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PERSPECTIVE

Do plant- and soil-mediated legacy effects impact future biotic interactions?

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Summary

1. Biotic interactions of plants can have legacy effects mediated by changes in plant traits and soil characteristics. Legacy effects are defined as effects that persist after the causal biotic interaction ceases, because plant traits and soil characteristics are plastic and modifications may be maintained for long time periods.

2. To date, studies on biotic interactions of plants with above- and below-ground organisms and their plant-mediated interactions have mainly focused on short-term effects in the continuous presence of interacting organisms.

3. Little is known about how long the changes in plant traits and soil characteristics persist after the biotic interaction ceases and indirectly affect future biotic interactions and community assembly. Further, since some organisms switch between above- and below-ground compartments during ontogeny, impacts on soil-dwelling larval stages can have direct legacy effects on their above-ground adult stages and vice versa.

4. Elucidating legacy effects of biotic interactions above and below the ground will provide a deeper insight into a better understanding of the importance of plant trait- and soil characteristic-mediated indirect interactions in shaping community assembly, biodiversity and ecosystem function.

Key-words: above- below-ground interactions, ecosystem function, history, indirect interactions, phyllosphere, plant traits, rhizosphere, soil, temporal aspects, trophic levels

Introduction

There is increasing awareness of the importance of linkages between above- and below-ground compartments of terrestrial ecosystems (Scheu 2001; Van der Putten *et al.* 2001; Wardle *et al.* 2004). Organisms above and below the ground change plant traits systemically and may indirectly interact mediated by changes in plant traits. For example, root-feeding insect larvae induce systemic changes in defensive compounds in leaves with negative consequences for above-ground herbivores and their natural enemies (Soler *et al.* 2005). These plant-mediated interactions between below-ground and above-ground organisms have been studied intensively in the last two decades, and several reviews were published on the topic. Since 1993, when the first conceptual model on plant-mediated interactions between root and shoot herbivores was published (Masters, Brown & Gange 1993), reviews have focussed on the role of changes in plant physiology (mainly plant defence) in mediating indirect interactions between above-ground insect herbivores and root herbivores (van Dam *et al.* 2003; van Dam & Heil 2011; Soler, Erb & Kaplan 2013), soil micro-organisms such as mycorrhizal fungi (Gehring & Whitham 1994; Koricheva, Gange & Jones 2009; Hartley & Gange 2009; Zamioudis & Pieterse 2012), and detritivores (Wurst 2010, 2013). Other reviews considered the role of above- below-ground linkages in a global context (De Deyn & Van der Putten 2005), for ecosystem processes such as plant succession and biological invasions (van der Putten *et al.* 2009; Harvey, Bukovinszky & van der Putten 2010), and to predict the impact of global change (van der Putten *et al.* 2009). Together, these reviews suggest that above- below-ground linkages are common, have important consequences for understanding a range of community and ecosystem processes, and may provide insight in a better understanding of the consequences of global change for terrestrial ecosystems.

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The work to date on above- below-ground linkages has addressed a wide range of promising research directions and areas – from natural to managed and disturbed systems – and proposed important approaches for studies on plant-mediated above- below-ground interactions. However, the majority of past studies have been short term, and it largely remains to be tested whether above- and below-ground interactions have long-term and/or legacy effects in terrestrial ecosystems. Here, we define legacy effects as effects that persist after the biotic interaction that caused the effect ceases. We suggest that legacy effects can be mediated by changes in plant traits and their zones of influence, in particular the soil. In general, we highlight the need of a community approach to understand the consequences of indirect, plant trait- and soil characteristic-mediated, interactions on community assembly, biodiversity and functions in terrestrial ecosystems.

Box 1:

Glossary

Phyllosphere: the aerial parts of living plants including leaves, stems, buds, flowers and fruits that provide a habitat for endo- and epiphytic micro-organisms.
Rhizosphere: plant roots and the surrounding soil that are directly affected by root activity and root inhabiting soil biota.
Short-term effects: effects that last for hours to days.
Long-term effects: effects that last at least several weeks, irrespective of presence or absence of the initiated interaction.
Legacy effects: a specific case of long-term effects that persist after the biotic interaction that caused the effects ceases.

Zones of influence of plants affected by above- and below-ground interactions

Plants interact with a variety of organisms above and below the ground. Biotic interactions of plants induce phenotypic changes in plants, and a wide range of local plant responses to organisms above and below the ground can systemically affect the whole plant. There are many examples of below-ground interactions affecting above-ground plant tissues and vice versa (reviewed by, e.g., van Dam *et al.* 2003; Bezemer & van Dam 2005; Wurst 2013). For example, root herbivory by wireworms can affect secondary metabolites in leaves (Wurst *et al.* 2008), and shoot herbivory by caterpillars may change secondary metabolites in roots (Soler *et al.* 2007a). However, the effects may not stop at the plant level but extend to the zones of influence: the phyllosphere and the air, the rhizosphere and the soil. Thus, biotic interactions in one compartment can have trait-mediated indirect effects of plants on biotic interactions in the other compartment involving the zones of influence.

THE PHYLLOSPHERE

Whipps *et al.* (2008) defined the phyllosphere as the aerial parts of living plants including leaves, stems, buds, flowers and fruits that provide a habitat for micro-organisms (see Box 1). The micro-organisms can be found both as epiphytes on plant surfaces and as endophytes within plant tissues. Plant species identity may determine phyllosphere microbial (Yang *et al.* 2001) and above-ground arthropod communities (Koricheva *et al.* 2000; Haddad *et al.* 2009), but herbivore-induced changes in plant traits may also determine above-ground communities (Ohgushi 2005). Although knowledge is limited, changes in phyllosphere microbial communities may cascade up to plant interactions with higher trophic levels, such as herbivores, pollinators and their natural enemies. This has been mainly studied in endophyte–grass symbioses that mediate resistance against herbivores (reviewed by Saikkonen, Gundel & Helander 2013). These symbioses depend, among others, on plant and fungal genotypes, life history of the symbiosis partners, and abiotic and biotic environmental conditions and their interactions. Additionally, it has been shown that leaf endophytes can affect above-ground arthropod communities (Omacini *et al.* 2001; Rudgers & Clay 2008; Jani, Faeth & Gardner 2010) and change vertebrate herbivore–predator interactions (Saari *et al.* 2010).

Similarly, but looking from the opposite direction, it has been documented that aphids, mediated by their honeydew excretion, and chewing insect larvae can have significant effects on phyllosphere microbial communities (Stadler & Müller 1996, 2000; Stadler *et al.* 2001a; Stadler, Solinger & Michalzik 2001b; Muller *et al.* 2003). Also higher tropic levels, parasitoids, can have indirect, herbivore-mediated effects on the diversity and structure of fungal communities in the phylllosphere (Perez *et al.* 2009). Whether pollinators influence phyllosphere microbial communities is largely unknown. There is evidence that bees can transfer bacteria between plant species (Johnson *et al.* 1993), and recently, it has been shown that the composition of epiphytic bacterial communities differs between leaves and petals (Junker *et al.* 2011) that may potentially have consequences for pollinators.

Below-ground interactions in the rhizosphere of plants can also have impacts on phyllosphere microbial communities. According to Whipps *et al.* (2008), there is increasing evidence that micro-organisms on seeds or roots can become endophytic in the roots, enter the vascular system and are transferred internally to the aerial parts of plants where they establish as phyllosphere endophytes (Lamb, Tonkyn & Kluepfel 1996; Wulff, van Vuurde & Hockenhull 2003). Plant-growth-promoting rhizobacteria (PGPR), root endophytes such as *Piriformaspora indica*, rhizobia and arbuscular mycorrhizal fungi (AMF) may modulate phyllosphere microbial communities by different mechanisms such as induction of resistance, changes in apoplastic pH in leaves and Ca^{2+} signalling (reviewed by Yang *et al.* 2013). Other root-associated organisms such as herbivores, pathogens and decomposers may affect phyllosphere microbial communities, but that remains to be tested.

In general, systemic and local changes in above-ground plant traits induced by biotic interactions may have effects on phyllosphere communities, with potential cascading impacts on above-ground communities ranging over several trophic levels. Changes in phyllosphere communities may also have effects on litter decomposition or nutrient dynamics (Choudhury 1988; Schweitzer *et al.* 2005; Frost & Hunter 2008). The impacts on these long-term processes and functions in terrestrial ecosystems have been little explored and provide ample opportunities for new insights in phyllosphere-mediated interactions in terrestrial ecosystems.

THE RHIZOSPHERE

Both above- and below-ground interactions of plants have impacts on the rhizosphere and associated soil organisms. The rhizosphere was first defined by Hiltner (1904) as plant roots and surrounding soil (Hartmann, Rothballer & Schmid 2008), which is directly affected by root activity and associated soil organisms (see Box 1). The extension of the rhizosphere can range from sub-μm to supra-cm scales depending on the activity considered such as root exudation, respiration, uptake of nutrients and water; the inner extension involving root tissues is not well defined (Hinsinger *et al.* 2009). The rhizosphere effects of shoot herbivores can be either mediated by rather short-term allocation of C to roots and enhanced root exudation, or by more long-term changes in root morphology and biomass (Bardgett, Wardle & Yeates 1998). Below-ground interactions with a variety of functionally dissimilar soil organisms such as root herbivores and AMF can also change plant C allocation to roots (Grimoldi *et al.* 2006; Schultz *et al.* 2013) and root exudation, involving also defence compounds (Wurst *et al.* 2010; Vos *et al.* 2012). Root exudates play an important role in defending the plants against pathogens and herbivores (Bais *et al.* 2006). For example, plant-parasitic nematodes can be repelled or paralysed by root exudates, but also attracted (Koltai, Sharon & Spiegel 2002). In general, the impacts of above- and below-ground interactions do not end at the root level, but expand to influence rhizosphere interactions and soil biota communities with potential feedback effects on plant performance.

THE AIR AND THE SOIL

Biotic interactions of plants both above- and below-ground can change emissions of information revealing chemicals to the air and soil surrounding plants to affect associated communities and ecosystem processes. There are a multitude of studies reporting changes in leaf volatiles following above-ground herbivory (reviewed by Dicke & van Loon 2000), but below-ground herbivory may also induce volatile and liquid exudates from roots (Rasmann *et al.* 2005; Wurst *et al.* 2010) and leaves (Wäckers & Bezemer 2003; Soler *et al.* 2007a,b). Thus, interactions in both compartments can induce the emission of chemicals mediating interactions with other organisms such as herbivores, their natural enemies (e.g. parasitoids and entomopathogenic nematodes) and neighbouring plants. Changes in volatile emission may play an important function in inter- and intraspecific communication of plants (Karban *et al.* 2003). However, effects on the air are likely short term, because the air around a plant is constantly exchanged and above-ground organisms are often highly mobile.

In contrast, the soil can be affected in more long term, by changes in resource input and soil biota communities, thereby influencing ecosystem functions such as decomposition processes, nutrient cycling and primary productivity. Changes in litter quality mediated by biotic interactions above and below the ground (e.g. Choudhury 1988; Schweitzer *et al.* 2005; Frost Hunter 2008) can affect soil biotic and abiotic characteristics with impacts on litter decomposition, nutrient cycling and potentially future plant performance and biotic interactions with higher trophic levels. For instance, the quality of leaf litter can be changed by above-ground herbivory with impacts on below-ground food webs (Bardgett, Wardle & Yeates 1998; Bardgett & Wardle 2003). The activity, composition and size of soil biota communities can be altered with consequences for decomposition, nutrient cycling and nutrient uptake by plants (Hamilton & Frank 2001).

Short-term versus long-term impacts of above- and below-ground interactions

The majority of studies on plant-mediated above- below-ground interactions have focused on short-term effects on individual plants and a single or a few plant–herbivore interactions. Changes in plant traits following herbivory, for example altered growth and chemistry, are measured and related to the performance of simultaneously interacting herbivores. However, herbivore-induced indirect effects through trait changes in plants occur not only among spatially separated organisms, but also among temporally separated organisms (Ohgushi 2005). For example, herbivore-induced effects can shape arthropod communities across several trophic levels and thus lead to biodiversity shifts that last over more than one growing season. This has been shown for above-ground plant–insect interactions, for example on the willow *Salix miyabeana* (Nozawa & Ohgushi 2002; Nakamura & Ohgushi 2003) and *S. eriocarpa* (Nakamura *et al.* 2005; Utsumi, Nakamura & Ohgushi 2009; Utsumi & Ohgushi 2009). However, long-term indirect interaction webs induced by herbivores, which range over more than a growing season, have to our knowledge not yet been studied in an above-below-ground context.

Table 1. Plant trait- and soil characteristic-mediated impacts of biotic interactions of plants

	Short term (hours to days)	Long term (weeks to months/years)
Changes in plant traits	Induction of qualitative or mobile defence compounds Changes in volatiles Changes in root exudates	Induction of quantitative and immobile defence compounds Induction of mechanical defence Nutrition (re)allocation Compensatory and regrowth Changed architecture Changed litter quantity and quality Priming Epigenetic changes
Changes in soil characteristics	Changes in pH Changes in microbial activity	Shifts in soil biota and microbial communities Changes in decomposition rates and nutrient cycling Changes in physical and chemical soil characteristics

Biotic interactions above and below the ground alter plant traits and soil characteristics with short- to long-term consequences for subsequent interactions. See Fig. 1 for illustration.

We propose that changes in plant traits induced by above- and below-ground herbivory can have both short-term and long-term effects on biotic interactions of plants (Table 1, Fig. 1). Short-term effects, ranging from hours up to several days, are caused by changes in induction of qualitative or mobile defensive substances (Karban & Baldwin 1997), volatile emissions and root exudates. Qualitative or mobile defences such as alkaloids, phenolic and cyanogenic glycosides are present in low concentrations, and their pool is continually turning over (Coley, Bryant & Chapin 1985). After an herbivore has been deterred by an induction of mobile defence, the levels of defence compounds may rapidly decrease to pre-induced levels (Baldwin 1989). When root feeding leads to enhanced root exudation and carbon leakages, the end of the feeding may reduce or stop these plant responses. On the other hand, immobile or quantitative defences (Feeny 1979; Karban & Baldwin 1997) such as polyphenols and fibre contents can also be altered by herbivory. They can be present in high concentrations and are fairly inactive metabolically and can be retained and even accumulate in the plant tissue until mortality (Coley, Bryant & Chapin 1985). Also, feeding by above- and below-ground herbivores may lead to resource reallocation and shifts in shoot-to-root ratios (Steinger & Müller-Schärer 1992; Rodriguez & Brown 1998). These changes are rather long term, lasting several weeks, months and even across years, and likely persist after the herbivore attack ceases (Tuomi, Fagerström & Niemelä 1991; Agrawal 2002). Recently, there is also a growing interest in the concept of priming of defences in plant–herbivore interactions (Hilker & Meiners 2010). Priming is defined as an enhanced ability of a plant to respond to a stress factors such as herbivory when it has already experienced this stress or indications of it (such as egg deposition) in the past. Experience with a first or priming stimulus is predicted to prepare the plant to respond in a quicker and/or more efficient way to a second or triggering stimulus. Evidence for priming in plant-mediated above- below-ground herbivore interactions is still lacking, but we consider priming as a possible long-term effect, because it would prepare the plant to respond to future attackers and is thus not only a short-term response that ceases when the interaction and its immediate response (e.g. induction of defence) has stopped. Under long-term effects, we also group compensatory regrowth of plants, which can be seen as alternative strategies to defence against herbivores (van der Meijden, Wijn & Verkaar 1988; Strauss & Agrawal 1999; Fornoni 2011). For instance, spring infection by aphids to *Solidago altissima* can greatly alter community composition of insect herbivores by enhancing shoot regrowth in autumn when the aphids are no longer present (Ando, Utsumi & Ohgushi 2011). Also, changes in litter quantity and quality due to biotic interactions above- and below-ground are defined as long-term effects, which may affect soil characteristics and feedback to plant performance and future interactions. Lastly, epigenetic changes could have long-term and transgenerational effects on biotic interactions of plants (Holeski, Jander & Agrawal 2012). For instance, above-ground insect herbivory during the vegetative phase of wild radish induces resistance in the seedlings of the next generation (Agrawal 2002). Also, caterpillar herbivory in the parental generation on *Arabidopsis* increased resistance in the subsequent progeny generation by enhancing jasmonate responsiveness to damage. This transgenerational resistance against chewing herbivores includes the priming of jasmonic acid-related defences and requires siRNA biogenesis (Rasmann *et al.* 2012). The authors suggested that DNA methylation is a possible mechanism for transgenerational inheritance. To our knowledge, it is not known whether transgenerational effects are also induced by below-ground herbivory.

Although we introduced plant-mediated effects now with a focus on herbivore interactions, the differentiation between short- and long-term effects is also valid and important for characterizing plant interactions with other biota such as decomposers or microbial symbionts and pathogens, which also affect plant traits through defence induction, changes in nutrient allocation and/or growth.

We hypothesize that, besides changes in plant traits, changes in soil characteristics have the highest potential to have long-term impacts on plant performance and their biotic interactions both above and below the ground. For soil, as for the plant traits, we distinguish short- and long-term effects of biotic interactions on its characteristics (Table 1,

Fig. 1). Short-term effects are defined as changes in pH and the microbial activity in vicinity of the roots. More long-term effects such as changes in soil biota communities and mineralization, nutrient cycling and decomposition rates may affect not only the rhizosphere but also the bulk soil. Additionally, long-term effects mediated by changes in quantity and quality of plant litter and other organic resource inputs (e.g. excrements and dead bodies) may lead to chemical and physical changes in the soil.

Legacy effects of above- and below-ground interactions

LEGACY EFFECTS MEDIATED BY PLANT TRAITS

Past biotic interactions can have legacy effects mediated by plant traits, because plastic plant traits may remain changed after the biotic interaction ceases. Thus, legacy effects can be seen as a specific case of long-term effects, when changes are still detectable in the absence of the organism(s) that induced the changes. Studies focussing on above-ground plant–herbivore interactions have been shown that past herbivory can have legacy effects on subsequent herbivores, mediated by induction of defence responses (Viswanathan, Narwani & Thaler *et al.* 2005; Poelman *et al.* 2008) and compensatory growth (Ando, Utsumi & Ohgushi 2011). The mechanisms of the legacy effects can be different, such as changes in defence responses, nutrient allocation and compensatory growth, or epigenetic changes of the plants (Table 1).

In the last decade, the interest in above- below-ground herbivore interaction research has mainly focused on plant defence mechanisms (e.g. van Dam *et al.* 2003; Bezemer & van Dam 2005; Soler, Erb & Kaplan 2013), while other mechanisms have received less attention. Alternative responses of plants to herbivory are tolerance, mediated by compensatory growth and alterations in morphology (e.g. shoot-to-root ratio), and changes in nutrient allocation and storage. It has been documented that plants reallocate nutrients and carbon to organs not under attack for regrowth (e.g. Schwachtje *et al.* 2006). These changes in morphology and allocation patterns are more long term than the immediate induction of defence responses and may influence future biotic interactions of plants. In general, long-term effects are good candidates for legacy effects, because they might still be present after the biotic interaction has ceased. Further, long-term and legacy effects may be more relevant for plant development and fitness, because they may cause long-lasting costs leading to trade-offs for the plants.

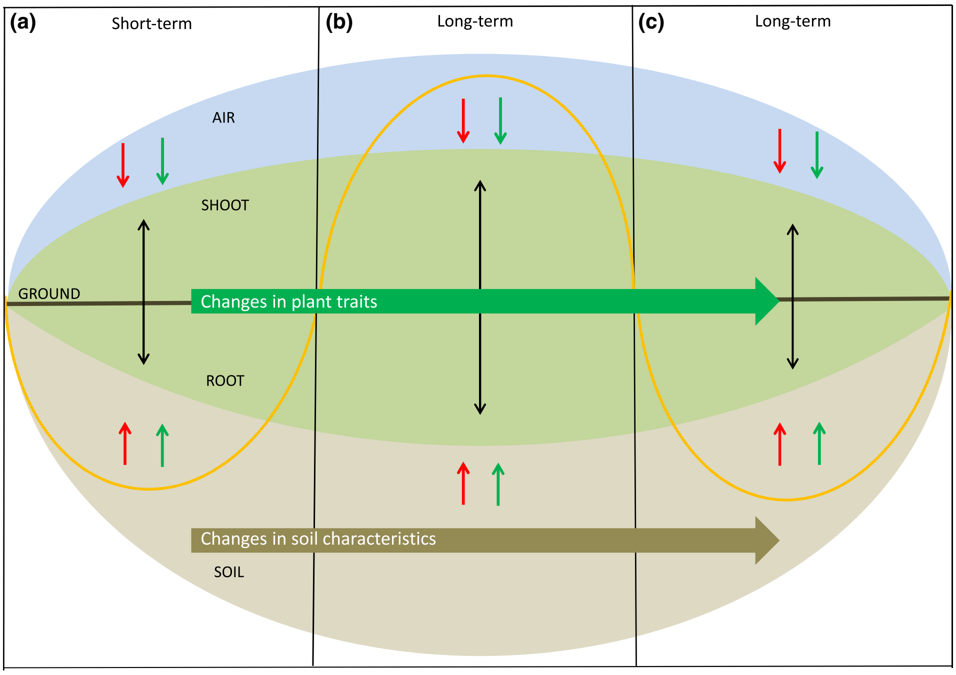

Fig. 1. Biotic interactions of plants can have long-term and legacy effects on future interactions by changes in plant traits and soil characteristics, and through ontogenetic niche shifts. Biotic interactions above and below the ground can be positive (vertical green small arrows) or negative (vertical red small arrows) and affect the plants systemically (indicated by the vertical black arrow connecting the shoot with the root). Biotic interactions of a plant at a given time (a) may differ from biotic interactions at later times (b) and (c), because of different interacting organisms during the course of the year or following years. Biotic interactions at a given time induce changes in soil characteristics and plant traits (indicated by the big horizontal brown and green arrows, respectively, see Table 1 for details) that may affect subsequent interactions of the plant with above- and below-ground organisms. Also, ontogenetic niche shifts of organisms, such as insect herbivores that have a root-dwelling larval stage and an above-ground adult stage, can mediate legacy effects of past interactions (indicated by the orange curve between the below- and the above-ground compartment).

LEGACY EFFECTS MEDIATED BY BIOTIC AND ABIOTIC SOIL CHARACTERISTICS

Past biotic interactions of plants can also have legacy effects in soils, because resource input into the soil alters soil characteristics that persist after the biotic interaction ceases. So far, we know little about whether and how long past biotic interactions of plants above and below the ground have legacy effects mediated by changes in biotic and/or abiotic soil characteristics. Recently, evidence was published for soil-mediated legacy effects in an above-below-ground context (Kostenko *et al.* 2012; Bezemer *et al.* 2013; Sonnemann *et al.* 2013). For example, Kostenko *et al.* (2012) reported that above- and below-ground insect herbivory on ragwort (*Jacobaea vulgaris*) induced effects on successive plants in terms of secondary metabolite content, biomass, and above-ground multitrophic interactions mediated by changes in the composition of soil fungi. The soil legacy effects induced by above- and below-ground herbivores differed significantly, indicating different mechanisms how above- and below-ground herbivores affect the soil and its biotic communities. Similarly, Sonnemann *et al.* (2013) reported soil legacy effects induced by a below-ground generalist herbivore (*Agriotes* spp.) in a grassland plant community context. Root herbivory by *Agriotes* larvae changed AMF communities in soil and led to enhanced productivity of the grassland plant community subsequently grown in the soil. Further, the root herbivore-induced soil legacy effect changed biotic interactions of plant species and enabled them to be less vulnerable to subsequent root herbivory and profit more from mutualists (AMF). In fact, the number of arbuscules, functional units responsible for carbon and nutrient exchange in arbuscular mycorrhiza, of *Plantago lanceolata* roots was less negatively affected by root herbivores, when the AMF had contact with root herbivores in the past. This suggests that the soil biota community may be changed by root herbivory with potential positive feedback effects on primary productivity. More research is needed to judge the generality of these findings and the importance of plant and soil-mediated legacy effects on biotic interactions and ecosystem functions. This is especially important as legacy effects caused by changes in plant traits and soil characteristics can generate indirect interactions between temporally separated organisms above or below the ground.

LEGACY EFFECTS MEDIATED BY ONTOGENETIC NICHE SHIFTS

Another potential pathway of legacy effects would be mediated by ontogenetic niche shifts in organisms. Several insects, mainly belonging to Coleoptera, Diptera and Lepidoptera, have a soil-dwelling larval stage and an above-ground adult stage. If one of the ontogenetic stages is affected by plant or soil characteristic changes, this is likely to carry over to the following life stage, resulting in the direct connection of the above- and the below-ground compartments (Fig. 1). In general, each stage of the life cycle of an organism is dynamically linked to the other through demographic processes of growth, survival and reproduction (Miller & Rudolf 2011). However, these legacy effects can only be addressed in long-term studies that allow ontogenetic shifts of the focal species and integrate their impacts on above- and below-ground interactions. To date, the interrelationship between the life stages of single species and their consequences on community dynamics have mainly been modelled (Schreiber & Rudolf 2008; Rudolf & Lafferty 2011) with a focus on aquatic systems in regard to comparisons with empirical data. In a recent study (Erwin *et al.* 2014), it has been shown that initial adult feeding by a specialist herbivore (*Tetraopes tetraophthalmus*) on common milkweed (*Asclepias syriaca*) increased root damage and survival of conspecific root-feeding larvae, suggesting a plant-mediated facilitation of larvae by initial adult feeding in this intraspecific comparison.

Consequences of plant trait- and soil characteristic-mediated above- below-ground interactions in terrestrial communities

The crucial question is how much above- below-ground interactions and their legacy effects matter for plant performance and ecosystem functions in terrestrial ecosystems? Plant performance is ultimately linked to productivity and reproductive success (i.e. fitness), but the impact of above- below-ground interactions on plant fitness parameters has been rarely assessed (van Dam & Heil 2011). For this, more long-term studies have to be performed that measure the consequences of above- and below-ground interactions for seed set and future abundance of the focal plant in the plant community. By including the measurement of fitness parameters, we can evaluate the adaptive value of the plant responses and the role of above- below-ground biotic interactions for evolutionary processes.

Further, plant trait- and soil characteristic-mediated impacts and legacy effects of biotic interactions may cascade up to higher trophic levels in multitrophic systems. A rather long-term study on the impact of plant species richness on higher trophic levels above and below the ground (Scherber *et al.* 2010) showed that the effects on abundance and species richness are dampened with increasing trophic distance. However, individual plants' below-ground interactions that change defensive chemistry systemically have been reported to cascade up to higher trophic levels above-ground, that is predators, parasitoids and pollinators (Poveda *et al.* 2007), and even change the performance of the forth trophic level, that is hyperparasitoids (Soler *et al.* 2005). Also, systemic changes in plant nutrient contents due to root herbivory can affect above-ground herbivores and their enemies (Johnson *et al.* 2013). Similarly, above-ground herbivory has been reported to affect an insect root herbivore and its parasitoid by changes in plant chemistry (Rasmann & Turlings 2007; Soler *et al*. 2007a,b) and may lead to shifts in soil microbial communities (Yang *et al*. 2011). Thus, changes in plant chemistry due to biotic interactions in one compartment either in the below-ground or in the above-ground can have cascading effects on higher trophic levels in the opposite compartment and change community assemblies and biotic interactions. Since biotic interactions are often crucial for the provision of ecosystem functions (Wurst, De Deyn & Owen 2012), the above-mentioned impacts may affect functions and services of terrestrial ecosystems. By changing species compositions and trophic structures of above- and below-ground communities, functions such as pollination, primary productivity, decomposition, nutrient cycling and carbon storage in soil can be affected. These functional consequences of the legacy effects are so far unknown and should be addressed in future studies.

Conclusion and future directions

Overall, we conclude that above- and below-ground interactions affect plants and their zones of influence with their diverse communities and interactions and can generate long-term and legacy effects on biotic interactions and functional processes in terrestrial ecosystem. Based on the above-outlined lack of studies on long-term and legacy effects of above- and below-ground interactions, which are likely mediated by changes in plant traits and soil characteristics, we propose the following promising directions for future research:

EXTENSION OF THE PARAMETERS MEASURED IN ABOVE- BELOW-GROUND INTERACTIONS

We propose that, as previous studies have mainly focused on induced defensive chemistry, more plant traits should be considered in above- below-ground interaction studies, including compensatory regrowth, nutrient content, morphology and reproductive traits such as number and quality of seeds produced. Changes in these plant traits may mediate long-term and legacy effects induced by the biotic interactions.

CONSIDERATION OF DIFFERENT TEMPORAL SCALES

Besides short-term impacts, more long-term effects of above- below-ground interactions should be considered with special focus on not only the linkage of temporally separated organisms, but also consequences for fitness of individual species and ecosystem functions. These long-term impacts are good candidates for legacy effects, which proceed when the interactions do not take place anymore. Practically, above- and below-ground manipulations and their impacts on future biotic interactions in the same and the opposite compartment could be performed similar to work on above-ground indirect interaction webs (Ohgushi, Craig & Price 2007) and/or long-term biodiversity experiments might be monitored to see whether and how above- below-ground linkages change over time.

INCLUDING ZONES OF INFLUENCE OF PLANTS

The effects may not stop at the plant level, but extend to the phyllo- and the rhizosphere and microbial and/or arthropod communities associated with the plant. The plant- and soil-mediated effects may cascade up to higher trophic levels, thereby affecting the structure of food webs. To address this, more well-designed experimental studies under natural conditions should be performed. This approach may also elucidate the zones of influence of legacy effects.

ELUCIDATING THE IMPACT OF LEGACY EFFECTS AND THEIR MECHANISMS

Because only a few studies to date have reported legacy effects, more studies are needed before we can make generalizations about the occurrence, ubiquity and ecological and evolutionary consequences of legacy effects in plant–soil systems. Also, the mechanisms should be better elucidated, that is finding out which factors are responsible for the observed legacy effects.

EVALUATING THE IMPORTANCE OF ABOVE- BELOW-GROUND INTERACTIONS FOR THE EVOLUTION OF PLANTS AND ECOSYSTEM FUNCTIONS

It is also important to better understand the functional consequences of above- below-ground interactions for individual plants (performance, survival and fitness) and for ecosystem functions (nutrient cycling, decomposition and productivity). For this, physiological changes of organisms and physiological processes and fluxes in whole ecosystems should be considered.

EVALUATING THE IMPACT OF ABIOTIC FACTORS (INCLUDING GLOBAL CHANGE FACTORS) ON ABOVE-BELOW-GROUND INTERACTIONS

Some studies have already addressed the impact of global change factors such as drought and changed nutrient availability on above- below-ground interactions (e.g. Haase *et al*. 2008; Tariq *et al*. 2013). More studies are needed to evaluate the effects of multiple global change factors on the long-term interactions and linkages between the above- and the below-ground compartment and the functional consequences for terrestrial ecosystems.

Altogether, we suggest that it is time to broaden our view on above- below-ground interactions of plants by considering the consequences for associated communities in the zones of influence of the plants, for their interactions and ecosystem processes, both in the short and long term. Long-term and legacy effects of above- and below-ground interactions are likely mediated by changes in plant traits and soil characteristics, but the mechanisms how information is stored and influences future biotic interactions await future research. We conclude that incorporating long-term and legacy effects into a conceptual framework on research of plant interactions above and below the ground will contribute to the understanding of the importance of plant trait- and soil characteristic-mediated indirect interactions in shaping community assembly, biodiversity and function in terrestrial ecosystems.

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Data accessibility

This manuscript does not use data.

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