developed for the Food and Agriculture Organization and the U.S. Department of Agriculture. While still concerned with fertility, soil science increasingly has turned to the ecological function of soils and to the degradation they suffer (*12*).

Nitrogen Synthesis

In von Liebig's lifetime, population growth and urbanization gradually intensified the problems of nutrient shortage. With improved transportation, however, modern farmers maintained soil fertility with fertilizers from afar, tapping the nutrient banks built up over millennia by seabird colonies. Guano from Chile and Peru counteracted soil fertility decline on the farms of Western Europe and eastern North America from the 1830s, but it was always scarce and expensive. The big breakthrough that made nitrogenous fertilizer comparatively cheap came with the work of the German chemist Fritz Haber (1868–1934). By 1913, Haber found a way to synthesize ammonia from the air, the basis of all subsequent nitrogenous fertilizer. For reasons connected to world wars and the

Great Depression, Haber's work had limited impact until the 1950s, but ever since, the problem of nutrient depletion has been treated by various forms of soil chemotherapy, chiefly nitrogenous fertilizer, at least by farmers who could afford it. Without it, the world's farms could feed only two out of three of today's 6.3 billion people (*6*).

Soil ecosystems remain firmly, but uncharismatically, at the foundations of human life. The intensity and scale of modern soil use and abuse suggest there is much yet to be discovered about soils and their relations with people. Equally, current behavior implies that there is much that is already known that is not yet converted into prevailing practices. Soil ecosystems are probably the least understood of nature's panoply of ecosystems and increasingly among the most degraded. Correspondingly, soil history remains the least understood, and least recognized, aspect of environmental history.

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REVIEW

Ecological Linkages Between Aboveground and Belowground Biota

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All terrestrial ecosystems consist of aboveground and belowground components that interact to influence community- and ecosystem-level processes and properties. Here we show how these components are closely interlinked at the community level, reinforced by a greater degree of specificity between plants and soil organisms than has been previously supposed. As such, aboveground and belowground communities can be powerful mutual drivers, with both positive and negative feedbacks. A combined aboveground-belowground approach to community and ecosystem ecology is enhancing our understanding of the regulation and functional significance of biodiversity and of the environmental impacts of human-induced global change phenomena.

The aboveground and belowground components of ecosystems have traditionally been considered in isolation from one another. There is now increasing recognition of the influence of these components on one other and of the fundamental role played by aboveground-belowground feedbacks in controlling ecosystem processes and properties (*1*–*4*). Plants (producers) provide both the organic carbon required for the functioning of the decomposer subsystem and the resources for obligate root-associated organisms such as root herbivores, pathogens, and symbiotic mutualists. The decomposer subsystem in turn breaks down dead plant material and indirectly regulates plant growth and community composition by determining the supply of available soil nutrients. Root-associated organisms and their consumers influence plants more directly, and they also influence the quality, direction, and flow of energy and nutrients between plants and decomposers. Exploration of the interface between population- and ecosystem-level ecology is an area attracting much attention (*5*, *6*) and requires explicit consideration of the aboveground and belowground subsystems and their interactions.

Here we discuss recent advances in our understanding of the links between these two subsystems. We first outline how the aboveground subsystem influences the belowground subsystem and vice versa. We then discuss biodiversity links between the aboveground and belowground subsystems. Finally, we explain how the study of aboveground-belowground interactions may assist our understanding of the consequences of human-induced global change phenomena.

How Aboveground Communities Drive the Belowground Subsystem

It has long been recognized that soil organisms are responsive to the nature of organic matter

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that enters the decomposer subsystem (7). However, there is increasing awareness that different components of the soil food web show a range of responses to these resource inputs because they are variably driven by top-down forces (regulation by their consumers) and bottom-up forces (resource quantity and quality) (3, 8, 9). Because plant species differ in both the quantity and quality of resources that they return to soil, individual plant species may have important effects on components of the soil biota and the processes that they regulate. For example, grassland plant species differ in the composition of microbial communities around their roots (10), which helps explain why soils planted with different grassland species support different abundances of soil microbes and microbe-feeding fauna (11). In forests, differences in the quality of litter produced by coexisting tree species explains the patchy distribution of soil organisms and process rates that result from "single tree" effects (12).

Plant community composition greatly influences the community composition of root-associated organisms (13), and studies have shown these effects to be much more specific than originally supposed (14–16). However, effects of plant composition on decomposer communities appear to be context-dependent. Recent large experiments point to a range of effects of plant communities on soil communities. For example, in an experiment performed in a New Zealand grassland, different subsets of the flora were excluded from different plots (17). Although major groups of soil organisms were mostly unresponsive to changes in plant community composition, the community structure of soil microbes, microbe-feeding nematodes, and herbivorous nematodes and arthropods was responsive. In a study in the Konza Prairie, Kansas (18), sampling of soils under various combinations of C3 and C4 grass species revealed that some bacterial and nematode groups were responsive to the presence of particular plant species, although no uniform pattern emerged. In a study of five abandoned ex-arable sites across Europe (19), manipulation of plant community composition exerted idiosyncratic effects on several components of the decomposer biota (i.e., microbes, nematodes, mites, and earthworms) and no clear effect on soil animals associated directly or indirectly with plant roots.

Several recent studies indicate that aboveground trophic interactions have indirect effects on soil biota by affecting the quantity and quality of resources that plants produce. In the short term, foliar herbivory can cause substantial release of carbon into the rhizosphere; this can positively affect microbial activity, causing an aboveground feedback by increasing nitrogen availability for the plant (20). In the longer term, herbivores can affect the quality and quantity of plant-derived resources for soil organisms through several mechanisms (4). Positive effects arise when herbivores promote compensatory plant growth, returning organic matter to the soil as labile fecal material (rather than as recalcitrant plant litter), inducing greater concentrations of nutrients in remaining plant tissues and impairing plant succession, thereby inhibiting ingress of plant species with poorer litter quality. Negative effects arise through impairment of plant productivity by tissue removal, induced production of secondary defenses, and promotion of succession by favoring the dominance of unpalatable plant species with poor litter quality. Whether net effects are positive or negative depends on the context (21–23). However, other groups of soil organisms that are more intimately associated with plant roots may show more uniform trends; most studies have found that arbuscular mycorrhizal infection of roots is impaired by foliar herbivory, probably as a result of reduced carbon allocation to roots (24).
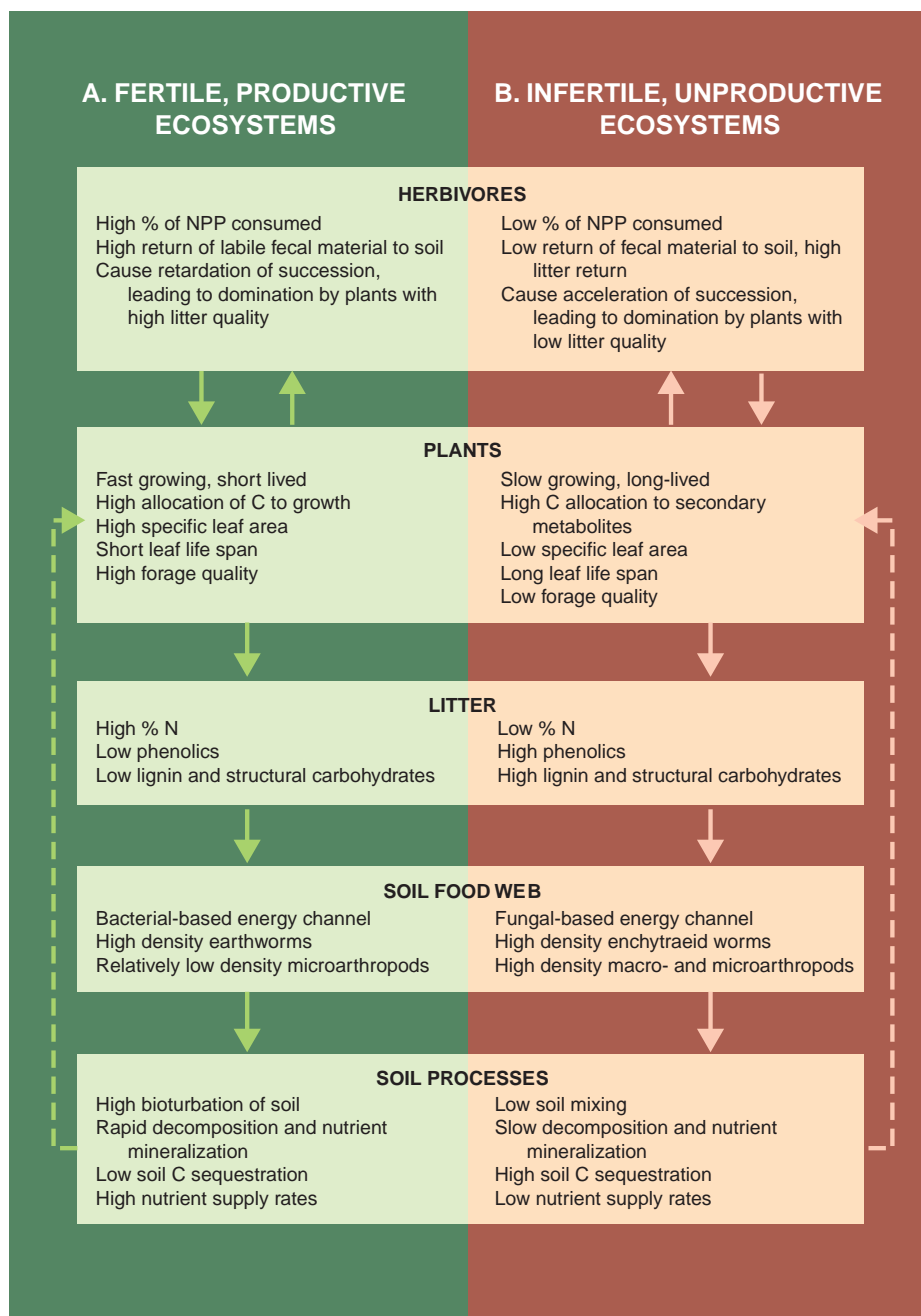

Fig. 1. One major ecological driver is the difference in fundamental plant traits between species that dominate (**A**) fertile systems that support high herbivory and (**B**) infertile habitats that support low herbivory. Plant traits serve as determinants of the quality and quantity of resources that enter the soil and the key ecological processes in the decomposer subsystem driven by the soil biota. These linkages between belowground and aboveground systems feed back (dotted line) to the plant community positively in fertile conditions (A) and negatively in infertile ecosystems (B).

Despite the level of unpredictability and context dependency of aboveground biotic effects on soil biota, consistent patterns do emerge at broad levels of comparison, such as across ecosystems. Plant species adapted for fertile conditions differ markedly in their ecophysiological traits from those best suited for infertile conditions, e.g., in terms of relative growth rate, carbon allocation strategies, leaf area characteristics, and tissue nutrient concentrations (3) (Fig. 1). These traits are important determinants of trophic structure, both above- and belowground. Ecosystems dominated with plant species adapted for fertile conditions can support high herbivore densities, with more than 50% of net primary productivity (NPP) being returned to the soil as labile fecal material. In infertile conditions, nearly all NPP is returned to soil as recalcitrant plant litter. Fertile soils also support soil food webs in which the bacteria-based energy channel, microfauna (nematodes and protozoa), and earthworms play an important role in nutrient cycling, whereas infertile soils tend to support food webs dominated by fungi and arthropods (notably mites, springtails, and millipedes) (3, 25). Fertile conditions are therefore likely to support rapid, leaky nutrient cycles and low net accumulation of soil carbon, whereas infertile conditions should support slow nutrient cycles in which nutrients are conserved and soil carbon sequestration is promoted (3, 25, 26). With regard to plant symbionts in the soil, a comparative study of 58 British plant species showed that plant species with traits associated with fertile, intermediate, and infertile habitats supported mainly arbuscular, ecto-, and ericoid mycorrhizal fungi, respectively (27). Such systematic comparisons have yet to be made for other obligate root associates such as root herbivores and pathogens.

How Belowground Biota Drives the Aboveground Subsystem

Although there is accumulating evidence that aboveground biota can have important effects on the belowground subsystem, for a feedback to occur it is also necessary that belowground organisms can influence aboveground community structure and functioning. The mechanistic basis by which primary productivity is regulated by belowground interactions is well understood (3). For example, the accumulation of parasites, pathogens, and root herbivores in the rhizosphere can directly remove carbon and nutrients from plant tissues and reduce root uptake capacity, producing a negative feedback on plant growth (16). In contrast, mutualistic symbionts such as mycorrhizal fungi can enhance access to limiting nutrients, with a positive feedback on plant productivity (28). Indirectly, the detrital food web can liberate nutrients locked up in dead organic matter or in microbes, thus increasing nutrient availability to, and pro-

ductivity of, plants (9, 29) (Fig. 2).

Recent studies have shown how biotic interactions in soil can regulate the structure and functioning of aboveground communities. Root pathogens and root-feeding invertebrates do not project an equal magnitude of negative feedback on all plant species within a community, and thus their presence can result in qualitative differences in plant community composition and in the structure of higher aboveground trophic groups (30, 31). Therefore, they can induce changes in the successional replacement of plant species both in early (14, 15, 32) and late (14, 33) successional stages. The rate of pathogen accumulation in the soil can also determine the abundance and invasibility of plant species in a community (34); rare plants tend to accumulate pathogens that limit their growth, whereas abundant and invasive species accumulate pathogens more slowly (34, 35). Mutualistic symbionts also confer different degrees of feedback on certain plant species within a community (36) and therefore influence plant community structure (36, 37) and populations of aboveground consumers (38). Mycorrhizal fungi associate with the majority of plants within any community, but each plant benefits most from a unique fungal isolate (39). As a result, changes in the mycorrhizal composition may influence biomass, nutrient status, and relative abundance of plants (37, 40), which can then either decrease (41, 42) or increase (43) the density of aboveground consumers associated with individual plant species (Fig. 2).

Indirectly, the structure of plant communities can be influenced by interactions in the detrital food web. For example, manipulation of the soil fauna in a model grassland ecosystem was found to alter the composition of the plant community (44). In the absence of soil macrofauna, changes were detected in microbial biomass and organic matter decomposition, resulting in altered nutrient dynamics and an increase in the abundance of grasses relative to other plant species (44). Similar ecosystem and community effects have been reported for larger soil
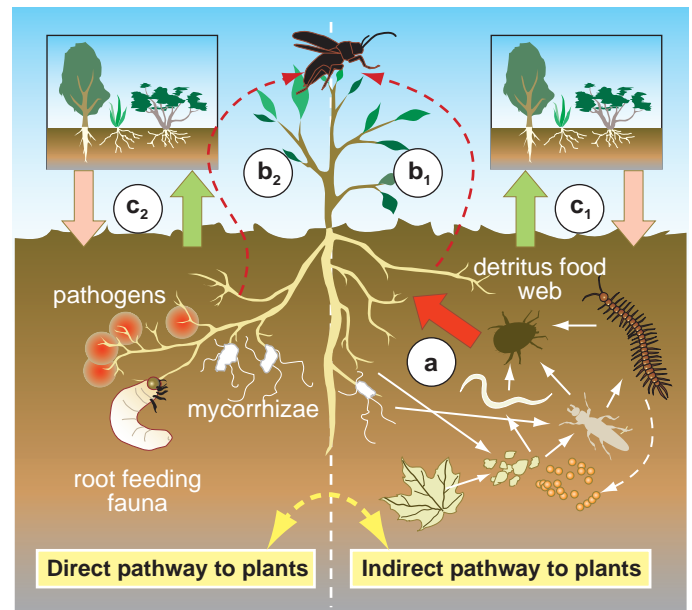

Fig. 2. Aboveground communities are affected by both direct and indirect consequences of soil food web organisms. (**Right**) Feeding activities in the detritus food web (slender white arrows) stimulate nutrient turnover (thick red arrow), plant nutrient acquisition (a), and plant performance and thereby indirectly influence aboveground herbivores (red broken arrow) (b_1). (**Left**) Soil biota exert direct effects on plants by feeding on roots and forming antagonistic or mutualistic relationships with their host plants. Such direct interactions with plants influence not just the performance of the host plants themselves, but also that of the herbivores (b_2) and potentially their predators. Further, the soil food web can control the successional development of plant communities both directly (c_2) and indirectly (c_1), and these plant community changes can in turn influence soil biota.

fauna, such as earthworms and some soil-inhabiting mammals, through mechanisms such as changes in the chemical and physical characteristics of the soil (45, 46) or the transport of microbial propagules and plant seeds (47). Because soil animals can stimulate nutrient mobilization and plant nutrient uptake, they also have the potential to indirectly affect aboveground consumers. For example, plant-sucking aphids were found to perform better when host plants were grown in the presence of microbial-feeding Collembola or earthworms than when these organisms were absent (48). Similarly, bacterial-feeding microfauna were found to indirectly increase the numbers and biomass of aphids on barley shoots through their positive effects on soil nitrogen turnover and the nutritional status of the plant (49) (Fig. 2). Such studies are beginning to provide evidence of important plant-mediated linkages between aboveground and belowground food webs.

Above- and Belowground Biodiversity—Linked or Living Apart?

If communities of soil organisms affect the productivity and composition of plant communities, what role does soil biodiversity play in the feedback between aboveground and belowground communities? The diversi-

ty of soil organisms is tremendous; 1 g. of soil can contain between 5000 and 10,000 species of microorganisms (*50*), but plants interact with only a subset of this large species pool (*51*). Every individual plant is also
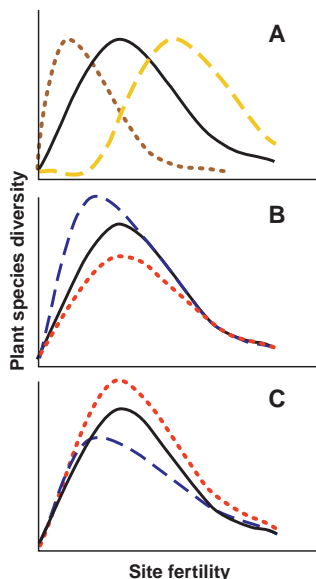

Fig. 3. Relationship between underlying site fertility and plant species diversity, in which diversity is maximized by intermediate fertility (the solid curve in all three panels), as proposed by Al-Mufti *et al*. (*76*). (**A**) Consequences of decomposer activity. When decomposer organisms alter nutrient availability, the response curve of plant species diversity to site fertility changes accordingly. If soil decomposers enhance nutrient availability, then the relationship between local plant diversity and site fertility shifts from the solid curve to the dotted curve, resulting in plant diversity being maximized in less fertile sites. Conversely, when decomposers reduce nutrient availability, local plant diversity shifts to the dashed line with maximal diversity in more fertile sites. Effects of decomposer diversity may be unpredictable (*58*), because diversity may enhance or reduce the availability of nutrients to plants and effects depend on initial site fertility. In practice, however, net primary productivity is probably relatively insensitive to decomposer diversity because of the generalist feeding behavior of most consumers in the soil subsystem (*77*), so that effects of decomposer diversity should be smaller than those for soil organisms that have a more intimate interaction with plant roots. (**B**) When targeted to subordinate or rare plant species, arbuscular mycorrhizal fungi enhance diversity (dashed line) (*37*), whereas root pathogens and herbivores reduce diversity (dotted line) (*34*). At a given site fertility, arbuscular mycorrhizal fungi should enhance plant phosphorous uptake, so that plant diversity peaks under lower site fertility (*28*). (**C**) When targeted to dominant plants, arbuscular mycorrhizal fungi (dashed line) reduce diversity (*78*), whereas root pathogens and herbivores increase plant species diversity (*14*). As in (B), the enhancement of plant phosphorous uptake by arbuscular mycorrhizal fungi means that maximal plant diversity should occur under lower site fertility (*28*).

exposed to potentially hundreds of species of soil fauna, mostly nematodes, microarthropods, insects, and earthworms. However, few studies have investigated the extent to which the aboveground subsystem depends upon this diversity of soil organisms.

Although the effects of decomposer diversity on aboveground plant productivity are poorly understood, these effects are likely to saturate at low levels of diversity. Microcosm studies (*52*, *53*) have shown that the presence of five mesofaunal species was sufficient to maximize growth of *Betula pendula* seedlings, and one of these (*52*) found that seedling production depended on the presence of the enchytraeid *Cognettia sphagnetorum* rather than on the number of animal species in the soil. Further, decomposer diversity effects on plant productivity may not necessarily be positive, especially at the functional group level. In a microcosm study, addition of protists and nematodes enhanced, whereas earthworms reduced, plant production (*54*). These positive effects only occurred when earthworms were absent (*54*), which is consistent with other studies that show the inclusion of larger bodied soil organisms to reduce the aboveground effects of small-sized soil organisms (*44*).

Intimate interactions between plants, soil pathogens, root herbivores, and mycorrhizal fungi may be direct drivers of plant community diversity (*55*), but consequences of the biodiversity of these soil organisms has been rarely studied. A study of the dune grass *Ammophila arenaria* showed additive effects of mixtures of soil pathogens (fungal species and a nematode) relative to the effects of pathogen monocultures (*56*). More diverse mixtures of arbuscular mycorrhizal species were found to promote both the abundance of rare plant species and total plant community biomass and diversity (*37*), although the mechanistic basis of these results remains unclear. Further, the aboveground effects of mycorrhizal fungi depend on soil fertility (*28*), and increasing diversity of ectomycorrhizal fungi has been found to promote tree seedling productivity in low-fertility but not high-fertility substrates (*57*).

Based on the limited evidence available, it appears that the effects of soil biodiversity on aboveground attributes (plant productivity, composition, and diversity) can range from positive to negative depending on context (*3*, *58*). In Fig. 3, we provide a conceptual framework for predicting how diversity of different subsets of the belowground biota may influence plant diversity. This framework suggests that the aboveground consequences of soil biodiversity are strongly dependent on context, such as the types of soil organisms considered, the role of plant species in a community (dominant versus rare or subordinate species), and site fertility. We also

predict stronger aboveground effects of the diversity of specialist soil organisms, such as those that are intimately associated with plant roots (e.g., mycorrhizal fungi and root pathogens) than of those that show low specificity (e.g., decomposer biota).

Implications for Global Change

Over the past century, much of the Earth's land surface has been transformed by a range of phenomena (*59*), such as invasions of alien species into new territories, alteration of climate through atmospheric CO_2 enrichment, nitrogen deposition, and land use change. Whereas the significance of these phenomena for ecosystem performance is widely recognized (*60*), the mechanisms that drive ecosystem responses to them are not well known. Understanding the consequences of these phenomena requires explicit consideration of linkages between aboveground and belowground biota. This is because, with the exception of some major disturbances that directly affect soil biota (*61*), global change phenomena indirectly affect soil biota and the processes that they drive through changes that occur aboveground, by changing plant community composition, carbon allocation patterns, or the quantity and quality of plant-derived organic matter, for example. In turn, such belowground responses to global change would create feedbacks that affect aboveground biota (*62*, *63*).

A growing number of studies point to how atmospheric CO_2 enrichment can affect ecosystem properties through aboveground-belowground linkages (*64*, *65*). Enhanced CO_2 can indirectly affect soil organisms through shifts in the quantity and quality of plant litter returned to soil, the rate of root turnover, and the exudation of carbon into the rhizosphere (*66–68*). Because of the variety of ways in which plants respond to atmospheric CO_2 enrichment depending on context (e.g., variations in soil fertility), positive, negative, or neutral indirect effects of enrichment on belowground organisms and nutrient mineralization can occur (*3*). Consequently, the direction and magnitude of aboveground feedbacks that result from these belowground changes are also variable, with the possibility of positive (*69*) and negative (*70*) responses.

Invasion of plants into new territories may greatly affect aboveground-belowground feedbacks, especially when the invading species has vastly different physiological traits from the native flora. These feedbacks may initially operate through interactions between invasive species and root-associated biota (*34*, *35*), but in the longer term they can also involve the effect of the invader on the quantity and quality of resource inputs to soil and on decomposer organisms and the processes that they drive (*71*). A classic example is the invasion of the actinorhizal shrub

Myrica faya into nitrogen-limited stands of *Meterosideros polymorpha* in Hawaii, which resulted in a more-than-fourfold increase in soil nitrogen input and a consequent increase in ecosystem productivity (*6*).

Less is understood about how invasion of soil organisms influences aboveground biota, although these effects should be strongest when the invading species has functional attributes that are not shared by the resident indigenous species. For example, exotic earthworms introduced to North American forests exert a greater effect on surface litter and soil structure than do native soil organisms, and they induce pulses of nutrient mobilization that result in altered plant growth and community composition, potentially leading to alternate steady-state systems (*72*). Similarly, predation and reduction of native earthworm populations by invasion of the New Zealand flatworm *Arthurdendyus triangulata* into the United Kingdom and Ireland may reduce their beneficial effects on soil conditions such as porosity and drainage, influencing plant community composition and productivity (*73*).

These examples show that effects of global change phenomena on ecosystems consistently involve linkages between the above- and belowground subsystems. In nature, ecosystems and communities are generally subjected to several global change phenomena simultaneously, and different communities are influenced by these phenomena in a variety of ways in the long term. However, ecological responses to global change over very long time scales (*74*) and to multiple stressors (*75*) have yet to be thoroughly considered in a combined aboveground-belowground framework.

Conclusions

Studies on aboveground-belowground feedbacks are now in the phase of exploring the effects that the two subsystems exert on each other, but to be able to generalize requires a better understanding of the mechanisms behind these effects. This understanding will be gained by evaluating how the plant functions as an integrator of these subsystems, because aboveground and belowground consumers are largely spatially separated with the plant as a connector. To date, mechanistic understanding has focused on the quality and quantity of resources that the plant produces both above- and belowground, but many unknowns remain on the role of plant physiological mechanisms, such as plant defense strategies and the proportional contribution of primary and secondary plant compounds (*1*, *31*). An emerging theme is that aboveground consequences of belowground interactions and vice versa are not easily predicted; an organism or group of organisms on one side of the aboveground-belowground interface can often exert positive, neutral, or negative effects on the other side of the interface depending on context (*2*, *3*, *16*, *22*). The nature of this context dependency is likely to be determined primarily by spatial and temporal scale and by abiotic factors; there is a need to determine how biotic relationships interact with abiotic agents to drive community and ecosystem properties. New insights from studies on aboveground-belowground interactions should be used to improve our predictions of the effects of human-induced environmental changes on biodiversity and ecosystem properties and to enhance the efficiency of human interventions in restoration and conservation efforts.

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