PERSPECTIVE

Soil biodiversity and human health

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Soil biodiversity is increasingly recognized as providing benefits to human health because it can suppress disease-causing soil organisms and provide clean air, water and food. Poor land-management practices and environmental change are, however, affecting belowground communities globally, and the resulting declines in soil biodiversity reduce and impair these benefits. Importantly, current research indicates that soil biodiversity can be maintained and partially restored if managed sustainably. Promoting the ecological complexity and robustness of soil biodiversity through improved management practices represents an underutilized resource with the ability to improve human health.

oils comprise a dynamic reservoir of biodiversity within which the interactions between microbes, animals and plants provide many benefits for human well-being; however, their potential use for the maintenance of human health has been less clear¹⁻³. Living soils are vital to humans because soil biodiversity, with its inherent complexity (the types, sizes, traits and functions of soil organisms), not only provides disease control but also influences the quantity and quality of the food we eat, the air we breathe and the water we drink⁴. The long-term provision of these benefits is dependent on careful and sustainable use of soils as a resource. Yet, soil biodiversity is often unintentionally affected by human-induced global changes. Land-use change, including urbanization, agriculture, deforestation and desertification, can have a ripple effect on soils and soil biodiversity that extends far beyond the original site of disturbance^{5,6}. For example, the increase in soil erosion by water and

wind contributes to the formation of dust storms and the dispersal of soil organisms and pathogens, with effects on soil biodiversity and ultimately on human, plant and animal health $^{7-10}$.

Research efforts are rapidly producing information about soil biodiversity and its functions, which can be combined with land managers' knowledge, to inform the development of sustainable soil-management practices^{1,11–13}. The resulting global preservation and restoration of soils would provide an additional path towards decreasing disease in and providing medicine for humans, plants and animals.

Here, we focus on the impacts of the use and mismanagement of land on human health due to (1) changes in the prevalence of antagonists for soil-borne pests and pathogens that cause diseases in humans, plants and animals, and (2) changes in soil biodiversity that affect the maintenance of health (Fig. 1). We use the integrated concept of human

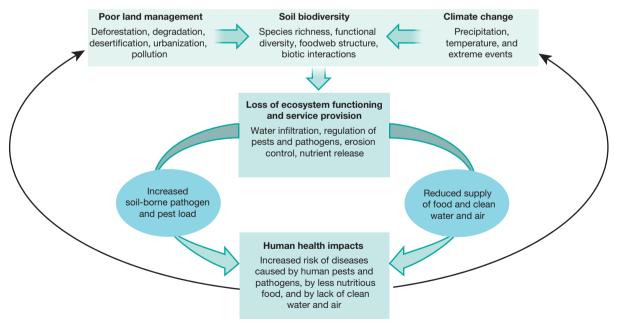


Figure 1 | Flow diagram illustrating the link between soil biodiversity and human health. Soil biodiversity is often negatively affected by the interaction between poor land management practices and drivers of climate change, both of which ultimately compromise ecosystem function

and services that are essential for human health (control of pests and pathogens, production of nutritious food, cleansing water and reducing air pollution). Responses to reduced human health can in turn affect management decisions that govern land use and climate change.

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Table 1 | Soil pathogens and parasites of humans, animals and plants

Host organism	Type of pathogen	Euedaphic pathogens		Soil-transmitted pathogens	
		Species name	Disease caused	Species name	Disease caused
Humans	Bacteria	Bacillus anthracis Listeria monocytogenes	Anthrax Listeriosis	Escherichia coli Salmonella spp.	Diarrhoea Salmonellosis, Typhoid fever Diarrhoea
	Fungi	Aspergillus spp. Coccidioides immitis Histoplasma capsulatum	Aspergillosis Valley fever Histoplasmosis		
	Protozoa Helminths (Nematoda)	Naegleria fowleri	Brain encephalitis	Toxoplasma gondii Ascaris lumbricoides Ancylostoma duodenale Necator americanus Strongyloides stercoralis	Toxoplasmosis Ascariasis Hookworm Hookworm Strongyloidiasis
	Platyhelminthes			Taenia saginata	Beef tapeworm
Animals	Bacteria Helminths (Nematoda)	Bacillus anthracis	Anthrax	Haemonchus contortus	Haemonchosis
Plants	Bacteria Fungi Helminths (Nematoda)	Agrobacterium tumefaciens Phytophthora infestans Meloidogyne spp. Bursaphelenchus xylophilus	Crown gall Potato blight Root knot Pine wood		

Following refs 19 and 89, pathogens are listed as euedaphic (true soil organisms) or as soil-transmitted (those temporarily living in soil and transmitted to a host).

health as defined by The World Health Organization and Convention on Biological Diversity¹⁴, which extends beyond disease and infirmity and recognizes human connections to other species, ecosystems and the ecological foundation of varied drivers and protectors of human health. We specifically discuss how knowledge of the linkages between soil biodiversity and human health can be strengthened for improved management of land. Some aspects of land-use change in relation to soil biodiversity and human health are covered elsewhere, including industrial pollution, radioactivity, landfills, resource extraction, and mineral toxicity; and are not included here^{15,16}.

Soil biodiversity and soil-borne pathogens

Most soil organisms pose no risk to human health; rather, evidence is accumulating that soil biodiversity can be of great benefit^{17,18}. Soil-borne pathogens and parasites that cause human diseases represent a minority of the species living in soils. There is a great opportunity to capitalize on the positive effects of soil organisms on human health through their roles (direct and indirect) in controlling soil-borne pathogens and pests (listed in Table 1).

Many animal, plant and human disease-causing organisms or their vectors live in soil, but their relationship to human diseases and the environment is not fully elucidated^{16,19–21}. To address soil management and public health we need an understanding of the organisms, their ecological interactions, and why they become prevalent or persistent in soils^{22,23}. Some soil-borne pathogens, such as the bacterial genera Pseudomonas and Enterobacter, are opportunistic species that can infect and cause diseases in humans but whose main functions in the soil foodweb are as antagonists against plant root pathogens, promoters of plant growth and decomposers^{20,24}. Other soil-borne pathogens are obligate parasites that require a host to complete their life cycle. Most of these organisms can survive in soils for weeks to years, including as spores and eggs or inside carcasses. Soil-borne pathogens causing human infectious disease can be either true inhabitants of soils (euedaphic) or are transmitted via soils (Table 1). Soil-transmitted pathogens are usually obligate pathogens and reside temporarily in soil before being transmitted to humans by contact, vectors or in faeces.

Soil and anthrax

Anthrax is a zoonotic disease infecting humans, wildlife and livestock caused by the bacterium *Bacillus anthracis*. Known in the USA as an agent of bioterrorism, *B. anthracis* is relatively common and found in soils worldwide, including within the USA. Anthrax spores can remain dormant in soils for decades, but with heavy rains they are brought to the soil surface and attach to roots and grasses, which are grazed by animals. There have been outbreaks in eastern Colorado and Texas, occasionally

resulting in die-offs of grazing animals, usually cattle. In contrast to this episodic occurrence, *B. anthracis* in Namibia and east Africa occurs annually in zebras and other grazing animals. In recent field experiments in Namibia, carcasses of animals infected with *B. anthracis* were shown to promote grass growth, which thus made the site more attractive for grazing wildlife²⁵. This mechanism provides *B. anthracis* with a wildlife host and continues the cycle of the infectious disease.

Hence, one of the more effective strategies to reduce anthrax prevalence is burning of the vegetation, especially at sites of carcass deposition. However, maintaining soil cover is also important to reduce dust formation by wind erosion because human infections of anthrax typically result from inhalation of airborne spores or via vectors.

In general, soils favourable for anthrax are calcium-rich with neutral to alkaline pH (that is, Chernozem soils) 26 . Studies on soils and anthrax disease ecology in the Kruger National Park in South Africa found that when soil calcium was >150 milliequivalents per gram and pH>7, the anthrax death rate for ungulates was seven times higher than in other nearby soils 26 .

Soil and helminths

The nematode *Strongyloides*, a soil-transmitted helminth and a parasite of humans and animals (Table 1), has a unique life cycle that alternates between free-living in soil and parasitic. The larvae are passed into soil in faeces and moult either (1) to become larvae that can infect humans or (2) to develop into adults that produce eggs and become a new free-living generation in soil. The free-living form feeds on bacteria as part of the soil foodweb, but its role in decomposition and nutrient cycling is not well understood. When infective larvae in soil come into contact with a suitable host, they penetrate the skin and eventually migrate to the intestine, where they reproduce. *Strongyloides stercoralis* infections occur in 10% to 40% of the human population in many tropical and subtropical countries²⁷, as a result of poor sanitation practices. In a study in rural Cambodia, about 45% of the people tested were infected, and a higher risk of infection was associated with lower organic carbon content of soils and land-use conversion from forest to cropland²⁸.

This strongly suggests that increasing the soil organic carbon levels in our croplands could be effective in reducing the prevalence of disease-causing helminths. Also included in the category of soil-transmitted helminths are hookworms and roundworms (Table 1), which infect many people globally. For example, in 2003, China and sub-Saharan Africa each had an estimated 200 million hookworm infections²⁹. The contributions of hookworms and roundworms to the soil foodweb and their relationship to soil properties, however, are not well known.

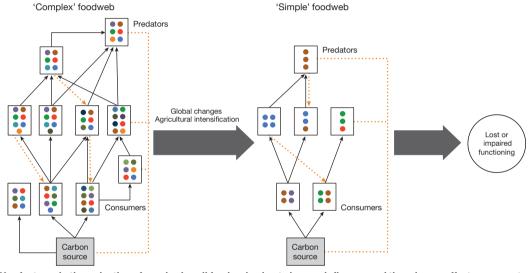
To understand and predict the incidence of soil-borne pathogens and parasites in the future, much can be gained by integrative studies on their

BOX 1

Human influence on soil foodwebs

Soil foodwebs are naturally complex entities that enhance ecosystem functions such as biogeochemical cycling and the suppression of pests and pathogens for plants, animals and humans. Global changes, however, can have detrimental impacts on soil foodweb complexity by reducing belowground biodiversity and affecting biotic interactions. Substantial advances have been made in understanding these impacts on ecosystem functioning over the past few decades^{1,3,65}. Furthermore, recent studies suggest that soil foodweb complexity is essential to maintaining high rates of ecosystem function^{45,46,65,86}. Thus, activities that cause belowground biodiversity losses (such as loss of taxa and trophic levels) contribute to a reduction in foodweb complexity and, thereby, the capacity of soils to perform ecosystem functions. See Box 1 Figure, in which

taxa are shown as coloured circles, trophic levels are shown as boxes, solid lines represent food sources and dashed lines indicate omnivory. The 'simple' foodweb on the right has been adversely affected by human-induced changes. Although these functions may not be lost completely, even reduced levels of functioning can influence human health directly (by reduced suppression of soil-borne diseases) or indirectly (by reduced provision of food, clean water and air). In some cases, these functions can be replaced through human interventions such as increased fertilizer and pesticide inputs, but promoting ecosystem functioning by managing soil biodiversity is likely to be more cost-effective and will ensure long-term sustainability.



 $Box\,1\,Figure\,|\,\,Key\,features\,in\,the\,reduction\,of\,species\,in\,soil\,food\,webs\,due\,to\,human\,influence\,and\,the\,adverse\,effect\,on\,ecosystem\,functioning.$

life cycles in soils, their role in soil foodwebs, and how they are affected by environmental variables. The resulting knowledge can be used to establish viable management options to reduce the impacts of soil-borne pathogens and parasites. Integrating this new soil-based knowledge with the experience of public health researchers would provide an enormous opportunity for new soil-based approaches and policies to control current and emerging infectious diseases.

Soil and allergies

Several studies have shown that exposure to soil microorganisms lessens the prevalence of allergic diseases^{22,30–33}. In particular, there is evidence that our immune system needs to be exposed to possible pathogens residing in soils in order to develop tolerance³⁴. For example, it was found that individuals living in more urban environments have a lower diversity of bacteria on their skin and lower immunity expression^{33,35}. It is predicted^{14,33} that nearly two-thirds of the global human population will be living in urban areas by 2050 (refs 14, 33), resulting in less stimulation of our immune systems by soil organisms, and leading to more allergic diseases. Management of urban areas could easily consider access to natural areas and small livestock (chickens, ducks, rabbits and goats) as a way of exposing the urban population to soil organisms.

Soil, antibiotics and antihelminth resistance

As soils are altered through global change and associated losses in biodiversity above- and belowground, there is concern that we are losing a possible source of antibiotics and medicines, as well as the biological controls needed to prevent human, animal and plant disease. Antibiotic resistance to microbial-derived medicines has increased rapidly, threatening the prevention and treatment of diseases caused by bacteria, fungi and parasites¹⁷. The development of new antibiotics using soil has been very slow, because about 99% of bacteria have yet to be cultured. However, a new technique recently identified an antibiotic from an uncultured soil bacterium that can kill Mycobacterium tuberculosis, the causal agent of tuberculosis¹⁷. This is very promising: other as-yet-uncultured species may also reveal novel antibiotics. Helminth parasitic worm infections in humans, cattle and other domestic animals are often treated with antiparasitic, antihelminthic drugs, which are showing increasing resistance. Fortunately, land-management practices, including rotating pastures with more-resistant animals, breaking up or removing manure piles in pastures, or managing for higher grass growth so that animals do not graze on the parasites found in soils, are useful options for reducing the risk of parasite infection^{36,37}.

Soil and biological control

Human health is influenced indirectly by our choice of agricultural management practices owing to changes in the nutritional value of the plants and animals we eat, and the quantity of food produced. Plants are subject to many diseases caused by bacteria, fungi, viruses and parasites, which affect plant growth, nutrient levels and the quality of our food. In agriculture, biocontrol of a soil-borne pest for plants is a management option that is based on the identification and ecology of a naturally occurring soil predator or parasite that reduces the pest or

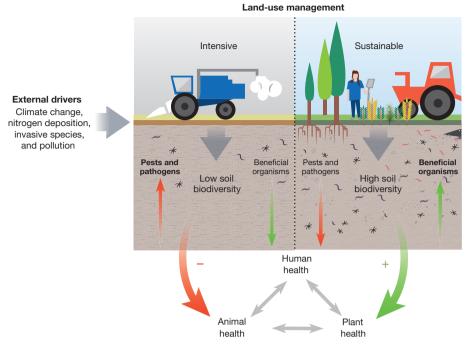


Figure 2 | A conceptual framework illustrating how decisions on land use and management are linked to human health through the effect on soil biodiversity. Soil biodiversity is strongly influenced by external drivers such as climate change and nitrogen deposition but also by landuse management. Land use such as agricultural intensification (left) can reduce the diversity and densities of beneficial organisms that control pests and pathogens, thereby negatively affecting the health of plants, animals and humans. Adopting less-intensive management practices (right) that enhance soil biodiversity can promote plant, animal and human health because the number of beneficial species will outweigh pests and pathogens. Moreover, soil biodiversity may help mitigate the impacts of external drivers of ecosystem functioning.

plant pathogen population and thereby enhances food quantity and nutrient content.

For example, the root weevil Diaprepes abbreviatus causes substantial damage to citrus plants. The damage is naturally controlled in some Florida soil habitats by species of indigenous soil entomopathogenic nematodes (EPN) that parasitize and kill the root weevil. A nematode species not native to Florida, Steinernema riobrave, is commercially available to control the root weevil in habitats where indigenous EPNs are less dominant, rather than using less effective, more costly chemical controls that move into groundwater and are harmful to human health 38,39. In addition to augmenting soils with EPNs, managing soil in ways that promote native EPN prevalence and diversity are used. For example, maintaining good soil drainage, low pH, and adding sand to soils that are low in EPNs before planting young trees are practices used to conserve native EPN species in citrus groves. There are many other examples of biocontrol delivered through a healthy soil foodweb, such as the use of the bacterium Pasteuria penetrans, a pathogen of plant parasitic nematodes, and Arthrobotrys anchonia, a nematode-trapping fungus that kills plant parasitic nematodes^{40–43}.

As recent evidence suggests, it is not only single organisms that should be considered as valuable for controlling soil-borne pests and pathogens of humans, animals or plants. The immense diversity and abundance of organisms found belowground in concert contribute to the control of pests and pathogens (Box 1) $^{44-46}$. Hence, control of soil-borne pathogens should not focus solely on specific beneficial soil predators or parasites, but rather on how a general increase in the complexity of soil biodiversity can reduce plant, animal and human diseases caused by soil-borne pathogens: the disease is suppressed as a result of the whole soil foodweb 47,48 .

Although the direct link between biodiversity and disease suppression has not been well established in soil owing to the complex interactions that occur belowground, there is growing evidence for the aboveground world: disease risk in wildlife plants and humans rises with biodiversity loss^{49–53}. For example, Johnson *et al.*⁵⁰ recently showed in wetland ecosystems that amphibian species richness moderated pathogen transfer and thereby limited disease prevalence in the animals. Soil biodiversity may similarly moderate the impacts of pests and pathogens both above- and belowground. One recent study⁵⁴ showed how increased microbial diversity reduced the success of a bacterial pathogen *in vitro*. Furthermore, temporary inhabitants of soil can also have positive

functions in ecosystems and thereby indirectly benefit human health; for example, some bumblebees well known for their benefits as plant pollinators live temporarily in soils. Burrowing vertebrates such as voles and prairie dogs can also indirectly benefit plant, animal and human health by mixing and enriching organic matter and nutrients in soils^{55,56}. These examples emphasize that many soil organisms contribute indirectly to soil functions that can ultimately benefit human health.

Maintaining soil biodiversity for health

To maintain soil biodiversity, it is essential to take into account the spatial distribution of belowground organisms. In recent years, the available information on biogeography of soil biodiversity has accelerated. Global distributions of soil taxa from microbes to larger animals shows that few species occur in all soils; instead many species are rare and show restricted distributions, often limited to particular soil types or geographical regions ^{57,58}. For example, some enchytraeid species occur primarily in rich Arctic peat soils, and many nematode and mite species are endemic to the Antarctic continent ⁵⁸. Likewise, a study of the soils of Central Park in New York City found almost as many distinct microbial communities and undescribed soil biodiversity (bacteria, archaea and eukarya) as occur in other global biomes ⁵⁹. Soil biodiversity, like soils themselves, is highly variable across fields and regions, highlighting the need to understand how soil communities organized in complex soil foodwebs differ spatially across a region and globally ^{57,58,60,61}.

In the next sections, we outline how soil biodiversity influences the production of food, fibre and biomass, and the provision of clean water and air, and illustrate how improved management of soil biodiversity can reverse to some degree the negative impact of humans on the depletion of global resources (Fig. 2).

Food, fibre and biomass production

With the exception of hydroponic horticulture, all terrestrial crop production is soil-based²¹. Given that crops support most of the human population, sustainable use of our soils is essential for long-term human health. In agricultural systems, soil-borne pathogens can disrupt the metabolic flow of nutrients within plants, reduce plant above- and belowground biomass, including fruits and other edible plant parts, or even kill the plant entirely, all leading to the production of less nutritious food. In humid and cooler climates, earthworms have been shown to increase crop productivity⁶², whereas termites can increase yields in warmer and

drier climates⁶³. Bender and van der Heijden⁶⁴ showed that enriched soil life increased nutrient-use efficiency, plant nutrient uptake and thereby crop yields. Moreover, enhancing the soil foodweb structure influences the resistance and resilience of other terrestrial ecosystems^{65,66}, and this knowledge can be used to promote sustainable use of our soils^{45,67}.

Soil symbionts have a particularly important role in sustainable production. Symbiotic soil microbes are essential for nutrient supply⁶⁸ and can contribute to biofortification of plants for important micronutrients such as zinc⁶⁹. Plant breeding and micronutrient fertilization are promising ways to address micronutrient deficiencies, but the bioavailability of the micronutrients is ultimately determined by soil microbial cycling of these micronutrients¹⁶. There is also evidence that fungi, in particular endophytes, promote plant stress tolerance⁷⁰.

It is evident from the above that soil biodiversity can play a crucial part in providing a more stable supply of food and a higher nutritional value of the food produced. However, the intensification of agricultural practices in the last century has ignored this role of soil biodiversity. The cornerstones of agricultural intensification—ploughing, and the application of agrochemicals and fertilizer—have been linked to a reduction of soil biodiversity^{3,6}. We stress that these are beneficial practices that should not be abolished, but instead should be used at the right time, rate and place.

Air quality

Land-use change has been tied to the frequency of dust storms, emissions of greenhouse gases, and the release of volatile organic compounds and biota in air 7 . Soil bacteria, fungi and some invertebrates, such as nematodes and mites, are transported several hundreds to thousands of kilometres by wind 71,72 . The misuse of land—such as overly intensive ploughing, leaving extended areas bare and fallow, and burning plant biomass from fields—increases dust and the formation of particulate matter of less than $10\,\mu m$ in size (PM10), with major consequences for human health in the form of respiratory problems, lung tissue damage, and even lung cancer 7,10 . Because soils are frequently polluted with heavy metals, harbour antibiotic-resistant organisms from animal feedlots, and contain pathogens for plants, animals and humans, the resulting dust can cause negative effects on human health 73,74 .

An example is valley fever in the southwestern region of the USA; outbreaks are caused by a soil fungus, *Coccidioides immitis*, that normally decays organic matter and helps to stabilize the soil surface, thus minimizing soil erosion. However, when the soil is disturbed, such as by agricultural practices, the fungus produces windblown spores that can cause lung disease in animals and humans and at worst result in death^{75,76}. In 2004, there were 6,000 cases of valley fever in the USA⁷⁴. Surveillance of dust storms with land–atmosphere modelling and remote sensing of dust storms is under way to enhance the epidemiology and decrease the number of cases of valley fever⁷⁴.

Here again the link between agricultural intensification, soil biodiversity, and human health is clear; intensive agriculture disturbs the soil and negatively affects soil organisms, such as arbuscular mycorrhizae, saprotrophic fungi, and earthworms, that play a key part in stabilizing soil and thereby reduce the potential of dust formation^{77,78}. Management options such as reduced tillage have been shown to reduce PM10 formation⁷³ and thus limit the risk of lung disease, cardiac arrhythmia, heart attacks and premature death⁷⁹. Other ways to reduce dust and conserve soil stability and biodiversity include agroecological management practices, such as planting windbreaks, adding manure, incorporating cover crops and retaining crop residues⁸⁰.

Water quality

The provision of clean drinking water is increasingly compromised by pollution (such as from mining, landfills and agrochemicals)⁸¹ and poor sanitation (contaminating drinking water with faecal-associated organisms)^{16,82}. Moreover, land-use changes, especially those accompanying urbanization, affect the relationship between runoff versus infiltration of water with potential impacts on local surface water bodies, groundwater

BOX 2

The UN Sustainable Development Goals

The successful implementation of the UN Sustainable Development Goals³⁰ in September 2015 that are aimed at ending poverty and improving the lives of the poor, are tightly connected to maintaining the biodiversity of soils. Yet only four of the seventeen targets specifically mention soil: Goal 2 (to end hunger, achieve food security and improved nutrition, and promote sustainable agriculture (Target 2.4), Goal 3 (to ensure healthy lives and promote well-being for all at all ages (Target 3.9), Goal 12 (to ensure sustainable consumption and production patterns (Target 12.4), and Goal 15 (to protect, restore and promote sustainable use of terrestrial ecosystems, sustainably manage forests, combat desertification and halt and reverse land degradation, and halt biodiversity loss (Target 15.3).

For example, Goal 3 (Target 3.9) focuses on substantially reducing hazardous chemicals and air, water and soil pollution. However, the connection between managing land for enhanced soil biodiversity and meeting Sustainable Development Goals such as ending epidemics of tropical and other communicable diseases (Goal 3, Target 3.3) or sustainable management of water and sanitation (Goal 6) is not recognized or incorporated.

To achieve the Sustainable Development Goals we stress that it is not enough to aim towards improvement of a single benefit related to 'food' or 'air' or 'water' or 'disease' control, because all are simultaneously dependent on soils and soil biodiversity. We propose a multiple-benefit focus for sustaining soils, biodiversity and global health that addresses many of the Sustainable Development Goals—such as Goals 1, 2, 3, 6, 8, 11 13, 14 and 15—through the following means:

- Include soil biodiversity and human, plant and animal health experts in integrated collaborative research, management and policy efforts to sustainably manage soils, food, water and air for improving human health
- Develop a global database of soil biodiversity to facilitate integrated and predictive use by scientists and health experts
- Establish a global archive of samples for the future benefits of health researchers that captures the interactions of total soil biodiversity (bacteria, archaea, eukaryotes)
- Utilize existing, new and local knowledge on successful management of lands to promote new options for longterm maintenance and conservation of soil biodiversity and improving human health
- Include soil biodiversity as a criterion for determining wilderness and protected areas
- Focus research on conservation of soil biodiversity as a management tool to improve human health in the long-term
- Coordinate scientific societies and other global efforts to educate and communicate results to land and water managers, public and policy makers, such as through the Global Soil Biodiversity Initiative (https://globalsoilbiodiversity.org), global conventions and scientific societies
- Broaden the disciplines of human health and soil biodiversity linkages to include the combined expertise needed to address the multifaceted climate and global environmental changes and to meet the Sustainable Development Goals

levels, areas downstream of point source pollution and the recharge of aquifers.

Soil biodiversity acts to enhance the structure of soils and thereby infiltration and percolation of water through the soil profile to (1) improve

water-use efficiency by crops, (2) limit the amount of agricultural runoff and associated contamination into adjacent land areas, and (3) filter out pathogens and contaminants by size exclusion, die-off and adsorption. Soil organisms can also degrade harmful pollutants and reduce the impact of poor sanitation^{83,84}. For example, *Enterobacter cloacae*, an enteric bacterium found in soils and water, is an effective means of bioremediating selenium-contaminated agricultural drainage water⁸². Selenium, an essential micronutrient for humans, occurs in groundwater and can accumulate in irrigated river basins and evaporative ponds. Implementing additional measures such as reduced irrigation, sealing earthen irrigation canals, and rotational land fallowing can further enhance the management of excess selenium⁸⁵.

Outlook

It is clear that soil biodiversity represents an underutilized resource for sustaining or improving human health through better soil management. As indicated above, some agroecological management options are known to maintain and increase soil biodiversity for human, animal and plant health. However, further development of viable practices and especially the promotion of their use as broadly as possible is urgently needed.

How to best manage the world's lands for improved human health? Some basic guidelines for management of soil biodiversity are offered here. We suggest that a new approach for land use and management is required that acknowledges that soil biota act in concert to provide multiple benefits, even if these benefits are not easily observed. Moreover, increased soil foodweb complexity promotes resistance and resilience to perturbation and may buffer the impacts of extreme events.

Agroecological practices that enhance soil organic matter content and soil biodiversity can promote nutrient supply, water infiltration and well-structured soil. Effective management options for cropping systems include reduced tillage with residue retention and rotation, cover crop inclusion, integrated pest management, and integrated soil fertility management (such as the combination of chemical and organic fertilizer). Expanding plant species diversity in crop and/or land rotations and adding organic amendments to pastures can increase soil biodiversity and mimic better the natural soil foodweb^{65,66,86}. Additionally, maintenance of soil biodiversity at the landscape level can be enhanced through buffer strips and riparian zones and land rotations. Drainage water management can reduce the movement of pollutants, agrochemicals and other contaminants to nearby landscapes¹³. Likewise, several forestry practices exist that promote soil biodiversity: re-established mixed deciduous forest stands in Europe were shown to have higher soil biodiversity than pure coniferous stands⁸⁷.

Management for conservation of land should include soil biodiversity as an important criterion in determining protected and wilderness areas, particularly in rapidly changing ecosystems, such as tropical forests, permafrost soils and alpine grasslands. Conservation of soil biodiversity should, in general terms, be based on existing knowledge of soil properties, the abundance, sizes and types of soil organisms, and vegetation. Nevertheless, conserving soil biodiversity could also be done through laboratory isolation of individual organisms or whole communities to maintain a reservoir of genetic and functional diversity appropriate for future disease prevention, biological technologies, and pharmaceuticals⁸⁸.

Soil archives that conserve live collections of interacting species of soil microbes and invertebrates in soil samples from different biomes are irreplaceable and essential; yet at present there are few such archives⁸⁸. Given the growing global demands placed on limited productive land and the projected increases in infectious diseases, there is an urgent need to implement these and other conservation measures as a stockpile for the future.

Ideally, the practices and conservation strategies outlined above that enhance soil biodiversity for the maintenance of human health should be incorporated directly into land-, air- and water-use policies at global and regional levels and integrated with public health organizations such as the United Nations (UN) World Health Organization.

Global conventions such as the UN Framework Convention on Climate Change, the UN Convention on Biological Diversity (CBD) and the UN Convention to Combat Desertification are all central to soils and global land use but often neglect soil biodiversity and our dependence on soil for human health, with the exception of the CBD¹⁴ through the Food and Agricultural Organization (FAO). Through the Global Soil Partnership, the UN FAO brings together global institutions and other interested parties to coordinate agreements and international challenges related to soil sustainability. The Global Soil Partnership is advised on global soil issues by a scientific Intergovernmental Technical Panel on Soils. Likewise, progress towards the UN Sustainable Development Goals can be achieved by incorporating knowledge of soil biodiversity into a broader spectrum of benefits that improve human health (see Box 2; ref. 89). Importantly, the Global Soil Biodiversity Initiative was established as an independent scientific effort to provide information on soil biodiversity to policymakers and is preparing to publish the first Global Soil Biodiversity Atlas in collaboration with the European Union Joint Research Centre. The Global Soil Biodiversity Initiative (https://globalsoilbiodiversity.org) is also working to have soil biodiversity considered in current international initiatives such as the Intergovernmental Platform on Biodiversity and Ecosystem Services and Future Earth.

Fortunately, there is increased recognition that developing effective management tools for soil biodiversity requires active information transfer between scientists and policymakers with new policies formed on current evidence-based knowledge and local cultural knowledge^{3,4}. However, we need to identify implementation mechanisms to encourage easier updates on best management practices and related policies to ensure long-term sustainable use of global lands under a changing global environment. This is particularly crucial given the rapid accumulation of new insights on how soil biodiversity can be managed to promote human health

We are losing soils and soil biodiversity at a rapid pace, with substantial negative ramifications on human health worldwide. It is time to recognize and manage soil biodiversity as an underutilized resource for achieving long-term sustainability goals related to global human health, not only for improving soils, food security, disease control, water and air quality, but because biodiversity in soils is connected to all life and provides a broader, fundamental ecological foundation for working with other disciplines to improve human health.

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- Bardgett, R. D. & van der Putten, W. H. Belowground biodiversity and ecosystem functioning. Nature 515, 505–511 (2014).
- Fisher, F. S., Bultman, M. W., Johnson, S. M., Pappagianis, D. & Zaborsky, E. Coccidioides niches and habitat parameters in the southwestern United States: a matter of scale. Ann. NY Acad. Sci. 1111, 47–72 (2007).
- 3. Wall, D. H. et al. Soil Ecology and Ecosystem Services (Oxford Univ. Press, 2012).
- 4. Wall, D. H. & Six, J. Give soils their due. Science 347, 695 (2015).
- Haddad, N. M. et al. Habitat fragmentation and its lasting impact on Earth's ecosystems. Sci. Adv. 1, e1500052 (2015).
- Tsiafouli, M. A. et al. Intensive agriculture reduces soil biodiversity across Europe. Glob. Change Biol. 21, 973–985 (2015).
 - This study, encompassing four agricultural regions across Europe, showed that increasing land-use intensity reduced soil foodweb diversity, functional diversity and taxonomic diversity.
- Garrison, V. H. et al. African and Asian dust: from desert soils to coral reefs. Bioscience 53, 469–480 (2003).
- Park, J. W. et al. Effects of ambient particulate matter on peak expiratory flow rates and respiratory symptoms of asthmatics during Asian dust periods in Korea. Respirology 10, 470–476 (2005).
- Quinton, J. N., Govers, G., Van Oost, K. & Bardgett, R. D. The impact of agricultural soil erosion on biogeochemical cycling. *Nature Geosci.* 3, 311–314 (2010).
- Schenker, M. Exposures and health effects from inorganic agricultural dusts Environ. Health Perspect. 108, 661–664 (2000).
- Dominati, E., Patterson, M. & Mackay, A. A framework for classifying and quantifying the natural capital and ecosystem services of soils. *Ecol. Econ.* 69, 1858–1868 (2010).
- Thiele-Bruhn, S., Bloem, J., de Vries, F. T., Kalbitz, K. & Wagg, C. Linking soil biodiversity and agricultural soil management. *Curr. Opin. Environ. Sustainability* 4, 523–528 (2012).

- 13. Nielsen, U. N., Wall, D. H. & Six, J. Soil biodiversity and the environment. Annu. Rev. Environ. Resour. 40, 63-90 (2015).
- World Health Organization and Secretariat of the Convention on Biological Diversity. Connecting Global Priorities: Biodiversity and Human Health. A State of Knowledge Review https://www.cbd.int/health/SOK-biodiversity-en.pdf (WHO,
- 15. Brevik, E. C. & Burgess, L. C. The 2012 fungal meningitis outbreak in the United States: connections between soils and human health. Soil Horizons 54, 1-4 (2013).
- Oliver, M. A. & Gregory, P. J. Soil, food security and human health: a review. Eur. J. Soil Sci. 66, 257–276 (2015).
- Ling, L. L. et al. A new antibiotic kills pathogens without detectable resistance. Nature 517, 455-459 (2015).
- Ferris, H. & Tuomisto, H. Unearthing the role of biological diversity in soil health. Soil Biol. Biochem. 85, 101-109 (2015).
- Brevik, E. C. & Burgess, L. C. Soils and Human Health (CRC Press, 2012).
- Bultman, M. W., Fisher, F. S. & Pappagianis, D. in Essentials of Medical Geology (ed. O. Selinus) Ch. 20 (Springer, 2013).
- Pepper, I. L., Gérba, C. P., Newby, D. T. & Rice, C. W. Soil: a public health threat or savior? Crit. Rev. Environ. Sci. Technol. 39, 416-432 (2009).
- Brevik, E. C. & Sauer, T. J. The past, present, and future of soils and human health studies. *Soil* **1**, 35–46 (2015).
- Myers, S. S. & Patz, J. A. Emerging threats to human health from global environmental change. *Annu. Rev. Environ. Resour.* **34**, 223–252 (2009). Berg, G., Eberl, L. & Hartmann, A. The rhizosphere as a reservoir for
- opportunistic human pathogenic bacteria. Environ. Microbiol. 7, 1673-1685
- Ganz, H. H. et al. Interactions between Bacillus anthracis and plants may promote anthrax transmission. PLoS Negl. Trop. Dis. 8, http://dx.doi. . org/10.1371/journal.pntd.0002903 (2014).
- Smith, K. L. et al. Bacillus anthracis diversity in Kruger National Park. J. Clin. Microbiol. 38, 3780-3784 (2000).
- Schär, F. et al. Strongyloides stercoralis: global distribution and risk factors. PLoS Negl. Trop. Dis. 7, http://dx.doi.org/10.1371/journal.pntd.0002288
- Khieu, V. et al. High prevalence and spatial distribution of Strongyloides stercoralis in rural Cambodia. PLoS Negl. Trop. Dis. 8, http://dx.doi. org/10.1371/journal.pntd.0002854 (2014).
- de Silva, N. R. et al. Soil-transmitted helminth infections: updating the global
- picture. *Trends Parasitol*. **19**, 547–551 (2003).

 Kay, A. B. Overview of "Allergy and allergic diseases: with a view to the future". Br. Med. Bull. **56**, 843–864 (2000).
- Matricardi, P. M. & Bonini, S. High microbial turnover rate preventing atopy: a solution to inconsistencies impinging on the hygiene hypothesis? Clin. Exp. Allergy 30, 1506-1510 (2000).
- Rook, G. A. W. 99th Dahlem conference on infection, inflammation and chronic inflammatory disorders: Darwinian medicine and the 'hygiene' or 'old friends' hypothesis. Clin. Exp. Immunol. 160, 70-79 (2010).
- Hanski, I. et al. Environmental biodiversity, human microbiota, and allergy are interrelated. Proc. Natl Acad. Sci. USA 109, 8334-8339 (2012).
 - This study provides evidence that people living near environmentally diverse areas had less propensity for allergies because of a greater diversity of commensal bacteria on their skin, most of which are also found in soil and vegetation.
- Haahtela, T. et al. The Finnish Allergy Programme 2008–2018—scientific rationale and practical implementation. Asia Pacific Allergy 2, 275-279 (2012)
- Ruokolainen, L. et al. Green areas around homes reduce atopic sensitization in children. Allergy 70, 195-202 (2015).
- Prichard, R. in Antimicrobial Drug Resistance (ed. Mayers, D. L.) 621-628 (Springer, 2009).
- Corbett, C. J. et al. The effectiveness of faecal removal methods of pasture management to control the cyathostomin burden of donkeys. Parasites Vectors **7,** 48 (2014).
- Epstein, L. Fifty years since Silent Spring. Annu. Rev. Phytopathol. 52, 377-402
- Campos-Herrera, R., El-Borai, F. E. & Duncan, L. W. in Nematode Pathogenesis of Insects and Other Pests (ed. Campos-Herrera, R.) (Springer, 2015).
- Charles, L. et al. Phylogenetic analysis of Pasteuria penetrans by use of multiple genetic loci. J. Bacteriol. 187, 5700-5708 (2005).
- Gray, N. F. Ecology of nematophagous fungi: *Panagrellus redivivus* as the target organism. *Plant Soil* **73**, 293–297 (1983).
- Stirling, G. R. in Biological Control of Plant-Parasitic Nematodes: Building Coherence Between Microbial Ecology and Molecular Mechanisms (eds Davies, K. G. & Spiegel, Y.) 1-38 (Springer, 2011).
- Stirling, G. R. Biological Control of Plant-Parasitic Nematodes: Soil Ecosystem Management Sustainable Agriculture 2nd edn (CABI, 2014).
- Costa, S. R., Kerry, B. R., Bardgett, R. D. & Davies, K. G. Interactions between nematodes and their microbial enemies in coastal sand dunes. Oecologia 170, 1053-1066 (2012).
- Ferris, H. et al. Diversity and complexity complement apparent competition: nematode assemblages in banana plantations. Acta Oecol. 40, 11-18 (2012).
- Sánchez-Moreno, S. & Ferris, H. Suppressive service of the soil food web: effects of environmental management. Agric. Ecosyst. Environ. 119, 75-87 (2007).

- This study showed that the prevalence of predator and omnivorous nematodes, which suppressed plant parasitic nematodes, was higher in soils with more complex foodwebs.
- Penton, C. R. et al. Fungal community structure in disease suppressive soils assessed by 28S LSU gene sequencing. PLoS ONE 9, http://dx.doi. org/10.1371/journal.pone.0093893 (2014).
- Weller, D. M., Raaiimakers, J. M., Gardener, B. B. M. & Thomashow, L. S. Microbial populations responsible for specific soil suppressiveness to plant pathogens. Annu. Rev. Phytopathol. 40, 309-348 (2002).
- Johnson, P. T. J. et al. Species diversity reduces parasite infection through cross-generational effects on host abundance. Ecology 93, 56-64 (2012).
- Johnson, P. T. J., Preston, D. L., Hoverman, J. T. & Richgels, K. L. D. Biodiversity 50. decreases disease through predictable changes in host community competence. Nature 494, 230-233 (2013).
 - This laboratory and field study showed that a richer host diversity reduced transmission of a parasite (the trematode Ribeiroia ondatrae) and reduced amphibian disease.
- Keesing, F., Holt, R. D. & Ostfeld, R. S. Effects of species diversity on disease risk. Ecol. Lett. 9, 485-498 (2006).
- Searle, C. L., Biga, L. M., Spatafora, J. W. & Blaustein, A. R. A dilution effect in the emerging amphibian pathogen Batrachochytrium dendrobatidis. Proc. Natl Acad. Sci. USA 108, 16322–16326 (2011).
- 53. Suzán, G. et al. Experimental evidence for reduced rodent diversity causing increased hantavirus prevalence. PLoS ONE 4, http://dx.doi.org/10.1371/ journal.pone.0005461 (2009).
- van Elsas, J. D. et al. Microbial diversity determines the invasion of soil by a bacterial pathogen. Proc. Natl Acad. Sci. USA 109, 1159-1164 (2012)
 - Experimental results showed that in soils with greater microbial diversity invading bacteria have a lower survival rate.
- Andersen, D. C. Belowground herbivory in natural communities—a review emphasizing fossorial animals. Q. Rev. Biol. 62, 261-286 (1987).
- Gehring, C. A., Wolf, J. E. & Theimer, T. C. Terrestrial vertebrates promote arbuscular mycorrhizal fungal diversity and inoculum potential in a rain forest soil. Ecol. Lett. 5, 540-548 (2002).
- 57. Bates, S. T. et al. Global biogeography of highly diverse protistan communities in soil. *ISME J.* **7**, 652–659 (2013). Wu, T., Ayres, E., Bardgett, R. D., Wall, D. H. & Garey, J. R. Molecular study of
- worldwide distribution and diversity of soil animals. Proc. Natl Acad. Sci. USA **108**, 17720-17725 (2011).
- Ramirez, K. S. et al. Biogeographic patterns in below-ground diversity in New York City's Central Park are similar to those observed globally. Proc. R. Soc. B 281, http://dx.doi.org/10.1098/rspb.2014.1988 (2014).
- 60. Lauber, C. L., Ramirez, K. S., Aanderud, Z., Lennon, J. & Fierer, N. Temporal variability in soil microbial communities across land-use types. ISME J. 7, 1641-1650 (2013).
- Tedersoo, L. et al. Global diversity and geography of soil fungi. Science 346, http://dx.doi.org/10.1126/science.1256688 (2014). This analysis indicates that the distribution and species richness of fungi is mostly determined by climate and not related to plant diversity on a global scale, except for root-related ectomycorrizal fungi; biogeographical comparisons of continents indicate efficient dispersal mechanisms for fungi
- compared to larger organisms. van Groenigen, J. W. et al. Earthworms increase plant production: a metaanalysis. Sci. Rep. 4, http://dx.doi.org/10.1038/srep06365 (2014).
- Evans, T. A., Dawes, T. Z., Ward, P. R. & Lo, N. Ants and termites increase crop 63. yield in a dry climate. Nature Commun. 2, http://dx.doi.org/10.1038/ ncomms1257 (2011).
- 64. Bender, S. F. & van der Heijden, M. G. A. Soil biota enhance agricultural sustainability by improving crop yield, nutrient uptake and reducing nitrogen leaching losses. J. Appl. Ecol. 52, 228-239 (2015).
- de Vries, F. T. et al. Soil food web properties explain ecosystem services across European land use systems. Proc. Natl Acad. Sci. USA 110, 14296-14301
- 66. de Vries, F. T. et al. Land use alters the resistance and resilience of soil food webs to drought. Nature Clim. Change 2, 276-280 (2012). This study compared nitrogen retention in extensive versus intensive grasslands and showed that species-rich extensively managed grasslands had greater soil nitrogen retention due to a higher fungal; bacterial abundance ratio compared to intensively managed grasslands.
- Wall, D. H., Bardgett, R. D. & Kelly, E. F. Biodiversity in the dark. Nature Geosci. 3, 297-298 (2010)
- 68. Rillig, M. C. & Mummey, D. L. Mycorrhizas and soil structure. New Phytol. 171, 41-53 (2006).
- Schulin, R., Khoshgoftarmanesh, A., Afyuni, M., Nowack, B. & Frossard, E. in Development and Uses of Biofortified Agricultural Products (eds Banuelos, G. S. & Lin, Z.-Q.) Ch. 6 (CRC Press, 2008)
- 70. Rodriguez, R. J. et al. Stress tolerance in plants via habitat-adapted symbiosis. ISME J. 2, 404-416 (2008).
- 71. Brown, J. K. M. & Hovmøller, M. S. Epidemiology—aerial dispersal of pathogens on the global and continental scales and its impact on plant disease. Science **297**, 537-541 (2002).
- Nkem, J. N. et al. Wind dispersal of soil invertebrates in the McMurdo Dry Valleys, Antarctica. Polar Biol. 29, 346–352 (2006).

RESEARCH PERSPECTIVE

- Madden, N. M., Southard, R. J. & Mitchell, J. P. Conservation tillage reduces PM10 emissions in dairy forage rotations. *Atmos. Environ.* 42, 3795–3808 (2008)
- Sprigg, W. A. et al. Regional dust storm modeling for health services: the case of valley fever. Aeolian Res. 14, 53–73 (2014).
- Nguyen, C. et al. Recent advances in our understanding of the environmental, epidemiological, immunological, and clinical dimensions of coccidioidomycosis. Clin. Microbiol. Rev. 26, 505–525 (2013).
- Tabor, J. A., O'Rourke, M. K., Lebowitz, M. D. & Harris, R. B. Landscapeepidemiological study design to investigate an environmentally based disease. J. Expo. Sci. Environ. Epidemiol. 21, 197–211 (2011).
- 77. Frey, S. D., Elliott, E. T. & Paustian, K. Bacterial and fungal abundance and biomass in conventional and no-tillage agroecosystems along two climatic gradients. *Soil Biol. Biochem.* **31**, 573–585 (1999).
- Six, J., Frey, S. D., Thiet, R. K. & Batten, K. M. Bacterial and fungal contributions to carbon sequestration in agroecosystems. *Soil Sci. Soc. Am. J.* 70, 555–569 (2006)
- Anderson, J. O., Thundiyil, J. G. & Stolbach, A. Clearing the air: a review of the effects of particulate matter air pollution on human health. J. Med. Toxicol. 8, 166–175 (2012).
 - This review provides an analysis of the complexity of particulate matter air pollution and its effects on human health.
- Nordstrom, K. F. & Hotta, S. Wind erosion from cropland solutions in the USA: a review of problems, and prospects. *Geoderma* 121, 157–167 (2004).
- Alavanja, M. C. R., Ross, M. K. & Bonner, M. R. Increased cancer burden among pesticide applicators and others due to pesticide exposure. CA Cancer J. Clin. 63, 120–142 (2013).
- 82. Frankenberger, W. T. & Arshad, M. Bioremediation of selenium-contaminated sediments and water. *Biofactors* **14**, 241–254 (2001).
- Abraham, J. & Silambarasan, S. Biodegradation of chlorpyrifos and its hydrolyzing metabolite 3,5,6-trichloro-2-pyridinol by Sphingobacterium sp JAS3. Process Biochem. 48, 1559–1564 (2013).

- Rayu, S., Karpouzas, D. G. & Singh, B. K. Emerging technologies in bioremediation: constraints and opportunities. *Biodegradation* 23, 917–926 (2012)
- Bailey, R. T., Romero, E. C. & Gates, T. K. Assessing best management practices for remediation of selenium loading in groundwater to streams in an irrigated region. J. Hydrol. 521, 341–359 (2015).
- Tiemann, L., Grandy, A., Atkinson, E., Marin-Spiotta, E. & McDaniel, M. Crop rotational diversity enhances belowground communities and functions in an agrosystem. *Ecol. Lett.* 18, 761–771 (2015).
 Chauvat, M., Titsch, D., Zaytsev, A. S. & Wolters, V. Changes in soil faunal
- Chauvat, M., Titsch, D., Zaytsev, A. S. & Wolfers, V. Changes in soil faunal assemblages during conversion from pure to mixed forest stands. For. Ecol. Manage. 262, 317–324 (2011).
- Cary, S. C. & Fierer, N. The importance of sample archiving in microbial ecology. Nature Rev. Microbiol. 12, 789–790 (2014).
- Jeffery, S. & van der Putten, W. H. Soil-Borne Human Diseases 1–56, http://dx. doi.org/10.2788/37199 (Joint Research Centre Scientific and Technical Reports, European Commission, 2011).
- United Nations Sustainable Development Goals. Open Working Group Proposal for Sustainable Development Goals, https://sustainabledevelopment. un.org/focussdgs.html (UN, 2014).

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