Soil Biodiversity and the Environment

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Annu. Rev. Environ. Resour. 2015. 40:4.1–4.28

The *Annual Review of Environment and Resources* is online at environ.annualreviews.org

This article's doi:
10.1146/annurev-environ-102014-021257

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Keywords

agriculture, ecosystem function, global change, land use, management practices

Abstract

Soils represent a significant reservoir of biological diversity that underpins a broad range of key processes and moderate ecosystem service provision. Our understanding of the role that soil organisms play in ecosystems is still developing, but the increased investigation into biodiversity-ecosystem functioning relationships in soils over the past couple of decades has provided insights that have greatly enhanced our ability to sustainably manage soil biodiversity. In this review, we synthesize emerging knowledge of soil biodiversity as a natural resource that supports the functioning of terrestrial ecosystems and their delivery of ecosystem services. We explore how environmental changes alter soil biodiversity and how this in turn can affect ecosystem processes as well as resistance and resilience to environmental changes. We then discuss ways to include soil biodiversity in management strategies for sustainable production and biodiversity conservation. We conclude by highlighting key research challenges to further improve our knowledge of soil biodiversity and its management.

Contents

1. INTRODUCTION

Soils form the terrestrial surface we live on and the basis for the vast majority of life on Earth, yet they are possibly the least understood and appreciated of Earth's ecosystems. Soil is considered to be among the most biologically rich habitats on Earth, with greater biodiversity per unit area than that observed aboveground, and is a center for biological interaction (1, 2). Soil biota are essential for a range of key ecosystem processes on which humans depend, including decomposition, mineralization, and nutrient cycling (3–5); and these biota mediate the provisioning of ecosystem services such as disease suppression and pollutant degradation through bioremediation, soil formation, and water infiltration, and climate regulation through their impacts on carbon (C) dynamics (6–8). Moreover, belowground communities are tightly linked to aboveground communities through trophic interactions, biogeochemical cycling, and plant-soil feedbacks, and these interactions ultimately govern ecosystem functioning (9, 10). However, our understanding of belowground communities is limited compared with our understanding of aboveground communities (2, 11). Although soils may appear highly resilient, their effective functioning can be highly fragile. Currently, soils and their biota are being threatened by degradation caused by global changes, including land use, climate change, chemical pollution, and invasions of new species, with potentially widespread impacts on Earth's ecosystems.

Global change in its broadest sense is considered the main concern for biodiversity conservation, ecosystem function, and service provision (12, 13). A substantial proportion of Earth's terrestrial surface area has been converted for human use (14), and more than 15% of soils worldwide are considered degraded with many areas highly impacted by pollution (15). Over 40% of Earth's land surface area is classified as arid to semiarid ecosystems, and this percentage is increasing owing to desertification (16). Furthermore, anthropogenic activities have resulted in substantial changes in nitrogen (N) and phosphorus (P) fluxes with inputs to the biosphere increasing from 15.3 to 175–259 teragrams (Tg) N year^{-1} and <0.3 to 14–16 Tg P year^{-1}, respectively, in the early twenty-first century compared to 1860 levels, altering global nutrient cycles and causing imbalances among C, N, and P (17). Associated with these observed global changes, there has been a loss of species in many terrestrial ecosystems and the introduction of novel species (9). Such gains and losses of species can be considered a consequence but also a driver of global change with potentially significant impacts on ecosystem functioning (18). Belowground communities are no less affected by environmental changes than aboveground communities, and significant responses to changes in land use, climate, nutrient deposition, invasive species, and other global changes are already evident with potential implications for ecosystem functioning in both natural and managed systems (19). These changes to soils are raising global attention toward efforts to sustain soils and their living capital for the future.

This review synthesizes current literature to provide an overview of the state of knowledge of soil biodiversity in its broadest definition (i.e., species richness and community composition); the relationship between soil biodiversity and ecosystem functioning and service provision; and the impacts of global changes and management practices on belowground communities. We then discuss how we may realistically improve in-field management of soil biodiversity to facilitate longer-term ecosystem functioning, biodiversity conservation, and soil health in natural as well as managed systems, and we conclude by outlining key research gaps and challenges.

2. SOIL BIODIVERSITY

Our knowledge of the distribution, biogeography, and functional aspects of soil biodiversity is rapidly evolving in part due to the increasing recognition of its substantial role in ecosystem processes and partly because of the benefit of healthy soils to human health and well-being. The continued technological development of molecular methods and equipment, greater sensitivity of analytical equipment and new analytical procedures, and increasingly sophisticated statistical tools (including bioinformatics pipelines) are facilitating the discovery of the true diversity and functional capabilities of the biota (eukaryotes and prokaryotes) found in small quantities of soil. The improved precision of techniques, such as stable isotope analysis, now reveals how small organisms aid the transfer of C and nutrients into the soil food web and helps determine how their functions are affected by soil disturbance (20). Remote sensing technology connects large spatial scale parameters (e.g., vegetation, land use, climate) with data on microbial and invertebrate distributions for use in predictive maps, models, and scenarios (21). The rapid advancement of these tools facilitates our understanding of belowground community diversity and composition, which allows us to link belowground communities to ecosystem functioning across local to global scales. This information can provide a framework for building scenarios of how soil biota will contribute to ecosystem functioning in the future. In this section, we provide an overview of the soil biota, their role in ecosystems, and examples of the application of new tools that have provided novel insights into the relationships between belowground communities and ecosystem structure and functioning in recent years.

2.1. Soil Biota

Soils support highly abundant and diverse communities of organisms that show a broad array of life histories and functional traits (**Figure 1**), and they range in body size from a few micrometers in some bacteria to several meters in length in the case of some earthworms (**Table 1**). However, the largest known soil organism is the pathogenic fungus *Armillaria ostoyae* (Romagn.) Herink. Several

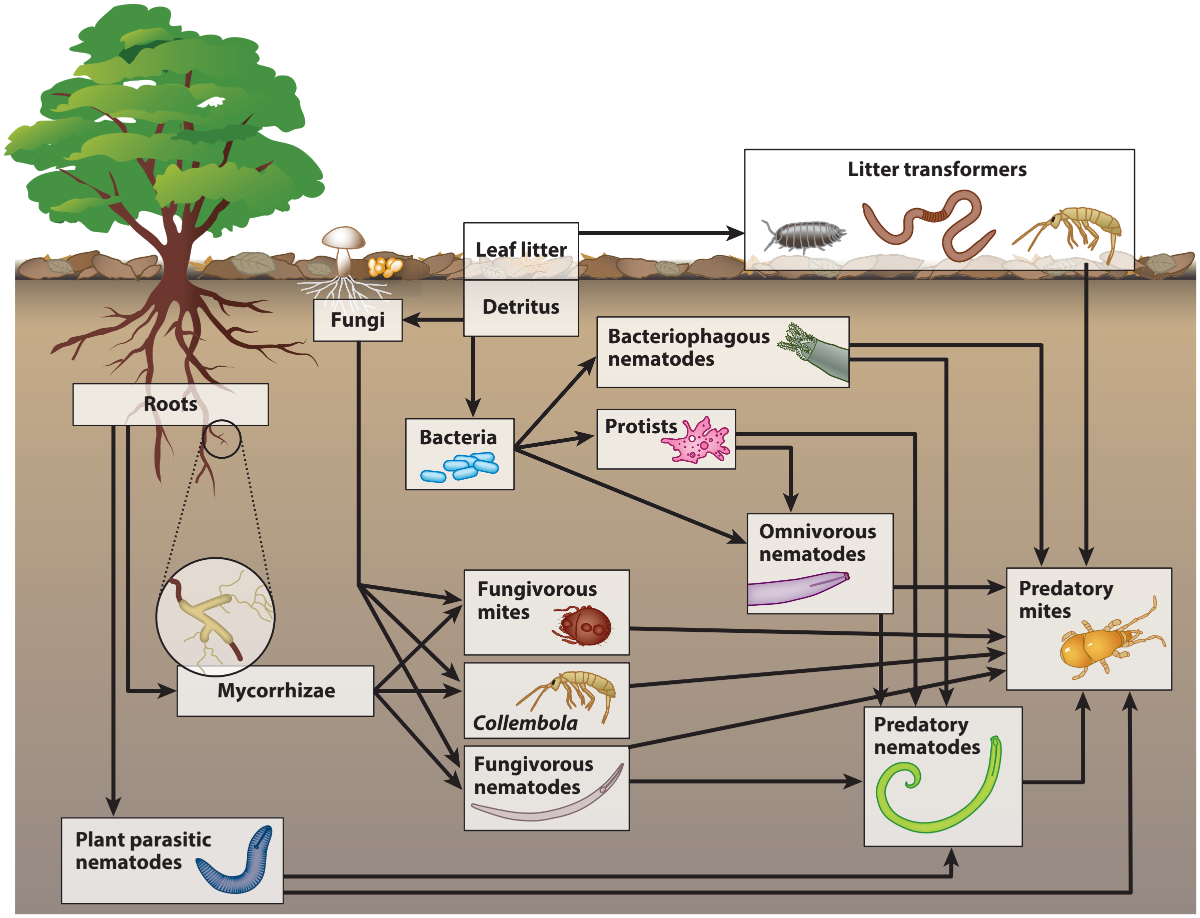

Figure 1

A simplified soil food web illustrating some of the key groups of soil biota. Fungi and bacteria form the basis of the soil food web acting as plant root symbionts or decomposers. Microbial feeders, such as protists, bacterial and fungal feeding nematodes, mites, and springtails, influence soil processes by moderating microbial biomass and activity, while in turn being prey to larger soil fauna such as predatory nematodes and mites. Plant roots are parasitized by different plant parasites including nematodes, while organisms such as isopods, earthworms and some microarthropods act as litter transformers that help fragment and incorporate litter into the soil horizon. Real-life soil food webs are substantially more complex and include many other groups of soil fauna.

genetically unique individuals growing in the Malheur National Forest in Oregon, United States, are estimated to cover hundreds of hectares each, weigh many tonnes, and are thousands of years old (22). The biotic interactions between this diversity of organisms occupying the soil ecosystem ultimately influence the impact of soil biota on ecosystem functioning (2, 23). Soil organisms are often classified into functional groups, such as ammonia-oxidizing bacteria, mycorrhizal fungi, plant parasites, and predators, or are compartmentalized on the basis of body size to provide insight into the potential functional role of soil organisms. In the latter case, three main groupings are generally considered according to Swift et al. (3): microbes (bacteria, fungi, archaea) and microfauna (i.e., protists, nematodes) with body widths less than 0.1 mm; mesofauna (i.e., mites, springtails, enchytraeids) with body widths less than 2 mm; and macro- and megafauna (i.e., earthworms, ants, millipedes, etc.). Although there is substantial variation in feeding types and

Table 1 Overview of average local species richness and approximate maximal abundances, number of known species and estimated global species richness of key soil microbial and invertebrate taxa

Taxa	Local species richness	Approximate maximal abundance	Known species[a]	Estimated richness
Prokaryotes	100–9,000 cm^{-3}	20×10^{9} cm^{-3}	4,500[b]	Up to 10^{9}[c]
Fungi	200–235 g^{-1}	100 m g^{-1}	100,000	5,000,000[d]
Protozoa	150–1,200 $(0.25\ \text{g})^{-1}$	10×10^{6} g^{-1}	40,000	200,000
Nematoda	10–100 m^{-2}	20×10^{6} m^{-2}	5,000	20,000
Acari	100–150 m^{-2}	400,000 m^{-2}	30,000	80,000
Collembola	20 m^{-2}	200,000 m^{-2}	8,000	24,000
Annelida	10–15 ha^{-1}	500 m^{-2}	3,600	7,000
Enchytraeidae	1–25 ha^{-1}	300,000 m^{-2}	600	1,200
Formicoidea	NA	NA	15,000[e]	No estimate
Isoptera	NA	NA	2,600	10,000

Abbreviation: NA, not applicable because these organisms live in colonies making it difficult to meaningfully estimate richness and abundance per unit area.

[a] The number of known and global species richness of microbes includes non-soil-specific species.

Modified from Bardgett & van der Putten (2), Barrios (6), and Brussaard et al. (1), with some additional references: [b] Dykhuizen (148), [c] Torsvik et al. (149), [d] Blackwell (150), and [e] AntWiki (**http://www.antwiki.org/wiki/**).

life history between species within these classifications, and many taxa span multiple functional groups and trophic levels, these groupings are useful for investigations into areas such as nutrient cycling and ecosystem dynamics. Moreover, our knowledge of species' functional characteristics is becoming clearer, thus constantly improving our understanding of the belowground ecosystems.

Microbes form the base of the soil food web, and they are of great significance to ecosystem functioning. The microbial community is largely dominated by bacteria and fungi that account for most of the belowground biomass, roughly equal to 0.6 to 1.1% of soil organic C (or 2 to 806 g C m^{-2}) (24), and represent a biodiversity pool with an estimated species richness of tens of thousands per gram soil (25). It is worth noting here that we still lack a clear definition of what makes a microbial species, and we often rely on sequence similarities of taxa-specific DNA subunits to distinguish between distinct organisms rather than morphological characteristics. We refer to these as operational taxonomic units rather than species. The soil bacterial communities are generally dominated by the phyla Acidobacteria, Actinobacteria, Proteobacteria, and Bacteroidetes (24), with community composition strongly related to soil pH at local to global scales. In particular, the relative abundance of Acidobacteria increases with a decrease in soil pH, whereas the relative abundances of Actinobacteria and Bacteroidetes increase with increased soil pH, with bacterial richness peaking at near neutral pH (26). Although Basidiomycota and Ascomycota dominate the soil fungal community, climate, vegetation, and edaphic characteristics influence fungal community composition, and functional groups show considerable variability in their relationship with these variables (27). The fungal:bacterial ratio can be predicted to some degree based on soil C:N ratios, possibly because fungi require more N per unit biomass than bacteria. In addition, fungi generally have higher relative abundances in forest biomes than in grassland and desert biomes at a global scale. Fungal species richness is positively related to mean annual precipitation (through both direct and indirect effects) and soil calcium concentration, with total richness increasing toward the equator (24). Archaea are also common in soils, but they are generally less abundant than bacteria, representing on average only 2% (ranging from 0 to 10%) of the prokaryotic community across soil types with greater relative abundance in soils with lower C:N ratios (28).

A meta-analysis by Fierer and coworkers (24) found that soil faunal biomass generally equals ~2% (ranging from 1.5 to 3.6%) of microbial biomass across biomes globally (excluding larger animals) with only weak relationships to plant biomass, but there is significant variation in the relative abundance of soil fauna across biomes. Apicomplexa, Cercozoa, Ciliophora, and Dinophyceae are the most abundant protists in soils, but local community composition is strongly related to climatic conditions. Species of Dinophyceae are particularly abundant in arid soils, whereas Ciliophora and Apicomplexa are more abundant in humid soils, and Cercozoa are more widespread (29). Nematodes are the most numerous multicellular soil animal in most ecosystems and dominate the soil faunal biomass in desert soils (24). Nematode community composition is strongly related to climate, and plant parasites tend to dominate warm, humid sites, whereas bacterial feeders dominate colder, drier sites (30). Mites and springtails are common in most ecosystems, but particularly high abundances are observed in forested ecosystems. Earthworms and enchytraeids dominate the soil faunal biomass in most biomes given their relatively large body size. Enchytraeids are particularly abundant in boreal forests, tundra, and heathlands, whereas earthworms are abundant in temperate grasslands, deciduous forests, tropical pastures, and rain forests, with limited abundances observed in acidic soils, desert soils, and arid grasslands (24). Ants are common in many temperate to tropical ecosystems. Termites are less widespread than ants but are abundant in many subtropical and tropical ecosystems, with increasing abundances toward the equator in wet ecosystems (31). Ants and termites were not explicitly incorporated in the meta-analysis mentioned above (24), and the contribution of larger soil fauna to belowground biomass may be somewhat underestimated.

Soil is a three-dimensional, highly heterogeneous environment in terms of physical structure, soil properties, and nutrient concentrations at very fine scales (32). This heterogeneity is generally considered the main driver of the high biodiversity observed in soils (33). Soil biota are not evenly distributed throughout the soil, and most activities take place in biological hot spots, such as the rhizosphere, i.e., the area around plant roots where soil biota are influenced by root exudates (34). Vegetation composition and biotic interactions, particularly between trophic levels, also influence soil biodiversity at fine scales (23). At local scales (i.e., meters to kilometers), variation in edaphic variables and vegetation composition become more important in shaping soil communities, but the relative importance of these factors depends on habitat characteristics and differs between functional groups (35). It is becoming apparent that factors such as climate, soil type, and geological history generally become better predictors of belowground community composition at larger scales, and this seems broadly applicable across different taxa (11, 29, 30, 36). Furthermore, there is increasing evidence that many belowground taxa have restricted distributions, with many taxa showing biogeographical patterns that are dissimilar in some ways to those observed aboveground (11, 29, 30, 37). For example, although many belowground taxa show decreased species richness at high latitudes, there is very limited evidence for strong latitudinal gradients in biodiversity belowground; nevertheless, termites seem to be an exception to this with higher species richness in the tropics where they often occur in great numbers (2, 31). Also, a global-scale study of soil fungal diversity found a decrease in species richness at higher latitudes even though several taxonomic and functional groups showed contrasting patterns (27). Interestingly, a study that compared the diversity of belowground communities of New York's Central Park with samples collected globally through sequencing found there was little difference in the number of species observed per unit sampling effort, with 6.5% and 26% fewer prokaryotes and eukaryotes, respectively, in Central Park compared to global samples (38). This study (38) stresses the importance of edaphic factors in structuring belowground communities, indicating that human-altered environments can conserve substantial belowground biodiversity. Global-scale patterns of belowground community composition and biogeographical patterns help define a basis for management in different regions.

2.2. Functional Roles

The soil biota regulate a broad suite of essential soil processes, including decomposition of organic material, which is the first step toward the release and recycling of C and nutrients tied up in aboveground plant and animal biomass. At large spatial scales, the rate of litter decomposition is mainly governed by climatic conditions, i.e., temperature and precipitation (39), whereas at smaller spatial scales nutrient and lignin content becomes more important (40). However, ultimately litter and soil organic matter (SOM) decomposition are governed by biotic activities (3, 41, 42). Soil microbes drive most functions with bacteria generally utilizing more labile material and compounds, and more recalcitrant plant-derived material is mostly degraded by fungi (4, 43). Hence, soil food webs are often described as being fungal or bacterial dominated. Bacterial-dominated food webs are generally characterized as representing disturbed soils with a fast and open nutrient cycling and low SOM content, whereas fungi dominate less-disturbed food webs characterized by slower, more conservative nutrient cycling, and greater SOM content (43, 44). The functional role of archaea in soil has not been thoroughly examined, but many archaea have been linked to N cycling and may be the dominant prokaryotic ammonia oxidizer (45).

Soil biota influence ecosystem functions through their interactions with the vegetation aboveground. For example, both soil microorganisms and fauna can moderate vegetation succession and plant diversity (46, 47). Symbiotic N-fixing bacteria and mycorrhizal fungi associated with plant roots aid in nutrient uptake, in particular N and P, respectively. It has been estimated that symbiotic microorganisms are responsible for ∼5–20% of all N (up to 80% in boreal and temperate forests) and up to 75% of P that is taken up by plants annually, and more than 20,000 plant species depend on microbial symbionts for growth and survival (44). Moreover, changes in the composition of symbiotic microorganisms may alter plant community dynamics by modifying plant-herbivore interactions and competition between different plant species (46). Similarly, pathogens strongly influence competition between plant species and can contribute to the persistence of rare species, maintain biodiversity by suppressing dominant species, and facilitate invasion of non-native species (44, 48). However, non-symbiotic soil microbes also influence nutrient dynamics. For example, free-living N-fixing bacteria are common in most terrestrial ecosystems, contributing a significant amount of N to soils with rates of up to >3 kg N ha^{-1} $year^{-1}$ in some dryland and tundra ecosystem types (49).

There is also mounting evidence that soil biota can significantly modify belowground-aboveground interactions mediated by changes in plant traits that are associated with water and nutrient uptake and the production of plant defenses, which in turn can influence aboveground communities of mutualists, herbivores, and predators (50, 51). Furthermore, rapid immobilization of N by soil microbes acts as a short-term N sink, preventing loss to groundwater or nearby ecosystems; later, this N can be released and act as a source of N for plant uptake (52). In addition, soil microbes contribute to plant growth through their role in the weathering of soils via exudation of organic acids and solubilization of precipitated P (53, 54). Conversely, microbes can have negative effects on plant growth by competing for nutrients particularly in nutrient limited ecosystems, by transforming N to more labile forms, or by reducing N pools through denitrification (44).

Soil fauna moderate microbial activities and through this influence ecosystem processes including decomposition and nutrient cycling (42, 55). It is well established that soil fauna influence microbial biomass and activity through grazing, fragmenting, and incorporating litter into soil, and build and maintain porosity and aggregation through burrowing, casting, and nesting, which together stimulate ecosystem processes (6, 56). Protists and nematodes are near the base of the food web feeding on microbes and stimulate microbial turnover and respiration. Some groups of nematodes can affect C and nutrient cycling indirectly by enhancing plant growth through predation or biocontrol of plant pathogens and directly by feeding on and reducing root biomass and plant growth (57). Protists play similar functional roles as microbial grazers, but the full extent of their importance in nutrient cycling is unknown (58). Ecosystem engineers, such as earthworms, ants, and termites in particular, have a significant impact on their environment. For example, termites play a particularly large role in litter fragmentation, decomposition processes, and nutrient cycling in subtropical and tropical savannas and forests as symbiotic microorganisms allow them to break down lignocellulose (31, 42). Similarly, earthworms influence their environment substantially, particularly by fragmenting and incorporating dead organic material into the deeper soil horizons where microbial activity is greater, and thereby influence ecosystem functioning. Importantly, a meta-analysis found that the presence of earthworms, on average, increased crop yield by 25% in agricultural systems, with the greatest effects observed in systems with high residue return and low soil N availability (59).

2.3. Emerging Insights

Metagenomics and the associated bioinformatics pipelines are increasingly being used to investigate the functional capacity of microbial communities and metabolic pathways. For instance, in a study on the effect of 10 years of elevated CO_2 (eCO_2) levels in a grassland, metagenomics was used to investigate microbial community responses. The study found that bacterial biomass and community composition responded to eCO_2, and there was an increase in the abundance of genes associated with the degradation of labile C and genes related to C and N fixation under eCO_2. The abundance of these genes was correlated to soil C and N content and plant productivity, indicating a relationship between gene abundance and ecosystem function (60). More recently, whole-community shotgun metagenomics was used to explore the impact of 10 years of 2°C warming on community metabolism in temperate grassland soil in the Midwestern United States. The authors found that warming enriched pathways related to C turnover (such as cellulose degradation, CO_2 production), N cycling (such as denitrification), and sporulation genes, indicating that microbial community responses mediate feedback responses to climate change (61). Similarly, another study used metagenomics to investigate the change in soil microbial functional gene abundances and pathways during permafrost thaw. The study showed that warming induced a rapid increase in genes associated with C and N cycling, and the authors were able to identify specific genes related to methane emissions (62). Such studies provide evidence for the mechanisms through which belowground communities influence ecosystem processes under current conditions, allowing us to make robust predictions of potential global change implications on ecosystem structure and functioning. Similarly, meta-transcriptomics is a promising tool to quantify changes in gene expression in response to environmental changes (63).

Stable isotopes have long been used to investigate nutrient flows through the soil food web, in particular C and N, but the improved sensitivity of analytical equipment has substantially improved the use of stable isotopes as a tool in ecological studies in recent years. For example, stable isotopes were recently used for the first time to quantify protist respiration rates and rates of bacterial ingestion by protists in an incubation study using ^{13}C- and ^{15}N-enriched bacteria to better quantify the contribution of protists to C and N dynamics belowground (20). Other emerging techniques that promise further insights include the development of novel tools for data processing, modeling, and mapping. For example, network modeling approaches have only rarely been applied to microbial communities but appear promising for elucidating the roles of microbes and linking this to emergent properties of ecosystems, particularly for developing hypotheses that can then be tested experimentally (8). As another example, Griffiths and coworkers (21) collected >1,000 soil samples using a grid to produce the first high-resolution map of bacterial communities

THE GLOBAL SOIL BIODIVERSITY INITIATIVE

The Global Soil Biodiversity Initiative (GSBI) is a platform for all scientists of all countries interested in communicating expert knowledge on soil biodiversity research and in learning how to incorporate this into environmental policy and sustainable land management. Research on soil biodiversity has rapidly accelerated in the last 10 years, increasing our knowledge of the identity of the many species belowground, their geographical distribution, and their influence on biogeochemical and hydrological cycling. Soil biodiversity is now seen as tightly linked to aboveground diversity and as having a significant influence on the maintenance of ecosystems. Life-supporting services to society that are provided by soil organisms include decay of organic matter; cleansing of water; regulation of pests; and nutrient cycling for food, feed, and fiber production. Land-use change, such as tillage, mining, paving of fertile soil, and afforestation, decreases soil biodiversity with impacts on Earth's ecosystems. Nevertheless, soil biodiversity is frequently overlooked in global environmental policies, and the GSBI platform aims to bridge the gap between research and environmental policy making. Projects of the scientists involved in the GSBI include the publication of the GSBI's findings, participation in working groups on methods harmonization, creation of the DataBase Platform on Soil Biodiversity, education for the public on the benefits of soil biodiversity, and development of global research experiments.

throughout Great Britain in one of the most rigorous landscape-scale studies of belowground communities to date. The study found that bacterial diversity was best explained by soil pH but also found a strong relationship between bacterial and plant communities, indicating that similar mechanisms may structure aboveground and belowground communities. Such large-scale spatially structured surveys, utilizing high-resolution molecular techniques in combination with spatial modeling, provide significant insights into belowground communities. In brief, significant insights are emerging from the development and refinement of technologies, and new global research collaborations, such as the The Global Soil Biodiversity Initiative (see sidebar), provide excellent frameworks for acquiring and incorporating new insights into soil management and policy making.

3. SOIL BIODIVERSITY AND ECOSYSTEM FUNCTIONING

There is growing recognition that soil biodiversity is essential to the provision of ecosystem services for human well-being. Soil biota moderate primary production through their role in (*a*) soil formation, decomposition, and nutrient cycling; (*b*) control or suppression of plant pests and diseases; (*c*) the production of plant growth hormones; (*d*) regulation of water supply by modifying soil structure and water infiltration and storage; and (*e*) promotion of flood and erosion control by modification of soil structure and water infiltration (6, 19). In addition, soil biota influence climate through storage of C and the production and consumption of greenhouse gases (6, 19). Scientists and policy makers are increasingly recognizing the benefit of including ecosystem services in decision making for global sustainability (19). However, despite the increasing awareness of the crucial role of soil for food production, hydrology, and greenhouse gas fluxes, soils are often considered as abiotic, without including knowledge of the biotic component that is integral to the provision of ecosystem services. For example, the role of biota in aerating, aggregating, and moving soil particles and elements affect ecosystem services in the short term and also assure the formation of stable soils over longer time scales. In this section, we discuss the relationship between soil biodiversity and ecosystem processes and provision of services. We focus on the role soil biodiversity plays in four ecological concepts of high importance to human well-being:

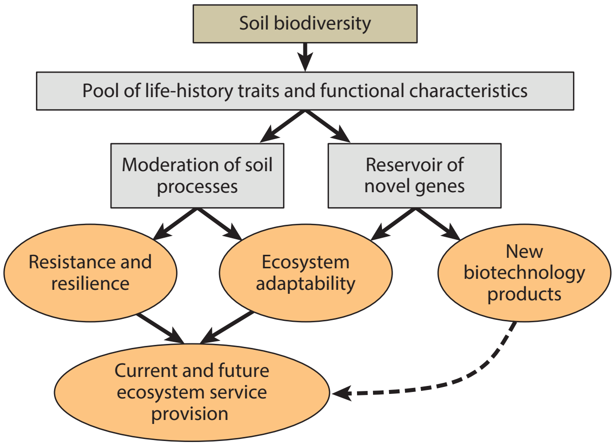

Figure 2

A schematic and simplified overview of the four main ecological concepts (*orange ellipses*) influenced by soil biodiversity and the pathways through which this occur. Soil biodiversity moderates soil processes, such as nutrient cycling, and through this directly influences the provision of ecosystem services. Soil biodiversity also influences the resistance and resilience of functions to perturbations such as pollution and extreme events, and the adaptability of ecosystems to environmental changes such as climate change, and through this the provision of ecosystem services. Moreover, soil biodiversity provides a pool of novel genes that may improve ecosystem adaptability but also represents a significant reservoir of genetic material that may be utilized for biotechnological products in industry. The dashed arrow indicates that some biotechnological products such as pharmaceutical products may be seen as services to human well-being even though they are not produced in the field.

(*a*) ecosystem service provision through moderating soil processes, (*b*) enhancement of ecosystem resistance and resilience to perturbation, (*c*) increased ecosystem adaptability to environmental change, and (*d*) as a reservoir for the development of potentially new biotechnological products (**Figure 2**). Although some biotechnological products may be considered ecod resilience to perturbation, (*c*) increased ecosystem adaptability to environmental chsystem services, we thought it pertinent to highlight this as a separate concept given that the products may be delivered off field (i.e., in the lab).

3.1. Soil Biodiversity and Ecosystem Functioning Relationships

Although it is well established that soil biota influence many soil processes, there is an ongoing investigation into how important soil biodiversity is to ecosystem functioning. In particular, studies are providing insight into what type of relationship between soil biodiversity and ecosystem functioning might exist and what the relative importance of community composition versus species richness might be. Soil microbial communities are generally thought to have some functional redundancy given the astounding diversity found belowground and are therefore expected to be highly resistant and resilient to perturbation (5, 64). A recent global-scale study, however, showed that the functional attributes of soil microbial communities differed between biomes and that there is a positive relationship between functional and taxonomic diversity (65), suggesting a potential direct link between biodiversity and ecosystem processes. Other studies have shown a similar relationship for microbial functional diversity (66, 67), with a positive species richness-functional diversity relationship appearing to exist across taxonomically diverse groups (68). One possible reason for this pattern is that ecosystem functions are not performed by whole ecosystems but rather by specific system components (69), for example, a specific group of microbes as in the case of nitrification. Moreover, there is evidence that suggests that soil biodiversity may be important to the maintenance of broad ecosystem functionality (70), i.e., soil biodiversity may have a greater role on ecosystems through space and time when considering more than one function in isolation.

Microbial communities are perhaps better assessed on the presence of their functional capacities rather than species composition per se (71). Importantly, some functions can be considered general functions that many organisms can undertake, while others can be considered specialized functions that only a few species can undertake. Such specialized functions may be more sensitive to species losses than general functions (5), and there is some evidence that specialized functions indeed occur at greater rates with higher biodiversity. For example, a study showed that increasing species richness of cellulose-degrading bacteria not only sustained greater bacterial densities and greater richness over time but also increased the rate of cellulose degradation under stable conditions (72), indicating that species richness can confer higher process rates even when species may be considered functionally redundant. Furthermore, a recent study found that long-term heavy metal contamination has significant effects on microbial community diversity and pesticide mineralization, and the study showed that even moderate biodiversity losses can impact specialized but essential ecosystem functions (73). There is also evidence that microbial functional capacity may be impacted by environmental changes even though community composition may be highly resistant (74). Perhaps this is why biodiversity-multifunctionality studies show idiosyncratic outcomes with soil community composition having seemingly divergent effects on ecosystem processes (75).

There is less support for a strong positive influence of soil invertebrate diversity on ecosystem function. It appears that community composition, or species identity, is a better predictor for process rates with species richness mainly being important in low-diversity ecosystems (5). It has been observed in laboratory studies that functional dissimilarity can contribute to diversity effects on soil processes (76), which might be a cause for the observed positive diversity-functioning relationships in low-diversity systems, where it is more likely that new species are functionally dissimilar from species already present in the community. However, given that species differ substantially in life history traits, functional roles and sensitivity to environmental change diversity may have more important roles in ecosystem functioning through time. A recent review of the role of soil invertebrates in wood decomposition supports this notion. The review concluded that the activities of the entire soil invertebrate community accelerate wood decomposition, although some groups such as wood-boring beetles and termites are particularly important to the process and the loss of these may significantly reduce the rate of wood decomposition (42). Furthermore, new research found that the increased richness of functionally dissimilar litter decomposers not only accelerated litter decomposition but also stabilized litter decomposition rates through time (77).

3.2. Soil Biodiversity, Resistance, and Resilience

Theoretically, soil biodiversity may confer greater functional resistance and resilience to disturbances, and there are some studies that indicate that diverse belowground communities are indeed more resilient and resistant to disturbances. For example, a recent paper (78) created a microbial diversity gradient using a dilution series and found that increased diversity enhanced community structural (i.e., composition) stability when exposed to heat stress and mercury pollution. Diversity also conferred functional (soil respiration) stability toward heat stress, but not mercury pollution, suggesting that the effect of diversity may be stress type dependent (78). Similarly, another study investigated the effect of benzene and mercury pollution on microbial community stability and functioning but using soils that naturally differed in bacterial diversity (79). There was no difference in the responses between soils to copper perturbations. Benzene, by contrast, had a significant impact on bacterial community structure in both high- and low-diversity soils, but no effect on diversity was observed in the high-diversity soil, suggesting greater structural stability. Moreover, benzene impaired a narrow-niche function (mineralization of 2,4-dichlorophenol) in both soils, but only the high-diversity soil recovered the ability to perform this function, indicating a positive effect of diversity on resilience to perturbation. Hence, there is evidence that diversity may play a significant role in the resistance and resilience of ecosystem functioning. Given the significant variation in life history characteristics, functional traits, and sensitivity to environmental change observed within and between taxa of soil fauna, it appears likely that increased diversity of soil fauna would have similar positive effects on functional resistance and resilience by providing a pool of species that can moderate functioning under different environmental conditions.

Many factors including the history of microbial community assembly processes are known to influence the resistance and resilience of microbial communities to disturbance (80), which makes it difficult to predict microbial responses to specific stresses (8). The resistance and resilience to perturbation differ substantially between microbial functional groups because of (*a*) differences in specific functions; (*b*) the groups' ability to acquire mobile genetic elements through, for example, horizontal gene transfer, genetic structure, and plasticity; (*c*) sensitivity to environmental factors; and (*d*) biotic interactions with taxa influenced by environmental factors (8). Hence, microbial communities may be best assessed on the presence of their capacity to perform certain functions rather than on species composition (71). However, the roles of soil biota in the resistance and resilience of ecosystem functions are moderated by environmental conditions, such as soil structure. Recent work has, for example, shown that reduced precipitation can promote the formation of microaggregates in which microorganisms are protected from adverse effects of lower soil moisture content, thereby providing sites for continued ecosystem function (81).

3.3. Soil Biodiversity and Suppression of Pests and Pathogens

Soil biodiversity includes organisms that are pests and pathogens that can directly impact plant production and cause economic loss in agriculture. However, there is mounting evidence that healthy soils may promote suppression of plant diseases, pests, and pathogens mediated by soil biodiversity through predation, competition, and parasitism (82). For example, it has been noted that the loss of plant species biodiversity, resulting from land-use practices such as forestry, and shifts in plant community structure, resulting from weed invasion, can influence the belowground communities of mutualists and pathogens (83). Alternatively, naturally complex plant communities can promote soil bacteria that enhance protection of plants from pathogens (84). Moreover, soils with long and complex food web structures are better at suppressing plant parasitic nematodes (85). Global change impacts on soil community diversity may therefore reduce plant health and growth.

4. GLOBAL CHANGE IMPACTS

Global change is unquestionably one of the greatest threats to soil biodiversity, with recent work indicating that global change impacts on soil biota moderate at least some ecosystem functions (86, 87). Although we are accumulating knowledge of the impact of global change drivers such as climate change, eCO_2 concentrations, and land-use changes, there is still much to learn before we can make any broad predictions about their impacts in the longer term. Moreover, the degree to which global change alters soil biodiversity and ecosystem functioning depends on the rates of change, the ecosystem, and the vulnerability of species. Some of the key concerns of global change impacts include a potential for a disconnect between aboveground and belowground communities, changes in plant-soil feedbacks, negative effects of soil biodiversity loss on the resistance and resilience of ecosystem functioning to perturbation, and decreased capability of ecosystems to adapt to environmental change. To anticipate and potentially mitigate such changes, we need to develop tools to quantitatively assess impacts on ecosystem services, based on factors such as the vulnerability and resilience of subsurface species and the individual species' or food web's contribution to a particular component of a function or service. The greatest impacts of global changes may be expected in low-diversity, less-resilient ecosystems, or in highly disturbed systems, but this is yet to be quantified explicitly.

In this section, we give a broad overview of the potential impacts of the most prominent and best researched global change drivers. It is worth noting that in most cases our understanding of global change impacts is limited to the impacts of each driver in isolation. Nevertheless, global changes rarely occur in isolation, and the net effect on ecosystems is moderated by interactions between the prevailing global change drivers under given circumstances (**Figure 3**). Furthermore, we acknowledge that several other global change drivers, including ozone, heavy metal pollution,

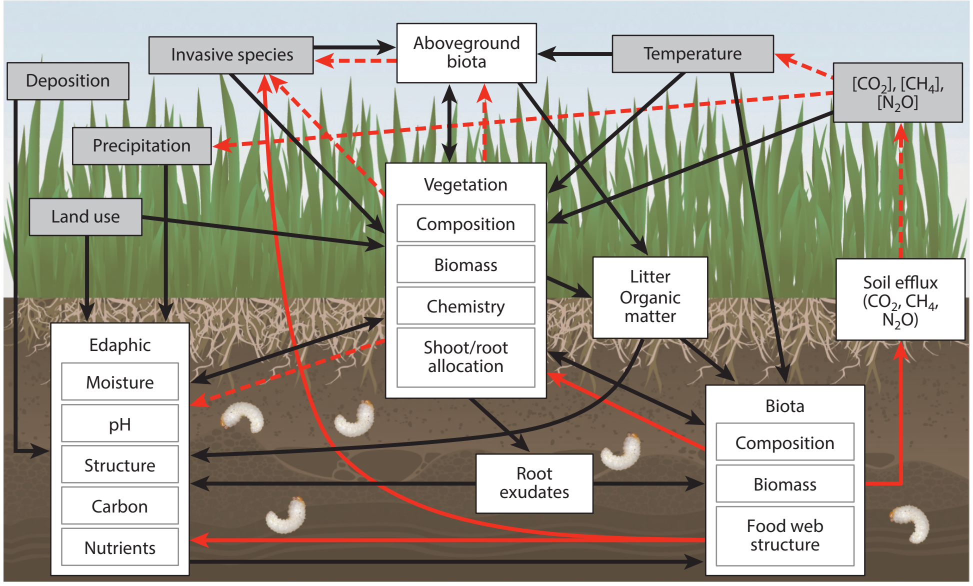

Figure 3

Schematic overview of the main direct and indirect pathways through which global change drivers impact belowground communities and the feedbacks caused by the changes in belowground communities. Note that only the pathways considered to be most important are represented. Gray-tinted boxes indicate the main global change drivers. Land use includes all physical (i.e., tilling), chemical (i.e., pesticides, fertilizer), and biological (i.e., crop) management options; deposition includes atmospheric deposition of nitrogen (N), sulfates, etc., as well as point source pollution. Invasive species include plants, animals, and microbes above- and belowground (although the latter is not explicitly indicated for simplicity). Black arrows indicate the main direct and indirect (i.e., through changes in soil properties and vegetation) pathways through which global change drivers influence belowground communities, and red arrows indicate direct (*solid*) and indirect (*dashed*) feedback effects of belowground biotic responses. Interaction between precipitation and temperature moderates local impacts, but this interaction is not illustrated explicitly for simplicity. Similarly, interactions between global change drivers more broadly influence belowground responses and feedbacks.

and increased UV-B, can influence belowground communities either directly or indirectly, but given limited space these are not discussed in detail here.

4.1. Climate Change

Changes in temperature and precipitation have been observed globally, and further climate changes, including potentially abrupt changes, are expected throughout the twenty-first century (88). Temperatures are expected to increase, and precipitation regimes (amount, seasonality, variability) will change at global scales, but there is some uncertainty on the effect sizes at smaller scales. Additionally, the increased frequency of extreme climatic events expected globally is likely to have disproportionally large impacts on ecosystems and their resident soil biota. Both changes in temperature and precipitation have significant effects on belowground communities, but the observed local responses are highly dependent on interactions between these two global change drivers. The effects of changes in precipitation may be ameliorated or amplified by simultaneous changes in temperature or may be moderated by the current temperature regime (i.e., effects may be greater at high or low temperatures) and vice versa. Hence, we discuss these two global change drivers in the same section.

Precipitation is one of the main constraints on soil biota in many ecosystems and one of the key factors governing microbial activities, mainly through its effect on soil moisture content. A recent meta-analysis found that reduced precipitation generally has negative impacts on fungal biomass, collembolans, and enchytraeids, and no consistent effects were observed on other taxa (89). Several taxa, including nematodes (90) and protists (91), are known to show predictable but context-dependent responses. Moreover, a study by Pereira and coworkers (81) showed that reduced precipitation alters microbial community composition, indicating potential impacts on ecosystem functioning even if the overall microbial biomass does not respond. Changes in the amount of precipitation, frequency, or seasonality are likely to have significant belowground impacts, particularly in dryland ecosystems where water is already limited (92). New research has shown, however, that the impact of precipitation changes is influenced by historical climate patterns (93, 94). For example, microbial communities that have experienced variable precipitation over years to decades respond less to changes in precipitation variability than microbial communities from systems with more stable soil moisture content in terms of both community structure and biomass (93, 94). Incorporating historical climatic regimes into ecosystem models that investigate climate change impacts may improve our predictive capacity.

As mentioned above, belowground communities are influenced by changes in temperature. Blankinship and coauthors (89) showed that increased temperature consistently increased nematode abundances, and García-Palacios and colleagues (87) found positive responses of fungal biomass. By contrast, increased temperatures can have negative effects on enchytraeid abundances (95). The effect of temperature on belowground communities is climate dependent with larger negative effect sizes observed in colder and drier biomes (89). However, belowground community responses to climate change are often idiosyncratic. This pattern may partly be related to differences in the soil food web structure between the ecosystems studied. For instance, a study that compared the resistance and resilience of intensively managed wheat with bacterial-based food webs and extensively managed grasslands with fungal-based food webs to drought found the latter to be more resistant, albeit not more resilient (96). Structural equation modeling showed that this difference was related to food web structure, indicating that land management influenced the ecosystem's response to climate change. Such information may be utilized to promote the resilience and resistance of managed ecosystems and may warrant further exploration. Managing soils to promote fungal-based food webs may further improve soil C sequestration and reduce N losses and thus be key to sustainable land-use practices (97).

4.2. Elevated Carbon Dioxide Concentration

Changes in CO_2 concentration are unlikely to have strong direct impacts on soil biota given the high concentrations encountered in the soil pore space (2,000–30,000 ppm) (98). Still, direct effects may occur as some belowground plant pests and entomopathogenic nematodes can utilize CO_2 gradients for host location (99). By contrast, strong indirect effects are likely through changes in the quantity and quality of single-species resources (litter, root exudates, root biomass) or as a result of changes in the aboveground community composition, as well as edaphic variables such as changes in soil moisture associated with increased plant water-use efficiency under eCO_2 (100). In particular, soil microbial communities associated with plant roots and the rhizosphere may be affected by changes in plant metabolism and root exudation (98), although this is not always observed (81). Several recent reviews agree that eCO_2 increases microbial biomass, thus favoring the fungal pathway and detritivores, but eCO_2 can have neutral or even negative effects on larger soil organisms (87, 89). This, in turn, can have cascading impacts on the soil food web structure that may result in functionally altered, and taxonomically simplified, soil communities (98, 101).

4.3. Nitrogen Deposition

Soils are increasingly being impacted by the introduction of N from external sources, mainly through fossil fuel derived atmospheric N deposition and the application of N-rich fertilizers, particularly in agricultural systems. Most studies to date have focused on N fertilizer application given that this is easier to simulate than atmospheric deposition. Increased N content through fertilizer application can have a negative impact on microbial biomass (102), although a 2015 meta-analysis found that N deposition increased bacterial biomass and also processes related to the soil N cycle (87). Moreover, N fertilization can influence belowground community composition as was observed for N-fixing bacteria (103), which has been shown to negatively impact nematode diversity (101). Higher nutrient loads are known to influence the efficiency of, and plant dependency on, mutualists, such as mycorrhizal fungi and N-fixing bacteria (104, 105), and may favor more parasitic strains (106). Moreover, high nutrient loads might promote more aggressive pathogens with greater disease emergence and pathogen impacts (107). It is clear that better guidelines for the application of N fertilizers and judicious use could significantly promote belowground biodiversity and its benefit to ecosystem N dynamics.

4.4. Land-Use Changes

Land-use changes have significant impacts on belowground communities. Intensive land-use management, particularly those activities associated with agricultural practices, impacts belowground communities differentially with larger organisms responding more strongly to changes in land-use type than smaller organisms (108, 109), often causing a shift belowground toward bacterial-dominated food webs because high levels of disturbance disrupt the fungal hyphal system (110). This, in turn, may influence nutrient dynamics and nutrient retention as bacterial-dominated food webs are considered less conservative with respect to nutrient dynamics than fungal-dominated food webs (111). The application of fertilizers and pesticides are important in agricultural and horticultural systems because they reduce the impacts of weeds, pests, and soil-borne diseases (112), but they often have negative impacts on soil biota (113). However, their efficiency in controlling pests and pathogens is decreasing owing to the increasing emergence of pesticide-resistant pests and pathogens, and alternatives to the more environmentally harmful pesticides are still being explored (114). Promoting management practices that minimize the use of these products where possible could have positive effects on soil biodiversity in agricultural systems and increase the benefits of soil biodiversity to the farmer. The main objection to limiting the use of pesticides and fertilizers is the concern that this might cause yield declines. Some farmers apply fertilizers at levels above that required for maximal crop yields, but high precision management of fertilizer application could potentially reduce inputs without significant yield declines. This could be of direct economic value, i.e., lower input costs, and limit the negative environmental effects of nutrients lost through runoff, leaching, or volatilization (115). There is also evidence that plant breeding has selected against traits that promote the plants' ability to host beneficial microorganisms that improve plant growth by suppressing diseases and pests (116, 117). By contrast, extensification can have positive effects on the abundance and diversity of soil biota; however, the time frame for response is taxa and life strategy dependent (108). Hence, conversion of former arable lands to less intensive land-use types may not restore soil biodiversity in the short term because the provision of ecosystem services by soils may be impacted for hundreds of years after the abandonment of agricultural lands (118).

Other land-use type changes that have significant impacts on belowground communities include the conversion of natural forests into pasture, forestry, agricultural lands, other production systems (i.e., production of biofuels), and urban areas. Recent cross biome work has shown that the conversion from forest to grassland has consistent directional effects on microbial community composition and catabolic profiles relevant to ecosystem function. Both bacterial and fungal biomass decreased in response to land-use conversion, and although the diversity of both groups increased, the effect size was moderated by soil texture with lesser effects observed on fine-textured soils (119). Such systematic global-scale work provides highly valuable insights and allows us to more accurately predict the consequences and develop management practices that minimize, or even mitigate, impacts of land-use changes.

4.5. Invasive Species

Invasive species is an increasing problem worldwide (18). The introduction of non-native (exotic) species can have significant impacts belowground through changes in plant-soil feedbacks (120) and mutualistic interactions (121). It is well established that invasive plant species influence belowground communities. For example, some exotic plant species produce allelopathic compounds that can affect mycorrhizal fungal communities with consequences for native plant species and potentially for ecosystem functions (122). Moreover, exotic plant species can alter soil communities with impacts on disease and pathogen suppression (123), and in some cases, they bring along nonnative symbionts that benefit their survival in the new habitat (124). Similarly, nonnative soil organisms can affect both belowground and aboveground communities. For example, nonnative species of earthworms have invaded several northern temperate forests in North America that lack native earthworm species. The invasion of some species, and in particular *Lumbricus terrestris*, can have substantial effects on their new environment, often accelerating organic matter decomposition (and through this cause a potential loss of soil C), altering the soil food web structure toward a bacterial-dominated food web, and negatively influencing native plant species diversity (125). However, the impacts of nonnative species, including animal, plant, and microbial, on their new environment are highly species specific, and we are yet to discover what life history or functional characteristics may determine their potential impacts.

5. MANAGING BELOWGROUND COMMUNITIES

In this section, we discuss how belowground communities can be managed in human-impacted ecosystems to facilitate conservation of soil biodiversity and promote the potential benefits received from this biodiversity. We focus on options for managing soil biodiversity in agroecosystems given the significant impacts that agricultural practices have on soil biodiversity, and the potential of soil biodiversity to promote sustainable production. We also discuss briefly how such management practices might further contribute to climate change mitigation, improve ecosystem resilience to perturbation, and increase the capacity of ecosystems to adapt to environmental change, in particular with reference to restoration ecology.

5.1. Management Options for Soil Biodiversity and Services

Soil biodiversity management is often disregarded in high-intensity agricultural systems as management's functional roles (i.e., physical manipulation of soil structure, pest control, nutrient cycling) are increasingly being replaced by human inputs, with substantial impacts on belowground communities. For example, Tsiafouli et al. (109) found not only that the diversity of many taxonomic groups decreased and communities were composed of more closely related species but also that some functional groups may be completely lost under intensive agriculture with potential implications for ecosystem functioning. Interestingly, this shift in food web structure was accompanied by an increase in the importance of nematode functional roles, which does suggest some flexibility in the soil food web structure to respond to external stimuli. However, an increased recognition of soil biodiversity's roles in ecosystem functions and a shift toward a more sustainable use of our resources have renewed our interest in soil biodiversity as an entity to assure continued provision of ecosystem services (1, 6). In particular, practices such as no-till and organic farming have been suggested as tools to increase the benefits of soil biodiversity. Yet, there is substantial variation in the effectiveness of these practices for maintenance of different soil biotic groups under differing management regimes.

No-till or conservation agricultural practices may improve soil health (i.e., improved soil structure, greater organic matter content, decreased weed and pest abundance) and ecosystem service provisioning, as well as aid agricultural adaptation to climate change (7, 126, 127). However, such practices need to be applied with care as a recent meta-analysis found that no-till practices, on average, reduced crop yields by 5.7% compared to conventional practices but could retain, or even exceed, yield levels if applied in combination with crop rotation and residue retention, particularly in dryland agricultural systems (128). No-till practices have also been suggested as a management practice to promote C sequestration, but current evidence suggests that there is limited potential for C sequestration by changing to no-till practices (127). One reason why conservation farming might enhance annual yields, or infer temporal stability in yield and through this greater long-term output, is that it may promote beneficial mycorrhizal associations by reducing disruption of hyphal networks and increasing mycorrhizal fungal diversity (129). No-tillage is also known to increase fungal biomass in general, which leads to improved soil structure that increases infiltration and reduces erosion, thereby increasing yield over the long term (43, 130). Moreover, chemical-fallow practices and past inclusion of non-mycorrhizal crops in the rotation moderate mycorrhizal associations (131) and should be incorporated into management practices with care.

Over the past few years, there has been an increased interest in organic farming practices, which could have benefits for soil biodiversity, particularly owing to a reduced use of pesticides. It is not yet clear whether organic management practices per se have any direct benefit to provision of ecosystem services. Although some studies have shown increased provision of these services in organic compared with conventional farming agroecosystems (132, 133), other studies found no difference between conventional and organic farming in ecosystem service provision (134, 135). This is likely because organic farming often utilizes so-called intensive practices, which may negate any beneficial influence of lower pesticide use, a factor to consider when developing standard practices for sustainable farming (135). However, there is certainly the potential for organic farming to have broader on-farm benefits, including increased connectivity within ecosystems and positive management of soil biodiversity and food web structure (96, 136).

There is growing evidence that crop production can benefit significantly from managing plant microbial symbionts, such as mycorrhizal fungi and N-fixing bacteria in root nodules, as well as from many novel plant growth-promoting microorganisms. Microbial symbionts are found in almost all types of plant tissue, and many of these symbionts help the plants grow under harsh environmental conditions by providing nutrients, pathogen protection, or improved stress resilience (137). For example, new research suggests that certain fungal endophytes promote stress tolerance (e.g., to stress caused by drought, heat, and salt) and provide disease protection in plant hosts (138). The ability to increase drought tolerance appears to be fairly common in these endophytes possibly because of a more ancient origin in the plant-microbe symbiosis, whereas the ability to promote heat and salt stress tolerance, and disease protection, is habitat specific, and only strains extracted from plants growing in stressed environments confer tolerance to plants inoculated under laboratory and field conditions. These endophytes often occur in low abundances in soils, but the loss of species could have significant impacts on plant performance (138). It is not clear how and when these fungal endophytes confer stress tolerance and disease protection. Increased research in this area could reveal novel microbial inoculants to increase agricultural and horticultural yield stability in stressed environments, including stresses associated with global changes.

A range of farming practices that act through management of soil biodiversity has been identified to improve ecosystem functioning in agricultural landscapes at various spatial scales (**Figure 4**). Rotation is a common practice in agriculture, has historically represented an important tool for management of soil biodiversity, and is often used for control of certain belowground plant pests, including plant parasitic nematodes, but can also be used to incorporate cover crops that can maintain soil biodiversity through providing a continuous plant cover and improved SOM content (139). A considerable cost in agriculture and other production systems is the management of C and nutrient availability, particularly through the application of fertilizers, but certain management practices can reduce the reliance on organic or inorganic fertilizer application. For example, the incorporation of legumes in pastures or as cover crops as part of the rotation can increase soil N levels considerably through N fixation by bacteria in their root nodules, and rhizodeposition of C by cover crops can promote soil C levels (140). In both cases, soil biota are responsible for the incorporation and retention of C and N, and some of this N is available for later uptake by plants. Moreover, improved soil biodiversity may be achieved in some agroecosystems through the incorporation of trees. For instance, conversion of traditional slash and burn practices to agroforestry in a Central American tropical dry forest had a positive impact on earthworm biomass and soil fertility (141). Another significant cost to production systems is the management of soil water content. No-tillage with residue retention and cover crops can promote water infiltration and holding capacities through improved SOM content and moderation of the soil structure. Moreover, maintaining soil biodiversity through on-farm establishment of buffer strips, riparian zones, and denitrifier trenches, and other techniques, may improve the capacity for degradation of pollutants and reduce nutrient and agrochemical loss to adjacent ecosystems, thereby limiting potential impacts on ecosystem services at the landscape scale (19). In sum, it is evident that land-use practices in agriculture that promote the maintenance and conservation of soil biodiversity also tend to improve the delivery of multiple ecosystem services.

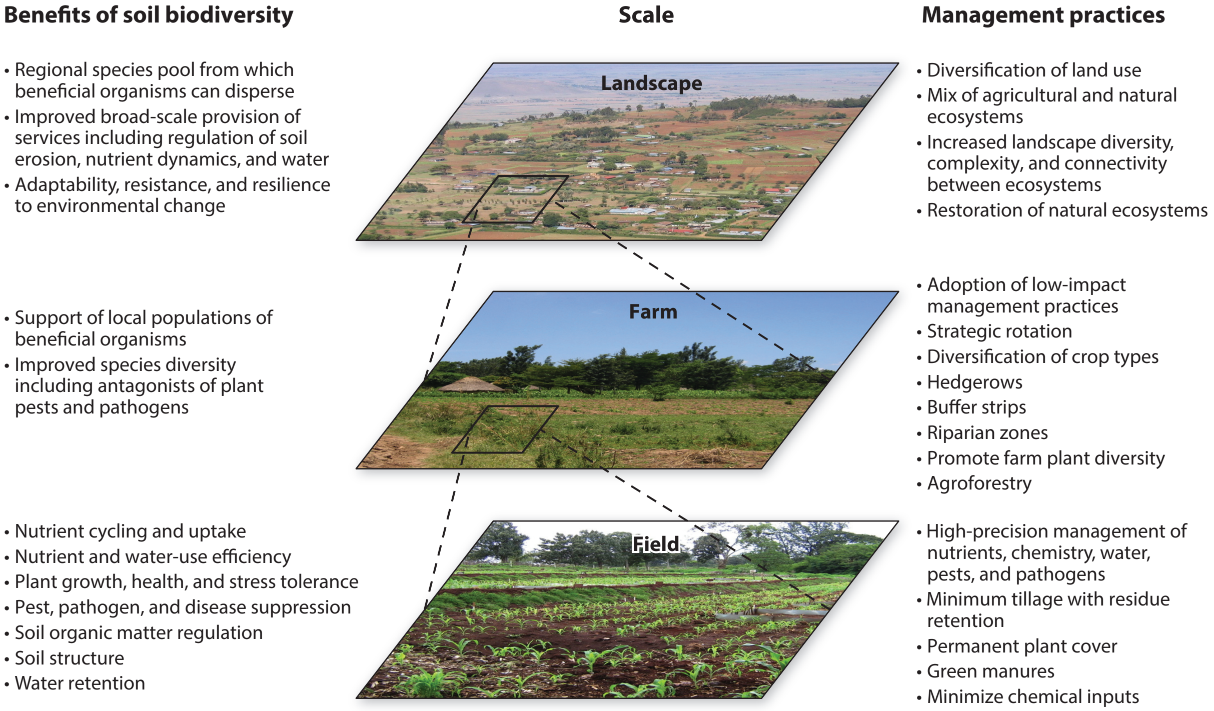

Figure 4

Schematic outlining (*left*) how soil biodiversity can benefit production systems at various spatial scales, and (*right*) how management practices at the same spatial scales may enhance the potential benefit of soil biodiversity in said systems.

5.2. Soil Biodiversity and Restoration Ecology

Ecosystem restoration is receiving significant attention given the impact of human activities on ecosystems as described above. A recent meta-analysis of studies that published results on the effect of restoration on biodiversity and ecosystem services in a range of ecosystem types found that restoration significantly improved both biodiversity and ecosystem function compared to degraded reference sites, albeit not to levels observed in "pristine" reference sites. Moreover, the meta-analysis showed that there was a strong positive correlation between biodiversity and ecosystem functioning in restored sites suggesting that restoration practices that promote the recovery of biodiversity may confer greater ecosystem functioning (142). The analysis did not explicitly consider soil biodiversity as a variable, but it appears likely that a similar relationship between soil biodiversity and ecosystem functioning would exist. Restoration practices that promote greater soil biodiversity, perhaps through active inoculation of beneficial soil organisms particularly where regional species pools are limited, may therefore benefit the restoration of ecosystem functioning and its resistance and resilience to perturbation. For example, there is evidence that belowground plant mutualists can ameliorate impacts of pollution on plant growth (143), and earthworms have been suggested as useful facilitators of ecosystem services in abandoned mining areas (144). Manipulation of vegetation may be used to promote key groups of soil organisms that facilitate certain ecosystem functions, such as the breakdown of pollutants, and through this speed up the rate of ecosystem recovery on degraded soils (145). Hence, soil biodiversity should be considered more carefully in restoration ecology as a tool to promote reestablishment of ecosystem functioning and to increase the resilience and resistance of restored ecosystems to disturbance, providing ecosystems with the capacity to adapt to future global changes.

6. SYNTHESIS AND PERSPECTIVES

Throughout this review we have provided an overview of our current knowledge of the diversity of organisms found belowground, their role in ecosystem functioning (and through this ecosystem service provision), and the potential impacts of global changes. Our knowledge of the belowground ecosystem has improved greatly over the past couple of decades and continues to evolve, but it is evident that global changes pose significant threats to soil biodiversity and its functional capacity. The conservation of soil biodiversity is of great importance to ensure that belowground communities continue to deliver the ecosystem services we depend on, and fortunately, current knowledge suggests that there is a great potential to sustainably manage soil biodiversity. To achieve this, it is critical that we think of soil biodiversity as a finite natural resource that can be depleted. New frameworks such as that brought forward by Dominati and coworkers (7), which aim to quantify the value of soils in terms of the natural capital and ecosystem services provided, explicitly recognize the role of soil biota. Such frameworks provide an excellent opportunity to improve the recognition of soil biodiversity's role in sustainable management of human-impacted ecosystems and to form a bridge between science and policy making. We have come a long way in developing such frameworks, as discussed in the previous section, and it is not too early to begin putting this knowledge into practice; nevertheless, there is still a need for additional data to guide the development and implementation of better management practices. In this final section, we present an overview of the research challenges to be resolved before we can effectively manage soil biodiversity for sustainability purposes.

The development of new molecular tools has greatly facilitated the discovery of novel soil biodiversity, but to fully appreciate the importance of this diversity, it is essential that we can attribute functional characteristics to the species we discover. Moreover, we need better insight into the current distribution of soil biota to monitor the loss and gain of species belowground and to determine how belowground communities may respond to global changes. There is, however, a vacuum of knowledge developing in terms of identification skills and capacity to describe the life history characteristics and functional traits of soil invertebrates, and new methods need to be developed that can provide insights into microbial species given that many of these cannot be cultured using traditional methods. Increased knowledge transfer between disciplines needs to be promoted to facilitate a holistic understanding of soil biodiversity and ecosystem function.

Another concern is that limited data exists on belowground responses to global change and, in particular, the integrated impacts when multiple global change drivers co-occur. This is compromising our capacity to establish general patterns and therefore our ability to predict and mitigate potential impacts through best management practices. This knowledge gap can be addressed by global-scale, cross biome studies. Researchers working with plant and animal communities aboveground have recognized this, and the development of multiple coordinated global-scale studies has begun. For example, the ongoing Nutrient Network experiment (**http://www.nutnet.org**) investigates the effects of fertilization, and the international drought experiment, Drought-Net (**http://www.drought-net.org**), investigates the impacts of reduced rainfall. Soil biodiversity would ideally be incorporated explicitly within both of these and other similar frameworks, but it is unlikely that all sites will have a substantial belowground component given logistical and funding constraints. Moreover, it is important that we elucidate how soil organisms act in concert to determine the full impact of global changes on different groups and soil processes. This requires a whole soil food web approach to belowground impacts. The development of more sensitive and less expensive analytical and molecular methods, and the development of standardized methods for quantifying belowground impacts, can greatly facilitate our ability to achieve this. Furthermore, this knowledge can be used to explicitly incorporate the effects of soil biota into ecosystem process modeling exercises, which is needed to improve our understanding of ecosystem processes under both current conditions and future conditions (92, 146). Moreover, ecosystem ecology would benefit from a better understanding of the links between aboveground and belowground food webs beyond plant-soil linkages; this knowledge could guide the development of better management regimes, for example, through enhanced biocontrol by belowground organisms in agroecosystems. Other key objectives are to establish direct links between soil biodiversity and crop production and to learn how to best manage soil biodiversity to benefit agroecosystems. Such knowledge would greatly improve our capacity to promote the incorporation of management strategies to guide new policies.

Lastly, it is increasingly important that we develop methods to conserve soil biodiversity at local to global scales. Recent work has brought to our attention that a substantial number of invertebrates, including species that inhabit soils at least in some life stages such as dung beetles, have been lost over the past few centuries and that the abundances of many others also decrease rapidly (147). The loss, or decreased abundance, of some of these species has already been shown to have important implications for ecosystem functioning. Future management practices of soil biodiversity for sustainable agricultural, conservation and restoration practices, and global change mitigation, should focus on reversing, or at least halting, this trend. However, it is important to recognize that not all soil biota are beneficial to human well-being. Many soil organisms, such as plant parasitic nematodes and fungal pathogens, have significant indirect impacts on human well-being by changing crop yields, but of more direct concern is that many potential human, and other animal, parasites and pathogens have life stages that occur in soil. Greater efforts should be given to develop management practices that minimize the potential impact of these parasites and pathogens, while maximizing the benefits of soil biodiversity more broadly.

SUMMARY POINTS

1. Soils represent a vast reservoir of biodiversity that is essential to ecosystem functions and service provision.
2. Our knowledge of soil biodiversity has increased substantially over the past couple of decades and continues to evolve.
3. The continued development of new tools and techniques provides great opportunities for new discoveries and further insights.
4. Global changes significantly impact soil biodiversity and through this ecosystem functioning and provision of services.
5. It is evident that soils can be managed to facilitate the conservation of soil biodiversity and the functions and services they provide.
6. Fungal-based food webs can improve soil C sequestration and reduce N losses, and fungal-based food webs may be key to sustainable land-use practices.
7. Fungal-based food webs may improve ecosystem resilience and resistance to perturbation.
8. Managing soil biodiversity may be a useful tool for improving restoration practices.

FUTURE ISSUES

1. There is a need to determine how soil organisms act in concert using a whole soil food web approach to determine their role in ecosystem functioning.
2. Soil biota could be explicitly incorporated into ecosystem process models.
3. More landscape- to global-scale, cross biome studies that explicitly incorporate soil biodiversity would support the formation of belowground ecological principles.
4. Ecosystem ecology would benefit from a better understanding of the links between aboveground and belowground food webs beyond plant-soil linkages.
5. There is a need to establish direct links between soil biodiversity and crop production to inform management practices.
6. Improved knowledge of management options to promote soil biodiversity is needed to support the development of better land-use management.
7. Developing policy frameworks that facilitate the implementation of soil biodiversity in management practices should be a priority.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

The authors would like to thank the editors of *Annual Review of Environment and Resources* for the opportunity to write this review and the two anonymous reviewers for their constructive comments. T. Fraser provided comments on an earlier version of the manuscript. D.H.W. acknowledges the Winslow Foundation for funding.

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