

Review

Soil Biodiversity Integrates Solutions for a Sustainable Future

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Abstract: Soils are home to more than 25% of the earth's total biodiversity and supports life on land and water, nutrient cycling and retention, food production, pollution remediation, and climate regulation. Accumulating evidence demonstrates that multiple sustainability goals can be simultaneously addressed when soil biota are put at the center of land management assessments; this is because the activity and interactions of soil organisms are intimately tied to multiple processes that ecosystems and society rely on. With soil biodiversity at the center of multiple globally relevant sustainability programs, we will be able to more efficiently and holistically achieve the Sustainable Development Goals and Aichi Biodiversity Targets. Here we review scenarios where soil biota can clearly support global sustainability targets, global changes and pressures that threaten soil biodiversity, and actions to conserve soil biodiversity and advance sustainability goals. This synthesis shows how the latest empirical evidence from soil biological research can shape tangible actions around the world for a sustainable future.

Keywords: belowground; diversity; microbes; worm; mite; insect; Sustainable Development Goals; Aichi Targets; land-use; climate change

1. Introduction

As the world's human population continues to rise and is expected to reach 8.6 billion by 2030 (UN 2017), it is paramount to respect and protect natural resources, including soil, water, air, minerals, and biodiversity that support life on Earth, including humanity. Current rates of consumption and inadequate management of resources are putting unprecedented pressure on global systems and it is estimated that one to six billion hectares (up to 30%) of land has been degraded globally [1]. Land degradation negatively affects 3.2 billion people, threatens sustained human well-being and is a major contributor to climate change and biodiversity loss [2]. Global initiatives to meet these challenges include the UN 2030 Agenda for Sustainable Development (Figure 1) and the UN Convention on Biodiversity's Strategic Plan for 2020 (Table 1). Broadly, these agendas address areas to improve human life and environmental sustainability, rely on the participation of all countries and stakeholders, and will require innovative, timely, and interdisciplinary approaches [3].



Figure 1. The UN 2030 Agenda for Sustainable Development centers around 17 Sustainable Development Goals (SDGs). These goals broadly address areas to improve human life and environmental sustainability and include 169 specific targets supported by member nations.

Table 1. The Aichi Biodiversity Targets are central to the UN Convention on Biodiversity’s Strategic Plan for 2020 and result from years of discussion and consensus building among more than 190 member nations. The targets are divided into strategic goals to be implemented by 2020.

Strategic Goal	Targets
Address the underlying causes of biodiversity loss by mainstreaming biodiversity across government and society.	1, 2, 3, 4
Reduce the direct pressures on biodiversity and promote sustainable use.	5, 6, 7, 8, 9, 10
Improve the status of biodiversity by safeguarding ecosystems, species, and genetic diversity.	11, 12, 13
Enhance the benefits to all from biodiversity and ecosystem services.	14, 15, 16
Enhance implementation through participatory planning, knowledge management, and capacity building.	17, 18, 19, 20

Soils are central to supporting natural systems and human well-being [4] (Figure 2), yet to date soil biodiversity—the diversity of life in soil which drives ecosystems, sustains life aboveground, and maintains healthy landscapes—has remained largely overlooked in global agendas. For example, the term ‘soil biodiversity’ does not appear in any UN documentation while forests, wetlands, rivers, and drylands have received specific attention to their benefit. Soil-dwelling organisms, including bacteria, fungi, nematodes, earthworms, moles, and even plant roots, contribute the majority of living biomass on Earth [5] and represent more than 25% of all described species [6,7], not to mention the genetic diversity represented within these species. The activity and complex interactions of soil organisms provides the backbone for many ecosystem functions, including nutrient cycling, pathogen control, water infiltration, foundations to food webs, and supporting agroecosystems (Figure 2). Our understanding of the critical connections between soil biodiversity and sustainability are rapidly progressing [8–10]. The time has come to incorporate this knowledge to bolster global actions and create a more holistic sustainability agenda that can simultaneously address biodiversity loss, climate change, and land degradation.

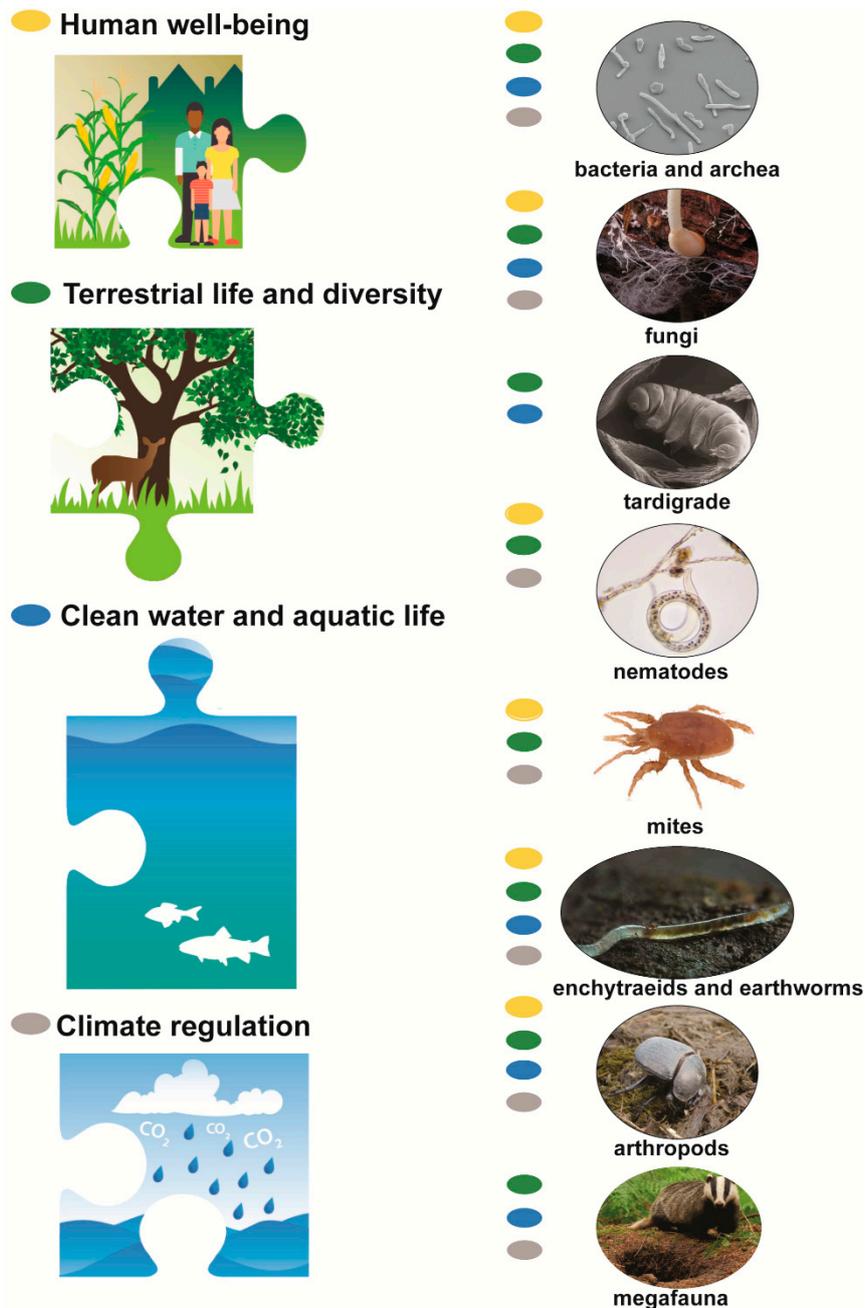


Figure 2. Soil organisms support multiple ecosystem services, which underpin global sustainability agendas. The colored circles next to each organism type represent which of the four overarching parts of sustainable development the organism contributes to directly. Image credit: K. Pintauro, E. Bach. Photo credits (top to bottom): E. Saunders, S. Axford, M. J. I. Briones, D. Robson, K. Markarov, A. Murray, M. P. Veldhuis, G. Faulkner.

Like most of the resources humans rely on, soils and soil biodiversity are under threat by land degradation, climate change, pollution, urbanization, and over-use and misuse [11]. Soils are a finite, non-renewable resource because they cannot be replenished within a human lifespan [12]. The formation of soils relies on a complicated balance between time, climate, topography, the underlying parent material, and of course organisms [13]. Therefore, timing—the swiftness in which we act to protect soils—is crucial. Several global efforts have recognized the urgency with which we must act. For example, the Global Soil Biodiversity Initiative launched in 2011 to bring together researchers and policy makers to integrate the knowledge we are gaining with actions for a sustainable future.

Other agencies have also started to include soil biodiversity in their consideration of soils, including the Global Soil Partnership, UN Food and Agriculture Organization, the Intergovernmental Platform on Biodiversity and Ecosystem Services (IPBES), and in 2019 the UN Convention on Biological Diversity requested a global report on soil biodiversity [14].

Prior to these recent efforts, integration of soil for nature and global sustainability largely focused on soil's physical and chemical properties with little consideration for biodiversity [15,16]. But, it is now accepted that including soil biota explicitly alongside soil abiotic factors in land management assessments can better serve sustainability goals than consideration of soil abiotic properties alone [8,17]. This holistic view of soils has gained traction from landowners, managers, and agencies and makes clear that diverse stakeholders are eager to protect this critical resource using interdisciplinary and sustainably focused methods. Despite this energy, more must be done to recognize and integrate the role of soil biodiversity in building a sustainable future. For example, the majority of soil biodiversity research examines diversity at a community level, across species and trophic levels; however, diversity within species is a critical component of biodiversity which has been all but ignored in soil habitats. Here, in an effort to guide global agendas and identify synergies between multiple sectors (research, users, public, and policy), we present (1) a synthesis of current research: Covering ways soil biodiversity can contribute to the global sustainability agenda; (2) global change and pressures that threaten soil biodiversity; (3) actions that will support conservation of soil biodiversity, while also affecting sustainability and biodiversity goals and targets; and (4) gaps in knowledge in linking soil biodiversity to sustainability.

2. Soil Biodiversity Contributes to Sustainability

2.1. Soil Biodiversity Supports Human Well-Being (Sustainable Development Goals (SDGs) 1,2,3,8; Aichi Targets 13,18,19)

Soils support the livelihood of the entire human population—more than 7.5 billion people—they are the foundation for numerous ecosystem functions that directly and indirectly support human health and well-being (Figure 1). This is most obvious when we view soil as the medium on which almost all food crops and livestock forage, including pastures, directly contribute to Sustainable Development Goals (SDGs) 2 and 3. It is the living communities—soil biodiversity—within soil that drive the processes central to plant growth, directly impacting human health and well-being through crop and livestock forage production [8,18].

Illustrations of the value of soil biota for supporting global food production are abundant and diverse. For example, soil fauna and microorganisms drive terrestrial nutrient cycling by decomposing dead plant and animal material and converting it to forms readily used by living organisms [19,20]. Nutrient cycling in soil is central to plant growth, directly impacting human health and well-being through crop and livestock forage production [8,18]. The value of soil biota is apparent in China where traditional rice-fish farming leverages rice paddies as fish habitat, where fish feed on microorganisms decomposing dead rice leaves. Fish feeding behavior loosens soil allowing more oxygen to infiltrate, further stimulating microbial decomposition of both plant material and fish excrement, which in turn liberates nutrients that are used by growing rice plants [21]. Similarly, in industrial row-crop systems, rotating legumes with grain crops leverages nitrogen (N)-fixing bacteria associated with the legumes to build soil N which grain crops like maize subsequently use.

Beyond supporting plant growth, soils influence human health and well-being as both a source and regulator of pests and pathogens, and disruptions to the diversity and interactions of soil biota can inhibit regulation of these diseases [22,23]. Crop and livestock pests and pathogens can have severe negative impacts on food production, human health, and well-being [24]. For example, in 2018, Anthrax bacterium (*Bacillus anthracis*) [25] emerged from soil killing more than 50 cattle across southeastern France [26], and from thawing permafrost in Siberia killing more than 1500 reindeer [27]. Soils are also home to disease-causing organisms that directly impact humans, such as helminth parasites (nematode *Strongyloides*), and brain encephalitis (*Naegleria fowleri*) [22], as well

as *Coccidioides immitis*, the fungus that causes Valley fever [22,28] (SDG 3). While disease causing organisms can be problematic and even dangerous, diverse soil communities are generally beneficial for human health, and provide a check on pathogens through competition with and predation of disease-causing agents for people, livestock, and crops [22,29]. Soil bacteria and fungi are also valuable sources for antibiotics, including long-established antibiotics like penicillin, produced by *Penicillium chrysogenum*, and emerging antibiotics from uncultured bacteria that show promise for preventing development of antibiotic resistance [30].

In addition to directly supporting food production through farming and ranching, soil provides access to economic livelihood [31], advancing SDGs 1 and 8 as well as Aichi Targets 13 and 19. Rural lifestyles and cultures centered around agriculture interface with soil, sometimes directly and often indirectly [32,33], contributing to Aichi Targets 13 and 18. For women farmers, these economic opportunities can also advance gender equality (SDG 5). Soil biodiversity contributes to many aspects of human health and well-being through multiple ecosystem functions [4,34]. Prioritizing soil biodiversity in policy and action also prioritizes this suite of benefits to human health and well-being, providing a coordinated opportunity to advance global sustainability agendas.

2.2. Soil Biodiversity Supports Terrestrial Life and Diversity (SDG 15; Entire Aichi Agenda)

Soil biodiversity supports life on land (SDG 15) and the entire Aichi agenda, including common and abundant species as well as rare and declining species [35]. Recognizing that soil organisms are part of global species loss is integral to preventing extinction generally (Aichi Target 12). A key step in preventing loss of soil-dwelling species is seeing soil as a habitat worthy of protection and conservation, directly advancing Aichi Target 5 (reduced loss of habitats). Soil organisms can also protect biodiversity by controlling invasive species (Aichi Target 9). For example, in Brazil the flatworm *Obama ladislavii* preys on an invasive snail species [36]. Soil and the life within it are essential to providing key ecosystem services (Aichi Target 14).

In addition to making up 25% of terrestrial biodiversity, soil organisms support life aboveground (SDG 15), both directly as a food source and indirectly through processes like decomposition and nutrient cycling [37] (Figure 2). Vertebrates, including amphibians, birds, mammals, and reptiles, rely on many soil invertebrates as food sources, and may use soil for shelter. For example, coyotes (*Canis latrans*) build dens belowground and feed on soil-dwelling mice, voles, and insects [38]. Evidence even shows that shore birds may consume large amounts of bacterial biofilms in their diets [39]. Soil organisms are also critical for plant growth and production, by cycling nutrients [40,41]. For example, the availability of N for plant uptake is dependent on microbial processes, such as N fixation which transforms dinitrogen (N₂) gas in the atmosphere to a bioavailable form [42]. In addition, an estimated 80% of all land plants rely on partnerships with mycorrhizal fungi [43] which deliver nutrients directly to plants. Above–belowground relationships are important drivers in ecosystems, shaping diversity and functioning [37]. Plants and other aboveground organisms also benefit from pollinators that live in soil, for some or all their life cycle. In turn, plants feed the soil food web through root exudates [44] and inputs of dead plant material [45]. Diversity of plant inputs as well as complexity of the habitat supports high levels of diversity [46], occurring at multiple scales (i.e., molecular, aggregate, horizon, and landscape) [47].

2.3. Soil Biodiversity in Hydrological Processes (SDG 6,14; Aichi Targets 6,8,11)

As water passes through soil on its way to creeks, streams, rivers, oceans, lakes, and groundwater, soil, and the life within it, integrates terrestrial and aquatic systems. During filtration water moves through soil pores, both large and small, which slow down flow rates and enable chemical and biological interactions. Water that exits soil where these processes function well is cleaner, which benefits people and aquatic life (Figure 2). Soil mediated water filtration advances SDG 6 (clean water and sanitation), SDG 14 (life below water), Aichi Target 6 (aquatic organisms managed sustainably),

Aichi Target 8 (reduced pollution, including nutrients), and Aichi Target 11 (protecting inland waters and coastal areas).

Soil biodiversity plays obvious roles in biological soil water use, but many organisms also facilitate physical and chemical interactions between water and the soil matrix [48]. For example, burrowing fauna including earthworms [49], ground beetles [50], and prairie dogs [51] influence the rate of water infiltration into soil through the development of mega- and macropores [52]. In Burkina Faso, increased termite foraging in restored forests increased water infiltration by 2–4 times over crop fields and bare ground [53]. This can alleviate flooding during high precipitation events, reduce soil erosion, and increase moisture in sub-surface soil. At the same time, plant roots and their excretions play critical roles in water flow dynamics in soil, which we are only beginning to understand through laboratory work with model organisms [54]. Further, biotic interactions between plants and microbes can directly impact hydrology and these interactions are impacted by changing climate [55].

Improving water infiltration also increases opportunity for plants and soil organisms to use dissolved and suspended nutrients such as nitrates and phosphates, reducing nutrient run-off into surface water and groundwater. Soil microbial metabolism of phosphates and nitrates recycles those nutrients within terrestrial systems and limits export to aquatic systems. Leveraging these ecological processes can be an important way to reduce reliance on fertilizer inputs and improve water quality, and reduce zones of eutrophication such as the large “dead zones” that appear in the Gulf of Mexico near the United States [56], the Sea of Oman between Iran and Oman [57], and the Yellow Sea near China [58]. In addition to nutrients, some bacteria and fungi are capable of degrading pollutants [59,60]. Linking soil biodiversity with water quality and hydrology is an area with great need for additional research as water quality and supply is a major challenge for communities world-wide, including wealthy nations.

2.4. Soil Biodiversity Regulates Climate (SDG 13; Aichi Target 15)

With more than 75% of soil organic carbon (C) residing in the top meter of soils, soil management plays a key role in how soils may act as a sink and store more C [61]. The pathway of C into the soil largely goes through plants, which take up carbon dioxide (CO₂) from the atmosphere during photosynthesis and use it as the building blocks for roots, stems, and leaves. Living plants move C belowground as root tissue and root exudates, which are readily incorporated into microbial biomass and either respired or deposited as complex organic molecules [10]. Because belowground C is stored as organic matter, it represents a dynamic pool that can be diminished through respiration, emitting greenhouse gases like CO₂, methane (CH₄), and nitrous oxide (N₂O), or enhanced through organic matter inputs, namely roots, detritus, and soil microbial biomass. Through these processes, soil is a critical part of addressing global climate change (SDG 13) and at the heart of Aichi Target 15 (protect and increase biodiversity contributions to C stocks). Soil is already part of some climate solutions. For example, the ‘4 per mil’ measure seeks to increase C pools in agricultural soils through changes in farming practices [62], although questions remain as to the extent this goal can be realized [63]. Soil biology plays a key role in better understanding how soil can be leveraged and managed to mitigate global climate change (Figure 2).

The role of soil biodiversity in regulating greenhouse gas emissions and storage of soil C, is well recognized [10,64]. The balance of C in soils is controlled by the interactive effects of climate, plant diversity, and soil biodiversity [65,66], and it is the soil community that ultimately controls the short and long-term fluxes and flows of C in and out of soils [67]. Much research has focused on the important role of soil microorganisms in plant litter decomposition, in large part because bacteria and fungi produce a suite of enzymes capable of breaking apart slow degrading plant molecules like cellulose and lignin. When assessing the ability of soils to store C we must also look at the specific functional types and traits within the microbial community [68]. For example, microbial traits or functional groups that would control C cycling and storage include: C use efficiency, community biomass turnover rates, microbial produced extracellular enzymes, and stoichiometry. Some of these metrics are being

incorporated into new C models such as Microbial Efficiency-Matrix Stabilization (MEMS) [69] and Microbial Mineral Carbon Stabilization (MIMICS) [70]. Soil animals also play important roles in litter decomposition and greenhouse gas emissions. Through leaf shredding, soil fauna increases the surface area of litter, which increases microbial decomposition rates [71]. Many soil animals consume leaf litter, digesting leaf litter and expelling excrement. Excrement from soil fauna decomposes more slowly than leaf litter [72]. Soil fauna generally increase litter decomposition rates in temperate and wet tropical climates, but not necessarily in cold dry environments [20,72]. Earthworm activity can both stabilize soil C [73] and increase greenhouse gas emissions [74] depending on local ecosystem conditions and climate. Soil biodiversity is an important avenue for deeper understanding, model prediction, and land use action to address climate change [67].

3. Threats to Soil Biodiversity

Despite the important role soil biodiversity plays across ecosystems, soil organisms face many of the same threats as aboveground organisms and receive far less research, media attention, and legal protection [35]. Habitat loss from land-use change, climate change, and invasive species, both above- and belowground, are as challenging for soil organisms as they are for terrestrial and aquatic organisms.

Habitat loss is the primary threat to soil biota. Agriculture is the largest driver of habitat loss and biodiversity declines globally [2], including land conversion to agricultural use and management practices within agroecosystems. Conversion of Amazonian forest to agricultural land-use results in the homogenizations of soil bacterial communities and loss of soil fungal diversity [75,76] as well as reductions in macrofauna [77]. Agricultural fields support smaller and less diverse soil communities than forests and grasslands [17] and agricultural intensification further reduces soil biodiversity, particularly larger bodied organisms (e.g., invertebrates) [78,79]. Even reduced tillage systems typically host less soil biodiversity than natural ecosystems, as shown by Domínguez et al. [80] in a study of grasslands and agroecosystems in Argentina. In addition to agricultural land use changes, urbanization and suburbanization leads to the destruction of soil habitats through building construction and pavement which results in soil sealing [81].

Habitat quality can be degraded through pollution, including excessive nutrient inputs, and invasive species. Heavy metal pollution can shift communities to become dominated by a few taxa that can tolerate, or even thrive with, high levels of chemical inputs with corresponding decreases in taxa abundant in unpolluted soils [82,83]. Increased N inputs, from atmospheric deposition or from direct fertilizer application, is also a form of pollution and can shift soil bacterial communities, decreasing *Acidobacteria* and *Verrucomicrobia* and increasing *Actinobacteria* and *Fermicutes*, and decrease overall microbial activity [84]. Habitat quality can also be impacted by invasive species. Invasive plants can alter belowground communities through release of exudates toxic to some soil organisms, such as arbuscular mycorrhizal fungi, changes in N-cycling, such as invasive legumes, shifts in fire frequency and intensity, and/or variations in plant litter and root inputs [85]. In some cases, invasive plants increase diversity and abundance of soil organisms, particularly when invasive plants result in increased litter and root inputs [86]. In other situations, soil organisms can be invasive species, reducing plant fitness and animal diversity and abundance [87]. Invasive earthworms in northern North America negatively impact native soil fauna, alter C and nutrient cycles [88], and affect plant community composition [89]. Enough research exists to know soil habitats face multiple threats, from direct and indirect inputs of pollutants and nutrients, to shifts in aboveground communities, including exotic species. However, habitat loss and degradation are not the only threats to soil biodiversity.

Climate change is the paramount challenge of our generation, and soil biota are impacted like all other life on Earth. Climate change includes a suite of environmental changes including atmospheric concentration of greenhouse gases, namely CO₂, precipitation quantity and frequency, and temperature. Globally, these variables are predicted to shift in different directions and magnitudes, and as such, understanding how soil biodiversity responds to climate change requires deep understanding of both soil biodiversity in biomes, predicted impacts of climate change, and how soil taxa populations and

communities may likely respond. A meta-analysis of soil microbial community studies found soil fungal abundance responses to elevated CO₂ varied by taxon and ecosystem [90]. Altered precipitation regimes impact insects, both above- and belowground. In an Australian grassland, summer drought periods corresponded with increased aboveground insect plant predator populations the following spring, but no changes in belowground invertebrates [91]. Decreased precipitation increased root-feeding nematode populations in mesic and semi-arid grasslands by decreasing predator nematodes, but this pattern was not observed in xeric grasslands where nematode communities are adapted to prolonged drought periods [92]. Temperature impacts soil communities in unique ways as well. Increased temperatures impact soil biota physiologically, as some taxa have a very narrow temperature range for optimal functioning and others can tolerate a broader range. In a study of springtails (Collembola) [93], an exotic species was more tolerant of higher temperatures than native springtail species, potentially increasing the risk that exotic invasive species could usurp native soil communities as climates change. Given the numerous interacting consequences of global climate change and the hyper-diversity of soil communities, there are many uncertainties in understanding climate change impacts on soil biodiversity.

4. Protecting Soil Biodiversity

Opportunities exist to protect and support soil biodiversity, which in turn sustains the diversity of life on Earth, including humanity. Many actions that support biodiversity aboveground also support biodiversity belowground. Because soil biodiversity is woven into many facets of ecosystems, explicit consideration of soil biodiversity can provide a holistic approach to advance many components of global sustainability agendas. Protecting existing natural areas, restoring degraded habitats, employing sustainable agricultural practices, and embracing urban biodiversity are all practices that reinforce and sustain diverse soil communities and the functions and services they provide across all ecosystems (Figure 3).

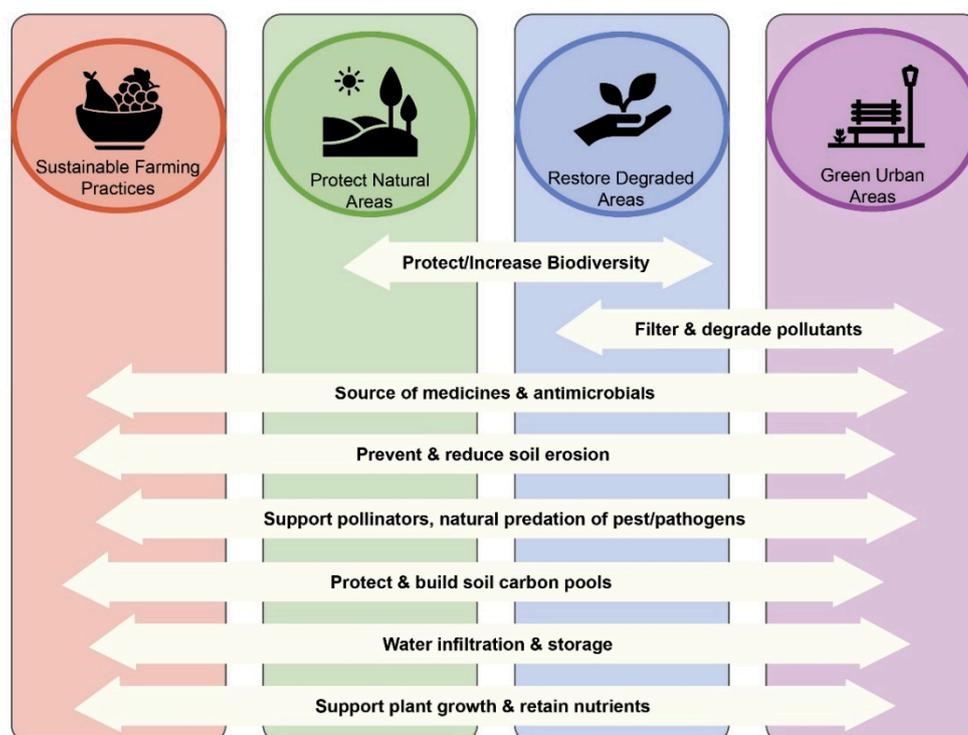


Figure 3. Broad actions that support soil biodiversity and multiple ecosystem services it supports. Enacting these practices can support multiple aspects of soil biodiversity, and in turn, advance multiple Sustainable Development Goals and Aichi Targets. Image credit: K. Ramirez, E. Bach.

4.1. Protect Natural Areas

Protecting natural lands is essential to protecting soil biota and the functions it provides (Figure 3). Prioritizing natural areas for protection has primarily focused on aboveground biodiversity [94], in large part because knowledge of soil biodiversity has lagged behind aboveground biodiversity. Protecting soil habitat in natural areas is an important source of this information, representing unique habitats and ecosystems with lighter human impacts. Soil biodiversity within natural areas improves water quality and can provide flood protection to populated areas in extreme events. Soil organisms in undisturbed soils are also critical to addressing global climate change, as they store C and regulate greenhouse gas cycling [95,96]. Models have shown that protecting areas from deforestation or conversion to agriculture can be a cost-effective way to prevent soil greenhouse gas emissions from microbial activity, conferring societal benefits far beyond estimated costs [97]. For example, in the Great Plains of North America, preventing cultivation of 10% of existing grasslands would avoid CO₂ emissions estimated to cost society \$430 million over 20 years [98].

Natural area protection and management is critical to sustaining biological diversity, both above- and belowground. Many land management decisions are driven by above-ground plants and animals, but soil organisms can provide an important focus for natural area management. For example, using prescribed fire to reduce and prevent woody plant or invasive species encroachment in grasslands benefits soil-dwelling insects and aboveground organisms that rely on open grassland habitats [99]. Timing and intensity of fire can be modified to protect abundance and diversity of soil-dwelling insects. Some invasive plant species impact soil organisms, including symbiotic mycorrhizal fungi, which can affect the ability of native plants to compete [85]. Such considerations are important for land managers making decisions about when and how to control invasive species in natural areas. There is much still to learn about soil communities across habitat types around the world, and natural areas are an important way to both protect soil communities and retain ecosystem services for a sustainable future.

4.2. Restore Degraded Ecosystems

Declines in biodiversity and ecosystem services from nature, largely from human land use, are globally pervasive. Ecosystem restoration is one of the best returns on investments to improve soil habitat and functioning to advance global sustainability [2,100]. Restoring ecosystems for soil biodiversity can provide numerous ecosystem functions and services that support global sustainability (Figure 3). Soil biodiversity, and the services it provides, can be both a goal of restoration and a means to restore degraded systems.

Restoration ecology has traditionally focused on above-ground metrics like plant and bird diversity; however, soil communities are central to ecosystem recovery and restoration. Soil fauna shift in community composition with time since restoration in North American tallgrass prairie [101–103], Costa Rican forests [104], and Australian mines [105], although in most cases, restored communities did not resemble communities in native reference ecosystems during the course of the study. Restoration practices in temperate woodlands and savannas increased collembola abundance and decreased non-native isopod habitat compared with no management [106]. Similarly, microbial communities show strong recovery trajectories with restoration in grasslands [107,108], wetlands [109], and forest [110], although they often fail to resemble native reference ecosystems. Considering ecosystem interactions, limited available data suggests trophic rewilding as a form of restoration has important feedbacks with belowground communities and their functioning including C and nutrient cycling [111,112]. Microbial communities can be managed in wetland restorations, to reduce N and phosphorous (P) export [109] through practices like altering hydrology to create anoxic conditions through flooding and select for anaerobic bacteria and metabolisms. Recent work with nematode communities in European grassland restored with seed addition and/or soil inoculum found it took seven years before differences in soil communities among the treatments was detected [113]. Similarly, Ribas et al. [114] found that ant communities had greater diversity, including some more conservative species, in gold mine tailings that revegetated naturally compared with planted grass and shrub,

although recovery may take longer. Recovery of soil organisms will vary by taxa and geography. Evidence is accumulating that soil biodiversity is an important part of ecosystem restoration.

Soil biodiversity can also be leveraged to restore degraded systems. For example, bacteria and fungi within soil can actively degrade chemical pollutants in soil like diesel [60] and glyphosate [59], and tolerate and chelate heavy metals [115,116]. Restoring belowground communities can stabilize soils and reduce erosion, and provide additional benefits in restored ecosystems, including faster recovery of soil C pools in restoration with high plant diversity compared with low plant diversity in North American grasslands [117]. In the tallgrass prairie of North America, certain arbuscular mycorrhizal fungi species can facilitate establishment and persistence of rare native plants [118]. Increasing the pace of ecosystem restoration is widely recognized as central to global sustainability agendas, including the UN declaration of 2021–2030 as the Decade on Ecosystem Restoration, and soil biodiversity provides a focus for both restoration practice and targets that integrates the multiple benefits gained from ecosystem restoration.

4.3. *Employ Sustainable Agriculture Practices*

Sustainable food production is essential to the future of humanity and nature on Earth, and as outlined above, soil and the biodiversity within it is the foundation of sustainable agriculture (Figure 3). Sustainable agricultural actions focused on soil biology are needed across cultures and farming contexts. There is an abundance of research from industrial row-cropping systems, including robust evidence that tillage negatively impacts soil organisms with larger body size [78,119], including earthworms [120], collembola [121], and mites [122]. No-till and reduced-till systems generally support a greater proportion of fungi than bacteria compared with conventional systems [119,123]. Tsiafouli et al. [79] found that management with annual tillage reduced soil biodiversity and shifted communities in favor of small-bodied organisms compared with grass/legume rotations and grasslands managed without any tillage. Smaller, less taxonomically diverse soil communities can lead to lower plant productivity, less N turnover, and greater P leaching [34], which could lead to reduced crop yields and increased loss of nutrients from agroecosystems. In addition to tillage, presence of cover crops and retention of litter are important factors for soil communities. Cover crops, which are grown in row-crop fields outside of the primary crop growing season, prevent extended periods of time when fields have exposed soil. Living roots from cover crops reduce soil erosion [124] and provide inputs, in the form of root tissue and exudates, that support numerous soil organisms including microorganisms, fungi, and nematodes [9,125]. Perennial crops generally improve habitats for soil organisms, reducing N loss [126,127] and building organic matter [128]. Diversity of plant inputs, through diverse rotations of crops and cover crops can shift soil microbial profiles and activity resulting in greater soil C accrual [129]. The retention of litter and a diversity of soil organisms play important roles in accruing and storing soil organic matter [130] and in some systems, increases in soil organic carbon (SOC) would also have the added benefit of increasing crop yields [131]. Furthermore, greater soil biodiversity and the functional redundancy it provides may increase the capacity of soil to continue functions like nutrient turn-over and plant productivity under global change scenarios.

Many traditional approaches to agriculture leverage crop diversity and rotation to improve production and break disease cycles. In the broad context of global agriculture, soil organisms play important roles across differing approaches and climates. In Honduras and other parts of Central America, crop rotation and wood ash application are leveraged to encourage soil-dwelling predators and reduce white grub outbreaks [132]. Pre-Columbian people in what is now French Guiana created raised fields that supported (and continue to support) soil engineers including ants, termites, and earthworms, which in turn increase soil nutrients and drain marshy soil, creating space for crop production [133]. Soil biodiversity is at the heart of sustainable agriculture, supporting crop and livestock production across all types of systems with fewer inputs that are costly to farmers and impact non-target species and habitats. Recognizing soil as complex, biological ecosystems that support

sustainable agroecosystems, rather than input/output systems to be optimized is a critical perspective shift necessary to advancing a sustainable future.

4.4. Adapt Urban Areas for Biodiversity and People

Approximately 55% of people world-wide live in urban areas and that number is expected to rise to 68% by 2050 [134]. Expansion of urban areas can lead to the destruction of soil habitats through building construction and pavements; however, urban areas can be home to diverse soil microbial and invertebrate communities. Soil is foundational to services provided by nature to urban areas (Figure 3). As mentioned before, soil organisms can directly degrade pollutants and chelate heavy metals in former industrial sites, improving safety of these sites within heavily populated areas. Urban soils support plants in green spaces and street curbs that can reduce air temperature in cities and provide space for play and relaxation. Soil fauna play key functional roles in urban rain gardens, which absorb stormwater and filter pollutants, reducing stress on storm water management systems.

Urban soils show some convergence, particularly with soil organic C and total N content, and some distinction from parent material and climate [135]. Biologically, a global survey of urban areas found convergence of archaeal and fungal communities, but not bacterial [136]. Studies of urban green spaces found similar levels of soil biodiversity as in a survey of soils in surrounding natural areas, although that pattern does not necessarily hold for some taxa [137].

There are many ways to support and encourage soil biodiversity in urban areas. Green spaces support the most soil biological diversity in cities [137,138]. Prioritizing green space in urban planning is an important way to maintain soil biodiversity and retain the ecosystem benefits it provides. In planning urban space use, including parks, using mulch for ground cover instead of rock increases earthworm abundance and reduces surface temperature [139], increasing water infiltration and alleviating “heat island” effects. Activity of soil organisms within rain gardens have the potential to enhance storm water infiltration, pathogen removal, and removal of excess nutrients and pollutants [140]. Soil compaction can be reduced with removal of disturbance (e.g., foot traffic or temporary structure). Green roofs can create additional habitat, supporting unique and diverse soil fungal [141] and beetle [142] communities. In addition, thoughtful urban development choices that ‘build up not out’ can be an important tool for protecting soil biodiversity and ecosystem services not only in urban areas, but also preventing conversion of natural areas and productive agricultural land. A co-benefit of many of these approaches is creating spaces for people to gather, share, learn, play, and relax. With most of humanity living in cities, and that percentage growing, urban areas are an important part of our present and future, and actions that support biological diversity belowground can make cities more livable and sustainable.

5. Knowledge Gaps

Global knowledge of soil biodiversity distribution lags markedly behind aboveground knowledge. New observations and understandings of soil-dwelling taxa and their habitats consistently come to light. Initiatives to bring together global datasets have created maps that show gaps in biogeography, biomass, and function, and species distributions of nematodes [143], bacteria [144], and fungi [145]. These synthesis efforts have highlighted knowledge gaps in distributions of soil taxa persist. Given the greater uncertainty around global distribution of soil biodiversity compared with aboveground biodiversity, analysis has shown only 37% of areas with the highest levels of both above- and belowground biodiversity overlapped [146]. More research is needed, particularly in the Global South, which is highly under-represented in the scientific literature, to refine these maps and build confidence needed to shape habitat conservation with soil biota in mind. Knowledge of soil microbial communities has grown exponentially in recent decades with the advent of molecular tools, but knowledge of many soil invertebrates has slowed as taxonomic expertise dwindles at many academic institutions. Understanding and appreciating soil biodiversity within taxa is a major knowledge gap. Soil organisms are estimated to have much higher proportions of undescribed species than larger terrestrial and aquatic taxa, which makes it challenging to evaluate which species may be in need of conservation and how best

to prioritize conservation efforts [35]. Furthermore, lagging understanding genetic diversity within soil biota, both fauna and microbial could slow discovery of pharmaceuticals [22,29] as well as capacity for soil communities to respond to changing climate. Understanding of soil organisms, both microbial and faunal, detailed enough to determine conservation status (e.g., common/rare/threatened/endangered) is needed to catch-up to aboveground knowledge and inform action.

Linking soil biodiversity with ecosystem services and functions is a crucial area in which to build information. We know soil organisms are central to nutrient cycling driving crop and livestock production, but we lack clear understanding of which organisms or communities are most directly involved. This leads to ambiguity around recommending actions for producers to leverage soil biology for sustainable agriculture. Water quantity and quality is a top concern for agriculture and humanity. Linking soil biodiversity impacts on water movement and quality at the watershed scale, perhaps through modeling, and scaling those findings up to landscape-scale actions appropriate for addressing current and developing water concerns is a priority. Scaling up soil biodiversity knowledge for global climate action is another key challenge. Recent work is advancing understanding of how soil biology can influence carbon cycling and next steps involve including biodiversity in climate change models to improve predictions [67].

Uncertainties also exist around threats to soil biodiversity and solutions to protect soil organisms and their contribution to sustainability. Enough research exists to know soil habitats face multiple threats, from direct and indirect inputs of pollutants and nutrients, to shifts in above-ground communities, including exotic species. However, many questions remain as to exactly how these factors impact understudied taxa like protists and enchytraeids. There is also a scarcity of soil biodiversity knowledge from certain habitat types, like urban areas, which have long been underappreciated by ecologists and soil experts. Even in well-studied systems, like agricultural production, there are knowledge blind-spots. Most research, including soil biodiversity research, has focused on industrial row-cropping practices with very little research on small-scale subsistence farming, which makes up a large portion of global agriculture. Increasing research in these areas will improve our understanding and increase expert confidence in recommending actions to protect soil biodiversity and leverage its functioning for global sustainability. We recommend additional research to build bridges between soil biodiversity expertise and real-world solutions for a sustainable future, and we also believe there is a need to act now, both to protect soil biodiversity and to advance sustainable development agendas.

6. Conclusions

Soil biodiversity knowledge and research is moving beyond academic circles and being used to support solutions to biodiversity loss, local (water quality, food security), regional (land degradation), and global (climate change) challenges. Managing soils, as the vibrant living systems they are, provides a new perspective for integrated actions and solutions. Soil organisms, microscopic and macroscopic, support all ecosystems: Cycling energy and nutrients to support plant and animal growth in terrestrial systems and maintaining nutrient balances in water, thereby affecting aquatic organisms and ecosystem health. The ways in which soil biodiversity interfaces with multiple ecosystem functions makes it a natural focus for advancing a holistic global sustainability agenda. Soil biodiversity is at the heart of natural solutions for climate, biodiversity, and humanity, including protecting natural areas, restoring degraded ecosystems, employing sustainable agricultural practices, and adapting urban areas for nature and people. As we work toward a sustainable future, let us not overlook the critical and diverse asset, right beneath our feet.

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