Chapter 15
Current Knowledge and Future Challenges of Aboveground and Belowground Community Ecology

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15.1 Introduction

Trait-mediated indirect interactions are a major component of community organization (Ohgushi 2005). There is increasing evidence that plant-based interaction networks in terrestrial systems involve numerous feedback loops, and many of these indirect interactions are mediated via herbivore-induced plant responses (Ohgushi et al. 2007, 2012). In this context, plant-mediated above–belowground linkages in terrestrial systems have received much attention in the past two decades (Bardgett and Wardle 2010). Research on interactions between above- and belowground organisms, communities, and ecosystem functions has clarified that plants and their variable traits are important mediators of these indirect interactions and above- and belowground communities. Thus, many of the above- and belowground processes in terrestrial ecosystems are indirectly linked to each other through plant-mediated mechanisms. To understand how terrestrial ecosystem functions will respond to global change (e.g., climatic changes, land use intensification, and biological invasions) and the loss of biodiversity, an integrative above- and belowground perspective is critical. The soil with its high diversity of species and functions is crucial for the performance of plants, which affect as primary producers

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associated interaction webs and communities above and below the ground, and should be integrated as a key component in community ecology. Also, for agriculture and sustainable resource use, it is important to understand the functional links in terrestrial ecosystems (i.e., the connection of above- and belowground ecosystem processes such as production, consumption, and decomposition).

This book offers an overview on basic and applied research on plant-mediated above- and belowground interactions and their functional consequences. It harnesses diverse expertise on a wide variety of aspects of above- and belowground interactions and considers different approaches ranging from single taxa and guilds to community and ecosystem level responses. These approaches span different scales and complexity and provide an in-depth overview of the current knowledge and future perspectives of above- and belowground linkages in terrestrial ecosystems. As far as possible, we focus on the community and ecosystem consequences of the linkage of above- and belowground through plant-mediated indirect interactions. In particular, we develop the evolutionary and community and/or ecosystem aspects of such interactions within the wider context of community ecology.

15.2 What Have We Learned from the Past Work?

The preceding chapters in this volume have identified key developments, discoveries, and conceptual advances in aboveground–belowground community ecology. In this section, we aim to summarize some of the most important advances in the research field, as a whole, drawing on the central conclusions from several of the chapters. Note that Bardgett (Chap. 1) provides a nice piece of historical review on the development of this research field in the past two decades, which we do not cover in this section.

In terms of investigating the belowground component of above- and belowground interactions, which is usually the most challenging aspect, Johnson et al. (Chap. 2) broadly describe a range of approaches applicable to laboratory and field studies. All of these approaches have strengths and weaknesses and there is no singular methodological development that could be regarded as a “breakthrough” or a “game changer.” Instead, the authors suggest that community ecologists have become increasingly aware of techniques traditionally used by soil scientists and progressively willing to incorporate these into above- and belowground experiments.

Complementing such experimental approaches with modeling is subsequently explored by Meyer (Chap. 3), which is especially relevant when one considers the high numbers of species and interactions involved in above- and belowground communities. Models in ecology can reveal mechanisms and consequences of assumptions where data are scarce, identify knowledge gaps, and generate testable hypotheses. Ecologists have made some progress in the research field of aboveground–belowground community ecology, although only a few of these models incorporate more than three species and more than one type of interaction. Further, many of the existing above- and belowground models have been developed in applied fields such as the agricultural sciences and are underrepresented in theoretical community ecology. Future above- and belowground modeling should thus more fully exploit the strengths of modeling approaches (i.e., include greater trophic complexity, explicitly address spatio-temporal scales, and emphasize close empirical-modeling cooperation).

The most widely studied, though perhaps still the most poorly understood because of their sheer diversity, component of belowground communities are soil microbial communities. Gadhave and Gange (Chap. 6) highlight how we have learnt much about how bacterial communities can have profound effects on foliar defensive chemistry and the herbivorous insects that feed on such foliage. This even extends to higher trophic levels, including predators and parasitoids of the herbivorous insects. Remarkably, changing the population of just one bacterial species can bring about such changes in plant chemistry and aboveground multi-trophic food webs. In terms of experimentation, the addition of rhizobacteria to soil is fraught with problems however. Of the most significant of these problems is that establishment of bacteria, and thus effects on the plant, is entirely context dependent, being influenced by the existing rhizobacterial populations, the soil, the plant itself, and the competitive ability of the introduced species. As many other chapters observe, most experiments have been done with crop plants, often in highly controlled conditions that do not mimic field conditions. There is, therefore, a very large gap in our understanding of above- and belowground interactions in natural communities. The authors also suggest that increasingly cheaper next generation sequencing technologies may help address this and unravel the nature of the plant microbiome in relation to above- and belowground interactions. In particular, they suggest that plant growth promoting rhizobacteria (PGPR) may be a major and widespread, but mostly unrecognized, driver of aboveground insect communities.

While PGPR have mainly beneficial effects on plants, with diverse effects on aboveground communities, Castagneyrol et al. (Chap. 7) point out that microbes which are pathogenic to plants can be involved in above- and belowground interactions. Direct interactions between pathogens and herbivorous insects when they share plant tissues (either roots or shoots) have been known for the last few decades, but only recently have ecologists studied indirect interactions between these groups when they occupy different parts of the plant. Such indirect, plant-mediated interactions remain poorly studied, but the fact we now know of their existence suggests that they should be incorporated more broadly into aboveground-belowground community ecology.

When it comes to above- and belowground interactions involving soil macro-invertebrates, Wurst et al. (Chap. 8) observe that ecologists have largely focused on the effects of earthworms and insect root herbivores on aboveground communities. A key finding in this area is that the effects of these taxa on aboveground organisms can either operate through systemic changes in plant traits (typically when organisms interact with plants simultaneously) or may operate through legacy effects. In the latter case, soil macro-invertebrates (the so called macrofauna) alter belowground conditions in a manner that affects future plant performance and plant traits, which then affects aboveground organisms. Above- and belowground organisms, therefore, do not necessarily interact with the plant at the same time as each other. Scaling up of such interactions appears to be particularly constrained by a lack of information on the spatio-temporal distribution of soil macrofauna. Some of the more recent approaches discussed by Johnson et al. (Chap. 2), particularly approaches such as meta-barcoding, may assist with this.

Ritzenthaler et al. (Chap. 9) consider that the most significant development in herbivore-microbial linkages has been the delineation of a feedback loop between herbivores and plants via microbial responses to herbivore deposition. More specifically, aboveground herbivores influence soil nitrogen and carbon cycles by introducing foliage, frass, cadavers, and honeydew into the soil. Ultimately, these inputs alter decomposition processes via changes in soil microbial communities. Consequently, these impacts on nutrient cycling influence the availability and quality of host plants for herbivores and higher trophic groups.

An early conceptual framework for considering interactions between above- and belowground invertebrates (mainly herbivores) came from the "stress response hypothesis" and the "defense induction hypothesis" discussed by Kergunteuil et al. (Chap. 10). The former tended to focus on changes in primary metabolites in plants, especially related to changes in nitrogen availability in the plant, whereas the second hypothesis was thought to operate mainly through systemic induction of plant defenses (e.g., secondary metabolites). While researchers often acknowledged these mechanisms could operate concomitantly, there was a tendency to consider above- and belowground interactions as being driven *either* by changes in primary *or* secondary metabolites. A significant shift in thinking has been to avoid this artificial dichotomy. Nonetheless, we know far more about how belowground herbivores affect aboveground herbivores than vice versa and have a fairly incomplete picture of general trends between the two groups. In response to this gap, Kergunteuil et al. (Chap. 10) propose a novel conceptual framework that uses environmental variation along ecological clines for disentangling the relative effect of biotic and abiotic factors. The aim of this framework is to better explain the evolution and maintenance of above- and belowground interactions in natural conditions.

Barber (Chap. 11) extends this to include interactions between plant antagonists (e.g., herbivores) and plant mutualists (e.g., pollinators). In particular, he emphasizes how the herbivore taxa and sequence of arrival on the plant are important for determining the existence and strength of any such interaction.

In terms of soil biota as drivers of plant community assemblies, Kardol et al. (Chap. 13) report how a key advance in the research field has been to establish that soil biota are important niche modifiers with significant consequences for plant growth and community assembly (i.e., how local assemblages are constructed from the regional species pool). Different functional groups of soil organisms modify plant niche space either through directly altering soil properties, for example, via bioturbation, or through altering the plant competition. Soil-biota-mediated niche modification in turn can cause species turnover (e.g., successional replacements) if soil biota make niches unsuitable for resident plant species by filtering them out, which creates opportunities for other species better adapted to the modified niche space. Further, soil enemy-free niche space can facilitate the establishment of exotic or range-expanding plants. Soil biota can also promote plant species coexistence and community diversity by niche diversification (i.e., an increase in total available niche space). Recent studies indicate that soil biota can even be used to steer plant community restoration through facilitating the establishment of certain target species.

An important recent development identified by Kaplan et al. (Chap. 14) has been to relate plant–soil feedbacks (PSF) to above- and belowground herbivory by insects. Herbivory induces changes in plant physiology (e.g., root exudation and leaf senescence), which in turn modify the soil biotic environment. In this context, herbivory can drive PSFs by changing the impact of a given plant in conditioning the soil for subsequent plant performance. In addition, herbivory is likely to differ on plants growing in soil conditioned by con- versus hetero-specifics due to changes in plant nutritional quality that alter insect preference or performance. Unlike PSFs on plant growth, which are often driven by the buildup of one or a few species-specific pathogens and conspecific feedbacks are usually negative, associations with insect herbivory likely involve holistic changes to the rhizosphere microbiome and are thus more difficult to predict. A current challenge is to steer PSFs in agricultural fields to make crops more resistant to insect pests and diseases.

15.3 Key Issues for Future Challenges

The reviews and syntheses covered in this book highlight several key issues for exciting challenges in promoting future research in this research field. These challenges involve (1) evolutionary perspective, (2) scaling-up to community and ecosystem, (3) global environmental changes and sustainable crop production. These critical issues, which previous studies have rarely considered, will undoubtedly stimulate further development of the research field of aboveground–belowground community ecology.

15.3.1 Evolutionary Perspectives

Eco-evolutionary dynamics, the interplay of evolution and ecological processes, is crucial for understanding the evolution of biological diversity, community structure, and ecosystem functions (Schoener 2011; Hendry 2017). Since there are multiple scales of biological organization from genes to ecosystems, ecologists have long recognized the importance of integrating across the biological scales. Despite that this issue is particularly important in above- and belowground interactions involved in multi-trophic systems, previous research has lacked a perspective of evolutionary consequences of above- and belowground linkages. For example, genetic variation in plant traits and subsequent evolution of those traits can affect species composition of soil microbial communities, which may in turn alter the evolutionary trajectory of plant traits (terHorst and Zee 2016). Also, particular genotypes of plants lead to soil microbial communities that are best suited to decompose the litter of that genotype, and this association can increase the success of seedlings of the same genotype (Madritch and Lindroth 2011; Schweitzer et al. 2014). To evaluate selective pressure of interactions on plant reproductive success, we need to explore fitness effects to reveal which of the observed responses are adaptive for whom and to quantify the importance of these interactions for the structuring of communities (Maron 1998; Van Dam and Heil 2011; Barber et al. 2015). Since selection pressure caused by herbivory in above- and belowground compartments varies temporally and spatially, the temporal and spatial variability of herbivore abundance may yield different patterns of eco-evolutionary dynamics in interactions between herbivores and plants.

In this book, several chapters principally challenge to answer the important questions of how trait evolution of plants and associated organisms plays a role in modifying higher biological organization of communities and/or ecosystems through a wide range of above- and belowground interactions (Chaps. 4, 5, 10, and 12) to more accurately understand communities and ecosystems within an evolutionary framework via the factors affecting the strength and direction of natural selection. In addition, several authors suggest the importance of phenotypic plasticity of plants to cope with heterogeneous environments, as well as trait evolution (Chaps. 4, 10, and 12; see Ohgushi 2016 for a review).

From a perspective of plant–soil feedbacks, Schweitzer et al. (Chap. 4) illustrate evolutionary consequences of the linkage of plants and soils through indirect genetic effects. Local adaptation and maladaptation will occur because of difference in feedbacks between plant traits and soil conditions due to variation of selective pressures from soil microbes or nutrients. Genetically based positive, neutral, and negative feedbacks may occur among genotypes within a population, among populations, and among populations along environmental gradients. Plant–soil feedbacks not only have ecological consequences but may also play unappreciated and critical roles in evolutionary processes. Strong selective gradients within and among populations can lead to matches and mismatches in ecological traits and soils that can change the selective landscape. Likewise, Kergunteuil et al. (Chap. 10) demonstrate the eco-evolutionary drivers of plant-mediated above- and belowground interactions along elevation gradients, which are well suited to disentangle the resulting eco-evolutionary factors affecting above- and belowground outcomes due to steady changes in abiotic factors along which biotic interaction variations can unfold. They focus on evolutionary forces driving plant defenses, because insect herbivory can exert strong selection on the evolution of anti-herbivore defenses. Not only genetic adaptation but also phenotypic plasticity enables plants to cope with a heterogeneous environment.

Plant traits can evolve in response to selective pressures from above- and belowground interactions of not only antagonists but also mutualists (Barber et al. 2011; van Geem et al. 2013). In this context, Barber (Chap. 11) documents how antagonists and mutualists in the above- and belowground compartments closely interact with each other, and that shifts in antagonistic and mutualistic interactions could feedback to influence plant fitness. If cross-compartment effects influence plant fitness and thus population dynamics, they may also lead to changes in plant community composition, as herbivory on both sides of the soil surface can affect plant community structure. In particular, we need to study feedbacks of indirect fitness effects on plants, with incorporating a wider range of organisms and scaling-up to different environmental and community contexts. Careful assessment of herbivore impacts on plants, including levels of herbivory to shoots and roots, growth effects, and plant fitness, will help to clarify the importance of indirect herbivore effects on plant communities.

It is imperative to include above- and belowground herbivores to extrapolate how ecological changes in herbivores drive trait evolution of plants and how evolution of plant traits influences plant–herbivore interactions (van der Putten et al. 2009; van Geem et al. 2013). Invasive plants are excellent candidates for exploring of the interplay between ecological and evolutionary processes. Huang et al. (Chap. 12) illustrate how the eco-evolutionary dynamics is critical to understand above- and belowground interactions of invasive plants. Specifically, invasive plants can escape selective forces of above- and belowground herbivores in native ranges and are exposed to new selective forces in introduced ranges. These ecological variations in herbivore pressure may drive evolutionary changes via plant fitness. Since novel arthropod communities established on invasive plants may each influence selection on their defensive traits, changes in above- and belowground herbivore interactions can drive adaptive evolution of defense strategies including resistance and tolerance of invasive plants. The difference in above- and belowground herbivore interactions between native and introduced ranges and feedback of genetic variation in defense against herbivores would be critical to understanding evolutionary trajectories of invasive plant defenses and corresponding ecological consequences. In addition, it should be noted that phenotypic plasticity in invasive plants would modify subsequent adaptive evolution and thus eco-evolutionary dynamics.

There is increasing evidence that fungi and pathogens mediate above- and belowground interactions in an evolutionary context. Bennett et al. (Chap. 5) argue that evolution can act in fungal-mediated above- and belowground interactions, and that there is a wide opportunity for exploring the role of natural selection in these interactions. In assessing whether fungal interactions alter evolution within above–belowground communities, the authors point out three basic areas in which selection influences fungal above- and belowground interactions: (1) one-way selective influences of fungi or aboveground organisms on each other, (2) evolutionary feedbacks and co-evolutionary arms races of above- and belowground organisms, and (3) the relative strength of indirect and direct selection on outcomes of above- and belowground interactions. Likewise, the outcome of above- and belowground interactions among pathogens and herbivores may be affected by trait evolution of plants, pathogens, and herbivores. For instance, Castagneyrol et al. (Chap. 7) suggest how evolution of plant resistance modifies pathogen-mediated above- and belowground interactions. Exploring the evolutionary consequences of belowground–aboveground interactions between insects and pathogens for terrestrial plant-based communities and ecosystems will be an exciting future avenue.

Consequently, ecology and evolution are influencing each other in interaction webs of above- and belowground organisms, in which the evolution of one species causes evolutionary and ecological outcomes that in turn produce additional evolutionary and ecological effects through a wide variety of direct and indirect pathways in combined above- and belowground interaction networks.

15.3.2 Scaling-up to Community and Ecosystem Level

15.3.2.1 Community Perspectives

Aboveground and belowground communities are intrinsically linked, and feedbacks between these compartments play a critical role in forming the plant-based community structure (van der Putten et al. 2009). Increasing appreciation is that species interactions should be understood in a community context, because other community members alter outcomes of a focal interaction within or among trophic levels, and thus the greater diversity of interactions (e.g., competition, facilitation, and predation) in a community produces different outcomes than individual interactions. Van Dam and Heil (2011) suggested that plants mediate multiple interactions between belowground and aboveground heterotrophic communities that have no direct physical contact. These interactions are positive or negative from the perspective of each player and can go from the belowground to the aboveground community or vice versa. Plant-mediated above- and belowground interactions occur between members of many different species, feeding guilds and phyla, and can be of antagonistic, synergistic, or neutral nature for one, several, or all members of the complex communities that are associated with a single plant species. Hence, several authors emphasize the importance of a community-based approach to scale up above- and belowground linkages and their feedbacks, by including multiple herbivore species and their natural enemies. For example, Bennett et al. (Chap. 5) provide the community-based approach that incorporates multiple species and interactions to understand communities of organisms in fungal mediated above- and belowground interactions. This is because plants rarely interact with a single fungus or insect species, but rather interact with a community of organisms. This greater diversity of interactions via competition, facilitation, or predation may produce a different landscape of outcomes than when a smaller suite of species is considered. Since we have a very partial and quite idiosyncratic picture of plant-mediated interactions between aboveground and belowground invertebrates, specific predictions in community linkage across soil boundaries have been poorly established.

Including multiple species of herbivores or microbes that directly consume a wide range of plant tissues is a first step to scale up from a pairwise interaction to the community scale. Recent above- and belowground linkage research has begun to consider interactions of multiple consumer species, by adding other key herbivores or microbes in both compartments. Such research has clarified that a focal above- and belowground interaction can be greatly modified by other species, depending on species identity or arrival sequences. Interestingly, the sequence of herbivore arrival can determine the outcomes of the above- and belowground interactions (Johnson et al. 2012, Chap. 11), indicating the importance of temporal aspects of the multiple interactions to form the plant-associated community. Wurst et al. (Chap. 8) highlight the impact of soil macrofauna on aboveground organisms. For example, root damage by insect herbivores impairs water and nutrient uptake as well as storage of resources in root tissues, and it can disrupt vascular connection between roots and shoots, thereby influencing aboveground herbivores. Additionally, insect root herbivores and earthworms can influence plant interactions with root colonizing microorganisms such as arbuscular mycorrhiza, pathogens, or symbiotic rhizobacteria. Note that the bacterial community belowground has large effects on foliar defensive chemistry, thus influencing insects that feed on the foliage and higher trophic levels (i.e., predators and parasitoids) in the aboveground compartment (Chap. 6). Although past studies have mainly focused on antagonistic interactions above- and belowground, Barber (Chap. 11) points out that mutualism, involving, e.g., pollinators and mutualistic soil microbes, should be included in above- and belowground community research. A few studies have tried to increase functional diversity of not only antagonists (e.g., herbivores and pathogens) but also mutualists (e.g., pollinators aboveground or mycorrhiza and rhizobia bacteria belowground), because herbivory belowground or aboveground can affect pollinator visitation for example (Poveda et al. 2007; Barber et al. 2011).

The second step to integrate multi-species interactions across trophic levels is to include natural enemies of herbivores (i.e., third trophic level) in above- and belowground systems. To do so, we need to investigate whether and how important indirect effects across multiple trophic levels, such as trophic cascade or apparent competition, work within and between above- and belowground compartments. Such indirect interactive effects across three trophic levels are caused due to changes in not only plants but also herbivore quality or quantity, which may in turn affect the abundance and performance of predators and/or parasitoids. In exploring three trophic-level interactions, Kergunteuil et al. (Chap. 10) highlight the current shift in above- and belowground research towards a multi-trophic context and the importance of considering the role of natural enemies. This is because population densities of herbivores and their natural enemies are intimately correlated and influence plant biomass available for both above- and belowground organisms. In addition, plants attacked by herbivores produce information-rich cues enabling natural enemies to locate their herbivore preys and consequently setting the stage for the tri-trophic interactions to unfold. Plant traits that regulate the recruitment of natural enemies are widespread in both above- and belowground compartments. On the other hand, Barber (Chap. 11) points out the importance of root herbivores to reduce preference and performance of parasitoids attacking aboveground herbivore hosts.

The past research interested in the tri-trophic interaction in above- and belowground systems has focused on chiefly bottom-up effects of herbivory on herbivore's natural enemies. However, because parasitoids and predators modulate the magnitude of herbivory, we can assume that top-down forces exerted by herbivore's natural enemies might also fashion above- and belowground interactions. Future research should take into account the influence of natural enemies according to their life history traits and the host stage attacked. Indeed, those ecological parameters may affect levels of herbivore pressures and plant stoichiometry differentially across soil boundary. Also note that the importance of three trophic-level interactions in forming aboveground communities has been widely accepted, but is little appreciated in belowground studies. Thus, we need to explore (1) the functioning of multi-trophic interactions in soil as compared with aboveground, (2) the links between above- and belowground multi-trophic interactions, and (3) the ecological and evolutionary consequences of these linkages across trophic levels. Another important perspective on above- and belowground interactions in plant-based communities is to focus on how these interactions determine community and biodiversity properties, such as overall abundance, species diversity and evenness, and community composition. In this context, Kaplan et al. (Chap. 14) show how plants influence the soil biotic community in a species-specific manner, and how the responses of a plant to changes in the composition or abundance of soil biota can also differ greatly depending on plant species.

Plant–soil feedbacks also influence diversity and composition of plant communities. Kardol et al. (Chap. 13) focus on how soil organisms influence plant community assembly through priority effects, soil legacy effects, and niche modification. They argue that different functional groups of soil organisms drive competitive interactions, species coexistence, and species turnover of plant communities by directly altering soil properties or competitive ability of plants. Plants can regulate the quantity and quality of resources available for the functioning of the soil biota. In turn, the belowground community can regulate plant growth and community composition indirectly via altering the physical, chemical, and biological environment in soils (Wardle et al. 2004). Therefore, future studies should place plant–soil feedbacks in a community context to examine in more detail how top-down effects across multiple trophic levels modify bottom-up effects and drive their feedbacks. Furthermore, as our understanding of community consequences of above- and belowground interactions has been largely dependent on short-term studies, we need to incorporate plant- and soil-mediated legacy effects across years into perspectives of above- and belowground linkages, by exploring how long the changes in plant traits and soil characteristics persist after above- and belowground interactions cease and thus indirectly affect future plant-based community assembly (Wurst and Ohgushi 2015).

15.3.2.2 Ecosystem Perspectives

Aboveground herbivores play a critical role in terrestrial ecosystems by creating feedbacks between plant properties and soil processes (Bardgett and Wardle 2003; Hartley and Jones 2004) and by enhancing nutrient cycling to the soil (Hunter et al. 2012). As a result, invertebrate herbivory can provide more N and P to the soil than other sources of the same nutrients from plant litter. In fact, N and P fluxes from dead herbivores to the soil are comparable to the main alternative pathway for these nutrients through plant litter (Hunter et al. 2012). These herbivore-mediated plant–soil nutrient fluxes are highly sensitive to the changes in ecosystem properties that occur during succession, suggesting that herbivores could influence the rate and pattern of the ecosystem development through shifts in nutrient cycling. Hence, aboveground invertebrate herbivores can make great contributions to acceleration of nutrient cycling by putting nutrients to soil and thus activating soil microbes, in particular in unproductive systems, and influence the rate and pattern of ecosystem development (Metcalfe et al. 2016). Also, herbivore-induced root exudation has impacts on ecosystem processes such as soil carbon cycling, soil CO_2 efflux, nutrient cycling of N and P, soil stability, and microbial mineralization and immobilization (Bardgett et al. 2014).

However, we know little about how the combined above- and belowground interactions contribute to ecosystem functions, the interactions among primary producers, herbivores, decomposers, and predators, and how the outcomes of these interactions are altered by changes in the abiotic environments (van der Putten et al. 2009). To expand the spatial scale to the ecosystem level, we should explore how above- and belowground interactions impact ecosystem functions and vice versa. Since soil microbes largely determine nutrient dynamics in decomposition processes, plant–soil feedbacks concern plant production processes, and thus above- and belowground interactions will provide a better understanding of biological interactions that generate ecosystem functioning (Bardgett and van der Putten 2014; van der Putten et al. 2016). In addition, belowground communities are remarkably diverse and they play a major role in shaping aboveground biodiversity and the functioning of terrestrial ecosystems (Bardgett and van der Putten 2014). It should be also noted that ecosystem functioning is greatly dependent on high functional redundancy in soil communities, and on belowground community composition, rather than species diversity. The challenge for the future is to use the insights into how plant–soil feedbacks affect aboveground biodiversity and functions to manage terrestrial ecosystems (van der Putten et al. 2013).

Two chapters directly deal with this issue. With regard to resource input from aboveground invertebrate herbivores to soil, Ritzenthaler et al. (Chap. 9) explore how various types of nutrient inputs from invertebrate herbivores to the soil are critical to soil microbial communities and thus subsequent nutrient cycling that governs ecosystem functioning and a feedback loop between herbivores and plants. Nutrient inputs can result physically from invertebrates or from their consumption of vegetation (i.e., litterfall and throughfall), thus invertebrate herbivores exhibit top-down control on the soil microbes. In contrast, the microbes are exhibiting bottom-up control on the vegetation by altering the quality and quantity of nutrients reaching the plants, inevitably altering the invertebrate herbivores that consume the affected plants. The plant itself also has a bottom-up control on the invertebrate herbivores because of the production of chemical defenses. Then, the authors argue that without considering the entire above- and belowground feedback loop, studies could miss vital ecosystem functions and a more complete knowledge of how they withstand environmental change.

How the plant–soil feedbacks govern ecosystem function is explored by Schweitzer et al. (Chap. 4). At the intra-specific level, variation in plant traits leads to conditioning of soil physical and chemical properties and biotic communities, which has feedbacks to plants. They can have positive fitness effects that lead to divergence of traits in plants, because the role of plant–soil feedbacks determines plant performance and fitness. In fact, the degree of soil N conditioning positively affected the feedbacks by soil biotic communities in the western USA. Importantly, differences in plant–soil feedbacks were driven by among-population level differences in growth. These results indicate that plant traits that strongly impact soil nutrients will lead to more positive plant–soil feedbacks and stronger patterns of local adaptation, and specific members of the soil biotic community that closely tie to N-cycling may be responsible for mediating these outcomes.

Note that ecosystem engineering, which can alter biotic and abiotic materials and create new habitats to a wide variety of organisms, plays an important role in niche construction, thereby forming communities and ecosystems. Kardol et al. (Chap. 13) argue that soil organisms can sway the selection of species able to coexist in the community through niche modification, such as changes in soil properties and microclimate and associations with plant roots that favor or suppress certain species in the plant community. Soil-biota-mediated niche modification can in turn cause species turnover (e.g., successional replacements) if soil biota makes niches unsuitable for resident plant species by filtering them out, which creates opportunities for other species better adapted to the modified niche space. Thus, it is important to examine how different functional groups of soil organisms and soil biodiversity affect plant community composition and ecosystem functions via plant–soil feedbacks. Wurst et al. (Chap. 8) highlight the important roles of earthworms and ants as soil ecosystem engineers, which exhibit cascading effects on communities and ecosystem functioning above- and belowground. Earthworms can affect soil physical properties through feeding behavior as they ingest soil mixed with organic material and by altering arrangement of soil organo-minerals, water infiltration, and pore volume. Earthworms also change soil chemistry by collecting and transporting soil organic matter within the soil profile and producing nutrient-rich castings on the soil surface and belowground. In addition, they can increase N leaching and C availability. Similarly, ants have impacts on soil physical properties by creating macro-voids, galleries, and chambers, and effects on chemical properties by collecting and transporting live and dead animal and/or plant materials to their nest structures, and the additions of salivary secretions and excreta in nest construction. As a result, ants may facilitate the flow of water through the soil by their channels and their effects on soil structure.

Consequently, understanding of how above- and belowground interactions control wide aspects of plant–soil feedbacks is critical for future development of above- and belowground community ecology.

15.3.3 Challenges and Chances: Global Environmental Changes and Sustainable Crop Production

The earth and thus humankind face great challenges, such as global climatic changes, land use intensification, biological invasion, and loss of species diversity, affecting ecosystems and their functions. The growing world population demands a growing production of food under less favorable and/or more variable environmental conditions. The knowledge on interactions and functional links between above- and belowground communities of terrestrial ecosystems is still in its infancy, but studies suggest that interactions and feedback loops between above- and belowground biota affect ecosystem functions and services such as productivity and pest control. Some urgent questions are: How do the interactions and feedback loops respond to global change such as climatic changes, land use intensification, and loss of species? How can we save and/or manage above- and belowground diversity in order to support ecosystem functions and services? These questions are still largely unanswered. This volume offers an overview over the rapidly expanding research field on above- and belowground community ecology and ideas how to proceed in the future.

The assembled knowledge on above- and belowground community ecology also points to challenges faced by the research field. Several chapters focus on plant–soil feedbacks considering the highly diverse microbial soil communities and their impacts on plant traits (Chap. 4), plant community assembly (Chap. 13), and aboveground herbivores (Chap. 14). This belowground microbial community approach needs new technologies and methods to assess species and functional diversity shifts in soil and their impacts on plants and higher trophic levels (Chap. 2). But also plant-associated aboveground biota such as herbivores and pathogens affect soil microbial communities (Chaps. 7 and 9), e.g., via changes in the deposition of carbon sources. Thus, there is more and more evidence for complex functional links between the below- and the aboveground compartment of terrestrial ecosystems, and a general challenge is to leave the single species approaches behind in order to acknowledge the diversity and complexity of the involved below- and aboveground communities.

A further level of complexity is imposed by integrating the impact of environmental changes and fluctuations (e.g., extreme weather events) in the research on above- and belowground communities and their functional links (Chap. 10). Global change factors such as land use change, shifts in temperature and precipitation regimes, elevated CO_2, and plant invasions and range expansions profoundly affect both above- and belowground communities with consequences on their interactions and functional links. Kardol et al. (Chap. 13) discuss the impacts of these global change factors on plant community assembly mediated by changes in the soil community. The effects, however, will not stop at the plant level, but cascade up to higher trophic levels above the ground as highlighted by Kaplan et al. (Chap. 14) showing the impacts of plant–soil feedbacks on aboveground herbivores. Additionally, feedback loops have to be taken into account, since shifts in aboveground herbivore communities may also impact belowground communities via plant-mediated changes in resources as shown by Ritzenthaler et al. (Chap. 9). The latter chapter also provides demonstrative examples how a rise in temperature will affect several components of the feedback loops such as metabolisms of invertebrate herbivores and microbes, C/N ratio of plants, the nutritional value of plant tissue and herbivore frass, the level of consumption, growth rates, and biotic interactions, with still largely unknown consequences for ecosystem functions. To predict the impact of climatic changes, interactions between the belowground and aboveground communities and the highlighted feedback loops need to be taken into account. In this respect, modeling approaches might be essential, because of the complexity of the systems and the limitations of experimental approaches in terms of replication and time. Meyer (Chap. 3) gives a summary on modeling approaches used to deal with above- and belowground interactions and provides suggestions for future modeling.

Besides changes in climatic conditions, the invasion of exotic species is another global change challenge. Huang et al. (Chap. 12) focus on the eco-evolutionary dynamics of above–belowground herbivores on invasive plants. Invasive plants respond differentially to above- and belowground herbivores than native plants, but few studies consider interactions with both above- and belowground herbivores. In illustrative examples, they show that the outcome of interactions depends on the herbivory in the other compartment. Tolerance to aboveground herbivores and a high growth rate seems to give invasive plants competitive advantages in their new range. The evolution of new plant traits is suggested to depend on herbivory in both compartments. In general, the success or failure of invasive plants may depend on interactions with above- and belowground antagonists and mutualists. The authors suggest that simultaneously releasing both above- and belowground host-specific herbivores or a single herbivore with above- and belowground life stages may make control of invasive plant species more likely.

Land use change is another important global issue that profoundly affects plant interactions with above- and belowground biota. Wurst et al. (Chap. 8) present a study (Sonnemann et al. 2016) showing that the plant-mediated above- and belowground interactions involving insect herbivores are modified by land use form and intensity. Impacts of land use on above- and belowground communities are well known, but how their interactions and feedback loops are influenced is widely unknown. To better understand and predict the impacts of land use change and/or intensity on plant and ecosystem performance, the interactions and functional links between above- and belowground communities should be considered.

In several chapters, the chances of integrating above- and belowground linkages in applied sciences are discussed. One field of application is restoration ecology, since soil communities have been shown to influence ecological processes such as the speed of plant succession (De Deyn et al. 2003; Kardol et al. 2006). These possibilities are addressed by Kardol et al. (Chap. 13). Another field of application is the manipulation of above- and belowground interactions in agricultural settings, e.g., for crop protection. Gadhave and Gange (Chap. 6) summarize the knowledge on plant-mediated interactions between rhizobacteria and aboveground insect herbivores. Plant growth promoting rhizobacteria (PGPR) are seen as a neglected part of plant insect community ecology deserving further attention, both in natural situations and in an applied aspect, through their potential role as “biofertilizers” and “bioprotectants.” Wurst et al. (Chap. 8) highlight the importance of soil macrofauna for sustainable agriculture. Besides their well-known benefits on physical, chemical, and biological soil characteristics, they may play a largely neglected role for plant health and pest resistance. For example, as macrofauna–microbe interactions may impact plant interactions with herbivores, they should be considered when developing microbe-based plant protection strategies in agricultural fields. Kaplan et al. (Chap. 15) discuss opportunities and challenges for manipulating plant–soil feedbacks in agriculture. Since plant breeding and synthetic fertilizers appear close to maximizing their impacts on yield (Mayer 2014), the manipulation of microorganisms in crop production seems a promising field of research and for further developments in agriculture. However, there are still great methodological challenges for manipulating the soil microbiome and the consistency of their effects on crop plants in time and space is questionable. Another aspect that needs more consideration is the impact of cross-compartment interactions on both plant antagonists and mutualists and their consequences for plant fitness discussed by Barber (Chap. 11). Above- and belowground mutualists such as pollinators and mycorrhizal fungi are influenced by herbivory in both compartments with so far largely unknown consequences for plant fitness. More focus on plant fitness is definitely needed, both in basic and applied studies, to estimate the influence of above- and belowground interactions on evolutionary traits and crop yield.

15.4 Conclusion

In general, the foundation is now in place to bring us a deeper understanding of aboveground and belowground community ecology. The linkages between aboveground and belowground communities are a crucial part of the structure of terrestrial ecosystems and contribute to their functioning, albeit our knowledge on the true complexity of ecosystems in space and time is still scarce. Based on the chapters of this volume, we highlighted some major challenges for the research field of aboveground–belowground community ecology such as strengthening the evolutionary perspective, scaling-up to community and ecosystem level, and developing applied solutions for global problems. These critical issues, which previous studies have little considered, will undoubtedly enhance the perspectives for further development of the research field. Also, they closely integrate evolution and ecosystem functioning via combining aboveground and belowground communities, which will develop and enrich the wide range of ecological perspectives. We hope that a deeper understanding of aboveground and belowground community ecology will help responding better to global challenges and adapting to the changing biosphere, now and in the future.

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