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Soil microbiomes and one health

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Title: **Soil Microbiomes and One Health**

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Abstract

The concept of one health highlights how human health is not an isolated component but is connected to the health of animals, plants, and environments. Here we demonstrate that soils are a cornerstone of one health and serve as a source and reservoir of pathogens, beneficials and the overall microbial diversity in a wide range of organisms and ecosystems. We list over 40 soil microbiome functions that either directly or indirectly contribute to soil, plant, animal, and human health. We identify microbes that are shared between different one-health compartments and show that soil, plant, and human microbiomes are perhaps more interconnected than previously thought. Our review further evaluates soil microbial contributions to one health in the light of dysbiosis and global change and demonstrates that microbial diversity is generally positively associated to one health. Finally, we present future challenges in one health research and formulate recommendations for practice and evaluation.

The one health premise highlights that the health and well-being of humans are inseparably linked to the health of other ecosystem components such as soil, plant, and animals (**Box 1**). We are gradually realizing that microbes are the critical conduit in one health because they inextricably connect each of these components, and the health of ecosystems heavily relies on the contribution of microbial communities[7]. A wealth of studies now demonstrate that microbial communities inhabiting plants, animals and humans act as a second genome[8], an extended genotype[9] or an eco-holobiont[10], and thus drive the fitness and performance of almost all organisms on Earth. A growing number of studies also suggest that microbial communities of different organisms are interconnected and form a circular loop[11]. Until now, the one health research landscape has been dominated by studies on microbial pathogens responsible for zoonotic diseases[12]. While the importance of pathogens is undeniably true, recent advancements in omics and statistical approaches have demonstrated that the microbiome associations go beyond just pathogens, and microbial symbionts, commensals, ammensals and the overall diversity have important implications for one health[7]. However, compared to plant, animal and human health, the appreciation for the soil microbiome and soil health remained understudied among one health researchers until now[3,13,14].

In this article, we discuss the importance of soil microbiomes for one health by highlighting the contribution of soil microbial communities to plant, animal, and human health. We assess how soils can be the source of microbiomes for other ecosystem components and we identify a set of microbial taxa that are shared between the different one health components. We then discuss various environmental factors that regulate soil microbial contributions to one health. We evaluate such contributions in the light of environmental perturbations and dysbiosis and discuss how soil microbiomes can respond to such changes. Finally, we present future challenges in one health research and formulate recommendations for practice and evaluation.

Soil as a potential source of microbiomes

Microbes are overwhelmingly abundant in soils, and after plants, microbes residing in the soil and deep surface represent the largest fraction of global biomass on Earth. Bacteria are the most abundant (15% of the total living biomass), however, the biomasses of fungi (2%) and Archaea (1%) are also larger than that of the animals (0.3%)[15]. Soils also harbor the most diverse and complex microbiome on earth with over 2500 ug of microbial biomass and >50,000 species per gram [16–18]. Bacteria and fungi are generally the dominant groups of microbes in soil with more biomass than protists and archaea[15]. Moreover, a gram of soil can also contain 10^7-10^9 virus particles[18]. Thus, from a source-sink perspective[19], one can consider soil as a major source of microbiomes on terrestrial ecosystems and thus, the foundation of one health (**Figure 1**). For example, specialized members of soil microbial communities assemble in the plant rhizosphere and get preferentially recruited into the roots, and as a result, plants receive a subset of the soil microbiome[20]. Estimates indicate that bulk soil is the most significant contributor to plant endophytic microbiota, contributing over two thirds of the bacterial and fungal diversity[21,22]. However, vertical transmission of plant growth promoting bacteria through seeds can also be an important factor[23,24] (see below). Indeed, a range of studies have shown that species specific microbiomes are common in plants[25,26]. Pie charts show the dominant phyla of each microbiome compartment (soil, plant, animal, human) (**Figure 1**). The composition is based on a synthesis of several studies conducted in the Midwest region of USA (Banerjee et al, unpublished) and the major phyla were consistent with other studies[18,27–29]. Overall, soil microbiome is the largest contributor of plant endophytic microbiota.

Geophagy, a deliberate consumption of soil or clay, is also common among animals. Sheeps, gorillas, bats, parrots are a few examples of geophagia in the animal world[30]. Biodiverse soils may also contribute commensal microbes to the animal gut microbiota[31,32]. Knowingly or unknowingly, farm animals also consume a significant amount of soil. For examples, it has been found that grazing sheep can consume up to 400 g of soil per kg of body weight[33]. For dairy cows, this number can be staggeringly high as they can consume up to 350 kg of soil per cow per year[34]. Estimates suggest that up to 3% of the rumen microbiome of sheep and cattle can be contributed by the ingested soil[35]. The skin microbiome composition of farm animals is indeed linked to the soil microbiome with *Arthrobacter* and *Sphingomonas* as the indicator taxa [36]. A recent study has found that dust microbes are associated with farm performance in commercial poultry [37]. Bacterial groups belonging to *Enterococcus* and *Candidatus Arthromitus* were linked to high-performing farms whereas groups belonging to *Nocardia*, *Lapillococcus*, *Brachybacterium*, *Ruania*, *Dietzia*, *Brevibacterium*, *Jeotgalicoccus, Corynebacterium* and *Aerococcus* were linked to low-performing farms. However, in cattle farms, soils can also be a recipient of the influx of the antibiotic resistance genes from the rumen microbiome [38].

Human geophagy has also been reported in many parts of the world including Asia, sub-Saharan Africa, Latin America and Pacific Islands[3940]. It is an epiphenomenon of nutrient deficiency whereby mineral and trace element rich soils are consumed by pregnant women as a prenatal dietary supplement [39]. Clay loam soil is negatively linked to the nasal microbiome diversity but positively associated with the rectum microbiome diversity [41]. Furthermore, soils with high cation exchange capacity often have higher nutrient content, leading to a higher soil microbial diversity, which has been linked to reduced risk of hospitalization for infectious and parasitic diseases in Australia [42]. Pet dogs and cats can regularly bring soil-associated microbes to built environments, resulting in exposures of their owners and other inhabitants [36]. Furthermore, the oral, nasal and skin microbiomes of farmworkers are linked to soil microbiome composition of their farms [43,44]. Overall, the soil microbiome can be a major contributor to microbial communities in other organisms and act as the foundation of one health. The following section will specifically discuss soil microbial contributions to various components of one health.

Soil microbial contributions to one health

Soil is the largest reservoir of microbial diversity on earth. Such an incredibly diverse microbial community can have direct and indirect influences on soil, plant, animal, and human health and wellbeing.

Soil health

Healthy soils are an invaluable resource for sustainable ecosystems and an important driver of one health. Soil health is the capacity of soil to function as a vital living system, to sustain plant and animal productivity, maintain or enhance water and air quality, and promote plant and animal health[45]. The quality and health of soils are intricately linked to global food and water security, and have important implications for energy security and climate change mitigation[46,47]. In recent years, the degradation of soils due to land use change, erosion, compaction and pesticide contamination has highlighted the urgent need of caring for soil's capacity to sustain ecosystem services[48]. Consequently, researchers are increasingly realizing that the role of microbial communities must be understood and incorporated to safeguard and enhance soil health[49] and there is a growing interest in the practices that can maintain healthy soils. For instance, several studies have shown that crop diversification[50,51], a reduction of synthetic pesticides[52,53], mineral fertilizers[35,42] and intensive tillage[54] can improve soil biodiversity and soil health.

Soil microbial communities play a pivotal role in ecosystem services and can have direct and indirect influences on a multitude of processes including nutrient cycling, organic matter dynamics, soil structure, carbon transformations and sequestration (**Table 1**). For example, the soil is the world's largest terrestrial pool of carbon, and a growing body of research suggests that microbial communities play an important role in soil carbon stability [86,87]. It has been reported that microbial biomass is not as labile as previously thought and fine-fraction stable organic matter can be of microbial origin[61,88]. Microbial biomass, complexity and presence of key microbial groups are associated with the stable pool of soil carbon, making microbial parameters essential for our predictive understanding of soil carbon sequestration[88,89]. Not only carbon, soil microbes are the critical determinants of other biogeochemical cycling including nitrogen, phosphorus, sulfur and iron, which have direct implications for all of the components of one health[17,18,90–92]. However, while the physical and chemical indicators of soil health have been emphasized in the literature, the soil biological indicators have received little or no recognition[45,47]. Furthermore, the current perception of microbial contribution to soil health is overly simplistic as studies often considered indices such as the overall microbial biomass, fungi:bacteria ratio or soil enzymes. Two recent articles have provided several recommendations and examples of microbial indices that can be employed in soil health assessment[47,49]. These include pathogen occurrence, the abundance of pathogenicity genes, overall microbial diversity, and specific soil functional groups as indicators of soil health characteristics.

Plant health

The contribution of soil microbes to plant health is indisputable and it serves as a cornerstone of terrestrial ecosystem functioning. Out of the approximately 29 essential elements for plants, 18 are obtained from the soil, and soil microbial communities play a central role in delivering these elements to plants[85]. Plants preferentially recruit microbes from the rhizosphere that are essential for their growth and development, and thus, plants receive a subset of the soil microbiome. Soil microbes can play a critical role in shaping the structure, composition and functioning of plant-associated microbiota. The rhizosphere microbiome strengthens the metabolic repertoire of plants and facilitates a range of processes including seed germination, seedling establishment, nutrition, water uptake, growth promotion, pathogen suppression, stress tolerance, and hormone regulation (**Table 1; Figure 2**)[8,29,68,73]. Up to 80% of plant nitrogen and 90% of plant phosphorus is acquired by microbes[16]. Even in intensively managed ecosystems, soil microbes can have a large impact on plants. For instance, legumes are well known for their ability to associate with nitrogen fixing bacteria, providing over 300 kg nitrogen per hectare and year[17,18,67]. Indirectly as well, microbes in the rhizosphere can influence critical functional traits including leaf area, leaf longevity, leaf nutrient levels and shoot:root ratio[74]. Bacteria such as *Rhizobium, Arthrobacter, Bacilus, Alcaligens, Rhodococcus, Methylobacterium, Pseudomonas,* and *Azospirillum* are known for their roles in plant nutrition, growth promotion, hormone regulation and stress control. One of the most well-known examples of plant beneficial microbes are the mycorrhizal fungi that form symbiotic associations with nearly 90% of land plants, including many crops[73]. Mycorrhizal fungi are recruited from the soil and colonize plant roots following an intricate molecular exchange. Mycorrhizae confer a wide array of benefits to the host plants[93]. For example, plants obtain water and essential micro and macro nutrients from mycorrhizal fungi and supply up to one fourth of their photosynthates in return[94]. The growth of a wide range of crops can be enhanced by mycorrhizal fungi and growth increases of up to 50% have been reported[95]. Field inoculation with mycorrhizal fungi can substantially promote plant yield, although effects are highly variable[96] and many commercial inoculants are of insufficient quality[97]. Fungi such as *Trichoderma* spp. or the endophytic fungus, *Piriformospora indica* are other examples of a beneficial microbes that can promote plant growth, stress tolerance and/or induce local and systemic resistance to pathogens [48,98]. Soil protists can also have a strong impact on plant nutrient availability and plant health by grazing on pathogenic microbes and stimulating mineralization[99]. However, not all soil microbes promote plant health and there are numerous soil-borne pathogens such as *Ralstonia, Rhizoctonia, Fusarium, Phytophthora, Gaeumannomyces* that cause deadly outbreaks in plants[59,72,100]. Numerous in-depth reviews are available on both beneficial and pathogenic microbes in the rhizosphere[8,74,101–103]. By promoting plant growth and seedling survival, microbes also contribute to the establishment and maintenance of green roofs and urban agriculture, which also creates a pleasant and healthy environment[104]. It is important to note that microbes do not act in isolation and an increasing number of studies demonstrate that a “systems” approach is required to understand microbiome functioning. For instance, microbial consortia, rather than individual microbes, may better explain the impact of microbiomes on plant growth and nutrient uptake[105], nitrogen use efficiency[106], pathogen success[84], and overall on the ecosystem multifunctionality[107]. In line with this, selective soil microbiome recruitment by plants has been found to be the key for plant survival[74], nitrogen use efficiency[106]and plant fitness[108].

Disease suppressive soils

Disease suppressive soils are one of the finest examples of soil microbiome-conferred protection of plants against soil-borne pathogens[63]. Disease suppressive soils are soils that due to their microbiome composition and activities do not allow pathogens to establish, or even if the pathogen establishes, it can only cause little or no damage [63,64]. Disease suppressiveness can persist in soil for more than 40 years even in the presence of soil borne pathogens[64]. Specific microorganisms can also confer disease suppressiveness, and an example is siderophore producing *Pseudomonas spp.* that can suppress the take-all by *Gaeumannomyces graminis var tritici* and wilt disease by *Fusarium* spp[109]. Interestingly, suppressiveness can also occur due to parasitic fungi such *Trichoderma* and *Verticillium* that are parasitic to potent fungal pathogens such as *Sclerotinia sclerotiorum* and *Rhizoctonia solani*[110]. Thus, disease suppressive soils may offer a plausible biocontrol solution and future studies need to assess how soil microbiome engineering can promote disease suppressiveness by inoculating specific microbes or altering soil management. While disease suppressive soils have been assessed for agricultural systems, we have limited knowledge about the prevalence of disease suppressiveness in native ecosystems. For example, future studies may wish to investigate if natural soils that are considered healthy, have greater disease suppressiveness. A relevant question is whether the heterogeneity of pathogens in natural soils increases the inoculum potential in the permanent or semi-permanent systems[111].

Animal and insect health

Beneficial roles of soils

Soil microorganisms also have beneficial roles in animal and insect health (**Table 1; Figure 2**). The soil environment can serve as a source of animal microbiomes and microbes that animals ingest through food (e.g., plants or other animals) finally originate from the soil. Many insects require endosymbionts such as various *Burkholderia* clades for their growth and survival[112]. These endosymbionts are not only transmitted vertically from parents to offspring, but an increasing number of studies show that insects acquire these microbes by feeding on plants or from the soil. For example, a recent study has demonstrated that foliar-feeding insects acquired microbiomes from the soil rather than the host plant, indicating that microbiome transmission in soil-plant-herbivore foodwebs may be widespread[113]. It has also been shown that insects can acquire soil microbes that depolymerize insecticides, making themselves insecticide-resistant[114]. Such findings indicate that there is an evolutionary benefit for imprecise vertical transmission and microbiome fidelity to acquire new microbes and enable adaptation to constantly changing environmental conditions[115]. Soil microbes can also directly act as food. Nematodes, one of the most abundant groups of soil fauna on earth, thrive on their bacterial and fungal preys[78]. Soil microbiomes can even influence the health and social behavior of soil-dwelling macroorganisms. For example, a recent study found that the abundance of butyrate-producing bacteria *Kineothrix alysoides* in the soil microbiomes was correlated to reduced anxiety in mice[31]. Similarly, exposure to soil can reduce allergic inflammation and have a positive influence on the gut-lung axis in mice[32]. Thus, a diverse soil microbiome can have positive implications for the gut health and mental health of soil dwelling mammals. However, to what extent the members of the soil microbiome can be found higher up in the food chain is poorly understood. For example, a substantial fraction of the microbiome in plants is acquired from the soil microbiome[116], but what fraction of this finally ends up in herbivores or carnivores is less clear. Also, while it is well known that microbiome composition influences animal health both directly or indirectly[80], it is still unclear how animal health might change in response to changes in the soil microbiome, i.e., when animals are fed with more diverse food or when they are grazing in more diverse environments.

Soil-borne animal pathogens

Animal diseases can also directly develop from infection sources in soil. Transmission may occur through the disintegration of infected carcasses, which can be contracted by the animals grazing nearby[117]. Soil-borne diseases in animals include nocardiosis, anthrax, malignant oedema, and blackleg[75,118]. Nocardiosis is a zoonotic disease in a range of animals including cats, dogs, guinea pigs and cattle. The disease is caused by a soil-borne actinomycete *Nocardia* and it involves localized or disseminated infection of the pulmonary tract[75]. While this could be a self-limited and transient infection, in adverse cases, it could also lead to tuberculous or a malignancy. Similarly, malignant oedema is an exogenous infection in sheep and other animals caused by soil-borne *Clostridium spp*[118]*.* There are also other deadly diseases such as ornithosis or psittacosis in birds, which are caused by soil-borne *Chlamydophila*[85].

Human health

Soils can influence human health and society in a multitude of ways, and thus, human health is intimately connected to soil health (**Table 1; Figure 2**). Humans are known to deliberately ingest soils as a supplement to their nutrient-poor local diet[40,83]. It is also common to use soils as detoxifying agents for making some food products edible, as well as for medicinal reasons such as gastrointestinal treatments[119]. Furthermore, people with more exposure to natural environments are less likely to suffer from allergic reactions, which may be linked to soil microbiomes[120] and when they inhale soil particles. The western lifestyle accompanying small family size, optimum hygiene, high antibiotic use, and urban homes is increasing around the world, and this has been linked to unwanted allergic responses, asthma, atopic dermatitis, and hay fever[121]. The increase in allergic responses has also been described with the biodiversity hypothesis which suggests that less contact with environments and microbial biodiversity results in insufficient stimulation of immunoregulatory circuits in people[120]. On the other hand, growing up in farming environments protects children from allergic sensitivity and asthma, which has been described as the 'hygiene hypothesis[122]. Together these hypotheses highlight the importance of natural environmental microbiomes for human health. Whether specific microbial groups are responsible for this remains unclear and this is an area that deserves more research attention. For example, identification or isolation of microbes or microbial consortia that are potentially responsible for increased resistance to allergies and disease are highly relevant. Soil microorganisms can also directly act as food. For instance, truffles, a fruiting body of some subterranean Ascomycetes fungi, is a highly prized food in modern gastronomy. Similarly, the entomopathogenic fungus *Ophiocordyceps sinensis*, a parasite of Himalayan caterpillars, is used for traditional medicine. This fungus has become one of the world’s most valuable biological commodities, having a per kg value three times higher than gold[123].

Humans also obtain several essential elements from plant-based food consumption and soil microbiomes not only regulate the cycling of those elements but also the health of all plants. For instance, arbuscular mycorrhizal fungi are known to deliver a range of trace elements to plants including, zinc and selenium, which are important for human health[94]. Furthermore, humans can only synthesize half of the essential amino acids themselves and they depend on food intake for the remaining amino acids as well as all of the essential vitamins[124]. Beyond the primary metabolites, plants only produce small amounts of secondary metabolites, but beneficial microbes associated with them can further enhance their production. For example, soil microbes can promote the production of important secondary metabolites (Omega-3 (n-3) polyunsaturated fatty acids, linoleic acid, L-carnitine, choline or sphingomyelin) by plants, which can subsequently be beneficial to animal and human health[124]. Additionally, food security is central to human health and well-being, and soil microbiomes are at the forefront of this provisioning service. Healthy soils are linked to good structure, optimum nutrients, and organic matter levels, which are important for construction and development. A wide range of environmental processes and soil ecosystem services including purification of drinking water, construction materials, carbon storage, and the production of greenhouse gases (production of nitrous oxide and methane) [43] are mediated by soil microbes, which have implications for human health. Indeed, soil microbiomes have a demonstrable impact on plants and animals consumed by humans and by doing so, soils indirectly influence human health.

Soil borne human pathogens

Not all microorganisms in soil are harmless and there are countless soil-borne pathogens that can be harmful to human health. There are over 300 soil fungi species that are known to cause disease in humans[82]. Coccidioidomycosis, also known as valley fever, is caused by the fungus *Coccidioides spp*. commonly found in soils of southwestern USA and Mexico[81]. Moreover, *Exserohilium rostratum* was responsible for the 2012 fungal meningitis outbreak in the USA[82]. Some protists can also cause human parasitic diseases such as diarrhoea and amoebic dysentery. Helminthiasis is a parasitic intestinal infection triggered by skin penetration by hookworm larvae in soil[59]. It affects millions of people and causes over 100,00 annual deaths worldwide. Soil can also be a source of *Bacillus anthracis*, the causal agent of anthrax in humans[59]. Another deadly disease is podoconiosis or chronic debilitating non-filarial elephantiasis caused by nematodes that affects 1 to 2 million people and results in chronic inflammation. In rare cases, tetanus can occur due to wound contamination with soils containing spores of *Clostridium tetani*[85]. Escherichia coli O157:H7 can persist for more than 90 days in soil[125]. This deadly pathogen causes 73,000 illnesses only in the USA annually[126]. There are also many facultative and opportunistic human pathogens that can thrive in soils[127]. It is concerning that many of such pathogens in soils can be multi-resistant including a range of enterobacteria[128]. While there are reports of human diseases from soil-borne pathogens, it is unclear what proportion of the human microbiome is directly or indirectly linked to the soil microbial reservoir. For a range of pathogenic fungi, it is known that they require alternate plant species to survive and reproduce[129]. Whether this is also the case for members of the human microbiome remains a speculation.

Factors governing soil microbial contributions to one health

Edaphic factors

Soil habitat properties have been shown to act as the proximal control of soil microbiome composition and functioning (**Figure 3**). For example, soil temperature, pH, moisture, redox status, organic carbon content, and spatiotemporal heterogeneity are the major drivers of soil microbial communities, with feedback to their contributions to ecosystem processes and one health[17,18]. Soil moisture and temperature exert overarching effects on microbial communities both directly by controlling their distribution and activities. One of the most well-established edaphic factors is soil pH. A myriad of studies have shown that soil pH is a key predictor of microbial community structure and composition at field- to continental scales[130,131]. Even when a wide range of soil properties were studied, pH emerged as the strongest predictor. Important microbial groups such as *Acidobacteria, Bacteroidetes* and *Actinobacteria* display predictable patterns across pH gradient in soil[130]. A range of recent microbiome studies have shown that soil pH drives, directly and indirectly, the effects of soil microbial communities on plant growth, ecosystem- or soil multifunctionality[132]. For instance, the ability of mycorrhizal fungi to forage for nutrients and deliver them to plants is directly linked to soil pH[52,133]. Interestingly, the reduced ability of mycorrhizal fungi to acquire nutrients at low soil pH is not only determined by soil pH but it is also linked to the dominance of specific bacteria with putative anti-fungal properties (e.g. specific Acidobacteria) that are more dominant at low soil pH[133].

Another important driver of soil functioning is the soil organic matter (SOM) content. SOM has an overall positive effect on soil microbial diversity and community composition (e.g., soil microbial biomass is strongly correlated to soil organic carbon content[88]), with direct positive feedback for soil microbial contributions to one health. This is because SOM not only offers carbon resources for microbial populations, and it is also linked to the cycling and availability of other nutrients[134]. Needless to mention, SOM also has a direct effect on soil structure, oxygen and water availability[135] The link between soil microbial diversity and soil or ecosystem multifunctionality is not necessarily linear, and recent studies have reported tipping points and thresholds in microbiome functioning and performance. A recent study showed a strong positive association between plant species richness and soil multifunctionality in less arid regions, whereas microbial diversity, in particular of fungi, is positively associated with multifunctionality in more arid regions[136]. However, such findings are not surprising since soil moisture availability is known to have an overarching effect on plant growth and microbial functioning[18].

Global change factors

Global change factors directly threaten microbial contributions to ecosystem services[137] and one health (**Figure 3**). Scientists across the world have recently issued a warning to understand the threat of climate change to soil microorganisms and how it could cause negative feedback[56]. One of the strongest consequences of global climate change is increasing occurrences of drought. Recent studies have shown that the decline of ecto-mycorrhizal fungal symbionts of trees due to warming and drought can cascade belowground and accelerate soil organic matter decomposition, reduce soil organic carbon content and alter ecosystem biogeochemistry[138]. Unlike drought, the effect of elevated CO_2 can be more convoluted and rising CO_2 can differentially alter microbial ecophysiological strategies with divergent effects on different functional groups. Another potent global change factor is rising temperature. For instance, it has been recently found that the proportional abundance of soil-borne pathogens may increase with rising temperature[139], altered humidity and precipitation[140]. Consequently, warming and altered humidity may enhance plant disease due to a microbial loop. However, context-dependency is a major factor here as some soil ecosystems (e.g., arctic and alpine) may respond more strongly than others. Moreover, it is important to consider that climate change may influence the eco-evolutionary interactions between the host and its microbiome with some associations becoming stronger while others may weaken[141]. A recent meta-analysis of 1235 global change experiments found that the net effects of global change factors (warming, elevated CO2, drought, fertilization and land use change) on microbial alpha diversity are highly variable with rare microbes more strongly affected by global change than the dominant taxa[142]. These findings are important because several studies have shown that rare microbes drive pivotal ecosystem functions[143] contribute to ecosystem multifunctionality[144].

Antimicrobial Resistance

Soil microbial communities and their contributions to one health are further threatened by chemical pollution with novel entities including microplastics[145] antibiotics[146] and pesticides (see below). While antibiotics are the foundation of global health, over 700,000 people die annually from antimicrobial resistant infections with a projection up to 10 millions by 2050[66,147]. It is concerning that as much as 32 tons of third- and fourth generation antibiotics are annually used in meat and dairy industries[65]. Such large use of antibiotics has led to the spread of antimicrobial resistance (AMR) genes and soil is one of the sinks for AMR. For instance, AMR genes can be detected 90 days after application in soils and can be transferred from manure amended soils to vegetables[148]. However, soil is also a natural source of a wide range of antibiotic resistance genes[149], used by microbes for survival and chemical warfare against competing microbes. Thus, while antibiotic resistance has a detrimental impact on human health, it is unclear whether it affects soil health because in many cases the presence of AMR genes in microbes do not necessarily enhance their survival in the soil environment (where usually no antibiotics are applied) nor do such genes influence important soil functions.

Land Use Intensification

Land-use intensification is a major anthropogenic factor of the 21st century that alters the local biodiversity and affects ecosystem processes[150,151]. The total area of cultivated land worldwide has increased over 500% in the last five decades with a 700% increase in fertilizer use and a several-fold increase in pesticide use[152]. Such intensive practices can reduce the diversity and complexity of microbiomes and negatively influence beneficial microbes in roots and soils[54,153–155]. Land-use intensification can cause a homogenization of soil microbial communities with dominance of a few taxonomic and/or trophic groups and a decrease in the overall diversity[156,157]. Fertilizer use and management type has a large impact on the soil microbiome and this in turn can influence a range of agroecosystem functions, partly mediated by changes in the microbiome[158]. An additional factor is the overuse of pesticides and plant protection products. These chemicals play an important role in conventional agriculture by controlling pests, weeds, and plant diseases. However, the use of such agrochemicals has increased over 40% in recent years, with as much as 1.2 million tons of active pesticide ingredients used annually[159]. A recent comprehensive study found that pesticides are widespread in soils[160] and residues can be detected even after 20 years of organic management that does not apply any synthetic pesticides[161]. While the effects of pesticides on soil microbes can be variable, a recent study found that pesticide residues had negative associations with the overall microbial biomass[149] and impair the nutrient uptake machinery of beneficial mycorrhizal fungi[52]. Thus, the overuse of pesticides poses a major threat to soil health, and soil microbial contributions to one health.

One Health, dysbiosis, and soil microbial diversity

Soil microbial diversity can influence one health in various ways **(Box 2)**. A range of studies has revealed that soil microbial diversity is positively linked to various components of one health, including aspects of soil[84], plant[25], and ecosystem[162] health. The positive effect of soil microbial diversity is explained by the fact that different microbes provide different functions. Moreover, the resistance of soil microbiomes to disturbance is expected to increase with microbial diversity i.e., some groups that are susceptible to perturbations may be replaced by new groups with similar functions and as a result, the microbiome would be performing at a similar level to its original state, albeit with a new composition when microbial diversity is high. In line with this, the disruption of microbiome homeostasis (i.e., dysbiosis) can cause impaired soil[107], plant[163] and human[164] health and this is often linked to reduced microbial diversity, indicating the importance of biodiversity. It is important to note that the link between soil microbial diversity and one health can vary depending on the habitat or species composition, and various relationships can emerge including microbial facilitation, alternative stable states, and no relationships **(Box 2).**

Outlook

In this review, we highlight that one health is woven by microbial health because the health of each of its components is determined by microbes. We propose that the soil may be a reservoir of microbes that determines the plant, animal, and human microbiome. We demonstrate that soil microbiomes, directly and indirectly, influence plant, animal, human and environmental health, and thereby one health. There are several important areas in one health research that require further elucidation.

Firstly, recent studies have shown that land-use intensification[156], urbanization[172] and landscape simplification[157] cause homogenization of the soil microbiome and reduce soil microbial diversity. Whether sites with impoverished soil microbiomes are less resistant to invasion by pathogens or can act as a reservoir or survival zone of pathogens or antibiotic-resistant bacteria require further investigation. Recent observations that soil microbiomes in urban sites contain more antibiotic resistance genes and genes associated to human pathogens[172] point in this direction. Moreover, animal livestock consumes the majority of the world’s antibiotics[173], and it is well known that this is a key source of antibiotic-resistant bacteria that can be distributed via seepage or manure to the environment. Future studies should explore how targeted soil management practices can help reduce the establishment and abundance of antibiotic-resistant bacteria.

Secondly, viruses may play a much more important role in soil communities than previously thought. A recent study measuring carbon flows with isotopically labelled plants, demonstrated that the most heavily labeled organisms in the rhizosphere ended up being two phages[174] and soils can act as reservoirs of substantial undescribed viral genetic diversity with viruses likely to be adapted to major microbial lineages[175]. How widespread viruses are in soils and to what extent they influence soil microbiome functioning, are still unclear. A first rough estimate suggests that 1.7 million viruses exist only in animals[176], but this number could even be higher considering the abundance of potential (microbial as well as invertebrate) hosts, including those living in soils. Another important question is how long plant, animal, or human viruses, can survive within the soil microbiome. Recent developments in sequencing approaches have made it possible to investigate the role of viruses in unprecedented detail. An assessment of whether soils can act as a reservoir of pathogenic viruses is a key priority for one health research.

Thirdly, chemical pollution is widespread[145] and it is not well understood how microbiomes are affected and whether this in turn affects to human or ecosystem health[177]. Moreover, the soil microbiome is simultaneously exposed to many chemical contaminants including antibiotics, micro-plastics, heavy metals, and pesticides. A recent study performed in small microcosms demonstrated that multiple stresses can impair soil functioning much more strongly than single stresses[137]. This area needs more attention and future studies should investigate how multiple abiotic stresses impair soil microbiome functioning and whether such stresses enhance the role of soils as a source of pathogens[178].

Fourth, it is still unclear whether impoverished microbial communities are less resistant to invasion by microbial pathogens or act as sources and vectors of microbial contamination[179]. Previous studies reported that pathogen invasion is hampered when soil microbial diversity is high[84]. Enhancing microbial diversity through targeted practices that are known to promote soil health and microbial diversity (e.g., crop cover, crop diversification, and reduced agrochemical use) may provide solutions and this area needs further investigation.

Fifth, a large number of studies sequenced and described the microbiome from a wide range of habitats. A next frontier is to understand microbiome processes and identify and isolate microbes (e.g., microbial consortia) important for soil, plant, animal, and human health. The relative importance of horizontal and vertical transmission is also an important question. For example, in plant microbiome research, future studies with a range of host species can show whether horizontal transmission via soil and the environment or vertical transmission through seeds is the major pathway for plant microbiome assembly. Scientists often focus on specific research areas and individual domains of life, and this is particularly true for the soil microbiome as most studies only focus on either bacteria, fungi or protists. Future studies interested in the role of soil microbes in one health, should not only consider different groups of soil microbiota, but also consider their associations with other groups including viruses, nematodes, earthworms, and soil arthropods.

Finally, while the state of aboveground biodiversity is easy to monitor and already assessed in many countries, underground processes are much more intricate and far less understood[180]. In view of the importance of the soil microbiome in determining the one health components (plant, animal, human and ecosystem), we recommend that governments initiate and support systematic monitoring tools to investigate the trends, threats, and long-term developments of the soil microbiome.

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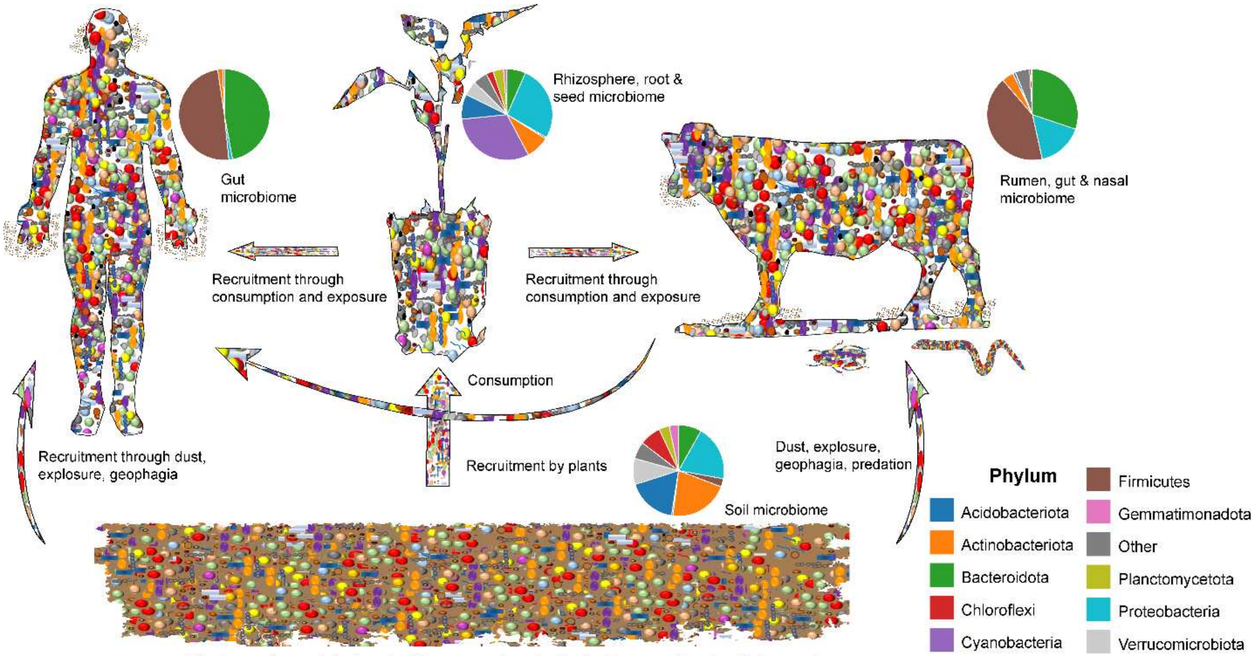
Figure 1: Microbes are the critical conduit that binds soil health, plant health, animal health and human health. Health conditions of all organisms in an ecosystem are interconnected through microbial communities. Soil harbors the most diverse and complex microbiome on earth and thus, can act as a microbial reservoir. Bulk soil is likely the largest contributor to plant endophytic microbiota, contributing over two thirds of the bacterial and fungal diversity. Diets play a major role in shaping the gut microbiome composition of both humans and animals. Based on the plant consumption, subset of plant microbiota that was originally derived from soil, could also make its way to the human and animal gut microbiome. Farmers or farm animals are regularly exposed to soils, and we also inhale soil particles, including soil microbes, through dust. Geophagy, a deliberate consumption of soil or clay, is common among animals and humans. Sheeps, gorillas, bats, parrots are a few examples of geophagia in the animal world. Human geophagy is also not uncommon. The thickness of the arrows suggests the potential strength of the associations. Pie charts show the top ten dominant phyla of each microbiome (soil, plant, animal, human). The composition is based on a synthesis of several studies in the Midwest region of USA (Banerjee et al, unpublished).

Figure 2: Soil microbiomes can have direct (solid arrows) and indirect (dotted arrows) influences on soil, plant, animal, and human health. Soil microbial communities play a pivotal role in ecosystem services and can have direct and indirect influences on a multitude of processes including nutrient cycling, organic matter dynamics, soil structure, carbon transformations and sequestration, all of which are critical to soil health. Soil microbes are also important determinants of biogeochemical cycling processes on earth, which have direct implications for climate change mitigation. Soil microbes such as mycorrhizal fungi, *Trichoderma,* and *Piriformospora* are also known for their roles in plant nutrition, growth promotion, hormone regulation and stress control. However, not all soil microbes promote plant health and there are numerous soil-borne pathogens such as *Ralstonia, Rhizoctonia, Fusarium, Phytophthora, Gaeumannomyces* that cause deadly diseases in plants. There are also many soil-borne pathogens that cause deadly diseases in animals including nocardiosis, anthrax, malignant oedema, and blackleg. Soil microbiomes can even influence the social behavior of animals. For instance, a diverse soil microbiome may contain important bacteria capable of resupplying the mammalian gut microbiome, with implications for gut health and mental health. Moreover, in mice, exposure to soil can reduce allergic inflammation and have positive influence on the gut-lung axis. Humans are known to deliberately ingest soils as a nutrient supplement, even use soils as detoxifying agents for making some food products edible and for medicinal reasons. People with more exposures to soils are less likely to suffer from allergic reactions. Soil-borne pathogens that can be harmful to human health. Coccidioidomycosis, fungal meningitis, diarrhea, amoebic dysentery, and helminthiasis are some examples of soil-borne diseases in humans.

Figure 3: Factors governing the soil microbial contributions to one health. The **inner circle** shows the association between soil microbial diversity and one health. The dashed lines indicate that this association may be context dependent. The nature and strength of this association will not only depend on the ecosystem but also on a range of environmental factors. The **outside circle** shows various edaphic and global change factors that can regulate the contribution of soil microbial diversity to one health. The **outside graphs** represent hypothetical relationships between various factors (X-axis) and soil microbial diversity (Y-axis). We speculate that these are the major factors, however, the list is not exclusive and there are many other factors that can influence the contribution of soil microbes to one health. The relationships between these factors and soil microbial diversity can vary with microbial groups and ecosystem types. To highlight such context dependency, three possible relationships have been shown for each factor.



Microbes as the conduit of one health components and soil microbiomes as the microbial reservoir

Figure 1

Figure 2

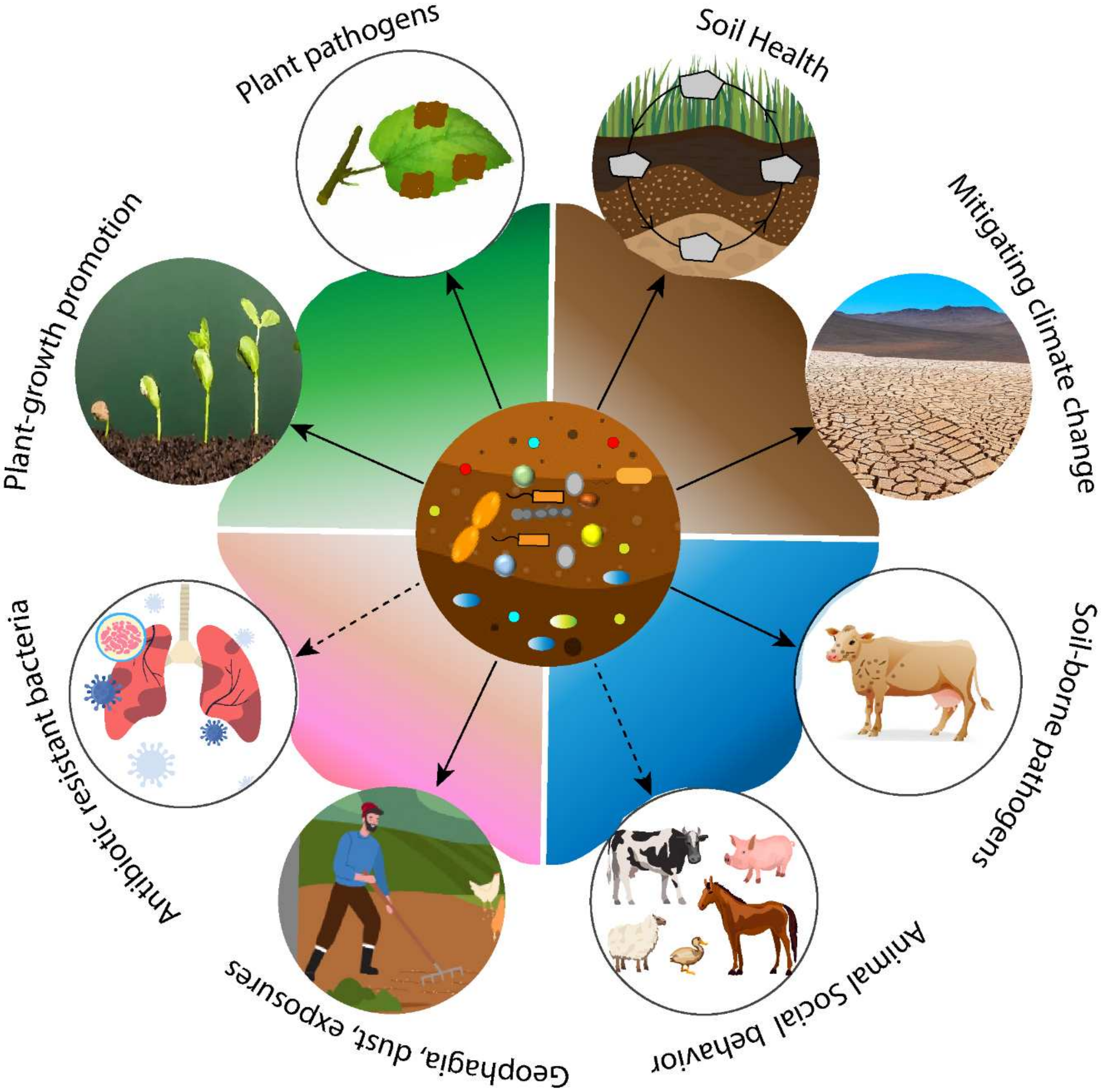
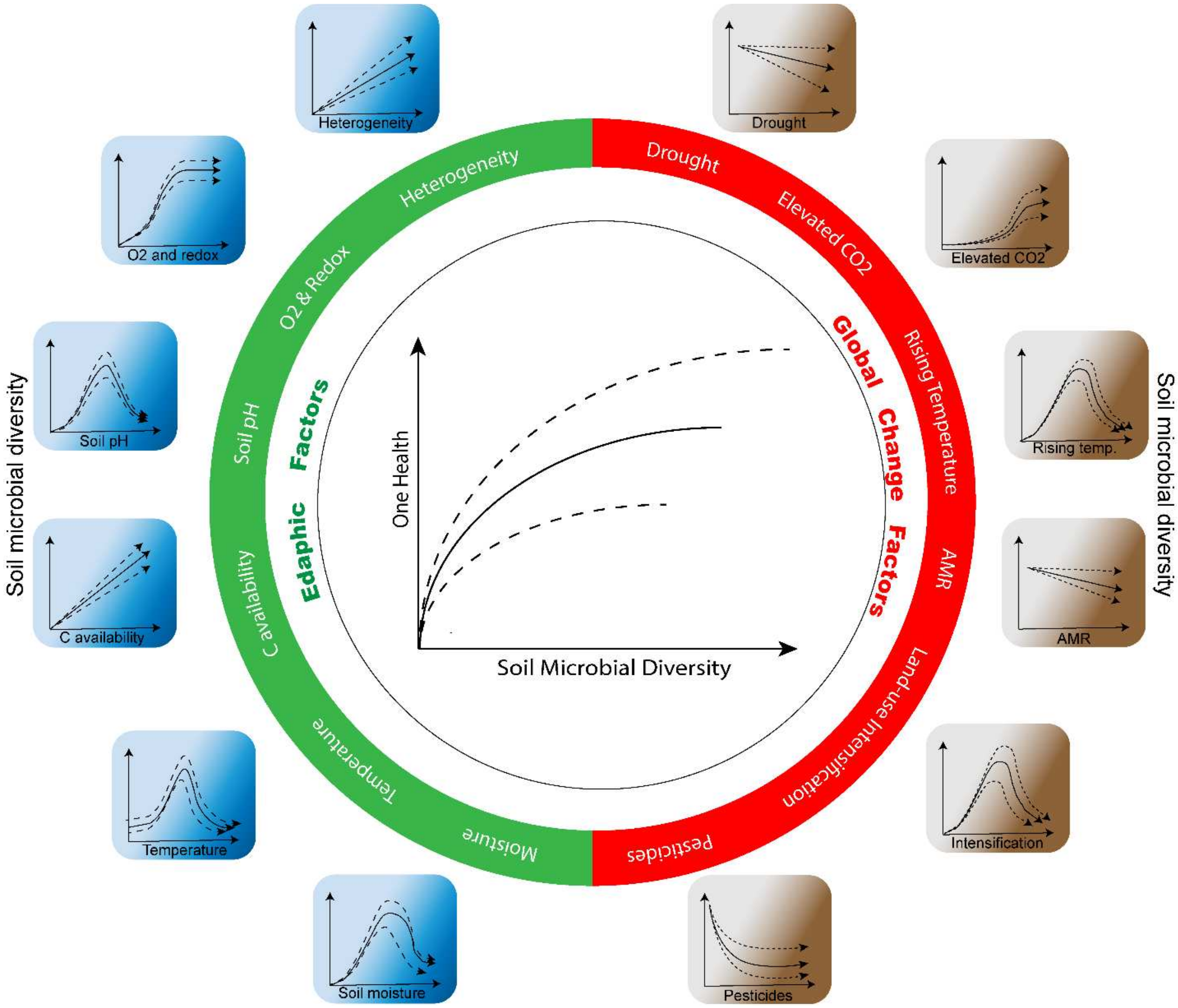
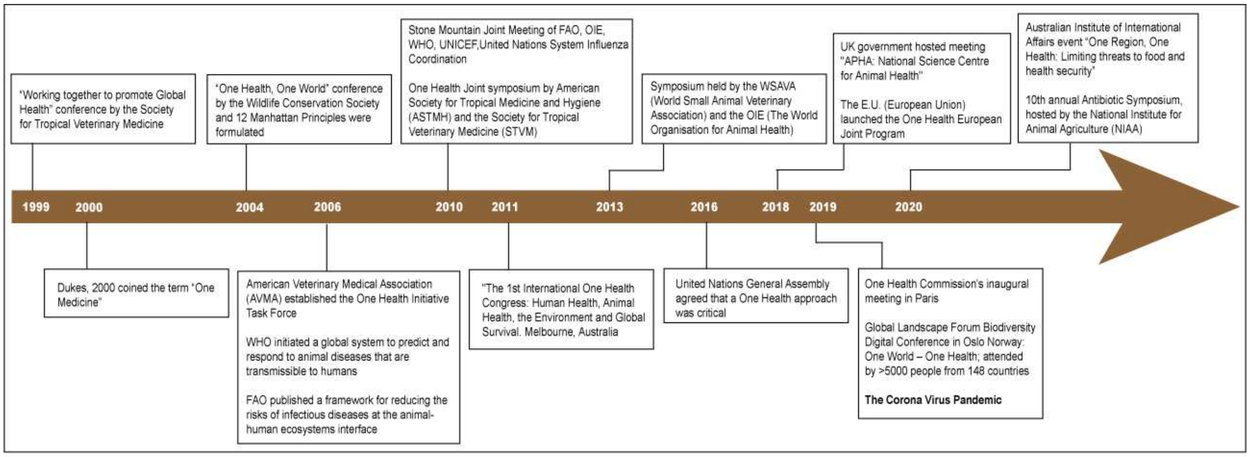

Plant pathogens
Soil Health
Mitigating climate change
Soil-borne pathogens
Animal Social behavior
Geophagia, dust, exposures
Antibiotic resistant bacteria
Plant-growth promotion

Figure 3


Heterogeneity
O2 and redox
Soil pH
C availability
Temperature
Soil moisture
Soil microbial diversity
Drought
Elevated CO2
Rising temp.
AMR
Intensification
Pesticides
Soil microbial diversity
Heterogeneity
O2 & Redox
Soil pH
C availability
Temperature
Moisture
Edaphic Factors
Drought
Elevated CO2
Rising Temperature
AMR
Land-use Intensification
Pesticides
Global Change Factors
One Health
Soil Microbial Diversity

Box 1. Evolution of one health

The importance of global health was noted in 1999 when the Society for Tropical Veterinary Medicine and the Wildlife Diseases Association organized a series of meetings on the topic 'Working together to promote global health[1]. In 2000, the concept of One Medicine was proposed[2]. In September 2004, a conference themed 'One World, One Health' was organized by the Wildlife Conservation Society in which the twelve Manhattan Principles were also formulated[3]. The Manhattan Principles are a list of recommendations for establishing a holistic approach to preventing threats to the health of life on earth and for maintaining ecosystem integrity[4]. The American Veterinary Medical Association formed the One Health Initiative Task Force in 2006[4]. The One Health concept was globally recognized after the American Medical Association proposed for strong partnership between the human and veterinary medical communities. In 2007, the Interministerial Conference on Avian and Pandemic Influenza (IMCAPI) was held in New Delhi, India. In 2008, the Food and Agriculture Organization, World Organization for Animal Health, and World Health Organization teamed up with the United Nations Children's Fund, United Nations System Influenza Coordination, and the World Bank to highlight the One Health approach to global health[1,3]. The WHO defines one health as an approach to formulating and implementing programs, policies, legislation and research in which multiple sectors communicate and work together to achieve better public health outcomes[5]. The FAO defines one health as an integrated approach that recognizes this fundamental relationship and ensures that specialists in multiple sectors work together to tackle health threats to animals, humans, plants and the environment[6]. The 1st International One Health Congress was held in Melbourne Australia in February 2011 where the interconnectivity of human health, animal health and environmental health was highlighted. in September 2016, The United Nations General Assembly unequivocally acknowledged the importance of One Health approach while addressing the threat of antimicrobial resistance[1,3]. In 2018, both UK and the European Union launched their one health programs.



Box 2. Health, One Health, and Dysbiosis

An important question that may arise when assessing the role of soil microbiomes in one health is what health is and if the conventional perception of health is sufficiently inclusive of defining and understanding microbial health. The WHO defines health as a state of complete physical, mental and social well-being and not merely the absence of disease or infirmity[5]. The importance of 'well-being' connects health to the one health premise. Maintaining a 'healthy' state requires 'eubiosis' of its microbial communities, which is typically associated with high diversity and uniformity of representative microbiota[7]. Considering the remarkable dynamics and inherent complexity of soil microbiomes, the task of identifying a healthy state can be daunting. Also, soil microbiomes may change during succession[150] and as such by definition microbiomes are not stable. A range of experimental studies have demonstrated that although microbiome performance increases when diversity increases (Panel A), there is a saturation point of that promoting role of diversity[153]. Thus, a basic level of microbiome diversity appears to be important, but further increase may or may not result in enhanced health or performance. This redundancy can be important, as it provides resilience and can act as insurance against perturbations (Panel B). Moreover, the importance of soil microbial diversity for one health, can also depend on the presence of specific taxa (e.g., keystone taxa[154]) that play an important role (Panel C) in microbiome structuring and perform ecosystem functions such as nitrogen fixation, detoxification, nitrification, pathogen suppression, facilitating one health. Thus, the establishment or disappearance of such taxa may lead to changes in one health. For instance, the establishment of mycorrhizal fungi in small islands can facilitates tree growth and change ecosystem performance[155]. Also, the establishment of specific soil pathogens in agricultural fields can cause crop failure with negative impacts on one health. Studies on lakes, coral reefs, oceans, forests, and drylands have also shown that smooth changes can be interrupted by sudden drastic switches to a contrasting alternative stable state[156] (Panel D). The role of soil microbes as moderators of such alternative stable states is not well-understood, but it could be potentially strong considering the intimate association between soil microbes and other organisms and ecosystem processes. For instance, a recent study has revealed that changes in nitrogen cycling by mycorrhizal fungi is linked to tipping points in carbon storage when forest expands into tundra[157]. Importantly, a healthy microbiome is not by definition diverse. While various studies report a positive link between soil microbial diversity and components of one health, there are also examples of no relationships and context-dependencies. For example, many of the taxa in the gut microbiome belong to Firmicutes and Bacteroidetes, which together represents nearly 70% of the total microbiota[158] and the dominance of a few taxa is adequate for usual functioning. Indeed, understanding the biology of a healthy microbiome state remains a major bottleneck.

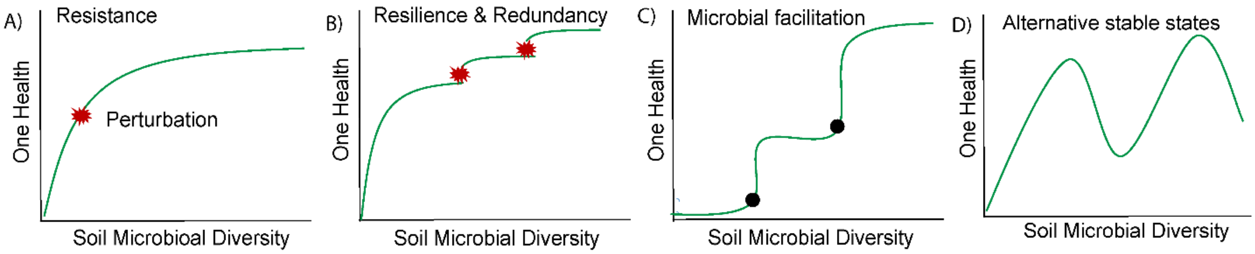


Table 1. Soil microbial contributions to one (soil, plant, animal, and human) health.

Soil Health	**Types of functions**	**Examples of involved groups[#]**
Direct effects		
Nutrient uptake and cycling[18]	Nitrogen fixation	*Rhizobium, Bradyrhizobium*
	Nitrification	*Nitrosomonas, Nitrobacter, Nitrospina, Thaumarchaeota*
	Denitrification	*Alcaligens, Pseudomonas, Trichoderma, Fusarium*
	Phosphate solubilization	*Burkholderia, Pseudomonas, Bacillus, Serratia, Arthrobacter, Penicillium*
	Siderophore formation	*Streptomyces, Azotobacter, Bacillus, Fusarium, Pseudomonas, Serratia*
Greenhouse gas fluxes[18,43–46]	Incomplete denitrification (N2O production), methanogenesis, microbial respiration	*Pseudomonas, Metahnosarcina, Methanobacterium, and wide range of microbes*
Water purification[36,47]		Wide array of microbes
Soil structure and prevention of soil erosion[48]	Soil aggregation & gluing of soil particles	Wide array of microbes
Soil carbon transformations and sequestration[45,49]	Soil organic matter stabilization	Wide array of microbes
SOM dynamics[50]	Decomposition	Wide array of microbes
	Detoxification of pesticides and contaminants	*Arthrobacter, Bacillus, Pseudomonas, Achromobacter*
Indirect effects		
Control of biological communities[51,52]	Disease suppressive soils	*Pseudomonas, Streptomyces, Paenibacillus, Penicillium*
Transfer of antibiotic resistance genes[53,54]		
Microbial reservoir and source of beneficial and pathogenic microbes		
Plant Health		
Direct effects		
Source of microbes[16,17]	Soil harbors incredible diversity of microbes that plants can recruit from including many beneficials, but also many pathogens	*Beneficials: Arthrobacter, Bacilus, Trichoderma, Fusarium, Glomus* *Pathogens: Fusarium, Phythopthora*
Plant Yield and Plant nutrition[55,56]	Nitrogen fixing bacteria mycorrhizal fungi, endophytes	*Rhizobium, Bradyrhizobium Glomeraceae, Gigasporaceae*
Plant growth promotion[57]	HCN production, hormone production, micronutrient	*Azospirillum, Burkholderia, Bacillus, Trichoderma*
Soil borne plant pathogens[58]	Harmful effects on plants	*Ralstonia, Rhizoctonia, Fusarium*
Pathogen suppression[8,59]	Antagonistic to pathogens, induced systemic resistance	*Trichoderma, Pseudomonas, Burkholderia, Bacillus*
Disease suppressive soils[51,52]		*Pseudomonas, Streptomyces, Paenibacillus, Penicillium*
Stress control[57,60]	ACC deaminase	*Alcaligens, Rhizobium, Rhodococcus, Methylobacterium*
Seed germination[57]		*Pseudomonas, Azospirillum, Cellulosimicrobium, Bacillus*
Hormone regulation[61]	IAA, cytokinins, gibberellins, ethylene regulation	*Pseudomonas, Enterobacter, Bacillus, Azotobacter*
Enhanced water uptake[16]	Mycorrhizae can access water from micropores in soil	*Glomus, Paraglomus, Diversispora*
Delivery of amino acids[62]		Mycorrhizas

Indirect effects [56,57,61,63]		
Signal interference[57]	Degradation of homoserine lactones	*Bacillus thuringiensis*
Leaf area and nutrient levels[57]		Wide range of microbes
Source of microbes		Wide range of microbes
Animal Health		
Direct effects		
Source of pathogens[64,65]	Nocardiosis, anthrax, malignant oedema, blackleg disease,	*Nocardia, Bacillus, Clostridium, Burkholderia, Chlamydophila*
Source of food[66,67]	Some vertebrates, but also nematodes and other groups feed on bacteria and fungi (fruiting bodies)	*Aphelenchus, Aphelenchoides, Rhabditis, Protorhabditis*
Social behavior[68,69]l	Reduction of anxiety in mice upon exposure to soils with high microbial diversity	Reptiles, insects, mice and chimpanzees
Indirect effects		
Geophagia[27,70]		
Source of microbes	Soil harbors incredible diversity of microbes that may be taken directly or indirectly	
Alleviation of toxic compounds[71]	Animals including cows	
Adaptation to environmental shifts[71]		Wild animals such as baboons and chimpanzees
Human Health		
Direct effects		
Source of food[16]	Truffles, root crops	Ectomycorrhizal fungi
Source of pathogens[47,72,73]	Fungal meningitis	*Exserohilium rostratum*
	Ringworm infection	*Trichophyton rubrum*
	Diarrhea and dysentery	Protists
	Gastroenteritis	*Campylobacter, Escherichia coli*
	Conjunctivitis, polio	Soil viruses
	Anthrax	*Bacillus anthracis*
Source of allergies[47]	Prevalence of allergens in soil	Wide array of microbes
Indirect effects		
Geophagia[32]	Deliberate intake of soil	
Protection against teratogens[32]	Clay can confer protection against teratogens	
Source of microbes[17]	Soil harbors incredible diversity of microbes that may be taken directly or indirectly	
Source of antibiotic resistant bacteria[47]		
Detoxification and Suppression of pathogens and viruses[74]		
Airborne dust[72,75]	Coccidioidomycosis	

[#]Examples are given for specific groups/processes. Major microbial groups are indicated, but often there are other microbes, even clades acting alone or as microbial consortia that can also contribute to the functions listed. General processes such soil structure or soil organic matter decomposition involve a wide range of microbes.