two-spotted spider mite *Tetranychus urricae* (**Figure 1A**) (Hoffmann et al., 2011c). Additionally, plant nutrient status often affects herbivore size, which in turn influences predator and parasitoid performance (Hunter, 2016). When the aphid *Rhopalossiphum padi* feeds on plants infested with free-living and root-feeding soil nematodes, it grows significantly larger than when feeding on plants without soil nematodes, resulting in higher emergence success of its parasitoid *Aphidius colemani* (Bezemer et al., 2005).

Root associates may also alter the quality of prey for natural enemies by their impacts on plant secondary chemicals, which occur both passively in the hemolymph and midgut of herbivores, or may be sequestered in herbivore tissues (Nishida, 2002; Lampert et al., 2011). For example, plant glucosinolates occurring within herbivore prey negatively affect a wide range of parasitoids (Gols and Harvey, 2009). While we focus here on root microbial mutualists, we note that there is now abundant evidence of root-feeding herbivores influencing the chemistry of plant tissues above ground, with subsequent effects on herbivore and enemy performance (Hunter, 2016). For example, root-feeding cabbage fly larvae (*Delia radicum*) induce higher glucosinolate concentrations in *Brassica nigra*. In turn, higher glucosinolate concentrations lead to longer development time and smaller size of both cabbage butterfly caterpillars (*Pieris brassicae*) and their parasitoid wasps, *Cotesia glomerata* (**Figure 1B**) (Soler et al., 2005).

Importantly, plant secondary metabolites also affect herbivore immune defenses against predators and parasites (Smilanich et al., 2009; Lampert, 2012). High concentrations of plant secondary metabolites tend to reduce immune defenses, probably because of their negative effects on insect growth rate and reduced allocation to immune functions. For example, hydrolysable tannins in quaking aspen (*Populus tremuloides*) correlate negatively with immune defense in the autumnal moth *Epirrita autumnata* (Haviola et al., 2007), and high iridoid glycoside concentrations in *P. lanceolata* compromise immune responses in the common buckeye caterpillar *Junonia coenia* (Smilanich et al., 2009). Lower immune defense can lead to higher performance of parasitoids (Reudler et al., 2011; Kos et al., 2012). While microbial root mutualists affect the expression of these (and other) secondary chemicals (tannins, Beyeler and Heyser, 1997; iridoid glycosides, Bennett et al., 2009), to our knowledge, no study has directly explored effects of soil organisms on host insect immunity through changes in secondary chemistry.

SOIL ORGANISMS AFFECT PATHOGENS OF HERBIVORES

Many of the same mechanistic pathways (chemical and physical traits) by which microbial root mutualists impact the efficacy of predators and parasitoids may also affect the pathogens of herbivores. Herbivorous insects are host to a wide diversity of disease agents, including protozoans, bacteria, and viruses. As with parasitoids and predators, the performance of herbivore pathogens is affected by both plant nutritional and secondary chemicals, and therefore influenced by belowground root mutualists. However, the effects of increased concentrations of nutritional chemicals on pathogens are not as readily predicted as they are for other types of natural enemy. This is because increases in plant nutritional quality can result in increased resources for pathogens, but can also result in improved host immunity (Povey et al., 2009; Cotter et al., 2011). Therefore, when associations with soil mutualists result in higher plant nutrient concentrations, any subsequent increases in rates of pathogen replication may be counteracted by concomitant increases in host immunity.

With respect to secondary metabolites, multiple classes of chemicals inhibit insect pathogens (Cory and Hoover, 2006). For example, plant pyrrolizidine alkaloids reduce the production of entomopathogenic nematodes feeding within woolly bear caterpillars, *Grammia incorrupta* (Gassmann et al., 2010). Likewise, when chlorogenic acid in tomatoes is oxidized to chlorogenoquinone, it binds covalently to occlusion bodies of the baculovirus HzSNPV and reduces their infectivity in the corn earworm *Helicoverpa zea* (Felton and Duffey, 1990). Similarly, in monarch butterflies (*Danaus plexippus*), the growth of its specialist protozoan parasite (*Ophryocystis elektroscirrha*) correlates negatively with foliar concentrations of cardenolides, toxic secondary chemicals in milkweed host plants (de Roode et al., 2008, 2011; Sternberg et al., 2012). In addition, the lifespan of infected butterflies correlates positively with cardenolides, a result of reduced parasite growth as well as increased monarch tolerance of infection (de Roode et al., 2008, 2011; Sternberg et al., 2012; Gowler et al., 2015). Because AMF associations belowground change the composition and concentration of milkweed cardenolides aboveground, AMF have substantial effects on monarch-parasite dynamics across milkweed hosts (Tao et al., 2015), an interaction across four biological kingdoms (**Figure 1C**).

When the infective stages of pathogens are released on plants, many plant traits affect their survival and persistence. For example, plant architecture, leaf form and color affect the amount of UV that is reflected onto the leaf surface, and thereby affect the survival of insect baculoviruses, which are sensitive to UV light (Hunter-Fujita et al., 1998; Cory and Hoover, 2006). Additionally, phylloplane microclimate and physiochemical properties affect pathogen infectivity and persistence (Der Geest, 2000). Currently, there remains limited information on whether microbial root mutualists affect these physical plant traits; if they do, belowground mutualists may have significant indirect effects on pathogen survival and persistence prior to infection.

Intraspecific variation in plant nutritional and secondary chemistry induced by root mutualists can also affect the foraging and oviposition behaviors of insect herbivores, with implications for herbivore contact rates and disease transmission. For example, AMF-associated *Baccharis halimifolia* and prairie C_3 graminoids experience higher herbivory than do plants without AMF (Moon et al., 2013; Kula and Hartnett, 2015), which may translate to higher rates of disease transmission among herbivores due to higher host density. Since transmission rate is fundamental to determining host-pathogen dynamics, understanding how microbial root mutualists affect disease transmission is important in both natural insect populations and in microbial biological control (Hunter, 2016). Although herbivore density and foraging behavior on individual plants clearly affect pathogen transmission (Parker et al., 2010), explicit links among root mutualists, plant traits, herbivore density, and disease transmission have yet to be made in the literature.

As we noted above for predators and parasitoids, soil mutualists affect multiple plant traits simultaneously, generating multiple mechanistic pathways by which root microbes influence tri-trophic interactions above ground. As with other enemies, the overall impact of root mutualists on disease dynamics will depend on the relative strength of each mechanistic pathway. Following the example of the monarch butterfly and its protozoan parasite described above, while cardenolides (secondary chemicals) reduce parasite numbers and increase the lifespan of infected butterflies (de Roode et al., 2008, 2011; Sternberg et al., 2012), macronutrients such as N and P also increase monarch performance (Tao and Hunter, 2012; Tao et al., 2014, 2015). Since associations with AMF change macronutrients and cardenolides simultaneously in milkweed leaves (Vannette and Rasmann, 2012; Tao et al., 2016), the net effects of AMF on butterfly-parasite interactions are best explained by the combined changes in milkweed P and cardenolide concentrations (**Figure 1C**) (Tao et al., 2015). Net effects on monarchs vary from positive, through neutral, to negative, depending on how particular milkweed species respond phenotypically to their root microbial mutualists.

MISSING LINKS

The last 15 years have seen an increase in the number of studies investigating indirect effects of belowground biota on aboveground tri-trophic interactions (Rasmann et al., 2017). As illustrated by our review, microbial root mutualists affect aboveground predators, parasitoids, and pathogens through a diverse set of mechanistic pathways, based on changes in the chemical and physical traits of plants engendered by root microbes. Specifically, chemical and morphological changes in plants alter the attractiveness of herbivore-infested plants to predators, the efficiency of their on-plant foraging behaviors, and the quality of herbivore tissues for enemy consumers. In addition, microbial root mutualists can change the efficacy of pathogens that attack herbivores above ground through their combined effects on plant morphology and plant nutritional and defensive chemistry.

However, the mechanisms of interaction documented to date (changes in plant nutritional quality, plant morphology, and plant secondary chemistry) represent a small subset of the potential pathways by which belowground biota more generally may influence tri-trophic interactions aboveground (van der Heijden et al., 1998; Smith and Read, 2008; Reinhart et al., 2012; Hunter, 2016; Rasmann et al., 2017). Unfortunately, the overall number of studies on this topic remains critically small, and most are focused on a few systems; as a result, significant knowledge gaps remain. Here, we highlight several of these gaps, in the hope that future studies will advance our understanding of these below-aboveground interactions.

(1) In reviewing this literature, we have been struck repeatedly by the difficulty of finding any generality in the magnitude and direction of effects of microbial root mutualists on tri-trophic interactions aboveground. One likely culprit is simply the small number of studies that have been conducted to date on this topic (**Table 1**); generality is hard to achieve when sample size is low. A major goal of this review is to support the call (Rasmann et al., 2017) for a concerted effort to understand how belowground organisms influence multi-trophic interactions aboveground. Pervasive effects of root biota on plant traits above ground are now well-documented (Hunter, 2016), but concomitant changes in the efficacy of predators and pathogens need much more attention.

Certainly, there is a clear need to look beyond effects mediated by mycorrhizal fungi and N-fixing symbionts, which still dominate the literature in this field. This is a two-part process: first documenting the diverse changes in plant physiology, chemistry, and morphology induced by different kinds of soil biota; second, linking explicitly these changes in plant traits to the expression of tri-trophic interactions. There has been substantial progress in the first of these, and minimal progress in the second. For example, evidence is accumulating that the rhizosphere is replete with other kinds of mutualistic microbe, including root endophytes and growth-promoting bacteria, which affect aboveground plant-herbivore interactions (Jaber and Vidal, 2010; Brunner et al., 2015). Similarly, soil macro-organisms, including dung beetles and springtails, are important ecosystem engineers that alter concentrations of the plant nutrients that are important to aboveground herbivores (Johnson et al., 2015c). Beyond root mutualists, there are well-characterized effects of root antagonists (root herbivores, pathogens, competitors) on plant phenotypic traits (Hunter, 2016), many of which are candidates for driving complex ecological interactions aboveground (Wyckhuys et al., 2017). Unfortunately, how these diverse soil biota influence tri-trophic interactions aboveground, either individually or interactively, remains largely unknown.

Beyond just a paucity of studies, a related barrier to generality is the apparent contingency in the responses of plant traits, and therefore tri-trophic interactions, to soil organisms (Barber et al., 2013). Within the microbial root mutualists, there have been several efforts to establish patterns among plant phenotypic responses based on plant phylogeny and life-history (Reinhart et al., 2012; Vannette et al., 2013). Unfortunately, the effects of microbial root mutualists on plant phenotype and herbivore performance seem to vary substantially among species of plant, species of microbe, species of herbivore, and environmental conditions (Garmendia et al., 2004; Gehring and Bennett, 2009; Grman, 2012; Grman and Robinson, 2012; Barber et al., 2013). To complicate matters further, the relative abundance of microbial root mutualists, and their degree of association with their hosts, also influences plant phenotype and herbivore performance (Garrido et al., 2010; Vannette and Hunter, 2011, 2013; Argüello et al., 2016). The unfortunate result is that, even within a single genus of plants, the impacts of microbial root mutualists on tri-trophic interactions do not conform to any readily identifiable phylogenetic or life-history pattern (Tao et al., 2015).

The antidote to idiosyncrasy is additional work. Ultimately, phylogenetically-controlled experiments (Reinhart et al., 2012; Vannette et al., 2013) must be combined with realistic ecological treatments of density and diversity (Vannette and Hunter, 2011; Argüello et al., 2016) to establish generality. We will not make progress until we accumulate laboratory and field studies in diverse ecosystems that control phylogeny, identity, density, and environmental conditions of all the interacting partners. These experiments must also measure simultaneously the suite of plant traits that microbial root mutualists influence aboveground. It is increasingly clear that interactions among multiple plant traits will combine to determine the net outcome of tri-trophic interactions aboveground (Tao et al., 2015, 2016).

(2) Similarly, studies of how belowground biota influence tri-trophic interactions above ground are limited currently to a narrow range of natural enemies. Most studies have focused on parasitoids, and we found only four studies on predators and one on insect pathogens. To date, we have no information on effects of soil biota on other key groups of enemies, such as vertebrate predators (e.g., birds, bats, reptiles), insect baculoviruses, or macro-parasites (such as nematodes) that are ubiquitous and economically important across ecosystems. There is no *a priori* reason to suppose that effects on these groups of enemies should be uncommon. For example, evidence suggests that vertebrate predators can use plant VOCs as foraging cues (Seymour et al., 2010; Amo et al., 2013). Given that some VOC production is mediated by root microbes (above), those microbes may also influence the foraging of vertebrate predators.

Beyond vertebrates, we suggest that interactions among soil biota, plants, herbivores, and pathogens will provide particularly intriguing opportunities for further study. It is now abundantly clear that plant chemistry is a major driver of animal disease across diverse terrestrial ecosystems (de Roode et al., 2013). Plant nutritional and defensive traits influence host quality, host immunity, host behavior, and thereby disease transmission. Given that diverse soil organisms influence plant chemistry above ground (Hunter, 2016), incorporating soil biota more generally in studies of disease spread is vital in placing disease dynamics within a community ecology context (Johnson et al., 2015b).

(3) Another critical missing link is to understand the effects of belowground organisms on interactions among multiple enemies above ground. For example, most of the studies in **Table 1** describe the effects of microbial root mutualists on a single species of natural enemy. Yet there is abundant evidence in natural and managed systems of interactions among natural enemies that influence subsequent prey suppression (Cardinale et al., 2003; Johnson et al., 2013; Painter et al., 2015). We might expect that (a) not all enemy species will respond in the same fashion to a given plant trait-change induced by a root mutualist, and (b) multiple phenotypic changes induced simultaneously by root microbes may have differential effects on different enemies. We need detailed experiments, manipulating multiple enemy species simultaneously, to explore effects of microbial root mutualists on herbivore suppression in a community context.

Most intriguing among such interactions may be those between predators and agents of disease. The ecological and evolutionary dynamics of such interactions might be particularly fascinating because predators can have large impacts on disease transmission. Such effects may be density-mediated: for example, by selectively feeding on infected prey, predators can decrease overall parasite transmission (Packer et al., 2003). On the other hand, indirect effects of predators on disease transmission can also be trait-mediated, operating through changes in host behavior, physiology or immune defense. For example, female Trinidadian guppies *Poecilia reticulata* display strong shoaling tendency in the presence of predators, thereby increasing the transmission of *Gyrodactylus* parasites (Stephenson et al., 2015). In the snail *Lymnaea stagnalis*, anti-predator behavior (blood expulsion) reduces their immunocompetence, which also renders them more susceptible to pathogens (Rigby and Jokela, 2000). Critically, the trade-offs between anti-predator and anti-parasite traits can be affected by host resource-availability (Roff and Fairbairn, 2007), and in the case of invertebrate herbivores, the quality of their host plants. Although there has been no direct evidence of host plant quality mediating these traits in herbivores, the trade-offs between anti-predator behavior and growth rate in tobacco hornworms *Manduca sexta* are more prevalent on well-defended tomato plants (Thaler et al., 2014). Overall, we suggest that it will be particularly informative to link the effects of belowground biota on herbivore densities and traits with the interactions between parasites and predators. We recommend manipulative experiments that vary the densities of infected and uninfected herbivore hosts, in the presence and absence of predators, across a broad range of associations with microbial root mutualists.

(4) Almost all of the mechanisms that we documented above were based on changes in plant chemistry (nutrients, toxins, VOCs) mediated by microbial root mutualists. However, traits such as plant architecture, domatia, trichomes and surface waxes are all subject to influences from soil organisms. These same plant traits mediate predator and parasitoid recruitment and foraging efficiency (Speight et al., 2008), and affect the viability of insect pathogens (Cory and Hoover, 2006). To date, there has been no exploration of the extent to which belowground organisms affect the third trophic level through these critical plant traits. This is particularly important in agricultural systems, where the behavior and persistence of biological control agents determine in part the success of pest management.

(5) Future studies should quantify more thoroughly the effects of belowground organisms on the fitness of all partners in the aboveground tri-trophic interactions. For example, while root colonization by AMF affects the fitness of infected monarch butterflies, parasite growth remains unaffected (Tao et al., 2015). In this case, the effect of belowground organisms on the aboveground tri-trophic interaction would have been missed entirely if only parasite performance had been measured. Because the ecological and evolutionary consequences of species interactions depend on the fitness of all interacting species, we

urge researchers to quantify as many life history parameters of as many participants as possible.

(6) While a majority of studies has examined these complex interactions uni-directionally from a bottom-up point of view, the third trophic level can also impact plants and soil organisms and create important feedback loops. For example, increases in predation pressure on herbivores that result from mycorrhizal associations can subsequently feedback to increase plant fitness (Hoffmann et al., 2011a). Moreover, effects of root microbial mutualists that first "cascade up" to increase the abundance or efficacy of natural enemies can then "cascade down" again to influence the fitness of plants and their mutualists, as well as the availability of nutrients in soils (Hunter, 2016). Future studies should assess the general frequency and strength of feedback processes that link upper trophic levels aboveground with soil biota below.

(7) By influencing some species more than others, soil organisms can change the structure and composition of herbivore and enemy communities. For example, AMF colonization alters arthropod predator community composition on *Deinandra fasciculata* (Schreck et al., 2013) and on *Glycine max* (Ueda et al., 2013). These important studies suggest that we need a community perspective to understand and integrate complex species interactions below- and aboveground.

(8) Abiotic factors, such as nutrient and water availability, strongly regulate the diversity and composition of soil organisms and their interactions with plants (Johnson et al., 2015a). It remains an open and urgent question as to how above- and belowground multi-trophic interactions are shaped by environmental stresses and global environmental change.

(9) So far, most studies have focused on agricultural systems or model systems. While these provide a starting point for understanding the mechanisms in well-studied and/or economically important systems, we also need to study systems that are more diverse, such as wild herbs and woody plants, to explore the generality of effects. Even where natural systems have been used, it remains unclear how these interactions play out in the field. For example, in our monarch butterfly studies, we used commercially available mycorrhizal strains, and it remains unclear how natural milkweed-AMF interactions influence interactions aboveground under field conditions (Tao et al., 2015).

In conclusion, it is clear that belowground biota have important effects on aboveground tri-trophic interactions. However, this topic remains in its infancy and many questions remain unresolved. We hope that our review will provide some guidance in designing future studies to better understand interactions between below- and aboveground subsystems of the integrated whole.

AUTHOR CONTRIBUTIONS

LT and JdR: conceived the idea for the review; LT: conducted the initial literature review; JdR and MH: provided additional literature to the review. All three authors contributed to writing and editing the manuscript.

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