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MAJOR REVIEW

The role of soil community biodiversity in insect biodiversity

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Abstract. 1. This study demonstrates that feedback loops between plants and insects contribute to both plant and insect diversity. Synthesis of several studies reveals that both bottom-up and top-down forces are important for plant and insect communities.

2. Feedback loops between plants and soil organisms contribute to plant and soil diversity. An analysis of multiple systems reveals that pathogens, mutualists, and a wide variety of soil fauna directly influence, and are influenced by, plant diversity.

3. The connection of plant–insect and soil–plant feedback loops leads to the maintenance of all three groups, and the maintenance of these feedback loops crucially affects insect diversity. Examples of the influence of soil community diversity on insect diversity, and the influence of insect diversity on soil community diversity, as well as feedbacks through all three trophic levels are provided.

4. Finally, means of conserving and restoring soil communities to influence the conservation and restoration of insect communities are discussed.

Key words. Arbuscular mycorrhizal fungi, bottom-up, conservation, feedbacks, herbivore, insect diversity, plant diversity, restoration, soil diversity, top-down.

Introduction

Insect community conservation and restoration have been identified as important yet difficult tasks (Arenz & Joern, 1996). This manuscript aims to address some of the difficulties associated with insect conservation and restoration by identifying the potential contribution of soil community composition and diversity to insect composition and diversity. Here, it is discussed that feedbacks between insect diversity and plant diversity contribute to diversity in both groups whereas feedbacks between soil diversity and composition and plant diversity contribute to diversity in both the soil and plant communities. Finally, it is hypothesised that these two feedback loops are linked such that soil microbial communities contribute to insect diversity via plant diversity, and vice versa, and the maintenance of these feedback loops between soil microbes, plants and insects affects insect diversity. These linked feedback loops have consequences for insect conservation and restoration.

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While there are many factors that contribute to soil, plant and insect diversity (including abiotic conditions, mammalian grazers, and competition between soil organisms, plants and insects), this study focuses on the contribution of soil community, plant and insect diversity to diversity among all three groups.

Diversity varies from local to global scales, and can be defined in many ways. Due to the difficulty of studying unseen organisms in the soil matrix, many measures of diversity aboveground, especially abundance, cannot be easily used belowground. While both species richness (the number of species) and diversity (the number and abundance of species) are easily measured aboveground, until very recently only species richness was estimable belowground for most organisms. Here, when diversity is discussed as a concept it will include measures of both species richness and diversity. Patterns of plant and insect diversity vary along latitudinal gradients. A satisfactory explanation for the latitudinal gradient in species diversity has yet to be identified and may vary by group (De Deyn & Van der Putten, 2005), and will probably operate in addition to the feedbacks among insects, plants and soil microbes that operate at smaller scales. Thus, this study will focus on terrestrial alpha diversity. Local scales, such as a field or park, are the most important for restoration and conservation biologists (Samson & Knopf, 1996; Packard & Mutel, 1997), and within alpha diversity feedback loops between microbes, plants and insects will probably play strong roles in structuring the diversity within each group.

The interaction between plant and insect diversity

Plant diversity contributes to insect diversity

The putative role of plant diversity in contributing to insect diversity has been discussed by a number of authors (e.g. Hutchinson, 1959; Southwood, 1966; Hunter & Price, 1992). Primarily these authors focused on whether plant diversity influences the diversity insect herbivores (Strong *et al*., 1984). For example, Southwood suggested that variation in habitats (plant communities) through time and space provides variation that supports multiple species (Fig. 1) (Southwood, 1977, 1988; Southwood *et al*., 1979). More recent studies have demonstrated that changes in plant diversity alter not only herbivore diversity, but also insect predator and parasitoid diversity (Siemann, 1998; Knops *et al*., 1999). There are also a number of direct mechanisms by which plants influence natural enemies, including volatiles released by attacked plants, the creation of structural refuges that shelter herbivores, structures such as trichomes that interfere with enemy foraging, and plant toxins that can be sequestered by herbivores as defences against enemies (Fig. 1) (Price *et al*., 1980). Thus, increased diversity and/or functional diversity of plant species increases the potential diversity of mechanisms by which plants can influence insect herbivores and their enemies (Price *et al*., 1980; Siemann, 1998; Knops *et al*., 1999; Perner *et al*., 2003).

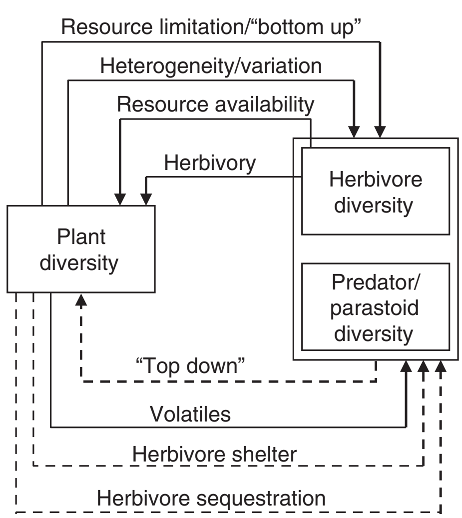

Fig. 1. A representation of the mechanisms discussed in the text that affect plant and insect diversity, and which contribute to feedbacks on diversity between the two sets of organisms. Direct mechanisms are represented by solid lines and indirect mechanisms are represented by dashed lines.

Numerous studies in a wide variety of systems ranging from grasslands to forests have demonstrated that plant diversity contributes to insect diversity (Murdoch *et al*., 1972; Southwood *et al*., 1979; Crisp *et al*., 1998; Siemann, 1998; Siemann *et al*., 1998; Knops *et al*., 1999; Koricheva *et al*., 2000; Perner *et al*., 2003). Other factors also influence insect diversity. A path analysis revealed that in diversity treatments the presence of legumes increased insect composition (Koricheva *et al*., 2000), whereas insect distribution was a product of irrigation treatment in a factorial design conducted in an arid climate (Wenninger & Inouye, 2008). Variation in species cover, plant biomass, soil nutrients and management regimes among 71 sites in Germany influenced arthropod abundance and functional group representation (Perner *et al*., 2005). Despite the influence of other factors, however, the overall pattern remains the same: plant diversity influences insect diversity.

Insect diversity contributes to plant diversity

Insect diversity is also a driver of plant diversity. For example, Huston (1979) suggested that plant diversity is a product of variation in the rate at which different plant species' competitive abilities are expressed, and these rates are influenced by external variables such as environmental regulation, nutrient availability, and, of course, herbivory. We know plant diversity can also be influenced by competition, stress tolerance, dispersal, facilitation, successional stage and environmental heterogeneity (reviewed in Lundholm, 2009). Insects can strongly influence the abundance and richness of plant species during insect outbreaks, which can limit the fitness and abundance of certain plant species [e.g. outbreaks of chrysomelid beetles on goldenrod species (Carson & Root, 2000)]. Even in non-outbreak scenarios insect herbivores have been shown to limit plant fitness (Schoonhoven *et al*., 2005), and even small amounts of insect herbivory can limit tree fitness (Crawley, 1985).

Insects clearly do not however decimate plant populations, and this is primarily due to the influence of herbivore enemies (Hairston *et al*., 1960; Lawton & Strong, 1981; Bernays & Graham, 1988). 'Top down' theory suggests that the prevalence of herbivore enemies limits herbivore populations preventing them from consuming all plants (Fig. 1). Several tests of 'top down' theory have demonstrated that herbivore enemies limit herbivore populations (reviewed in Hunter, 2001b), and plant adaptations such as volatiles may aid in top-down regulation (reviewed in Howe & Jander, 2008, Fig. 1).

Insect diversity–plant diversity feedbacks

Feedbacks between insect and plant diversity contribute to diversity in both groups. Despite earlier debates over the quantification of relative top-down and bottom-up effects (Hunter *et al*., 1997; Hassell *et al*., 1998), the current consensus is that both top-down and bottom-up effects influence ecosystems (Chapin *et al*., 2002). Feedback loops in ecological systems restrict the existence of unidirectional pathways (such as top-down or bottom-up effects) within ecological systems, because time can shift systems from top-down to bottom-up effects and vice versa, changing unidirectional pathways over time resulting in feedback loops (Hunter, 2001b). The relative importance of top-down and bottom-up interactions also depends upon environmental heterogeneity [factors such as water availability (Chase *et al*., 2000; Boyer *et al*., 2003; van Bael *et al*., 2003), light availability (Chase, 1996; Richards & Coley, 2007), nutrient availability (Denno *et al*., 2002) and spatial structure (Preszler & Boecklen, 1996; Gripenberg & Roslin, 2007)]. Thus, insect herbivores and their natural enemies affect plant diversity (through top-down mechanisms) whereas plant diversity affects the diversity of higher trophic levels (through bottom-up mechanisms) (Hunter & Price, 1992; Hunter, 2001b; Walker & Jones, 2001). This suggests that diversity of plants contributes to diversity of insects, and vice versa (Fig. 1).

The interaction between plant and soil community diversity

Soil community diversity contributes to plant diversity

Are insects the only organisms responsible for the maintenance of plant diversity? Hunter and Price (1992) suggested that members of soil microbial communities, including decomposers, pathogens and mutualists, probably influence plant community structure as well. Environmental regulation and nutrient availability, factors often regulated by the soil community, probably play a role in mediating plant competitive abilities (Huston, 1979), and other factors, such as stress tolerance and facilitation are probably somewhat regulated by interactions with soil communities. The diversity and activity of soil microbial biomass also contribute to the maintenance of plant diversity (reviewed in van der Heijden *et al*., 2008). For the sake of simplicity, belowground insects will be included as members of the soil community.

Pathogens

Soil pathogens strongly influence plant survival, abundance and diversity (van der Putten *et al*., 1993, 2007; Bever, 1994; De Rooij-van der Goes, 1995; Mills & Bever, 1998; Packer & Clay, 2000; Kardol *et al*., 2006, 2007). Pathogens may facilitate succession through the species-specific suppression of early colonisers allowing resistant later-successional species to colonise (van der Putten *et al*., 1993; Kardol *et al*., 2006, 2007). Pathogens are also agents of negative feedback that contribute to plant diversity (Bever, 1994; Mills & Bever, 1998; van der Putten *et al*., 2007). The Janzen–Connell Hypothesis (Janzen, 1970; Connell, 1971) proposed a mechanism by which the high variation in tree diversity in tropical climes could be maintained through host-specific pathogen attacks. This mechanism operates in both tropical (Wright, 2002) and temperate regions (Packer & Clay, 2000). Thus, pathogen diversity probably contributes to plant diversity in a wide variety of environments and conditions (Fig. 2).

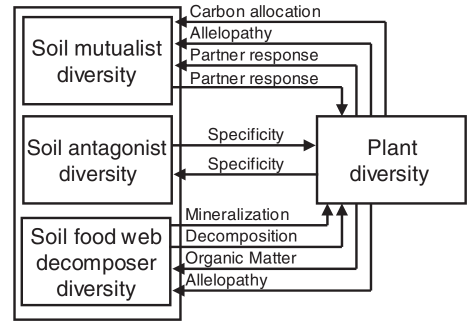

Fig. 2. A representation of the mechanisms discussed in the text that affect soil and plant diversity, and which contribute to feedbacks on diversity between the two sets of organisms. Direct mechanisms are represented by solid lines and indirect mechanisms are represented by dashed lines. Soil diversity is split into the three general categories of organisms discussed: Soil Mutualists (such as mycorrhizal fungi and rhizobia), Soil Antagonists (including pathogens, root herbivores, etc.), and the Soil Food Web and Decomposer community.

Mutualists

Due to early work by Bever (1994, 1999, 2002a,b, 2003) as well as van der Heijden *et al*. (1998), there has been a research emphasis on the contribution of soil mutualists, particularly mycorrhizal fungi to plant diversity. Mycorrhizal fungi associate with plant roots, delivering nutrients in return for carbon. The two most common types of mycorrhizal fungi are ectomycorrhizal fungi (EM fungi), which deliver nitrogen to their primarily woody hosts, and arbuscular mycorrhizal fungi (AM fungi), which deliver phosphorus to a wide variety of herbaceous and deciduous tree hosts (Smith & Read, 1997).

There are two hypothesised mechanisms for how mycorrhizal fungi might contribute to plant diversity. First, increasing the number of mycorrhizal fungal species may increase pathways of negative feedback that contribute to plant diversity. Research in microcosms has identified the presence of negative feedback loops between plants and the AM fungal species they host (Bever, 2002a,b). These feedback loops work when plants (or fungi) promote the fitness of partners that, in turn, are of greater fitness advantage to *other* plant (or fungal) species in the community, as demonstrated with *Panicum sphaerocarpon* and *Plantago lanceolata* grown with the co-occurring fungal species *Scutellospora calospora*, *Acaulospora morrowiae* and *Archaeospora trappei* (Bever, 2002a,b). *Panicum sphaerocarpon* promoted *A. trappei* and *A. morrowiae* which in turn promoted the growth of *P. lancoeolata* which in turn promoted *S. calospora* which in turn benefited *P. sphaerocarpon* thereby promoting diversity among both fungi and plants. Negative feedback loops generate a system of frequency-dependent selection. Negative feedback and frequency dependence will contribute to the maintenance of species diversity in both plant and fungal communities (Fig. 2).

The second hypothesis suggests that increasing mycorrhizal fungal diversity increases fungal functional diversity, and increasing functional diversity will increase the availability of resources for host plants under a wide variety of conditions (Read, 1998). A variety of theoretical and empirical work has suggested that different mycorrhizal fungal species may access different sources of nutrients (Reynolds *et al*., 2003b), vary in life-history strategies that probably influence foraging abilities (Hart & Reader, 2002, 2005), or mediate competition between plant species (Moora & Zobel, 1996; Rejon *et al*., 1997; van der Heijden, 2002, Fig. 2).

Greenhouse experiments show that increasing AM fungal richness leads to increasing plant community stability and diversity (Grime *et al*., 1987; Gange *et al*., 1993; van der Heijden *et al*., 1998). A field observation in an oak savanna showed a positive correlation between plant species richness and AM fungal richness (Landis *et al*., 2004), and in a series of field studies that reduced AM fungi through application of a fungicide there were significant shifts in plant species composition as well as reductions in plant cover and recruitment (Gange *et al*., 1990, 1993). Later field studies showed the potential for root-feeding insects to reduce the benefit of AM fungi (Gange & Brown, 2002).

The majority of plant species associating with EM fungi are slow-growing tree species. How EM fungi influence plant diversity has rarely been tested due to the impracticality of long-term manipulative experiments. EM fungi, however, may still contribute to plant diversity in manners similar to AM fungi. Variation in competitive outcomes between trees associated with different EM fungal communities has been demonstrated (Hoeksema, 2005; Kennedy *et al*., 2007), and transfer of carbon between adult trees and seedlings (Newman, 1988; Perry *et al*., 1989; Simard *et al*., 1997; Leake *et al*., 2004) could decrease competition and increase co-existence resulting in increased plant diversity (Kernaghan, 2005). There is also evidence that individual EM fungal species produce host-specific (Molina *et al*., 1997) and succession-specific growth patterns (Twieg *et al*., 2007), which represent the basic conditions for feedback among EM fungal hosts.

Rhizobia within legumes have also been shown to contribute to the diversity of aboveground plants (Van der Heijden, 2006). Rhizobia fix atmospheric nitrogen for their leguminous hosts. Nitrogen fixation often results in increased nitrogen availability for neighbouring non-leguminous species (Hooper *et al*., 2005). Grassland mesocosms inoculated with a variety of rhizobia bacterial species produced greater community productivity and evenness than mesocosms lacking rhizobia (Van der Heijden, 2006). This increase in evenness (a component of diversity) in grasslands is probably a result of facilitative interactions between leguminous plants and forb species that reduce competition for the limiting nutrient nitrogen. The interaction of multiple mutualist partners, or mutualist guilds, with plant hosts may be the norm (Stanton, 2003), thereby suggesting that a wide variety of belowground mutualists contributes to aboveground diversity.

Soil food web/decomposers

Through decomposition and mineralisation soil microbes are predicted to have large impacts on plant productivity, species diversity and richness. Decomposer communities have often been thought to be highly redundant, but that redundancy probably occurs primarily within groups (e.g. fungal decomposers, bacterial decomposers, etc.) and may be a product of great spatial variability (reviewed in Seälä *et al*., 2005). Unfortunately, there is still much work that needs to be done examining the role of soil food webs in ecosystem functioning, but preliminary conclusions suggest two important points. First, keystone species, often earthworms (Lavelle *et al*., 1997; Bonkowski *et al*., 1998; Scheu *et al*., 2002; Partsch *et al*., 2006), diplopods (Bonkowski *et al*., 1998; Seeber *et al*., 2008), or enchytraeid worms (Cole *et al*., 2000, 2002a,b; Seeber *et al*., 2008), have dramatic impacts on ecosystem functioning that can often translate into impacts on plant diversity through changes in plant productivity (reviewed in Scheu, 2003; Huhta, 2007).

Communities of invertebrate soil fauna have been shown increase plant species richness (Brown & Gange, 1992; Gange & Brown, 2002; De Deyn *et al*., 2007), favour late successional species resulting in an increase in local plant species diversity (De Deyn *et al*., 2003), and increase in the rate of succession (Brown & Gange, 1992), although variation in functional group richness, and not species richness, may explain these results (Heemsbergen *et al*., 2004). Specialist root herbivores can alter plant community composition by targeting specific members while generalists are more likely to influence composition through variation in preferences (which can be influenced by host plant quality) (reviewed in Mortimer *et al*., 1999). Root herbivores have also been shown to increase plant species richness (Brown & Gange, 1992; Gange & Brown, 2002; De Deyn *et al*., 2007), and this effect may be due to selective feeding or reduced competition between plant species caused by root herbivory (Agrawal, 2004). Large insects, such as cicadas and scarab larvae have been shown to have strong impacts on plant survival and density in tallgrass prairies (reviewed in Whiles & Charlton, 2006). Periodical cicadas have been shown to influence strong resource pulses in both grasslands (Whiles *et al*., 2001) and forests (Yang, 2004). Agricultural studies reveal that various wireworm species show preferences for different potato (Jonasson & Olsson, 1994; Olsson & Jonasson, 1995; Kwon *et al*., 1999; Johnson *et al*., 2008) and sweet potato (Thompson *et al*., 1999) genotypes. Although most agricultural studies focus on genotypes of a single species, there is evidence that variation in preference among genotypes scales up to variation in preference among species (Hemerik *et al*., 2003).

Preliminary conclusions suggests that the composition and diversity of the active decomposer component of food webs (primarily fungi and bacteria) often have the strongest influence on ecosystem functioning and plant productivity (Laakso & Setala, 1999; van der Heijden *et al*., 2008), and this effect is often not influenced by the presence of soil fauna that feed upon these bacteria and fungi (Fig. 2) (VreekenBuijs *et al*., 1997; Mikola & Setala, 1998). Soil community composition has also been shown to influence plant species composition in the absence of effects on productivity (Bradford *et al*., 2002). Soil community components can also act as checks on other productivity limiting organisms (e.g. Piskiewicz *et al*., 2007). As a result, factors such as the composition of the soil food web (Huhta, 2007; van der Heijden *et al*., 2008), the presence or absence of keystone species (Huhta, 2007), indirect effects between soil community members (Laakso *et al*., 2000) and the composition of the decomposer community (van der Heijden *et al*., 2008) will all have important consequences for the diversity of plants.

Plant diversity contributes to soil community diversity

Plant diversity also influences soil community diversity. Studies of single species plant communities in the field and the greenhouse have revealed that they support vastly different communities of AM fungi (Eom *et al*., 2000; Johnson *et al*., 2004), saprophytes (Wardle *et al*., 2003), nematodes (De Deyn *et al*., 2004; Viketoft *et al*., 2005; Viketoft, 2008), microbes (Innes *et al*., 2004), and mites (Badejo & Tian, 1999). We see similar patterns of unique soil communities beneath plants contained within communities in the field (Berg & Hemerik, 2004; Ahulu *et al*., 2006; Sýkorová *et al*., 2007; Viketoft, 2007; Viketoft *et al*., 2009). Also the assemblage of plant species is just, or more, important than the sum of its parts. For example, soil mite assemblages appear to respond not to single species, but to entire plant assemblages (St John *et al*., 2006b), creating a nonlinear positive correlation between plant species richness and mite species richness (St John *et al*., 2006a). In contrast, in some cases the distribution of nematodes can depend strongly on individual plant species, although this varies among studies (Viketoft *et al*., 2009). In addition, variation in plant communities creates variation in organic matter (reviewed in Ehrenfeld, 2003) and microbial biomass (Haynes *et al*., 2003). Plant biomass also plays an important role in determining soil community diversity through the regulation of resource availability (Mikola & Setala, 1998; Degens *et al*., 2000). Plant-induced variation in microbial communities appears to vary in effect between groups of soil organisms (Porazinska *et al*., 2003), and seems to be strongest for soil organisms directly interacting with plant hosts, such as mutualists and pathogens (Wardle, 2006).

In mesocosms using plants and microbes that regularly interact, variation in soil microbial communities in response to plant diversity is often not observed (reviewed in Wardle, 2006; Huhta, 2007). This may result from the exclusion of important organisms (e.g. larger invertebrates) (Wardle, 2006), limited dispersal capabilities within mesocosms, different effects dominating at smaller scales (Huhta, 2007), or temporal effects not simulated in mesocosms. Spatial effects also probably have a strong influence over the distribution and diversity of soil organisms living in structured environments (soil) with limited dispersal (Bardgett *et al*., 2005).

Some of the best evidence from field studies for plant-induced changes in soil community diversity involve invasive plant species (reviewed in Wolfe & Klironomos, 2005). Shifts in AM fungi (Hawkes *et al*., 2006; Stinson *et al*., 2006; van der Putten *et al*., 2007) and EM fungi (Orlovich & Cairney, 2004), rhizobia (Vitousek & Walker, 1989), and indicators of whole microbial communities (Batten *et al*., 2008) as well as nutrient cycles (Vitousek *et al*., 1987; Liao *et al*., 2008) have all been reported in association with the introduction of novel species. In most cases, how invasive plants influence their associated microbes is unclear, and more experiments are needed to identify the mechanisms behind these changes.

Some research has hinted at mechanisms by which plants can influence their soil communities. We know that plants vary in their carbon allocation to roots (reviewed in Litton *et al*., 2007), as well as the pattern of root exudates (reviewed in Rengel, 2002, Fig. 2). Variation in the different compounds released from plant roots have been shown to favour different soil organisms over others (reviewed in Bais *et al*., 2006) in combination with temperature (Kuzyakov *et al*., 2007), soil type (Berg & Smalla, 2009), and other factors. In addition, direct interactions between plants and the soil community can influence the diversity of mutualists and pathogens, indirect interactions can influence decomposers through litter inputs, and plants can use allelopathy to disrupt soil communities (Fig. 2).

Mutualists

Negative feedback loops between plants and AM fungi (and possibly EM fungi) contribute to the diversity of mycorrhizal fungi in soils. Different plant hosts promote fungal fitness differently generating a system in which increasing fitness of one AM fungal species feeds back to create an increasing fitness advantage for competing AM fungal species (Bever *et al*., 1996; Bever, 2002a,b, Fig. 2). A meta-analysis of studies investigating AM fungal diversity at sites varying in anthropogenic disturbance found that AM fungal diversity and composition declined as plant diversity declined (Opik *et al*., 2006), and in an oak savanna plant species richness was positively correlated with AM fungal species richness (Landis *et al*., 2004).

Pathogens

In order for pathogens to be responsive to plant community diversity, they must have some level of specificity for host plants. Generalist pathogens should respond only to changes in plant productivity, not plant diversity. Many pathogens are specialists and respond to the presence of only a few plant species (Bever *et al*., 1997; Marilley *et al*., 1998; Kowalchuk *et al*., 2002). As a result, a greater diversity of plant hosts should support a greater diversity of pathogens (Fig. 2). To date, however, this author knows of no direct test of this concept.

Litter inputs

The senescence of plant tissue that falls to the soil surface directly impacts soil communities, particularly decomposer bacteria and fungi. Plant species identity has been shown to influence decomposer communities (reviewed in Wardle, 2005), and monocultures of leaf litter have been shown to support different communities of decomposer invertebrates (Hansen, 1999; Wardle *et al*., 2006, Fig. 2). Species mixes of litter have been shown to increase soil invertebrate diversity in most cases (reviewed in Wardle, 2006). Species and genotypic diversity of litter may influence changes in soil microbial communities through responses by decomposer bacteria and fungi to rates of organic matter return (Diaz *et al*., 2004), variation in carbon to nitrogen ratios (Madritch & Hunter, 2002), association with leaf endophytes (Omacini *et al*., 2001), and the presence of tannins and other secondary compounds in leaf tissue (Wardle, 2006). In addition, variation in litter structure has been suggested to improve habitat and diversity of litter invertebrates and EM fungi (reviewed in Wardle, 2006).

Allelopathy

Allelopathic plant compounds can influence both plants and soil microbial communities (Stinson *et al*., 2006; Lankau & Strauss, 2007). Although this has yet to be demonstrated, allelopathy could alter plant communities resulting in altered microbial communities. Allelopathic chemicals can also negatively impact soil organisms, and reductions in soil communities then feed back to impact negatively neighbouring species (Fig. 2; Stinson *et al*., 2006; Lankau & Strauss, 2007). For example, release of glucosinolates by the invasive garlic mustard (*Allaria petiolata*) has been shown to impact negatively AM fungal spore production (Stinson *et al*., 2006) and EM root tip abundance (Wolfe *et al*., 2008), and black mustard (*Brassica nigra*) plants with high levels of glucosinolates have been shown to reduce AM fungal infection and growth promotion in neighbouring species (Lankau & Strauss, 2007). Both of these studies suggest two things: first, allelopathic plants may be targeting not just neighbouring plants but the soil communities they depend upon thereby providing a twofold strike on competitors, and second, future studies of allelopathic plants will probably discover effects of allelopathy cascading through a wide variety of soil organisms.

Feedbacks between soil community diversity and plant diversity

There is significant evidence to support feedbacks between soil community diversity and plant diversity. Feedbacks between plants and AM fungal mutualists that affect the diversity of both groups (Bever, 2002a,b) have already been discussed above. Many studies have examined how plant-induced changes in soil communities influence future plant communities (reviewed in Bever *et al*., 2002; van der Putten, 2005; Wardle, 2005; Kulmatiski *et al*., 2008), although the direction and strength of feedbacks can be altered by nutrient levels or change through time (van der Putten, 2005). A recent study showed invasive plant species *Aegilops triuncialis* changes in soil microbial biomarker fatty acids negatively impacted growth of the native species *Lasthenia californica* (but not the growth of native species *Plantago erecta*) (Batten *et al*., 2008). Other interactions may also strengthen feedbacks. Soil meso- and macrofauna have been shown to limit root growth into nutrient patches (Bradford *et al*., 2006) which may actually increase plant dependence on nutrient-uptake mutualist partners. As a result, plant-induced changes in soil diversity can feed back to influence plant diversity, and the maintenance of these feedback loops are probably strong contributors to both plant and soil community diversity.

The interaction between soil community diversity and insect diversity

Here, it is hypothesised that plant–soil diversity and plant–insect diversity feedback loops are mediated via plants. The evidence for this hypothesis is examined in the following sections.

Soil community diversity affects insect diversity

To date, this author knows of no study testing the direct effects of soil community diversity on aboveground insect diversity. In a study examining the influence of root herbivores and nematodes on aboveground grasshopper growth, De Deyn *et al*. (2007) found that nematodes negatively influenced grasshoppers while the presence of root herbivores negated any effects on grasshoppers via changes in plant biomass. Root herbivores and nematodes, together and alone, have been shown to increase aphid and aphid parasitoid abundances, while only root herbivores influenced pollinator visitation in wild mustard (Poveda *et al*., 2005). Interactions between root and shoot herbivores via their host plants have been shown to vary among habitats and systems (reviewed in Masters *et al*., 1993). For example, Masters and colleagues have shown that root herbivory on *Sonchus oleraceus* benefits aboveground invertebrate herbivores from a wide variety of classes (suckers, chewers, and miners) (reviewed in Masters & Brown, 1997). There are several possible mechanisms through which soil community diversity could contribute to insect diversity. First, soil organisms could simply increase the diversity of plant species available to herbivores. Second, soil organisms could contribute to phenotypic variation within species by modifying plant size or quality (Karban *et al*., 1997; Bennett *et al*., 2006). Modifying plant defences or growth rates would create a patchy distribution of plant phenotypes, and thus greater overall variation for insects to utilise (Karban & Baldwin, 1997). Finally, soil organisms could alter both plant inter- and intra-species variation in traits that directly or indirectly affect herbivores and other insects resulting in greater insect diversity (Fig. 3).

How might soil organisms contribute to intra-species variation in plants? The direct interaction between plants and herbivores can be modified through variation in plant quality and quantity (Schoonhoven *et al*., 2005). Pathogens and mutualists alter growth and reproduction of host plants. Different AM fungal species and communities of species have been shown to alter plant tolerance to herbivory (Borowicz, 1997; Gange *et al*., 2002; Kula *et al*., 2005; Bennett & Bever, 2007), constitutive levels of plant defence compounds (reviewed in Gehring & Whitham, 2002; Strack *et al*., 2003; Gange, 2007; Gehring & Bennett, 2009), induced direct responses to herbivory (Pozo & Azcon-Aguilar, 2007; Bennett *et al*., 2009), and volatile release (Gange *et al*., 2003; Guerrieri *et al*., 2004; Bezemer & van Dam, 2005). Nematodes with or without a soil microbial community

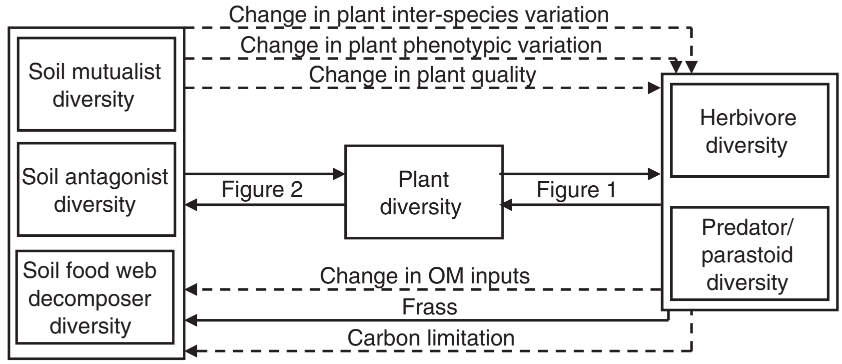

Fig. 3. A representation of the mechanisms discussed in the text that affect soil and insect diversity via plant diversity, and which contribute to feedbacks on diversity between the two sets of organisms. Direct mechanisms are represented by solid lines and indirect mechanisms are represented by dashed lines. The mechanisms that maintain soil and plant diversity, and plant and insect diversity are found in Figs 1 and 2 and are represented as such in this figure (to avoid complication).

reduced aphid parasitoid mortality in grassland mesocosms (Bezemer *et al*., 2005) while root herbivores reduced aboveground parasitoid and hyperparasitoid adult biomass (Soler *et al*., 2005) through changes in plant defence compounds or plant quality (Bezemer *et al*., 2005; Soler *et al*., 2005). Black mustard root herbivores can change the quality of volatile releases in a way that results in a decrease in parasitoid oviposition on aboveground herbivores (Soler *et al*., 2007b). A non-mutualistic fungal root endophyte (*Acremonium strictum*) has also been shown to reduce quantity but increase the variety of volatiles emitted resulting in increased oviposition deposition by moths (Jallow *et al*., 2008). The presence of rhizobia has also been shown to increase the palatability of plants to mammalian herbivores (Ritchie & Tilman, 1995). Decomposer bacteria and fungi release nutrients which can directly influence plant growth and reproduction. Thus, soil organisms can produce variation in the quantity and quality of plant tissues, the quantity and quality of plant tissues directly influence herbivore growth and survival (Schoonhoven *et al*., 2005) and probably influence herbivore enemies through quality of volatile release or abundance and quality of prey items.

Interactions among soil microbes or between soil microbes and larger soil fauna have been shown to produce a wide variety of responses in plants. For example, earthworms have been shown to alter foliar nitrogen (Newington *et al*., 2004), and combinations of earthworms and mycorrhizal fungi alter plant quality through changes in constitutive levels of plant defensive compounds (Wurst *et al*., 2004). The distribution of litter has also been shown to influence plant defensive compounds (Wurst *et al*., 2004).

Much less is known about how the soil communities might influence non-herbivorous insect species. Increases in herbivore number and diversity probably translate into greater herbivore enemy numbers and diversity. AM fungi can influence visitation by aphid parasitoids (Guerrieri *et al*., 2004), and AM fungal species identity influences the rate of parasitism of leaf miners (Gange *et al*., 2003) presumably through changes in released volatiles. Root herbivores have been shown to alter the composition of volatile compounds released (Soler *et al*., 2007b), and changes in nutrient availability also alter the release of plant volatiles (Schmelz *et al*., 2003; Lou & Baldwin, 2004). Soil microbial community changes in nutrient availability probably cascade up to herbivore enemies if not countered by other changes in plant quality (Bezemer *et al*., 2005; Soler *et al*., 2005). In addition, soil organisms could directly impact herbivore enemy diversity and abundance through alterations in plant quality, plant structure that alters enemy search patterns or movement, or creation of structural refuges (Price *et al*., 1980). Climate change, however, may alter the relationship between above- and belowground organisms and between trophic levels (Hartley & Jones, 2003; Voigt *et al*., 2003; Staley *et al*., 2007).

Pollinators are also probably influenced by changes in plant structure or nutrients that alter the quality and volume of pollen and nectar production. Several studies have demonstrated that AM fungi can influence host plant architecture in ways that translate into variation in pollinator visitations (Gange & Smith, 2005; Wolfe *et al*., 2005). The elimination of mutualistic AM fungi changes plant community structure resulting in changes in the community of pollinators visiting plants (Cahill *et al*., 2008). Thus, mutualistic insects are also influenced by changes in soil communities.

Insect diversity affects soil community diversity

Does insect diversity influence soil community diversity? Some recent research has focused on the influence of aboveground herbivores on belowground herbivores (Soler *et al*., 2007a), primarily through induction of defences in plant tissues (van Dam *et al*., 2003; Bezemer *et al*., 2004; Hol *et al*., 2004). In addition, foliar herbivory has been shown to influence negatively parasitoids of root herbivores (Soler *et al*., 2007a). The majority of research in this area, however, has primarily been focused on how herbivores and herbivore enemies influence decomposer systems and mycorrhizal fungi.

Insect influences on decomposer systems

Invertebrate herbivores and their predators are most likely to influence soil communities indirectly through the abundance and variety (or quality) of litter (or organic matter) entering the soil system (Pastor & Naiman, 1992; Bardgett & Wardle, 2003; Cebrian & Lartigue, 2004). While other factors, such as mammalian herbivores, pathogens, temporal changes, and abiotic factors are known to influence decomposer systems, this study will focus on the contribution of insects to microbial decomposition. In grassland mesocosms, the addition of aphid herbivores alone benefited soil decomposer bacteria at the expense of decomposer fungi as well as herbivorous nematodes (Wardle *et al*., 2005) and microbe feeding nematodes (Wardle *et al*., 2004), but the addition of aphid enemies reversed these effects and benefited primary and tertiary consumers through changes in plant biomass and community composition (Wardle *et al*., 2005). Similarly, Dyer and Letourneau (2003) found that aboveground predators influenced decomposer faunal communities primarily through regulation of plant biomass. Siberian moth frass had effects on soil organisms lasting up to 3 years, while greenfall from Siberian moth herbivory had short-term effects on soil community activity (Krasnoshchekov *et al*., 2003; Krasnoshchekov & Bezkorovainaya, 2008). Thus, insects can influence the diversity and abundance of soil organisms (Fig. 3).

Aboveground insects may also influence belowground communities through other direct and indirect pathways (Hunter, 2001a). The quantity and quality of plant biomass have the strongest influence over soil detrital communities (Wardle *et al*., 2006). Herbivore changes in litter composition through the induction of secondary compounds in leaf tissue will probably influence decomposer communities (Fig. 3) although this has yet be explicitly tested. Aboveground invertebrate herbivory has also been shown to influence negatively root feeders (reviewed in Masters & Brown, 1997). Herbivory by aphids, but not grasshoppers, has been shown to increase collembola populations in the top soil layer where host plant root density is reduced (Sinka *et al*., 2007, 2009).

All herbivores (both vertebrate and invertebrate) can directly influence soil nutrient inputs through excrement (frass). Frass inputs from canopy insect herbivores have been shown to influence soil invertebrates and alter nitrogen and carbon cycles (Reynolds *et al*., 2003a), and variation in soil nitrogen has been shown to alter plant diversity (Wedin & Tilman, 1996, Fig. 3).

Insect influences on mycorrhizal fungi

Herbivory by insects has been shown to reduce both AM and EM fungal colonisation in host plants (reviewed in Gehring & Whitham, 1994, 2002; Wamberg *et al*., 2003; but see Hokka *et al*., 2004; Gange *et al*., 2005; Gange, 2007), and these patterns of colonisation reduction vary with the degree of defoliation, can persist through time, and can result in changes in species composition (reviewed in Gange, 2007). Gange (2007) hypothesised that the level of herbivory will determine the effect of herbivores on mycorrhizal fungal richness, with the greatest richness occurring between low and moderate levels of defoliation. Reduced colonisation by mycorrhizal fungi may be a result of carbon limitation given that both herbivores and mycorrhizal fungi act as carbon sinks for host plants (Gehring & Whitham, 2002; Gange, 2007, Fig. 3). The opposite pattern (increasing mycorrhizal colonisation) occurs for plants experiencing root herbivory, and this pattern may be due to changes in root exudation that attract mycorrhizal fungi (reviewed in Gange, 2007).

Soil community diversity is important for insect diversity

Soil community diversity affects plant diversity which, in turn, affects insect diversity which feeds back to affect plant diversity and thus affect soil community diversity. This feedback loop has strong consequences. In an age where many insect species face extinction, the question of insect conservation has been pushed to the forefront. Due to their great mobility and small size, however, the conservation of insects creates great challenges. Plant and insect conservation should also include soil conservation. Understanding how disturbance and habitat fragmentation influence belowground organisms and produce cascades through ecosystems should be a priority for insect conservationists.

So then, how does one conserve soil communities? Many factors that influence plant and insect communities also influence soil communities. In particular, disturbance, such as tillage agriculture, can reduce soil diversity (Douds & Millner, 1999; Oehl *et al*., 2004), and, as discussed above, agricultural monocultures and invasive-dominated systems can limit soil community diversity. Thus, conservation efforts should focus on reducing disturbance at all trophic levels.

In the case of restoration, restoring the links between soil, plant and insect diversity has often been difficult to establish through simple broadcast of plant seed. The inoculation of disturbed soils with soil mutualists such as AM fungi and rhizobia has been shown to increase plant diversity in restorations in Mediterranean climates (Estaun *et al*., 2007), restorations following desertification (Requena *et al*., 2001) and prairie restorations (Smith *et al*., 1998; Bever *et al*., 2003). In addition, inoculation with whole soil communities from areas similar to the idealised reference state (Kemery & Dana, 1995) have been shown to increase establishment, growth and diversity in prairies (Bever *et al*., 2003). Field inoculation is best achieved by outplanting plant plugs that have grown in soil from the idealised reference state into the restoration site (Bever *et al*., 2003) to provide a host for rhizosphere organisms.

Feedbacks between soil and insect communities suggest that any increase in plant diversity resulting from inoculation with appropriate soil communities should cascade up to influence insect communities (and then back to down to influence soil communities). Thus, the maintenance of multiple links in the feedback loops between soil organisms and insects is a key factor in the restoration and maintenance of insect diversity.

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