Putting the ‘upstairs–downstairs’ into ecosystem service: What can aboveground–belowground ecology tell us?

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HIGHLIGHTS

- Aboveground–belowground interactions influence ecosystem function.
- Root and shoot herbivory weaken antagonism of the spatially-separate herbivore.
- Decomposers and mycorrhizae increase shoot herbivore performance or antagonism.
- Shoot herbivory stimulates nutrient cycling by decomposers.
- Root herbivory and mycorrhizae increase floral attractiveness to insect pollinators.

ABSTRACT

Interactions between spatially-separated aboveground and belowground biota exert important influences on the functioning of terrestrial ecosystems. Plant root exudates and litter inputs affect root-associated and decomposer sub-communities, which, in turn, regulate nutrient availability and plant growth. Ecosystem services theoretically attributed to specific functional components of aboveground or belowground biota are, therefore, influenced by indirect (plant-mediated) interactions with the wider community. Some recent studies have considered aboveground–belowground interactions in a climate change context, with implications for altered ecosystem service provision. This review is a conceptual discussion of the mechanisms by which aboveground–belowground interactions affect specific ecosystem services: control of herbivores by natural enemies, insect pollination and nutrient mineralization by soil decomposers. While some mechanisms are well-characterized, others are poorly understood. Reducing root and shoot herbivory, in addition to the direct plant benefit, indirectly promotes antagonism of the spatially-separate herbivore by its natural enemies. Soil decomposers and mycorrhizal fungi can increase shoot herbivore performance such that control by natural enemies is weakened, or initiate bottom-up trophic cascades which strengthen antagonism of shoot herbivores. Aboveground herbivory generally stimulates nutrient cycling by decomposers. Root herbivory and mycorrhizal association both appear to increase floral attractiveness to insect pollinators. Mechanisms reflect alterations to plant growth, nutritional quality and chemical defenses. Climate change has considerable potential to alter aboveground–belowground interactions, with largely unexplored implications for biological control, pollination and soil nutrient cycling.
1. Introduction

The functioning of an ecosystem is regulated by the interactions that occur between the organisms within it. Interactions between aboveground and belowground biota, via plant-mediated mechanisms, are potentially as important for ecosystem structure and function as those between spatially co-existing species (Bardgett and Wardle, 2010; see Dreyer and Gratton, this issue for a discussion of linkages between horizontally adjacent habitats). While both aboveground (Bale et al., 2002; Grime et al., 2000) and belowground (A’Bear et al., 2013; Jones et al., 1998) sub-community dynamics and processes are known to be affected by global climate change factors, only recently have studies begun to consider interactions between these spatially-separated biota within a climate change context. Plant inputs to soil (roots, their exudates and litter material) can determine sub-community composition by influencing root-associated and decomposer organisms. These, in turn, regulate plant growth and nutrient availability (Bever et al., 1997; Wardle et al., 2004). Feedbacks of this nature between spatially-separated sub-communities influence plant (Bradford et al., 2002; De Deyn et al., 1993), microbe (De Deyn et al., 2011; de Vries et al., 2012; Kostenko et al., 2012), detritivore (Hedlund et al., 2003; Wardle et al., 1999), herbivore (Bunkowski et al., 2001; Scheu et al., 1999; Wurst et al., 2003) and natural enemy (Bezemer et al., 2005; Gange et al., 2003) activity and population dynamics. As a consequence, ecosystem services (e.g. biological control of herbivore populations by natural enemies, pollination, decomposition and nutrient cycling) theoretically attributed to specific functional units within aboveground or belowground subsystems are, in reality, influenced by indirect interactions with other components of the community (Fig. 1).

Nutrient exchange intimately links aboveground and belowground biota; dead plant material provides the organic carbon required by the soil decomposer subsystem, the activity of which regulates the supply of mineral nutrients to plants, herbivores and natural enemies (van der Heijden et al., 2008). Plant-associated organisms, either aboveground (e.g. leaf herbivores and pollinators) or belowground (e.g. root herbivores and mycorrhizal fungi), influence one another through changes to plant productivity (e.g. due to mycorrhizal association; Gange et al., 2003) or induced defensive chemistry (e.g. terpenoid or glucosinolate production, due to herbivory; reviewed by Bezemer and van Dam, 2005), indirectly influencing higher trophic levels (Gange et al., 2003; Wardle et al., 2004). Belowground inputs, such as root exudates, litter fall and herbivore frass, influence the composition and activity of the decomposer community (Ayers et al., 2007; Jones et al., 1998; Krasnoschekov and Vishnyakova, 2003). Intense competition also occurs between plants and soil microbes, as they are limited by the same nutrients (Wardle et al., 2004). The wide range of mutualistic, facilitative and antagonistic feedbacks that occur between aboveground and belowground organisms are also influenced when interacting components are affected by changes in the abiotic environment (Stevnbak et al., 2012; Tylianakis et al., 2008). The direct effect of, for example, elevated CO2, warming or altered precipitation, on one species has the potential to indirectly influence members of the wider community (see also: Schmitz and Barton, this issue; Tylianakis and Binzer, 2013; Welch and Harwood, this issue). Ecosystem structure and function is, therefore, a consequence of this complex network of dynamic interactions.

Previous reviews have considered the ecology of specific aboveground–belowground interactions. These include the interactions between root and foliar herbivores (e.g. Bezemer and van Dam, 2005; Johnson et al., 2012), decomposers and foliar herbivores (e.g. Bardgett et al., 1998; Scheu, 2001), and mycorrhizal fungi and plant community dynamics (e.g. Gange and Brown, 2002; Hart et al., 2003). Several conceptual models have been suggested to describe the mechanisms by which different components of aboveground and belowground communities influence one another (e.g. Bever et al., 1997; Masters et al., 1993; Moore et al., 2003). Mechanistic understanding of these interactions provides the potential to regulate them for biological control and the provision of ecosystem services. The present review is a conceptual discussion of how interactions between aboveground and belowground sub-communities influence ecosystem function and service. We explore the mechanisms by which aboveground–belowground interactions regulate the control of herbivory by natural enemies, pollination and nutrient mineralization by soil biota (Fig. 1). These interactions have implications for biological control, productivity and soil fertility in natural and managed ecosystems. Within the context of each of the aboveground–belowground interactions reviewed, we draw on the limited available evidence to consider the potential for climate change to influence ecosystem service provision mediated by these feedbacks.

2. Effects of belowground biota on aboveground biota and ecosystem services

2.1. Root herbivore effects on natural enemies of aboveground herbivores

Root herbivores have been shown to affect a number of aboveground insect herbivores (reviewed by Johnson et al., 2012). Recent studies have begun to explore the implications of these effects for...
the regulation of insect herbivore populations by their natural enemies, particularly parasitoids (Soler et al., 2012), with implications for the management and efficacy of applied biological control. While root herbivory most frequently reduces aboveground parasitoid recruitment or performance (Bezemer et al., 2005; Rasmann and Turlings, 2007; Soler et al., 2007a,b; White and Andow, 2006), neutral (Kabouw et al., 2011; Olson et al., 2008) and positive (Johnson et al., 2013; Masters et al., 2001; Poveda et al., 2005) effects have also been reported.

The mechanisms determining belowground herbivore influences on aboveground parasitoids are not always pinpointed, but often reflect changes in herbivore-induced plant volatile (HIPV) production, or nutrient limitation (due to impaired root function) reducing prey density or quality. Root herbivory can reduce the effectiveness of HIPVs in parasitoid attraction (Pierre et al., 2011b; Soler et al., 2007b) or promote production of these (Olson et al., 2008) and other (Wackers and Bezemer, 2003) chemical cues important in natural enemy recruitment. Parasitoids have also been reported to avoid plants on which herbivore host performance is poor, as a result of root herbivory reducing shoot tissue quality (e.g. low nutrient or high secondary metabolite concentrations; Soler et al., 2012).

Most studies of root herbivore effects on aboveground natural enemies have considered parasitoids. One study that considered a broader range of herbivore antagonists found that field planted blackcurrant (Ribes nigrum) plants subject to root-feeding vine weevils (Otiorhynchus sulcatus) sustained higher populations of both parasitoids and predators, including braconid wasps (Aphidius spp.) and two ladybird species (Adalia bipunctata and Coccinella septempunctata) (Fig. 2; Johnson et al., 2013). In this study, however, aphid natural enemy abundance increased in a density-dependent manner, reflecting increased host abundance and may not have involved HIPVs (Johnson et al., 2013).

Root herbivory often, but not consistently, reduces the effectiveness of aboveground herbivore natural enemies. Where this does occur, control of root herbivores could help to maximize the efficacy of aboveground herbivore biological control agents. Even where root herbivory reduces shoot herbivore performance (see Johnson et al., 2012 for examples), an advantage to the plant is unlikely, since it is still under simultaneous attack. In addition to this dual herbivory, top-down control would likely be compromised by reduced parasitoid attack rates on inferior quality host herbivores (Godfray, 1994). In contrast, where production of natural enemy recruitment cues is increased due to root herbivory (e.g. Wackers and Bezemer, 2003), this raises the intriguing possibility of artificially activating the same mechanism to enhance recruitment of biological control agents (e.g. natural enemies).

The effects of global climate change on insect root herbivores have received little empirical attention (Staley and Johnson, 2008). Three studies have quantified the effects of elevated atmospheric CO2 on root herbivores, reporting positive (Johnson and McNicol, 2010), neutral (Salt et al., 1996) and negative (Johnson et al., 2011a) responses. Better studied is the effect of elevated CO2 on root growth, which generally increases relative to shoot growth (Rogers et al., 1994, 1996). Enhanced root growth is usually beneficial for root herbivores (e.g. Clark et al., 2011): more extensive plant damage due to herbivory might be expected as a result. This could increase attenuation of signaling (e.g. HIPVs) and reduced recruitment of natural enemies. The reported positive effects of O. sulcatus on aphid natural enemies (Fig. 1; Johnson et al., 2013) are likely to be reduced under elevated CO2 concentrations since, contrary to expectations, R. nigrum root growth and O. sulcatus larval performance have both been reduced under these conditions (Johnson et al., 2011a). While not considering root herbivores, Vuorinen et al. (2004) demonstrated that elevated CO2 reduced emissions of HIPVs from shoots in Brassica plants, which resulted in reduced orientation efficacy of natural enemies. It therefore appears likely that, where root herbivory reduces the recruitment of root herbivore antagonists, this may be exacerbated by elevated CO2.

2.2. Belowground herbivore effects on pollinator attraction

Entomophilous pollination is, perhaps, one of the most conspicuous insect-delivered ecosystem services, and one that arouses intense research interest. Kessler et al. (2011) distinguish two mechanisms by which insect herbivory can influence pollinators. The first, immediate interaction, is characterized by pollinator avoidance of plants because the herbivore has damaged or altered floral displays (e.g. Cunningham, 1995), or is physically occupying flowers (e.g. Lohmann et al., 1996). The second mechanism, subsequent interaction, describes herbivore-induced plant growth and, or, metabolic (e.g. HIPV production) changes affecting pollinator behavior (Lucas-Barbosa et al., 2011).

In this review, we consider how root herbivory and mycorrhizal association (Section 2.5) affect pollinators. Root herbivores usually impose fitness costs on plants (Johnson and Murray, 2008; Zvereva and Kozlov, 2012), resulting in trade-offs between re-growth, development and reproduction. An adverse effect of root herbivory on pollinator visitation might be expected due to increased limitation on the energy a plant can invest in floral displays and production of pollinator-attracting HIPVs. While the effects of leaf herbivory on pollinators have been addressed in a range of systems, root herbivore impacts on pollinators have only been considered in three; wild mustard (Sinapis arvensis), butternut squash (Cucurbita moschata) and cucumber (Cucumis sativus). Contrary to the expectation that root herbivory reduces pollinator visitation, S. arvensis and C. sativus experienced increased pollinator visitation when exposed to root herbivores (Table 1; Barber et al., 2011; Poveda et al., 2003, 2005). In these species, root herbivory resulted in either more frequent pollinator visits (Poveda et al., 2003, 2005) or longer visitation time (Barber et al., 2011). Pollinator visitation to C. moschata was not affected by root herbivory; no treatment effects were observed on plant traits (Table 1).

The mechanism underlying increased pollinator attendance of root-infested plants is unclear, though enhanced water and nutrient uptake due to stimulated lateral root production has been suggested (Poveda et al., 2003). The generality of observed root herbivore...
 effects on pollinators is, as yet, unknown (Barber et al., 2011), but a mechanistic understanding of how root herbivory enhances pollinator recruitment to certain plants might provide a means of enhancing pollination. Ultimately, if the plant traits promoting pollinator visitation could be triggered in the absence of root herbivores, this could have beneficial effects on agricultural productivity. A recent meta-analysis demonstrated that root herbivory (Zvereva and Kozlov, 2012), in contrast to shoot herbivory (Nykänen and Koricheva, 2004), usually promotes photosynthesis. Enhanced rates of photosynthesis might stimulate flowering traits and further strengthen positive effects of root herbivory on pollinator visitation. Given that global climate change is likely to have significant effects on pollinator physiology and distribution (Hoover et al., 2012), the potential positive indirect effects of root herbivory on pollinators (Table 1) might be relatively insignificant.

2.3. Soil decomposer effects on aboveground herbivores and their natural enemies

Much of our understanding of soil decomposer community impacts on aboveground trophic interactions is derived from faunal manipulation studies. The activity of soil fauna, at levels of complexity varying from single- to multi-species detritivore communities containing broad functional representation, generally increases plant growth and nutrient (e.g. nitrogen and phosphorus) uptake and concentrations in foliar tissues (Bonkowski et al., 2001; Newington et al., 2004; Poveda et al., 2005; Setala and Huhta, 1991; Wurst et al., 2003). Both neutral (Scheu et al., 1999; Wurst and Jones, 2003) and negative (González-Megías and Müller, 2010) detritivore effects on the nitrogen content of aboveground tissue have, however, been reported in nutrient poor soils. This could be a dilution effect; more nitrogen is taken up but biomass increases such that nitrogen concentration in the tissue is reduced. Soil decomposer microbiota have received less attention than fauna with regard to their effects on aboveground trophic interactions; this is mainly due to the fact that their communities are far more difficult to manipulate empirically. Microbial activity in soil also stimulates plant productivity by increasing nutrient availability. Combined decomposer fungal (Fusarium graminearum) and faunal detritivore (earthworm, Aporrectodea caliginosa) activity has been reported to generate additive and over-additive impacts on plant (winter wheat, Triticum aestivum) performance traits (Eisenhauer et al., 2010). Mechanisms by which decomposer activity increases plant productivity include the promotion of nutrient mineralization and favorable alterations to soil structure (Setala and Huhta, 1991). Positive detritivore–microbe interactions facilitating decomposition (additive promotion of nutrient availability; Eisenhauer et al., 2010) and reduced microbial competition for nutrients due to faunal microbivory (e.g. by colembola; Bardgett and Chan, 1999), also promote plant performance.

Improved nutritional quality of plant tissue due to soil decomposer (e.g. earthworm or colembola) activity can increase susceptibility to pests, improving leaf-chewing caterpillar (Newington et al., 2004) and aphid (Bonkowski et al., 2001; Eisenhauer et al., 2010; Poveda et al., 2005; Scheu et al., 1999; Wurst and Jones, 2003) herbivore performance. In contrast, reduced aphid performance (delayed development and decreased reproduction) on nitrogen-enriched plants has been attributed to increased foliar concentrations of plant secondary metabolites (e.g. glucosinolates, phytosterols; Lohmann et al., 2009; Wurst et al., 2003, 2004a,b). Induced plant defense is, therefore, not only a potential response to herbivory, but could also be enabled by decomposer-mediated nutrient mineralization. Whether soil decomposer activity stimulates plant susceptibility to, or defense against, herbivory is likely to depend on the system and nutrient status of soil. Earthworm activity in relatively nutrient rich soils generally promotes plant growth; this has been reported to increase susceptibility to aphid herbivory for hairy bittercress (Cardamine hirsuta; Wurst and Jones, 2003), wild mustard (Sinapis arvensis; Poveda et al., 2005) and winter wheat (T. aestivum; Eisenhauer et al., 2010), but stimulate secondary metabolite-mediated defense against aphids for white mustard (Sinapis alba; Lohmann et al., 2009) and plantain (Plantago lanceolata; Wurst et al., 2004a,b). If productivity is prioritised over defense in agricultural crop cultivation, soil fertilization and soil biotic factors that reduce carbon:nutrient ratios, promoting plant growth and quality, could have the potential to increase susceptibility to herbivory.

The complexity, and poor taxonomic and functional resolution of belowground communities, coupled with the assumptions that functional redundancy is high, and that species present in low abundance exert little influence on community interactions and ecosystem services (Degens, 1998; Griffiths et al., 2000; Wertz et al., 2006), have meant that the majority of empirical manipulations have involved common faunal detritivore species (e.g. earthworms and colembola). Subordinate (low relative abundance within a community) soil microbes have, however, recently been implicated in reducing crop biomass, but increasing defense against herbivory (Hol et al., 2010). Removal of subordinate microbial species from soil increased yield production by two crop species (Beta vulgaris and Brassica oleracea), but also increased plant nutritional quality and aphid (Brevicoryne brassicae and Myzus persicae) herbivore body size. Subordinate microbes enhanced glucosinolate concentrations in B. oleracea shoots under aphid herbivore attack. Decomposer organisms occurring in low abundance within their communities could, therefore, be exerting influences on ecosystem service provision that are disproportionately relative to their biomass. This is a particularly pertinent consideration where soil

### Table 1

<table>
<thead>
<tr>
<th>Study system</th>
<th>Herbivore</th>
<th>Pollinators</th>
<th>Responses to root herbivory</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Plant</td>
<td></td>
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<td>Shoot mass</td>
<td>Root mass</td>
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<tr>
<td>Wild mustard (Sinapis arvensis)</td>
<td>Wireworms (Arigotes sp.)</td>
<td>Honeybees (Apis mellifera), hover flies (Syraiphidae), bumblebees (Bombus sp.) and flies</td>
<td>0</td>
<td>0</td>
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<td>Butternut squash (Cucurbita moschata)</td>
<td>Striped cucumber beetle (Acalypma vitattum)</td>
<td>Squash bees (Pepopanis prunisus), bumblebees (Bombus sp.), honeybees (A. mellifera)</td>
<td>0</td>
<td>0</td>
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<tr>
<td>Cucumber (Cucumis sativus)</td>
<td>Striped cucumber beetle (A. vitattum)</td>
<td>Bumblebees (Bombus sp.), honeybees (A. mellifera)</td>
<td>–</td>
<td>0</td>
</tr>
</tbody>
</table>

Symbols indicate positive (+), neutral (0) and negative (−) plant and pollinator responses to root herbivory. Pollinators in bold were the most abundant groups.

* 35% fewer female flowers.
* 119% more time spent per visitation.
microbial communities are simplified, or diversity is reduced, as a result of land-use intensification (Giller et al., 1997; Gomez et al., 2004; Graham and Haynes, 2005). This could decrease their insurance value in controlling herbivores and other pests (Hol et al., 2010).

The implications for plant productivity when herbivore performance is increased depend, in part at least, on the effectiveness of population control by natural enemies. Both neutral (Wurst and Jones, 2003) and positive (Poveda et al., 2005) responses of parasitoid populations have resulted from decomposer-mediated increases in plant tissue quality. The positive responses reflected a bottom-up influence of increased nutrient availability; this was prevented by soil nutrient limitation in the case of the neutral response. Increased parasitoid abundance, but an unaltered rate of parasitism in a mixed aphid community (dominated by B. brassicae; Poveda et al., 2005), implies that even when parasitoids do respond to aphid abundance, the strength of the regulatory control may not be sufficient to prevent increased herbivory. Failure of Aphidius colemani parasitoid abundance to increase with that of the herbivore resulted in decreasing percentage parasitism as aphid (M. persicae) numbers increased (Wurst and Jones, 2003) and, consequently, a reduced capacity for population control. Nutrient mineralization by soil decomposers could, therefore, limit the efficacy of biological control agents. Rates of herbivore parasitism and predation can, however, be higher in nutrient-enriched soils (Bentz et al., 1996; Forkner and Hunter 2000; Wimp et al., 2010; Wurst and Jones, 2003). This suggests that fauna-mediated maintenance of soil nutrient status may have the potential to alleviate negative effects (e.g. of root herbivory; Section 2.1) on the effectiveness of shoot herbivore control by natural enemies, but is dependent upon the bottom-up trophic cascade being transmitted to the third aboveground trophic level.

The aforementioned studies of three aboveground trophic levels considered the effect of single earthworm species mediated by plants in monoculture. Functional biodiversity in complex soil communities can also affect aboveground tri-trophic interactions. Altered size class (often used as a proxy for functional diversity in soil) representation (microbiota [microbes and microfauna] only, microbiota and mesofauna, and microbiota, meso- and macrofauna) influenced the interaction between the cherry-oat aphid (Rhopalosiphum padi) and a parasitoid (A. colemani), mediated by both a grassland plant community and the dominant species (Agrostis capillaris) in monoculture (Eggers, 2004). Foliar quality (nitrogen content and carbon:nitrogen ratio) was unaffected by functional diversity. Aphid performance reflected system-specific soil biotic effects on plant free amino acid (the dominant source of nitrogen in phloem sap) concentrations from the α-ketoglutarate pathway. Amino acid concentrations were lowest in the plant community microbiota treatment, whereas, in the A. capillaris monoculture, they were lowest in the meso- and macrofauna treatments. In both systems, in the presence of parasitoids, aphid abundance increased where amino acid concentrations were lowest. For example, in the A. capillaris monoculture, high aphid abundance in the macrofauna treatment corresponded with reduced concentrations of arginine, an amino acid essential for parasitoid development (Fig. 3). The requirement for arginine by the aphids could have been satisfied by their obligate symbiont, Buchnera, which converts non-essential amino acids on the α-ketoglutarate pathway into essential amino acids (Sasaki and Ishikawa, 1994). Soil biota-induced reduction in the availability of essential amino acids is likely, therefore, to be more limiting for parasitoids than aphids, weakening top-down control of herbivory. Whilst the mechanism behind the differing effects of soil functional diversity in the community and monoculture is unclear (competition and altered plant species composition in the community could have contributed; Bradford et al., 2002), free amino acid concentrations appear at least as important as traditional plant quality indicators in regulating the performance and antagonism of phloem-feeding herbivores.

Altered patterns of precipitation (increased frequency and duration of drought, and prolonged precipitation episodes), predicted as a consequence of climate change will have considerable potential to affect the influence of soil decomposers on aboveground herbivory. This arises as a consequence of alterations to soil moisture content; one of the most important abiotic determinants of belowground sub-community dynamics and processes, due to the desiccation sensitivity of soil biota (reviewed by A’Bear et al., 2013; Blankinship et al., 2011). Detritivory, and rain addition or exclusion, have been shown to interact in their effects on aboveground herbivores. In a dryland ecosystem, rain addition and M. persicae biomass, has been intensified by earthworm (Agrostis capillaris) activity (particularly in plant monocultures; Johnson et al., 2011b). This had cascading effects on parasitoids (Aphidius ervi), beyond that expected as a consequence of aphid density decline, suggesting that prey quality, as well as quantity, was reduced. The negative effect of stressful abiotic conditions is, therefore, likely to over-ride any positive bottom-up trophic cascade to aboveground plant associates that might result from soil biotic activity under ambient conditions. Environmental change factors with the potential to stimulate soil biotic activity (e.g. elevated temperature,
when moisture is non-limiting) could increase the intensity of decomposer effects on aboveground multitrophic interactions. This could reduce the efficacy of biological control agents, where the antagonist cannot keep pace with enhanced herbivore performance.

2.4. Mycorrhizal effects on the natural enemies of aboveground herbivores

Given the ubiquity of plant association with mycorrhizal fungi, their role in aboveground-belowground ecology is under-represented. Mycorrhizal fungi influence the performance of aboveground insect herbivores, with mechanisms differing between mycorrhizal types (arbuscular mycorrhizae and ectomycorrhizae being most studied), herbivore feeding guilds, and mycorrhizal and herbivore species (reviewed by Bennett et al., 2006; Hartley and Gange, 2009; Koricheva et al., 2009). Herbivore responses generally reflect whether the mycorrhizal association improves plant biomass, nutritional quality, tolerance or defense. Taxonomic bias in the literature (e.g. many studies have considered a narrow range of arbuscular mycorrhizal Glomus species) and the system-specificity of interaction outcomes have resulted in very few of these mechanisms being well characterized.

Over the past decade a handful of studies on the impacts of mycorrhizal association on the natural enemies of foliar herbivores have been published. Understanding the natural enemy response is crucial within an applied biological control context, particularly in interactions where the mycorrhiza improves plant nutritional quality and herbivore performance. The first study to investigate the influence of mycorrhizal colonization on aboveground herbivore antagonism reported decreased leaf miner (Chromatomyia syngenesiae) parasitism on the ox-eye daisy, Leucanthemum vulgare (Gange et al., 2003). A complementary laboratory experiment exploring the mechanisms underlying this result revealed mycorrhizal species-specific and interactive effects, resulting in positive, neutral and negative responses of herbivore and parasitoid performance. Mycorrhizal colonization of a coastal shrub (Baccharis halifolia) increased gall maker (Neolasioptera lathamii) and leaf miner (Amauromyza maculosa and Liriomyza trifolii) densities, and decreased percentage parasitism (Moon et al., 2013). Plant size or leaf number was increased by mycorrhizal association in both studies; this could have reduced parasitoid searching efficiency (Gange et al., 2003).

In contrast, increased performance (in terms of oviposition rate, development time and population size) of phloem- and cell-feeder antagonists has been reported in response to mycorrhizal colonization (Hempel et al., 2009; Hoffmann et al., 2011a,b; Wooley and Paine 2011). The induced emission of bean plant (Phaseolus vulgaris) volatiles (e.g. β-ocimene and β-caryophyllene) by spider mite (Tetranychus urticae) herbivory is altered by mycorrhiza, resulting in increased predatory mite (Phytoseiulus persimilis) attraction (Schausberger et al., 2012). Further, a mechanistic prey-choice study in which the predator was presented with spider mites fed on mycorrhizal or non-mycorrhizal bean plants revealed that the prey selection reflected the mycorrhizal status of the plant on which it fed (Hoffmann et al., 2011c). Prey-related cues, which appeared to originate from their eggs, enabled the predator to recognize the improved quality, and preferentially oviposit in the vicinity of prey fed on mycorrhizal plants.

Available evidence suggests that herbivore feeding guild determines the form of interaction that occurs between mycorrhizal fungi and the herbivore’s natural enemies. Parasitism of leaf mines and galls appears to be reduced by mycorrhiza, mainly as a consequence of reduced parasitoid searching efficiency on larger plants (Gange et al., 2003; Moon et al., 2013). In an agricultural context, there would likely be a trade-off between mycorrhizal promotion of plant productivity and weakening biological control of mining and galling insects. In contrast, increased natural enemy populations, as a result of a bottom-up trophic cascade, appear able to compensate for the mycorrhiza-mediated promotion of phloem- and cell-feeding herbivore abundances (Hempel et al., 2009; Hoffmann et al., 2011a,b; Ueda et al., 2013). This proposed mechanism requires wider verification as impacts are also mycorrhizal species-specific (Gange et al., 2003). An important role for mycorrhizal fungi in the transfer of induced defense signaling between plants has recently been revealed. Arbuscular mycorrhizal (Glomus intraradices) association can enable the induction of parasitoid (A. ervi)-attracting HIPV (particularly methyl salicylate) production, ahead of potential pea aphid (Acyrthosiphon pisum) attack, when herbivore-free bean plants (Vicia faba) share a network of mycorrhizal mycelium with an infested plant (Babikova et al., 2013).

Elevated atmospheric CO2 increases belowground allocation of photosynthetic carbon. This can stimulate mycorrhizal colonization of roots (Garcia et al., 2008; Staddon and Fitter, 1998). Evidence for a significant effect of warming on belowground carbon allocation by plants is more limited (Olson et al., 2010; Staddon et al., 2003). The consequences for foliar herbivores and the regulation of their populations by natural enemies have yet to receive empirical attention. Increased mycorrhizal colonization could intensify the effects of the symbiosis on aboveground tri-trophic interactions. Stimulation of plant growth (Staddon and Fitter, 1998) could further reduce the searching efficiency of leaf gall and leaf miner parasitoids, potentially weakening biological control. In contrast, decreased shoot nitrogen as a consequence of progressive nutrient limitation (particularly under elevated CO2; Alberton and Kuyper, 2009) could negatively affect foliar herbivore performance. The response of the proposed bottom-up trophic cascade, from mycorrhizae to phloem- and cell-feeder parasitoids, to climate induced stimulation of mycorrhizal colonization is likely to depend on the nutrient status of soils. As nitrogen limitation progressively increases, the control of herbivory by antagonists could be weakened; declining plant and herbivore nutritional quality could negatively affect natural enemy performance. Mycorrhizal association is an important, but so far overlooked, consideration in the management of applied biological control under global change scenarios.

2.5. Mycorrhizal effects on pollinator attraction

As well as influencing foliar properties, belowground mutualism with mycorrhizal fungi has long been known to influence several plant floral traits. Mycorrhiza-induced increases in flower number and duration of flowering (Bryla and Koide, 1990) have implications for the attraction of aboveground mutualists – plant pollinators. Although several studies have investigated the influence of mycorrhizal association on plant reproductive traits (e.g. seed and pollen production; reviewed by Koide and Dickie, 2002), few have considered the associated crucial ecosystem service mediated by pollinator visitation to flowers.

Early studies of the impacts of mycorrhizae on pollinator visitation were ‘pot’ experiments, which, collectively, employed four different plants and three different mycorrhizal inoculation treatments (Gange and Smith, 2005; Wolfe et al., 2005). All investigated combinations revealed that inoculation with arbuscular mycorrhizal fungi increased pollinator visitation. Mechanisms of attraction were plant species-specific, reflecting mycorrhizal-induced increases in flower number per plant, individual flower size or nectar standing crop (Gange and Smith, 2005; Wolfe et al., 2005). A subsequent grassland field study reported a marked (67%) drop in floral visitation due to suppression of mycorrhizae, evident across the community of 23 flowering species (Cahill et al., 2008). This decrease in visitation in the absence of...
mycorrhizal activity was accompanied by a shift in visitor community composition, changing from large-bodied bees to small-bodied bees and flies. Further investigation across a broad range of species is required to verify the generality of mycorrhizal-induced promotion of pollinator activity.

Warming is already causing earlier initiation of spring flowering by many plants (Menzel and Fabian, 1999; Walther et al., 2010). Non-additive interactive effects of warming, elevated CO2 and nitrogen deposition on plant (pumpkin, Cucurbita maxima) nectar chemistry (sugars and amino acids) and pollinator (bumble bee, Bombus terrestris) performance have also been reported (Hoover et al., 2012). Such effects are often disruptive to the plant–pollinator mutualism. Mycorrhizal association is likely to exert important influences on floral trait and pollinator attraction responses to climate change, which remains to be investigated.

3. Effects of aboveground biota on belowground biota and ecosystem services

3.1. Aboveground herbivore effects on natural enemies of belowground herbivores

Natural enemies of root herbivores include fungi and nematodes (Johnson and Murray, 2008), as well as viruses, bacteria and predators. Indirect defenses, whereby roots damaged by herbivory emit volatiles that recruit entomopathogenic nematodes (EPNs), have been reported (Ali et al., 2012; Rasmann et al., 2005; van Dam, 2009; van Tol et al., 2001). Can these indirect defenses, of direct relevance to applied biological control, be altered by aboveground herbivores? It is known that systemic induction of direct chemical root defenses by shoot herbivores is less common and weaker than root herbivore-induced shoot defense (Kaplan et al., 2008), but it is less clear whether the same holds true for indirect defenses that involve recruitment of root herbivore natural enemies. Emission of (E)-β-caryophyllene from maize roots damaged by the Western corn rootworm (Diabrotica virgifera virgifera) is known to attract EPNs (Rasmann et al., 2005). Recruitment of EPNs was 43% lower in shoot herbivore (Spodoptera littoralis) infested plants, concomitant with reduced (E)-β-caryophyllene emission from roots (Rasmann and Turlings, 2007), implying a weakening of root herbivore biological control.

To our knowledge, only one study (Pierre et al., 2011a) has addressed whether shoot herbivory affects the parasitoid of a root herbivore. Females of the cabbage root fly (Delia radicum) parasitoid (Trybbiographa rapae) forage aboveground and burrow into the soil to parasitize their root-feeding host (Jones, 1986). Foliar herbivory by Pieris brassicae reduced parasitism of D. radicum by T. rapae in the field by 87% (Pierre et al., 2011a). This was associated with an altered composition of emitted HIPVs by plants sustaining both root and shoot herbivory (Pierre et al., 2011b). Although this study considered shoot HIPVs (the means by which T. rapae females locate root-infested plants), rather than root HIPVs, belowground natural enemy efficacy was weakened by shoot herbivory. More research is needed to further mechanistic understanding of the factors implicated in systemic root signaling (see discussion of this topic in Hiltpold et al., 2011). Maintaining plant free of shoot herbivores will most likely optimize the effectiveness of belowground biological control agents (e.g. commercial EPNs). Altered precipitation patterns are among the most significant aspects of global climate change likely to modify the effects of shoot herbivory on belowground natural enemies. In particular, drought conditions increase soil porosity; this reduces EPN motility, but increases the diffusion of volatile signals emitted from roots (Erb and Lu, 2013). Lower soil water content generally reduces EPN populations and their efficacy against root herbivores (e.g. Frew et al., 2013). Moreover, erratic or highly variable precipitation patterns cause temporal mismatches between root herbivores and EPNs (Preisser and Strong, 2004), reducing the capacity of EPNs to control root herbivore populations. We therefore predict that altered precipitation patterns are likely to further exacerbate the negative effects of shoot herbivory on the biological control of root herbivores.

3.2. Aboveground herbivore effects on soil decomposers

Invertebrate and mammal aboveground herbivory influences soil biota through altered exudation of carbon compounds from plant roots (Bever et al., 1997; Wardle et al., 2004). Results from early grazing studies (reviewed by Bardgett et al., 1998) generated the consensus that aboveground foliar herbivory stimulates root exudation, increasing microbial biomass and activity, and soil fungal abundance. This generalization was supported by subsequent work in mammal-grazed grassland systems where increased soil microbial biomass, due to the assimilation of root carbon exudation, generated a positive feedback to soil nitrogen mineralization and plant uptake (Hamilton and Frank, 2001; Hamilton et al., 2008). Increased abundance of root-associating soil fauna has also been reported as a consequence of mammal grazing-induced stimulation of root growth (Schon et al., 2010). Aphid (Stobion avenue) herbivory in contrast, reduced Poa annua root biomass, but still increased soil fungal (collomeloba, Folsomia candida) abundance, most likely as a consequence of root exudate-induced stimulation of fungal biomass (Sinka et al., 2007, 2009). Low soil carbon availability and primary production (Sankaran and Augustine, 2004), strong seasonal influences on microbial biomass and activity (e.g. in arid regions; Classen et al., 2006), and nitrogen limitation in nutrient-poor soils (Virtanen et al., 2008) can all limit the impacts of grazing on soil decomposer properties.

Artificial defoliation has been employed in several studies to replicate the sudden removal of shoot tissue by vertebrate grazing and insect herbivory. Such studies have generated equivocal results. In contrast to the general trend identified from herbivory, neutral (Bazot et al., 2005; Mikola et al., 2000, 2001b) and negative (Medina-Roldán and Bardgett, 2011; Mikola et al., 2001a; Sørensen et al., 2008) microbial biomass responses to artificial defoliation have frequently been reported, with variable impacts on soil fauna (Ilmarinen et al., 2005; Mikola et al., 2005; Pietikäinen et al., 2009; Sinka et al., 2007). Whilst some evidence exists for plant species (Hokka et al., 2004; Medina-Roldán and Bardgett, 2011) and growth phase- (Ilmarinen et al., 2005) specific plant biomass and root carbon exudation responses, much of the uncertainty derived from contrasting results is likely to reflect differential timing of rhizosphere sampling relative to the defoliation event. Studies that have sampled repeatedly over time have revealed a transient peak in root exudation up to 3–5 days following artificial defoliation, which is entirely diminished within one week (Henry et al., 2008; Mikola and Kyttövita, 2002; Paterson and Sim, 1999; Paterson et al., 2005). Further, artificial removal of aboveground plant biomass does not increase belowground resource availability in the same way as natural herbivory in which inputs of severed plant material and excrement from aboveground herbivory influence soil decomposer activity, as well as changes in root exudation.

Defoliation mediated by natural outbreaks of foliar herbivores has the potential to exert strong and prolonged influences on microbial community biomass and activity. Soils of fir forest defoliated by the Siberian moth (Dendrolimus superbus sibiricus) were characterized by a covering of zoogenic fall, comprising herbivore excrement and the bodies of dead larvae (Baranchikov et al., 2002). This altered abiotic conditions within the soil (increased temperature and moisture compared to non-defoliated forest) and stimulated microbial biomass and activity, such that a 50%
greater soil CO$_2$ efflux was still evident three years after defoliation (Fig. 4a). Experimental addition of *D. s. sibirius* frass to the forest floor confirmed the marked increases in microbial biomass, mineralization of several litter chemical elements (Fig. 4b) and CO$_2$ production as a direct consequence (Krasnoshchekov et al., 2003). The increase in microbial biomass developed during the first three months following frass addition and was detectable for several growing seasons. Defoliation, consequent alterations to soil chemical and microbiological properties, and associated cessation of root competition with the tree stand had promoted successional development of the plant cover within six years (Krasnoshchekov and Vishnyakova, 2003; Krasnoshchekov et al., 2003). Moth herbivory and frass deposition have also stimulated soil nutrient availability and turnover in birch (*Betula pubescens*) and oak (*Quercus rubra*) stands (Frost and Hunter, 2004; Kaukonen et al., 2013).

Whilst aboveground herbivores have obvious potential to influence belowground decomposer activity, microbial species and functional group dynamics are particularly difficult to assess. Few studies have attempted to reveal mechanisms and consequences of microbial community responses to foliar herbivory. Aboveground herbivory by the cabbage moth (*Mamestra brassicae*) on ragwort (*Jacobaea vulgaris*) altered soil fungal communities as well as plant chemical defense, generating a plant–soil feedback that influenced multi-trophic interactions mediated by plants growing later in the same soil (legacy effect; Bezemer et al., 2013; Kostenko et al., 2012). Soils that had previously contained plants subjected to foliar herbivory (conditioning phase) supported reduced root biomass and shoot pyrrolizidine alkaloid (defensive chemical) concentrations in later colonists, promoting aboveground herbivore performance and parasitoid emergence. Because root pyrrolizidine concentrations increased due to foliar herbivory in the conditioning phase, it was concluded that the effects on subsequent plants and trophic interactions were mediated by other factors, such as root exudation and pathogenic fungi (Bezemer et al., 2013; Kostenko et al., 2012). Further research is required into the possible mechanisms regulating foliar herbivore-induced impacts on plant–soil feedback, particularly in light of the implications for the performance of plants growing subsequently in the same soil.

Climate change and its associated causal factors will influence plant productivity and alter resource quality for both herbivores and decomposers. The potential for elevated CO$_2$, in particular, to reduce plant tissue quality is established, usually characterized by higher carbon:nutrient ratios and secondary chemical concentrations (Bezemer and Jones, 1998; Stiling and Cornelissen, 2007). The influence of aboveground herbivory on microbial activity and nutrient mineralization might be expected to reduce nitrogen limitation imposed by increased photosynthesis and plant growth under elevated CO$_2$. Reduced grasshopper (*Chorthippus brunneus*) herbivory (on grass, *Deschampsia flexuosa*) under elevated CO$_2$ has, however, increased nitrogen limitation as a consequence of intensified plant–microbe competition for nutrients (Stenbak et al., 2012). Minimal effects of elevated CO$_2$ on the quality of caterpillar (*Orgya leucostigma*) frass and aspen (*Populus tremuloides*) and birch (*Betula papyrifera*) greenfall exerted little influence on microbial biomass and respiration (Hillstrom et al., 2010). Input quantity, however, had a much stronger effect, suggesting that when herbivory is reduced, resource (frass and greenfall) availability could limit microbial activity.

Other studies reporting more marked plant tissue chemical changes under elevated CO$_2$ have not considered the transmission of effects belowground. Although there is much evidence for decreased foliar herbivore performance due to CO$_2$ elevation, increased performance has also been reported, with the direction and magnitude of effects depending on insect feeding-guild (reviewed by Bezemer and Jones, 1998; Zvereva and Kozlov, 2006). Elevated temperature will directly affect insect herbivores (and the biological control of their populations; Schmitz and Barton, this issue; Tylianakis and Binzer, 2013) with significant species- and context-dependency (reviewed by Bale et al., 2002). This will interact with warming effects on plant productivity, resulting in increased or decreased herbivory in different systems – a context-dependency which will make predictions difficult – and unknown effects on belowground biota.

**4. Conclusions**

The ecosystem services attributed to aboveground or belowground biota are strongly influenced by feedbacks between these spatially-separated sub-communities. Whilst the mechanisms regulating certain aboveground–belowground interactions are well characterized, others remain poorly understood. Maintaining plants free from root or shoot herbivory, as well as being of direct benefit to the plant, also appears indirectly to promote antagonism of the spatially-separate herbivore by its natural enemies. Soil decomposer activity and mycorrhizal association can increase shoot herbivore performance such that natural enemy control is weakened, or generate bottom-up trophic cascades which promote antagonism of aboveground herbivores. Soil nutrient status and herbivore feeding guild are important determinants of the prevailing mechanism. Aboveground herbivory generally stimulates the cycling of nutrients by soil decomposers, but there will be an important balance between the stimulation of plant growth by increasing nutrient availability and excessive damage by the herbivore. Root herbivory and mycorrhizal colonization both appear to promote floral attractiveness to pollinating insects. These tentative
conclusions concerning the multitrifrophic and functional implications of aboveground–belowground interactions are derived from limited empirical attention. The potential for climate change to alter these interactions is recognized, but any strong conclusions relating to this would be purely speculative. Further mechanistic understanding of how interactions between spatially-separated biota regulate ecosystem service provision and responses to climate change are tantalizing prospects for future research.

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References


