A temporal approach to linking aboveground and belowground ecology

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Ecologists are becoming increasingly aware of the role of aboveground–belowground relationships in controlling ecosystem processes and properties. Here, we review recent studies that show that relationships between aboveground and belowground communities operate over a hierarchy of temporal scales, ranging from days to seasons, to millennia, with differing consequences for ecosystem structure and function. We propose that a temporal framework is crucial to our understanding of the nature and ecological significance of relationships between aboveground and belowground communities.

Introduction

The study of belowground biological communities and their influence on ecosystem properties is a relatively new field of ecology. Although it has been long known that soil organisms are integral to soil fertility, it is only during the past few decades that ecologists have begun to explore belowground communities and their functional significance for plant communities and ecosystem processes. This interest is due, in part, to technological advances that have enabled scientists to extract and characterize soil microbial communities and to assess their function [1]. However, it is also due to an increasing recognition by ecologists, who have traditionally focused on aboveground organisms, of the importance of belowground organisms as structuring forces in terrestrial ecosystems [2–4].

Although there is still much uncertainty about the role of the soil biological community as a driver of ecosystem function, several studies have now shed light on this issue. For example, there is an increasing body of literature showing that individual functional groups of soil biota, and changes in the functional composition of soil biological communities, can act as important drivers of ecosystem functions, such as decomposition, nutrient cycling and plant production [2–6]. There is also an increasing

acceptance that plant–soil biological community feedbacks are major structuring forces in plant communities [3,7,8]. Our understanding of relationships between aboveground and belowground communities, however, is complicated by the fact that they operate at a relatively wide range of spatial and temporal scales [3,9,10]. The spatial and temporal scales at which plants and soil organisms operate at also differs, depending on the body size and life history of the organism concerned and the size of its habitat unit or domain [9,10].

Ettema and Wardle have argued the importance of a spatial scale for understanding the nature of relationships between plant and soil communities [9]. Similarly, in this themed issue of *TREE*, De Deyn and Van der Putten [10] argue the importance of spatial scale for understanding the functional role of linkages between aboveground and belowground diversity. Recent studies indicate that a temporal understanding is equally important, in that the nature and significance for ecosystem properties of aboveground–belowground relationships depends on the timescale within which they occur. Here, we review recent studies that show how plants and soil biological communities interact over a hierarchy of timescales, involving different mechanisms, and discuss the significance of these different types of temporal relations for ecosystem properties. We identity characteristic timescales as being those that occur over: (i) short timescales of hours to seasons, which involve highly dynamic interactions among plant roots, soil microbes and their consumers and which affect the cycling of nutrients, thus influencing plant nutrient supply and growth; (ii) intermediate timescales of tens to thousands of years, which involve changes in resource supply to soil, and feedback mechanisms between individual plants and their soil biological communities, with important consequences for nutrient cycling and vegetation succession; and (iii) long timescales of thousands of years to millennia, which involve long-term changes in nutrient availability and resource supply with consequences for decomposer communities and ecosystem productivity. Our aim is to illustrate the strong interdependence between plants and soil biota, and how

relationships between them operate over a hierarchy of temporal scales.

Aboveground–belowground relationships over short timescales
Dynamic interactions over hours to days
The abundance of activity of soil microbes varies greatly over short timescales of hours to days [2,4]. Many factors contribute to this, such as predation of microbes by soil animals and the action of abiotic stresses (e.g. wet–dry and freeze–thaw cycles) [4]. However, of primary importance is temporal variation in the supply of carbon (C) and other nutrients from roots to soil, via root death and turnover, and through the leakage, or exudation, of easily degraded compounds into soil. About 5–10% of the C that is taken up by plants during photosynthesis is excreted into the soil via the roots [11], and compounds lost via this route (including organic acids, sugars and amino acids) represent a high-quality nutrient source for microbes, stimulating their growth and thereby increasing prey availability for their consumers, such nematodes and protozoa [2,4]. Exudates also contain important signal molecules that have important multitrophic effects and influence plant growth [12,13]. The use of ^{13}C stable isotope techniques has revealed the dynamic nature of root exudation patterns and their influence on the activity and abundance of soil biota. For example, Ostle *et al.* [14] pulse-labelled aboveground tissue of grassland plants with ^{13}C–CO$_2$ and found that $>70\%$ of the label was released from the plants to soil within 48 h, either through root respiration or exudation. A large proportion of the fixed ^{13}C (5–8%) was allocated directly to arbuscular mycorrhizal fungi that associate with plant roots. This C is then rapidly turned over by the arbuscular mycorrhizal fungi [15] and transferred to other organisms in the soil food web, such as bacteria, decomposer fungi and their consumers [14].

An increasing number of studies reveal the ecological significance of changes in root exudation patterns for belowground properties and plant nutrient acquisition and growth. Although several factors can influence root exudation patterns, the clearest evidence of its ecological significance comes from studies that seek to determine a mechanistic basis for plant responses to herbivory. It has been shown that foliar [16,17] and root [18] herbivory lead to short-term pulses in root exudation, stimulating the biomass and activity of microbes [17,19] and the abundance of their faunal consumers [20,21]. These positive effects subsequently have a positive feedback to the plant through a temporary increase in soil nitrogen (N) mineralization and plant N acquisition, ultimately benefiting plant growth in the longer term [17,22]. The ecological significance of these short-term responses to herbivory is substantial, in that they explain, in part, the compensatory response of plants to grazing in natural ecosystems [17,23]. A range of abiotic and biotic factors, such as climate change, parasite attack and soil nutrient availability, also affect belowground C allocation and root exudation patterns [4,23]. Therefore, it is likely that similar mechanisms will operate to enable plants to compensate for these stresses in their natural environment.

Plant–soil interactions over seasonal timescales
Relationships between plant and soil biological communities also operate over seasonal timescales, involving several mechanisms that are of importance for the supply of plant nutrients during the growing season. There is a rich literature describing seasonal dynamics of many components of the belowground community in a range of natural and farming ecosystems [2,4]. However, recent studies in alpine regions provide novel insights into microbial community dynamics and their link to plant nutrient supply and nutrient cycling. Here, as in other seasonal ecosystems, the general assumption has been that soil microbes are inactive during the winter. However, Schadt *et al.* [24] found that the biomass of microbes in alpine soils was at its annual maximum during late winter, when soil is frozen, and showed a significant decline thereafter. These seasonal changes in microbial biomass are also associated with shifts in microbial community composition: in winter, fungi that utilize complex plant residues dominate, whereas in summer, bacteria that thrive on root exudates are more active [25]. There is also an almost complete turnover of the microbial community between winter and summer, with many novel DNA sequences [24] with different functional attributes [25,26] occurring at both times. This suggests that different microbial communities operate during winter and summer, and that one-time, static, surveys might underestimate microbial diversity.

These seasonal dynamics in microbial communities are important because they control the temporal partitioning of nutrients between plants and soil microbes over seasons. This was shown by Jaeger *et al.* [27], who studied seasonal partitioning of N between plants and microbes in an alpine meadow in Colorado. Here, the dominant plant species *Kobresia myosuroides* took up N maximally after snowmelt, whereas soil microbes immobilized N maximally in the autumn after plant senescence, and retained it throughout the winter [27]. The release of microbial N for plant uptake in spring appears to be facilitated by a significant decline in microbial biomass after snowmelt, leading to a pulse of soluble N, in the form of protein, into soil [25,26]. Interestingly, this pulse coincides with a peak in soil protease activity, which facilitates the supply of amino acids for plant uptake, and also the growth of soil microbes that are able to utilize amino acids [26]. This is of significance for plant nutrition because it concurs with the observation that plants and microbes compete for amino acids in these ecosystems during the growing season [28], and that amino acids represent an abundant form of N used by plants in N-limited ecosystems [29,30]. Little is known about the mechanisms responsible for the decline in the winter microbial community, and consequent flush of N. However, it has been suggested that changes in C-substrate availability, and increases in soil temperature and freeze–thaw activity after snowmelt are probable drivers [27]. When considered together, these studies indicate that, in N-limited ecosystems, the cycling of labile N pools over seasons relies on intimate, temporal coupling between plants and microbes and their resource demands (Box 1).

Box 1. Seasonal dynamics of alpine plant and microbial resource interactions

In alpine ecosystems, which are characterized by long, cold winters followed by short, cool growing seasons, the cycling of labile N pools over seasons relies on intimate, temporal coupling between plants and microbes and their resource demands. Here, the linkage between plant and heterotrophic microbial communities exhibits pronounced seasonal shifts that influence the temporal and spatial variation in diversity of both biotic groups. The supply of limiting resources determining production and species composition is dependent on fluxes of labile C and N between the two groups. Microbial biomass is largely dependent on C supply from plants, whereas plant production is limited by labile forms of N (small amino acids and inorganic N) derived from microbial degradation of soil organic matter. The supply rates of these resources change seasonally depending on climatic constraints and the abundance and activity of microbes and plants. Plant and microbial functional group composition also varies spatially, influencing the diversity of the other group.

Autumn phase

Senescing plants provide a pulse of labile C to support microbial growth (Figure Ia). Variation in the chemistry of these compounds provides a potential source to promote diversity in the microbial community. For example, litter that is rich in low molecular weight phenolic compounds enhances overall microbial biomass, particularly fungi, whereas litter that is rich in carbohydrates and sugars enhances bacterial growth [58].

Winter phase

Microbial biomass continues to increase in soils warmer than $-5°C$ as C and N in plant litter is consumed and mineralized (Figure Ib). Less easily degraded polyphenolic compounds promote dominance by fungal species [24].

Spring phase

Rapid changes in microclimate and the exhaustion of labile C compounds lead to turnover of microbial community, with concomitant release of labile N for plant uptake (Figure Ic) [26].

Summer phase

Plant uptake of N to meet growth demands occurs during the early summer [27], followed by a period of C sequestration and loss to soil microbes (Figure Id). Some slow-growing phenolic-rich plant species (e.g. the alpine herb *Acomastylis rossi*) exude C into the soil to manipulate microbial immobilization of N, promoting low nutrient conditions [64], whereas other, fast-growing species (e.g. the grass *Deschampsia caespitosa*) exhibit high turnover of fine roots, promoting more fertile conditions [58]. Variation in plant-derived C substrates influences microbial diversity, whereas microbial activity, biomass, and immobilization of N influence plant diversity.
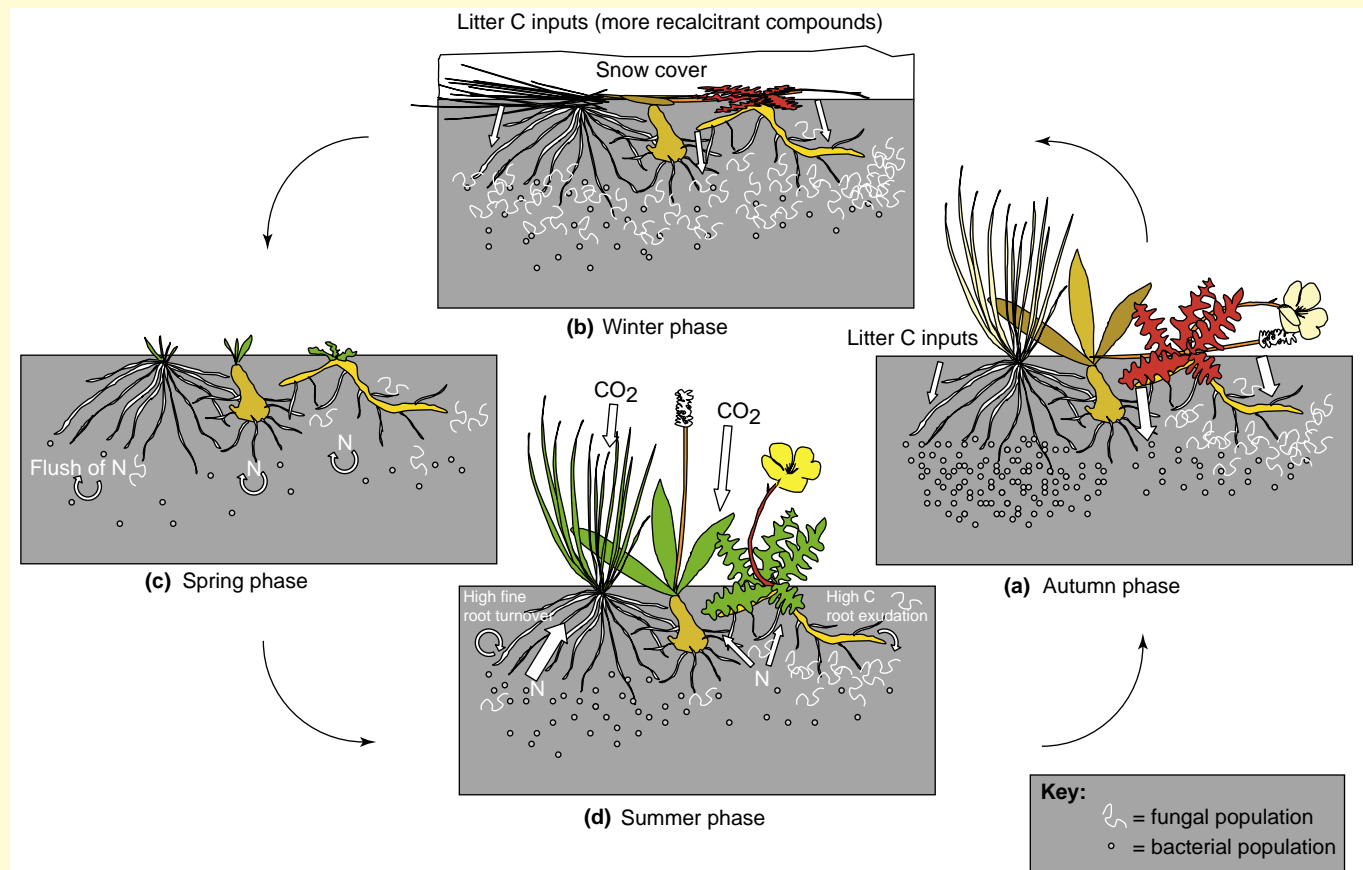

Figure I.

Aboveground–belowground relationships over intermediate timescales

Patterns over successional timescales

Soil biological communities change over successional timescales of tens to thousands of years, with important

implications for nutrient cycling and vegetation change. Studies of glacier forelands (Boxes 2,3), for example, reveal distinct patterns of soil microbial community development that parallel changes that occur above ground. In particular, soil microbial communities become

increasingly abundant and active as succession proceeds towards the maximal plant biomass phase [31–34] (Boxes 2,3). There are also changes in the diversity and composition of microbial communities: microbial communities switch from being bacterial dominated, during early stages of succession, to being fungal dominated at the maximal biomass phase [31] (Boxes 2,3). Microbial communities also become increasingly diverse as succession proceeds, in terms of the variety of resources that they can utilize [35]. These changes in the soil community parallel the build up in soil organic matter and N, which typically limits plant and microbial growth in early succession [33,34].

Mycorrhizal fungi, which are known to benefit the performance of their host plants due to improved plant uptake of water and nutrients and also increased protection against attack by pathogens and herbivorous insects, also increase in abundance and diversity as succession proceeds, corresponding to an increase in host plant diversity and changing habitat attributes [36,37]. The character of the mycorrhizal community also changes: in early succession, most colonizing plants are non-mycorrhizal, whereas in mid-succession, the dominant herbaceous plants tend to have a facultative requirement for arbuscular mycorrhizal fungi, and, in late succession trees and shrubs, which typically dominate the vegetation, have an obligate need for ectomycorrhizae [38]. Similar to plants and their symbionts, soil animal communities also change dramatically as succession proceeds. For example, studies of soil food web development reveal that soil animal communities become more complex and stable, with increasing food chain length, as succession proceeds [39]. However, in a study of surface-active invertebrates of glacier foreland in Austria, Kaufmann [40] showed patterns of invertebrate trophic development that were contrary to expected. Although rates of faunal colonization and succession generally followed a predictable pattern (with a rapid increase in diversity during early stages of succession), the first colonizers were almost exclusively predators, and herbivores and decomposers appeared later (Boxes 2,3). Predators have also been found to be the first colonizers of newly exposed glacier moraine in the High Arctic [41].

Many factors influence belowground community development (e.g. abiotic factors, such as climate and disturbance), but of primary importance is the build up in the amount and complexity of organic matter, which provides valuable resources (e.g. C and N), and changes in the quality of resource inputs to soil resulting from vegetation change. Plant species that dominate different stages of succession have different sets of ecophysiological traits [42], and these sets of traits can exert strong effects on soil biological properties [43,44], selecting for decomposer food webs with certain basic attributes [2,4]. Fast-growing species, for example, that typically dominate in early succession and produce large amounts of high-quality (i.e. N-rich) litter will promote bacterial-dominated food webs, whereas slow-growers that dominate in late succession produce low-quality, phenolic-rich litter that will favour fungal-dominated food webs [2,4]. This is consistent with the observation that soil food webs are dominated by bacteria and their consumers in early successional communities, whereas those of late succession have more complex food webs that are dominated by fungi and their consumers [31]. It is therefore reasonable to propose that changes in the functional composition of vegetation with succession will exert a strong selective effect on the belowground community.

Feedback mechanisms
Changes in belowground communities during succession will feedback to the plant community through a variety of mechanisms. One potential mechanism is via the build up in the abundance, activity and complexity of soil food webs with succession, which will positively feedback to the plant community through improvements in rates of nutrient recycling, especially of N [2,4]. The shift from bacterial-dominated to fungal-dominated food webs with succession might also positively influence rates of decomposition and nutrient cycling: bacterial-dominated food webs that occur during early succession are typically associated with 'fast' and 'leaky' nutrient cycles, whereas fungal-dominated food webs of late successional communities promote 'slow' and highly conservative cycling of nutrients [2,4,34]. It is probable, therefore, that belowground communities become more efficient in nutrient cycling as succession proceeds, leading to greater retention of nutrients in the system.

Another mechanism by which the soil biota feedback to alter plant community development is via the action of root-associated organisms (e.g. symbionts and root pathogens), which become more abundant and diverse as succession proceeds [40]. For example, arbuscular mycorrhizal fungi enhance plant species diversity in early successional communities [45–47] because they promote

Box 3. The Rotmoos glacier as an example of a chronosequence

The Rotmoos glacier in the Central Alps has been retreating since AD 1858, creating a well preserved chronosequence where disturbances have a minor role, and altitude is relatively constant along the sequence (Figure Ia; aerial photograph: BEV Vienna 1997). The succession of plants and animals has been well documented and there is little stochasticity in patterns of colonization of plants and animals. However, local factors, such as temperature, moisture and snow cover, do influence succession pathways and there are also hints that climate change (the cause of glacial recession) affects initial colonization [40].

Basic knowledge of this kind is mandatory for designing experiments to investigate the nature and ecological significance of aboveground–belowground interactions across temporal scales. The chronosequence approach also enables combined assessment of rates of change, a point in favour of long-term ecological experiments. The use of this chronosequence approach on glacier forelands has revealed patterns of belowground community development. For example: in Figure Ib, the soil microbial biomass (black bars) and the functional diversity (grey bars) of the microbial community increases significantly with increasing terrain age on the Rotmoos glacier foreland, Austria, reflecting an increase in resource availability, especially carbon and nitrogen. [Functional diversity was calculated as the diversity (Shannon diversity index) of a range of enzyme activities] (Data from [32]); in Figure Ic, the ratio of active fungal to bacterial biomass increases significantly with increasing terrain age in front of the Lyman Glacier, Washington, USA. This change might indicate a progressive shift towards a fungal-dominated food web in older sites, reflecting increased complexity and abundance of resources, and more efficient nutrient cycling (Data from [31]). Figure Id details the trophic composition of invertebrates along the Rotmoos glacier foreland in the Central Alps, Austria. The first invertebrate colonizers on still barren moraines are usually predators (ground beetles and spiders); various herbivorous groups appear after 40–50 years with the developing plant cover, and; detritivores (mostly millipedes) finally become abundant after 100 years, when an organic soil horizon has developed. The data were recorded from pitfall traps along the chronosequence and from mature reference sites outside the glacier foreland (rightmost points) (Data from [40]).
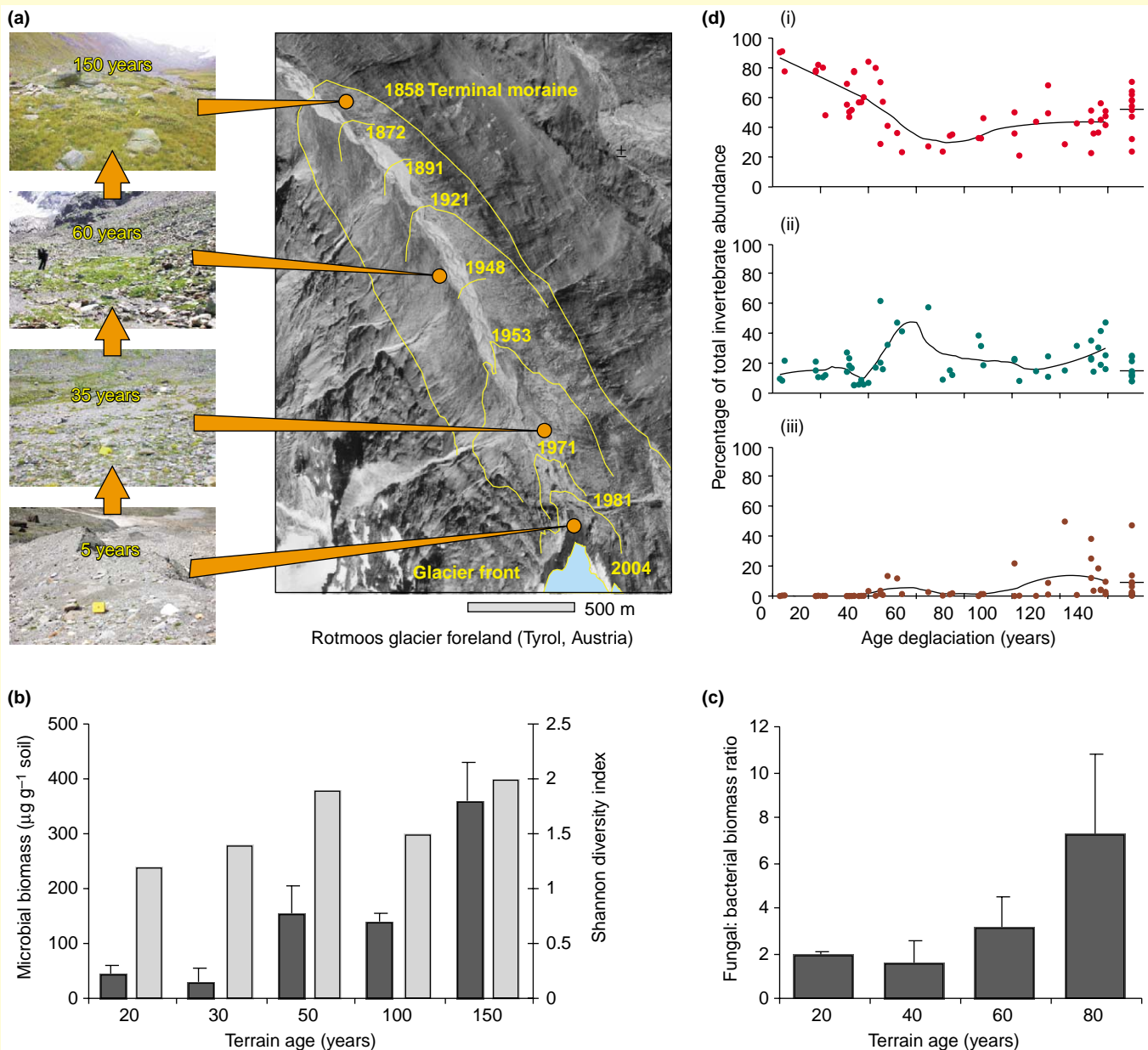

Figure I.

subordinate herb species relative to dominant graminoids and also increase interplant transfers of C and nutrients via hyphal links, leading to a more even distribution of resources within the plant community and reducing the ability of certain species to monopolize resources [48]. The build up of root pathogens during succession also exerts a powerful influence on vegetation change. For example, Van der Putten *et al.* [49] showed that, in sand dunes, a build up of root pathogens and root-feeding nematodes in the root zone of marram grass *Ammophila arenaria* led to a decrease in the abundance of this plant and its replacement by another species, *Festuca rubra*, that was not susceptible to these pathogens. Similarly, seedling mortality of invasive temperate tree species in tropical forests is due to the build up of fungal pathogens [50]. The build up of insect root herbivores, which feed selectively on early successional herb species thereby facilitating colonization by late successional species, also promotes vegetation succession [51]. Selective feeding by insect herbivores might also reduce the biomass of dominant species, enabling subordinate plant species to proliferate [8].

There are a wide variety of feedback mechanisms between plants and their soil biological communities and conceptual models are being developed of their role in vegetation change. These models are based on the concept of positive and negative feedback mechanisms that are generated by the specificity of response of interactions between plants and soil organisms [52–54]. Positive feedback occurs when a plant species influences the soil community in a way that benefits that plant, for example by promoting decomposer organisms that increase soil nutrient availability to that plant, thereby improving its performance in the community over time. This kind of feedback will enforce the dominance of this plant species, at the expense of other plant species, thereby reducing plant species diversity [52–54]. By contrast, negative feedback occurs when a given host plant performs worse in its own soil community over time, for example owing to the accumulation of host-specific pathogens or through the encouragement of mycorrhizal fungi that promote the growth of competing species. Such negative feedback will prevent any single species from becoming dominant within a locality, thereby promoting plant species co-existence [52–54].

This concept of feedback has been used to explain plant community dynamics in an increasing number of situations. For example, the invasibility of plants in grasslands is related to the ability of invading species to promote positive feedback, whereas negative feedback contributes to rarity owing to the accumulation of pathogens that limit growth [7]. Similarly, the invasibility of exotic trees into European forests is facilitated by positive feedback with the soil community [55], and the success of the European invasive weed *Centaurea maculosa* in North America might be related to its ability to cultivate soil biota that benefit its growth [56]. The concept of feedback has also been applied to plant succession. Reynolds *et al.* [52] suggested that positive feedback was more important as a driver of vegetation change during initial stages of succession, for example owing to N-fixing plants that result in positive feedback through the build up of soil N reserves (this initially benefits the N-fixing plant but, over time, also benefits neighbouring species, thereby leading to species replacement, i.e. facilitation). By contrast, the authors proposed that negative feedback is of limited importance during initial stages of succession, because host-specific pathogens are typically absent. However, as plant host densities and soil resources increase, a better environment is created for pathogens and mycorrhizal fungi, thereby increasing the role of negative feedback. Much is still to be learned about the mechanisms involved in positive and negative feedback, but such models provide a basis for testing the role of these mechanisms as drivers of vegetation change.

Although there is increasing recognition of the importance of feedback mechanisms between plants and their soil biological communities in vegetation change, their nature and the rate at which they occur will be altered by several external factors. For example, grazing by aboveground herbivores can accelerate or retard rates of vegetation succession, altering the quantity and quality of litter inputs to soil, which in turn affects soil biota and rates of soil nutrient cycling in both positive and negative ways [3,23]. Likewise, accelerated vegetation change resulting from global change phenomena, such as atmospheric N deposition, which promotes fast-growing species such as grasses at the expense of slower-growing herbs [57], might set in motion feedbacks to the decomposer community and soil N cycling, thereby further accelerating vegetation change [58]. In these situations, N-conserving species of infertile environments will be replaced by more competitive species, with traits that promote bacterial-dominated soil food webs and more rapid N cycling in soil [2–4,58]. Under such conditions, the new state would be preserved, even in the absence of additional N inputs, until N reserves in soil are exhausted, whereupon species adapted to low N conditions will re-establish [58].

Aboveground–belowground relationships over long timescales

Little is known about the nature and significance of relationships between plant and soil communities that operate over long timescales (i.e. over thousands of years or millennia). In a study of ecosystem development, Wardle *et al.* [34] provided insights into the functional significance of aboveground–belowground relationships in relation to nutrient cycling in extremely old ecosystems. These authors studied patterns of aboveground and belowground community development in a range of long-term chronosequences formed by different agents of disturbance. Each of the sequences had extended for sufficient time (i.e. 6000 to over four million years) for a decline in standing plant biomass to occur, known as the decline phase. Previous studies have linked this decline phase to long-term reductions in the availability of soil phosphorus (P), owing to leaching and occlusion of P in strongly weathered soils [59]. In accordance with this, Wardle *et al.* [34] found that, at all sites, the decline phase was associated with increasing N:P ratios of soil organic matter and litter of dominant plant species, suggesting an increasing substrate P limitation for decomposers.

Furthermore, they found that this reduction in substrate quality was paralleled by significant reductions in the biomass of decomposer microbes and shifts in the composition of microbial communities towards increasing fungal dominance, which together resulted in reduced rates of litter decomposition and mineralization of nutrients. These findings suggest, therefore, that as ecosystems develop, P becomes increasingly limiting. This sets in motion a negative feedback whereby low foliar and litter nutrient status reduces decomposer activity, which further intensifies nutrient limitation, leading to ecosystem decline [34].

Conclusions and future challenges

Thus, a consideration of temporal scale is crucial to our understanding of aboveground–belowground relationships and their significance for ecosystem properties. In particular, we identify a hierarchy of timescales within which different forms of aboveground–belowground relationships operate, each involving a different set of mechanisms with differing consequences for ecosystem properties. These range from highly dynamic interactions between plant roots and soil microbes that operate over short timescales, involving root exudation and the turnover of recent organic matter inputs, to longer term interactions that occur over thousands to millions of years, involving changes in the composition of soil organic matter and vegetation related to nutrient limitation. The greatest opportunity for aboveground–belowground interactions to influence ecosystem properties occurs at intermediate timescales, of tens to hundreds of years; here, a wide variety of feedback mechanisms, both positive and negative, operate between plants and soil biota, which strongly influence rates of nutrient cycling and vegetation change.

We highlight three major challenges that face ecologists working on aboveground–belowground relationships and their significance for ecosystem function. First, in relation to short timescales, there is a need to further understand the factors that regulate the transfer of plant C to soil and to determine its significance for the microbial community dynamics that influence plant nutrient supply and production, and global C cycling. A range of stable isotope approaches is available for exploring plant–soil C transfers [60], but conceptual frameworks, such as those generated by studies of herbivory [3,23], are needed to place the increasing number of studies of plant–soil C transfers in context of ecological processes at the ecosystem scale. Second, there is a need for a deeper understanding of the role of aboveground–belowground feedback mechanisms in plant community dynamics and vegetation change, and to integrate this knowledge into successional models that traditionally focus on vegetation-based mechanisms [61–63].

Finally, because the consequences for aboveground communities of belowground interactions, and vice versa, are not easily predicted [3,10], a major challenge is to unravel their context dependency, which is probably related to the spatial and temporal scale at which they operate, and also to abiotic factors that interact with biotic interactions to drive ecosystem properties. This presents a major challenge that can only be tackled effectively if soil ecologists work with scientists from other disciplines, such as plant ecologists, soil physicists and chemists, and theoreticians. The future, therefore, relies on interdisciplinary ecology and explicit recognition of aboveground–belowground relationships as regulatory forces in terrestrial ecosystems.

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