

Belowground biodiversity and ecosystem functioning

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Evidence is mounting that the immense diversity of microorganisms and animals that live belowground contributes significantly to shaping aboveground biodiversity and the functioning of terrestrial ecosystems. Our understanding of how this belowground biodiversity is distributed, and how it regulates the structure and functioning of terrestrial ecosystems, is rapidly growing. Evidence also points to soil biodiversity as having a key role in determining the ecological and evolutionary responses of terrestrial ecosystems to current and future environmental change. Here we review recent progress and propose avenues for further research in this field.

The last two decades have witnessed an enormous research effort directed at understanding how biodiversity loss impacts ecosystem functioning, and the influence of this on the goods and services that ecosystems provide¹. This research has led to the general consensus that biodiversity loss reduces most ecosystem functions and impairs their stability over time, and that functional traits of species have a major role in determining diversity effects¹. The majority of research on this topic, however, has had an aboveground focus; as a result, our understanding of the functional consequences of biodiversity loss belowground is less well developed. This lack of knowledge hampers our ability to predict the consequences of realistic scenarios of diversity change, especially since belowground biodiversity represents one of the largest reservoirs of biological diversity on Earth^{2,3}.

Soil communities are extremely complex and diverse, with millions of species and billions of individual organisms being found within a single ecosystem (Table 1), ranging from microscopic bacteria and fungi, through to larger organisms, such as earthworms, ants and moles (Fig. 1). Our understanding of this hidden biodiversity is limited, at least compared to what is known about aboveground diversity. But the last decade has witnessed a growing number of studies testing how belowground communities are distributed in space and time, how they respond to global change and what the consequences of biodiversity change are for plant community dynamics, aboveground trophic interactions, and biogeochemical cycles. Moreover, soil biodiversity research is now entering a new era: awareness is growing among scientists and policy makers of the importance of soil biodiversity for the supply of ecosystem goods and services to human society⁴; and a new generation of tools are available to interrogate the biology of soil and its ecological and evolutionary role.

Here we explore advances in our understanding of the roles of belowground biodiversity, and propose a pathway to further unravel its ecological and evolutionary function in the face of global change. Soil organisms perform a myriad of functions, but we focus here on their roles in nutrient and carbon cycling, plant community dynamics, and the eco-evolutionary responses of ecosystems to global change. We first bring together recent studies that have advanced our understanding of how soil biodiversity is distributed, and how soil diversity regulates ecosystem functions and the structure of terrestrial ecosystems. We then examine how soil biodiversity can mediate impacts of global change on the composition and functioning of terrestrial ecosystems, and explore emerging evidence for the role of soil biodiversity in the evolutionary dynamics of ecosystems. Finally,

we highlight research challenges for the new era of soil biodiversity research, and propose a pathway for advancing understanding of the role of soil biodiversity in determining eco-evolutionary responses to global change.

Spatial patterns of soil biodiversity

There is much dispute about how soil biodiversity is distributed across continental and global scales^{5,6}. Historically, soil microbial ecologists have been led by the view developed by Baas Becking in 1934 that “everything is everywhere, but, the environment selects”. Recent evidence, however, challenges this long-standing view⁷. Studies using molecular techniques, for example, show that bacterial, protistan⁸, mycorrhizal^{9,10} and faunal¹¹ taxa in soil have restricted global distributions due to variations in climatic, soil and plant conditions. Also, knowledge that exotic plant species are released from soil-borne pathogens in their new territories challenges the view that everything is everywhere⁷, and adds weight to the growing view that most soil organisms are restricted in their global distributions^{8–11}.

Another long-standing view in ecology is that species richness is maximal in the tropics and gradually declines towards the poles¹². The global biogeography of soil biota is uncertain due to a lack of data on patterns of occurrence across the world. What data are available indicate that while soil community composition varies across biomes^{2,11,13}, clear relationships between latitude and species richness do not exist belowground as they do for many taxa aboveground. Other than for termites¹⁴, we are not aware of any evidence that species richness of belowground taxa peaks in the tropics. For soil animals, including nematodes, mites and earthworms^{2,15}, and mycorrhizal fungi^{9,10}, the only clear pattern is that diversity is high along most of the latitudinal gradient, and that it drops towards the poles. This suggests a lack of coupling between aboveground and belowground diversity at global scales, a view supported by the finding that areas considered aboveground biodiversity hotspots¹⁶ had lower soil animal diversity than those that are not¹¹. This lack of coupling suggests that patterns of aboveground and belowground diversity are governed by different mechanisms^{3,12}, which are also scale dependent: local soil biodiversity is strongly driven by spatial heterogeneity, and the diversity of microhabitats found within a single, three-dimensional soil profile could be equivalent to that found aboveground within an entire ecosystem¹⁶.

Spatial patterns of soil biodiversity are shaped by a hierarchy of environmental factors, intrinsic population processes, and disturbance and recolonization events operating at different spatial and temporal scales¹⁷. At the smallest spatial scale (micrometre to millimetre), for example, distribution

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Table 1 | Estimated diversity and abundance of soil taxa according to published literature, supported by expert judgment

Taxon	Diversity per amount soil or area (taxonomic units indicated below)	Abundance (approximate)
Prokaryotes*	100–9,000 cm ⁻³	4–20 × 10 ⁹ cm ⁻³
Fungi†	200–235 g ⁻¹ ‡	100 mg g ⁻¹
AMF (species) ^{99–102}	10–20 m ⁻²	81–111 m cm ⁻³
Protists ⁸	150–1,200 (0.25 g) ⁻¹ §	10 ⁴ –10 ⁷ m ⁻²
Nematodes (genera) ^{103–105}	10–100 m ⁻²	2–90 × 10 ⁵ m ⁻²
Enchytraeids ¹⁰⁶	1–15 ha ⁻¹	12,000–311,000 m ⁻²
Tardigrades ¹⁰⁵	?	?
Collembola ¹⁰⁵	20 m ⁻²	1–5 × 10 ⁴ m ⁻²
Mites (Oribatida) ^{105,107}	100–150 m ⁻²	1–10 × 10 ⁴ m ⁻²
Isopoda ¹⁰⁵	10–100 m ⁻²	10 m ⁻²
Diplopoda ¹⁰⁵	10–2,500 m ⁻²	110 m ⁻²
Earthworms (Oligochaeta) ¹⁰⁸	10–15 ha ⁻¹	300 m ⁻²

Units can vary strongly between taxonomic groups, which is in part related to their size, but also whether the organisms are microscopic or macroscopic and whether identifications are based on morphology or on molecular and operational taxonomic units, or whether they are collected per gram, 100 g, or other soil volumes or surfaces. Estimates may differ substantially among soil types and ecosystems. A number of taxa have not been listed, including insects, ectomycorrhizal and ericoid mycorrhizal fungi, and vertebrate organisms (such as moles and voles). Numbers should be taken as preliminary given that most soil species have not yet been described, and because most estimates are based on single ecosystems or regions. We have used data proposed by the following experts: M. van der Heijden (arbuscular mycorrhizal fungi); V. Behan-Pelletier (mites); S. Geisen (protists); H. Helder (nematodes); M. Briones (enchytraeids and tardigrades); P. Lavelle and O. Schmidt (earthworms); supported with published data. Worldwide diversity includes aquatic and marine species¹⁰⁵. Estimate of 7,000 earthworm species worldwide is gross underestimation due to endemism¹⁰⁹.

* Bacteria and Archaea (genome equivalents)⁹⁵; estimation of worldwide diversity⁹⁶.

† Ref. 97 (also includes mycorrhizal fungi)⁹⁸.

‡ Operational taxonomic units.

§ Sequences.

|| There are some 1,500 species of tardigrades known worldwide, but no estimate can be made about numbers of species and numbers of individuals per unit soil.

patterns of soil biota are determined by microscale soil heterogeneity caused by variation in soil architecture and biotic interactions in pore space, including predator–prey interactions, ecosystem engineering by soil animals and rooting patterns of plants. Root exudates also contribute to fine-scale (millimetre to centimetres) spatial patterns in microbial and animal communities^{18,19}, serving to trigger specific groups of microbes in the rhizosphere, such as nitrate-reducing bacteria and denitrifiers²⁰ and attract symbiotic organisms to roots, including mycorrhizal fungi and rhizobia²¹, entomopathogenic nematodes²² and microbial antagonists of soil pathogens²³ through chemical signals. At the local scale (centimetres to metres), spatial patterns in soil biota are often explained by variation in the physical and chemical properties of soil, such as soil water, and carbon and nutrient availability, along with the identity of dominant plants, which determines the quantity and quality of substrates entering the soil³. At ecosystem, regional and continental scales (metres to thousands of kilometres), other factors such as climate, topography, soil abiotic conditions, such as pH, carbon and nutrient content, and continental isolation, have a more important role²⁴.

Studying spatial variability of soil biota is challenging given the enormous differences in the size of different soil organisms, which range from 2 µm for bacteria to more than 10 cm for earthworms, and up to a hectare for some soil fungi. Also, while microorganisms and some smaller fauna may be dispersed by wind, dispersal of larger-sized soil biota is limited by active movement, which is generally slow, ranging from 10–100 cm per year for nematodes to tens of metres per year for earthworms. As a result of these factors, coupled with inherent spatial variation in soil abiotic properties and the patchiness of plants, soil organisms are not distributed homogeneously in space; rather, belowground community composition is very fragmentary. In forests, for example, differences in litter quality beneath

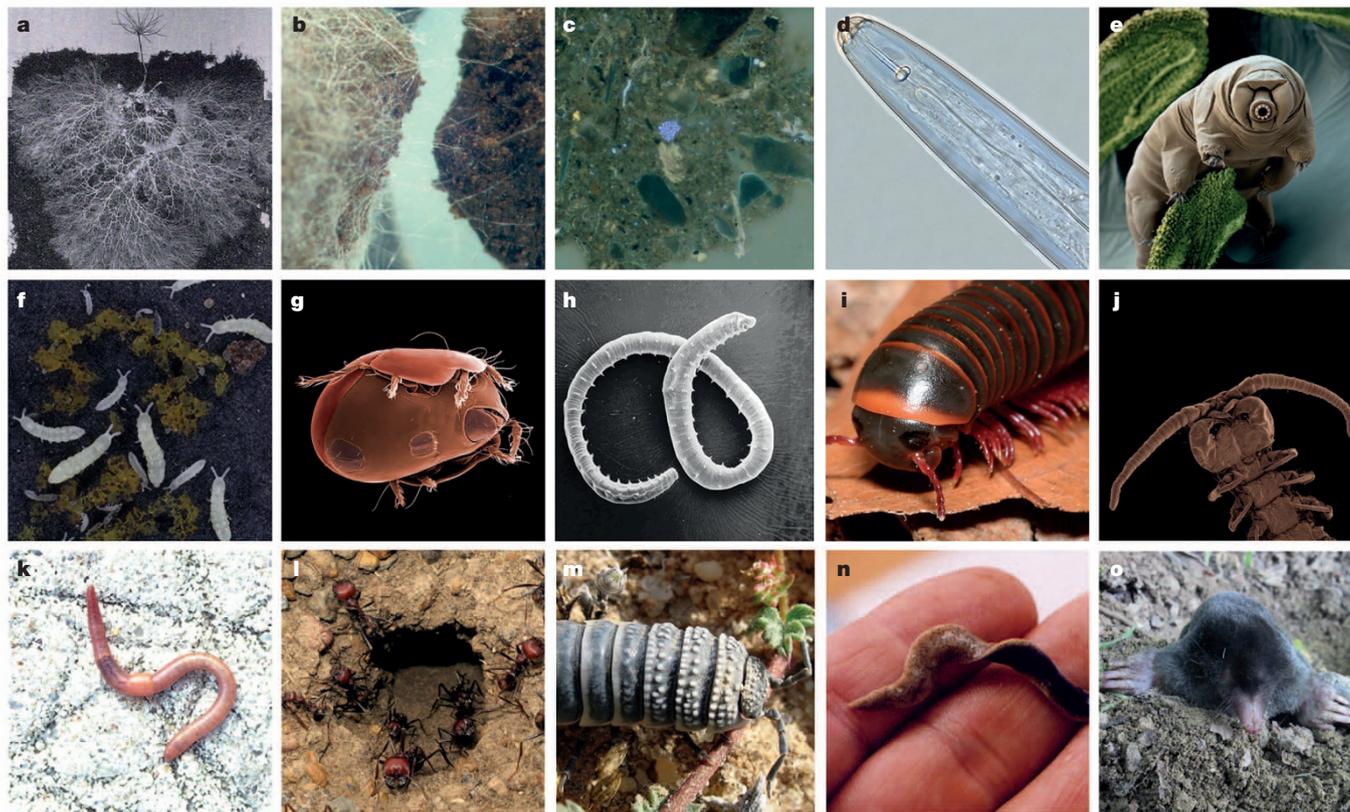


Figure 1 | A selection of organisms of the soil food web. a–o, The selection of organisms includes ectomycorrhizal (a) and decomposer fungi (b), bacteria (c), nematode (d), tardigrade (e), collembolan (f), mite (g), enchytraeid worm (h), millipede (i), centipede (j), earthworm (k), ants (l), woodlice (m), flatworm (n) and mole (o). All photographs are from the European Soil Biodiversity

Atlas, courtesy of A. Jones; individual photo credits are: K. Ritz (b, c); H. van Wijnjen (d); Water bear in moss, Eye of Science/Science Photo Library (e); P. Henning Krog (f); D. Walter (g); J. Rombke (h); J. Mourek (i, j); D. Cluzeau (k); European Soil Biodiversity Atlas, Joint Research Centre (l, n); S Taiti (m); and H. Atter (o).

dominant tree species lead to patchy distributions of soil organisms²⁵, whereas in semi-arid ecosystems, patterning of soil biota and nutrients are related to isolated areas of vegetation that create islands of fertility²⁶. Even in cultivated soils, patchy distribution of soil abiotic properties, such as pH and nutrient content, leads to strong patterning of soil organism distribution²⁷, and in non-vegetated ecosystems, such as the Dry Valleys of Antarctica, distribution patterns of soil organisms are related to spatial patterns in soil carbon and moisture availability²⁸.

Temporal patterns of soil biodiversity

Surprisingly few studies have examined temporal variability in soil biodiversity, but those that have reveal that population sizes of soil organisms vary over timescales of days to seasons, to decades and millennia. Over short timescales, major drivers of microbial community dynamics are resource pulses, which trigger rapid microbial responses. For example, recent work using molecular tools has shown that sudden increases in soil water availability following rainfall events after prolonged drought cause rapid and sequential resurrection of distinct, phylogenetically clustered groups of microorganisms over timescales ranging from minutes, to hours and days. Moreover, these rapid microbial responses are associated with significant pulses of nitrogen mineralization and CO₂ production from soil^{29,30}. Resource pulses from root exudates also drive short-term temporal dynamics of soil biota, with consequences for nutrient cycling and plant nutrient supply. Research has shown, for example, that the time between photosynthesis and the transfer of carbon from leaves to soil organisms is extremely rapid, taking hours in grassland³¹ or days in forests³². Also, as much as half of this photosynthetic carbon can be lost from soil by respiration within hours or days^{19,32}, again pointing to the role of root exudation as a major driver of the short-term dynamics of soil communities. Root exudation is also stimulated by biotic interactions with foliar³³ and root herbivores³⁴, which trigger short-term pulses of microbial activity and nitrogen cycling in the rhizosphere that increase plant nutrient uptake and growth^{35,36}.

Soil biological communities also vary over seasonal and successional timescales of tens or thousands of years, driven by changes in soil moisture and temperature, and shifts in resource supply in relation to the growth of plants. The few studies that have examined seasonal patterns in soil animal and microbial communities paint a complex picture. Studies of alpine ecosystems, for example, show that microbial communities display a complete turnover between winter and summer, with taxonomically and functionally distinct communities occurring at both times³⁷. In agricultural soils, seasonal patterns in soil communities are also highly complex, varying with land use and crop type³⁸ and from year to year³⁹. Even less is known about belowground community development over successional timescales, but a broad pattern appears to exist: at the onset of succession, soil food webs are composed of simple heterotrophic, microbial communities, and photosynthetic and nitrogen-fixing bacteria, but with time they become more complex and stable, with increasing food chain length⁴⁰, a reduced role of soil pathogens⁴¹ and greater reliance on mycorrhizal fungi for plant nutrition⁴².

Soil biodiversity and ecosystem processes

Ecologists first began to seriously explore the importance of trophic interactions in soil for ecosystem processes in the early 1980s, with microcosm studies revealing their role in stimulating processes of decomposition and nutrient mineralization, and plant nutrient acquisition and growth^{43–45}. These studies paved the way for an explosion of research over the last two decades exploring the importance of belowground trophic interactions for example^{46,47}, and trophic cascades^{47,48} for ecosystem processes. Modelling studies have explored the consequences of changes in the architecture and connectedness of soil food webs for energy flux, food web stability and ecosystem processes in real ecosystems^{49,50}. While these studies have increased recognition of the functional importance of soil organisms for biogeochemical processes, our understanding of the impact of species loss belowground still has many gaps. From the research that has been done to examine relationships between soil species richness and ecosystem functioning, the main messages to emerge are that for nutrient cycling, diversity effects are of most importance at the low end of the diversity spectrum, and they are

dependent, in part, on species traits rather than species richness per se^{51–53}. As a result, a common view is that there is high functional redundancy in soil communities for nutrient mineralization, and that changes in belowground community composition, rather than species diversity, are of most importance for ecosystem functioning.

New insights into the functional importance of belowground communities have emerged from studies done in the field. For instance, a field experiment set up across a gradient of sites from the subarctic to the tropics showed that reductions in decomposer functional diversity consistently slowed rates of litter decomposition and carbon and nitrogen cycling⁵⁴. Statistical models have also been used to show that changes in soil food web structure resulting from different land use intensities predicted processes of carbon and nitrogen cycling across a range of European sites, again demonstrating that shifts in soil food webs, in this case due to land use intensification, influence soil functioning under real-world field conditions⁵⁵. In a related study, intensive agriculture was found to impair the resistance and resilience of the soil food web to drought, leading to increased loss of carbon and nitrogen from soil as greenhouse gases and in drainage waters; this was related to a reduction in the 'slow' fungal relative to the 'fast' bacterial energy channel caused by intensive land use⁵⁶, suggesting that changes in the asymmetry of these channels, in this case from land use, disrupts ecosystem functioning.

The use of molecular approaches linked to field-based measures of soil carbon cycling has also shown that soil microorganisms regulate impacts of experimental warming on soil carbon and nitrogen dynamics in tallgrass prairie through differential stimulation of microbial populations and the signal intensity of genes involved in decomposition and nitrogen cycling⁵⁷. Similar approaches have been used to reveal the functional role of root-associated fungi involved in ecosystem carbon dynamics in boreal forest⁵⁸, and to show how the compositional and functional attributes of soil microbial communities vary across continental gradients⁵⁹. These are just a few examples, and while none explicitly test for soil diversity effects per se, they point at the diverse functional roles of soil organisms in biogeochemical cycles *in situ*.

Soil biodiversity and community dynamics

Over the last two decades, a major focus of soil biodiversity research has been to understand how soil biota impact vegetation dynamics. Traditionally, vegetation dynamics have been explained on the basis of abiotic factors, such as climate and soil physico-chemical properties, and biotic factors such as aboveground herbivory. In recent years, however, it has become widely accepted that vegetation dynamics are also strongly influenced by interactions between plant roots and soil-borne herbivorous, pathogenic, symbiotic and decomposer organisms, especially at local spatial scales⁶⁰. There was already some awareness in the 1990s about the role of soil biota, especially mycorrhizal fungi, root-feeding insects and soil-borne root pathogens as drivers of vegetation dynamics^{61–63}. But this became more widely recognized after the turn of the millennium with studies demonstrating the role of plant–soil feedbacks as drivers of plant diversity, abundance and succession^{41,64–66}, and ecosystem engineers, such as earthworms, in regulating vegetation dynamics⁶⁷.

Few studies have tested for effects of soil biodiversity on plant community composition, and these have either focused on soil diversity within single taxonomic groups, such as mycorrhizal fungi^{68,69}, or on manipulating coarser taxonomic units, for example based on organism body size^{70,71}. These studies show that belowground diversity can influence plant community diversity in both positive^{68,69,71} and negative⁷⁰ ways, which points to the myriad of mechanisms by which complex soil communities impact plant growth, and the potential for differential effects of soil biota to cancel one another out⁶⁰. Indeed, effects of soil biodiversity on vegetation dynamics operate through a variety of biotic interactions, which influence plant performance and vegetation dynamics directly, through altered herbivory, symbiosis, or pathogenesis, or indirectly through changing soil nutrient availability, predation on the plant-feeding organisms or symbionts, or changing interactions between plants and their aboveground multitrophic communities^{60,72}. In the short term, these biotic interactions can change

the capacity of plant species to compete, facilitate, and reproduce, whereas longer-term effects influence fitness and evolutionary adaptation.

An area that is especially rich in new discoveries concerns the role of plant secondary metabolites and defence signals in regulating belowground–aboveground interactions^{73,74}. It was recently discovered that belowground hyphal networks of arbuscular mycorrhizal fungi act as a conduit for defence signals from plants attacked by herbivorous insects to adjacent non-attacked plants, thereby acting as an early warning system for herbivore attack⁷⁵. Also, foliar and shoot herbivory has been shown to exert a unique soil legacy effect which greatly influences the production of defence chemicals in succeeding plants, and that this legacy effect is mediated by alterations in soil fungal community composition⁷⁶. These studies illustrate that soil biota can impact plant growth by modifying biotic interactions between plants and their natural enemies, but the role of soil biodiversity in these processes remains unresolved.

Considerable recent progress has been made in understanding the role of soil biodiversity in relation to disease suppression and symbiosis, and the use of molecular tools has revealed a previously unexpected diversity of rhizosphere microbes involved²³. A number of mechanisms have been put forward to explain why and how some soil-borne species contribute to disease suppression, including competition, predation and chemical communication, which collectively contribute to a form of soil biostasis from which many species cannot escape⁷⁷. However, new mechanisms are being proposed, such as the notion that the rhizosphere is a market place where roots and symbionts exchange carbohydrates for nutrients where cooperation can be rewarded, whereas cheating may be discouraged⁷⁸.

Eco-evolutionary dynamics and environmental change

Soil biodiversity is currently under threat from a range of anthropogenic pressures, but our understanding of how soil organisms adapt to rapid changes in their environment, whether they can do this fast enough to cope with novel environments, and how this adaptive capacity may relate to the level of soil biodiversity, is limited. A key challenge, therefore, is to determine how soil species respond to rapid environmental change, either through phenotypic plasticity, range shifts or by evolutionary adaptation, how these changes impact aboveground community re-organization and ecosystem functioning, and how the level of soil biodiversity may influence these processes (Fig. 2).

Although scant, evidence is emerging that certain soil organisms have the capacity to respond rapidly to climate change. An analysis of temporal

trends in fungal fruiting patterns in southern England, for example, revealed that climate change has advanced the first and extended the last fruiting date of many fungal species, with probable consequences for decomposition processes in soil⁷⁹. Similarly, an analysis of herbarium records in Norway has revealed that the time of fruiting of mushrooms has changed considerably over recent years, although changes differ across taxa⁸⁰. Whether or not these responses were due to plasticity or evolutionary adaptation has not been established. However, it was recently shown that individual species of decomposer fungi can acclimate to climate change, with warm-acclimated fungi reducing their growth and respiration following warming⁸¹. Given that fungi are the primary agents of decomposition, these results suggest that thermal acclimation of fungi could potentially alter decomposition processes in a warmer world⁸¹. It was also recently shown that exposure to a new environment can trigger rapid evolutionary change in life history traits of a soil mite, *Sancassania berlesei*, which ultimately alters population dynamics of this species⁸². Although not tested, such eco-evolutionary responses are likely to be widespread with impacts on community dynamics and ecosystem functioning in soil.

Changes in soil microbial community structure also have an impact on evolutionary processes, including patterns of natural selection on plant traits and plant responses to environmental change (Fig. 2). There is a huge body of historic literature reporting how rhizosphere microbes have an impact on plant traits related to nutrient acquisition, drought tolerance, and disease resistance, and ultimately plant fitness, although few studies have been done in non-managed ecosystems⁸³. Recent research also shows that modification of soil microbial communities can impact selection on plant traits with, for example, drought-adapted microbial communities increasing plant fitness under this stress⁸⁴. Similar specificity in selective advantage is exemplified by the finding that litter decomposition can be more rapid in soil beneath the host plant species, compared to when beneath a different plant species, the so-called home-field advantage⁸⁵. Home-field advantage effects are not always found and when they are, their strength is highly variable and context dependent. However, recent synthesis suggests that home-field effects are strongest when the quality of ‘home’ and ‘away’ litters become more dissimilar, and hence that dissimilarity in plant communities and litter quality between the ‘home’ and ‘away’ locations are the most significant drivers of home-field effects⁸⁶. The mechanisms involved in these various community responses still need to be resolved, but it is evident that soil biodiversity has the potential to impact both evolutionary and ecological processes under global change through direct effects

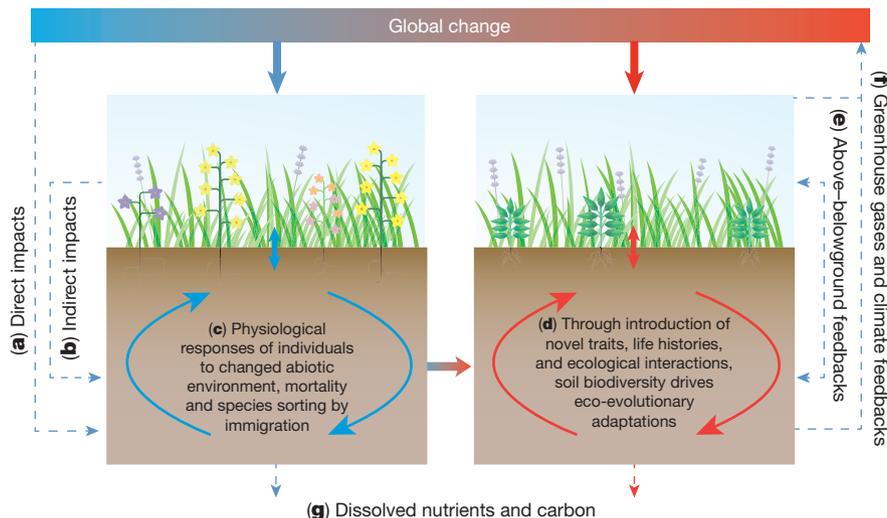


Figure 2 | Belowground responses and feedbacks triggered by climate change. Climate change impacts soil biodiversity directly (a), through changes in temperature and moisture, and indirectly (b), through shifts in resource supply from plants. Combined, these cause changes in the physiology and growth of individual soil organisms, leading to changes in the diversity and composition of soil communities through altered functional responses

and biotic interactions (c). As a result, selection for new traits and life histories within soil communities will take place, which in turn drives eco-evolutionary dynamics of aboveground communities (e) and ecological feedbacks to ecosystem processes, including greenhouse gas emissions and leaching of dissolved carbon and nutrients from soil (f).

of pathogens, symbionts or root herbivores, as well as by indirect effects involving decomposer organisms in the soil.

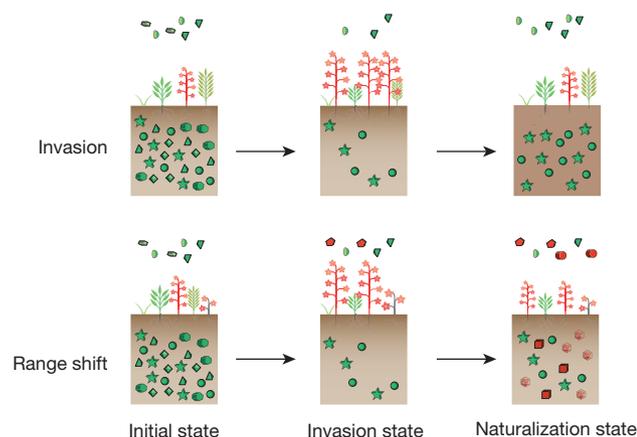
Soil biota may also have a role in eco-evolutionary dynamics of introduced exotic plant species (Box 1). An increasing number of studies show that introduced plant species have escaped negative feedback effects from soil biota⁸⁷, thus supporting the enemy release hypothesis. As time proceeds following invasion, however, the negative soil feedback may become

restored^{88,89}, which would predict that invasiveness ultimately declines with increasing time since introduction (Box 1 Figure). In one study on *Prunus serotina* (black cherry), soil pathogens were more virulent in the native than in the non-native range⁹⁰. These studies suggest that either the original pathogenic soil biota that cause negative feedback sooner or later are co-introduced, or that native soil pathogens in the new range become more virulent by rapid evolution. Indications of such rapid evolution emerge from studies on the introduced crucifer *Alliaria petiolata* in North America, which showed that soil decomposer communities of recently invaded sites are less capable of decomposing the toxic compounds of the introduced plant than microbial communities from sites that were invaded earlier⁹¹. Also, following invasion, decomposer richness has been shown to decline and then increase again, suggesting that microbial communities may adapt⁹² or become reorganized through dispersal, colonization and establishment processes.

BOX 1

Soil biodiversity, invasions and range shifts

Conceptualized relationship between soil biodiversity and the introduction of invasive exotic plant species that originate from other continents (top row) and plant species that expand their range within the same continent (bottom row). All native biota (plants, aboveground insects and microbes, and belowground microbes and invertebrates) are in green and exotic biota in red. In the initial state (left), abundance of exotic plant species is low and impacts on belowground and aboveground biodiversity are minor. During the invasion state (middle), exotic plant species become disproportionately abundant and might evolve increased competitive ability in the absence of specialized enemies. This process may be more pronounced for intercontinental exotic plant species (top row) than intracontinental range shifts (bottom row), where aboveground enemies also can shift their ranges. In this invasion stage, soil and aboveground biodiversity usually declines owing to loss of specific host plant species, or because of exotic plant species that suppress specific biota by novel chemistry. During the naturalization state (right), soil microbial taxa might rapidly evolve under the influence of the exotic plant species, leading to native pathogens and decomposer organisms adapted to the exotic plant species. As specific pathogenic effects are usually stronger than specific decomposer effects, exotic plants become controlled. If soil biodiversity controls pathogen evolution, the chance of such evolution occurring is greater in the case of intercontinental exotic plant species (top row) than intracontinental range-shifting (bottom row) plant species, as the latter become colonized by range-shifting soil biota from the original range (red symbols). As a result, the abundance of exotic plant species becomes controlled, thereby contributing to their ecological naturalization. Intracontinental range-expanding plant species (bottom row) might enter a naturalization state faster than intercontinental exotics (top row), because aboveground enemies and, later on, soil biota from the native range can shift range as well, but at different rates. Note that these are only some examples for which evidence can be found in current literature; many other scenarios are possible as well, but these need further testing.



Outlook and challenges

The last two decades of soil biodiversity research has revealed that belowground communities are remarkably diverse and that they have a major role in shaping aboveground biodiversity and the functioning of terrestrial ecosystems, as well as their ecological and evolutionary responses to environmental change. One of the biggest challenges for soil ecologists is to integrate this new understanding into existing and novel ecological frameworks in biodiversity-functioning research. Indeed, theory has lagged behind experimental work in soil ecology, and there is a pressing need to adapt existing and develop new theoretical models to explain patterns of belowground community organization and use this to understand their impact on aboveground community dynamics and ecosystem functioning.

There is also a need for improved understanding of the mechanisms that shape complex soil biological communities at different spatial and temporal scales. There is a dearth of information on spatial and temporal patterns of soil biodiversity, and this makes it difficult to develop new models explaining the structuring of soil communities. But the availability of soil biodiversity data is growing rapidly and with this comes the opportunity to develop new frameworks for explaining patterns of community organization at different spatial and temporal scales, and to identify the ecological and evolutionary mechanisms that underlie them. Progress has been made in this area, for example through the use of network analysis to determine patterns of coexistence in soil microbial communities^{57,93} and the application of new theories to the stability of food webs in soil⁹⁴. However, a remaining challenge is to merge the complex tangle of biotic interactions that operate in soil into single integrative frameworks that also take into account the structural and chemical complexity of soil.

It is now clear that soil biodiversity affects multiple ecosystem processes, including biogeochemical cycles and eco-evolutionary dynamics in plant and aboveground communities in response to global change. However, questions remain over the relative roles of genetic, species and functional diversity in driving these processes, and the role of extrinsic factors in modulating biodiversity-function relations, such as variations in soil fertility and the structural complexity of soil. Moreover, hardly anything is known about how belowground communities acclimate and adapt to rapid environmental change, although responses of soil biodiversity appear to impact aboveground evolutionary processes, including selection of plant traits in response to environmental change (Box 1 Figure). Such eco-evolutionary responses of belowground communities to rapid environmental change also have the potential to impact community dynamics and ecosystem functioning in soil, but so far this remains unexplored.

Finally, a major goal for soil biodiversity research is to integrate what we learn into sustainable land management decisions, especially regarding new approaches to the maintenance and enhancement of soil fertility for food, feed and biomass production, the prevention of human disease, and the mitigation of climate change. As we highlight here, a new age of research is needed to meet these scientific challenges and to integrate such understanding into future land management and climate change mitigation and adaptation strategies.

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