



# Soil microbiomes and one health

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**Abstract** | The concept of one health highlights that human health is not isolated but connected to the health of animals, plants and environments. In this Review, we demonstrate that soils are a cornerstone of one health and serve as a source and reservoir of pathogens, beneficial microorganisms and the overall microbial diversity in a wide range of organisms and ecosystems. We list more than 40 soil microbiome functions that either directly or indirectly contribute to soil, plant, animal and human health. We identify microorganisms 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 with one health. Finally, we present future challenges in one health research and formulate recommendations for practice and evaluation.

## Microbiome

A characteristic microbial community occupying a reasonably well-defined habitat which has distinct physio-chemical properties. Thus, the microbiome is holistically defined as the microorganisms and their structural elements including nucleic acids, proteins, lipids, polysaccharides as well as various metabolites. Microbiomes also encompass microorganisms and their activities, including their spatiotemporal dynamics, which results in the formation of specific ecological niches.

The one health concept highlights that the health and well-being of humans are inseparably linked to the health of other ecosystem components such as soil, plants and animals (BOX 1). We are gradually realizing that microorganisms are crucial in one health because they connect each of these components, and the health of ecosystems heavily relies on the contribution of microbial communities<sup>1</sup>. A wealth of studies now demonstrate that microbial communities associated with plants, animals and humans function as a ‘second genome’<sup>2</sup>, an ‘extended genotype’<sup>3</sup> or an ‘eco-holobiont’<sup>4</sup>, and thus drive the fitness and performance of almost all organisms on Earth. A growing number of studies also suggests that microbial communities of different organisms are interconnected and form a circular loop<sup>5</sup>. Until now, the one health research landscape has been dominated by studies on microbial pathogens responsible for zoonotic diseases<sup>6</sup>. Although pathogens are undeniably important, recent advances in omics and statistical approaches have demonstrated that microbiome associations go beyond just pathogens, and microbial symbionts, commensals, amensals and the overall diversity have important implications for one health<sup>1</sup>. However, compared with plant, animal and human health, the importance of the soil microbiome and soil health has received less attention among one health researchers until now<sup>7–9</sup>.

In this Review, 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 microorganisms for other ecosystems and we identify microbial taxa that are shared between the different one health components. We then discuss 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 source of microbiomes

Microorganisms are overwhelmingly abundant in soils, and, after plants, microorganisms residing in the soil and deep surface represent the largest fraction of global biomass on Earth. Bacteria are most abundant (15% of the total living biomass), but the biomasses of fungi (2%) and Archaea (1%) are also larger than that of animals (0.3%)<sup>10</sup>. Soils also harbour the most diverse and complex microbiome on Earth, with often more than 0.5 mg of microbial biomass carbon and >50,000 species per gram<sup>11–13</sup>. Bacteria and fungi are generally the dominant microorganisms in soil with more biomass than protists and archaea<sup>10</sup>. Moreover, a gram of soil can contain 10<sup>7</sup>–10<sup>9</sup> virus particles<sup>13</sup>. Thus, from a source–sink perspective<sup>14</sup>, one can consider soil as a major source of microorganisms in terrestrial ecosystems and, thus, the foundation of one health (FIG. 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<sup>15</sup>. Estimates indicate that bulk soil is the most important contributor to plant endophytic microbiota, contributing more than two-thirds of the bacterial and fungal diversity<sup>16,17</sup>. However, plant growth-promoting bacteria can also be transmitted vertically through seeds<sup>18,19</sup> (see below). Indeed, a range of studies have shown that species-specific microbiomes

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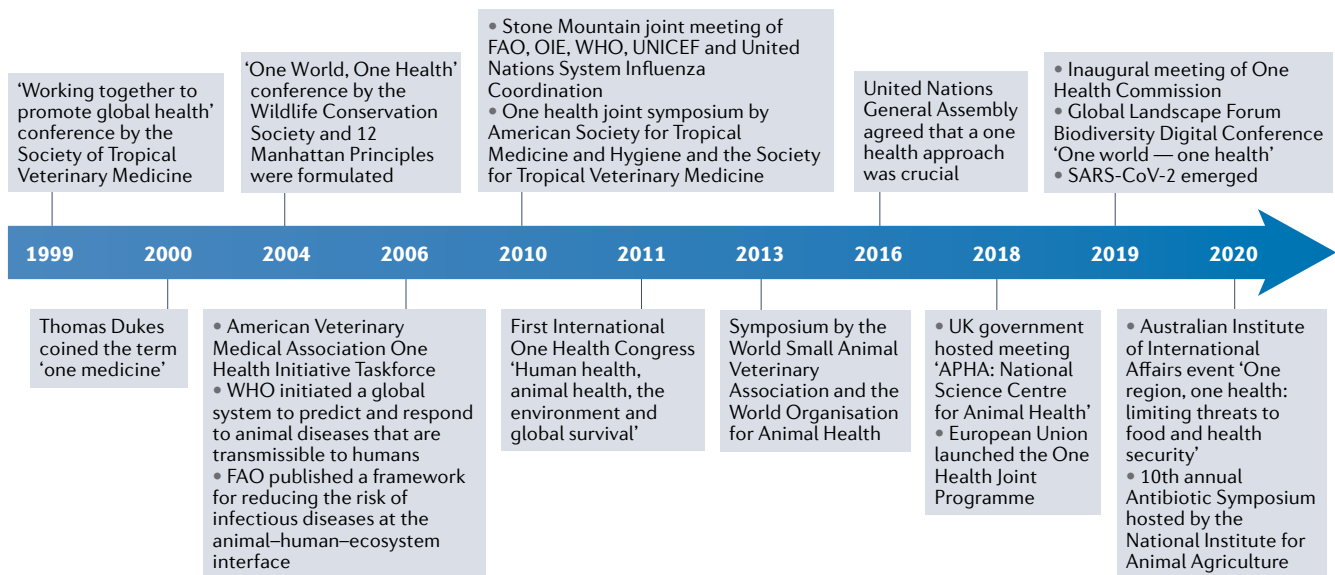
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## Box 1 | Evolution of one health

The importance of global health was noted in 1999 (see the figure) 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'<sup>171</sup>. In 2000, the concept of One Medicine was proposed<sup>172</sup>. In September 2004, a conference themed 'One World, One Health' was organized by the Wildlife Conservation Society in which the 12 Manhattan Principles were also formulated<sup>7</sup>. 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 (One Health Commission). The American Veterinary Medical Association formed the One Health Initiative Task Force in 2006. The one health concept was globally recognized after the American Medical Association proposed a 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 (FAO), the World Organisation for Animal Health (OIE) and the World Health Organization

(WHO) teamed up with the United Nations Children's Fund (UNICEF), the United Nations System Influenza Coordination and the World Bank to highlight the one health approach to global health<sup>7,171</sup>. The WHO defines one health as an approach to formulating and implementing programmes, policies, legislation and research in which multiple sectors communicate and work together to achieve better public health outcomes (WHO One Health). 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 (FAO One Health). The First 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 the one health approach while addressing the threat of antimicrobial resistance<sup>7,171</sup>. In 2018, both the United Kingdom and the European Union launched their one health programmes.



APHA, American Public Health Association.

are common in plants<sup>20,21</sup>. The dominant players of each microbiome compartment (soil, plant, animal, human) vary considerably (FIG. 1). For example, the human gut microbiota is less diverse and is dominated by the members of Bacillota and Bacteroidota. Animal microbiomes are relatively more diverse with a notable presence of Pseudomonadota. On the other hand, soil and the rhizosphere are highly diverse but dominated by Pseudomonadota, Actinomycetota, Cyanobacteria and Acidobacteriota. The composition is based on a synthesis of several studies conducted in the Midwest region of the United States, and the major phyla were consistent with other studies<sup>13,22–24</sup>.

Geophagy, a deliberate consumption of soil or clay, is common among animals. Sheep, gorillas, bats and parrots are a few animals that perform geophagia<sup>25</sup>. Biodiverse soils may contribute commensal microorganisms to the animal gut microbiota<sup>26,27</sup>. For instance, soil-dwelling mice can directly acquire microorganisms from the soil that can alleviate inflammation and allergic diseases<sup>28</sup>. Unknowingly as well, farm animals can consume a significant amount of soil adhered to plant shoots.

For example, grazing sheep can consume up to 400 g of soil per kilogram of body weight<sup>29</sup>. For dairy cows, this number can be staggeringly high as they can consume up to 350 kg of soil per cow per year<sup>30</sup>. Estimates suggest that up to 3% of the rumen microbiome of sheep and cattle can be contributed by the ingested soil<sup>28</sup>. The skin microbiome composition of farm animals is also linked to the soil microbiome with *Arthrobacter* and *Sphingomonas* spp. as the indicator taxa<sup>31</sup>. Bacterial groups belonging to *Enterococcus* and *Candidatus Arthromitus* are linked to high-performing poultry farms whereas groups belonging to *Nocardia*, *Lapillococcus*, *Brachybacterium*, *Ruania*, *Dietzia*, *Brevibacterium*, *Jeotgalicoccus*, *Corynebacterium* and *Aerococcus* are linked to low-performing farms<sup>32</sup>. However, in cattle farms, soils can also be a recipient of antibiotic resistance genes from the rumen microbiome<sup>33</sup>.

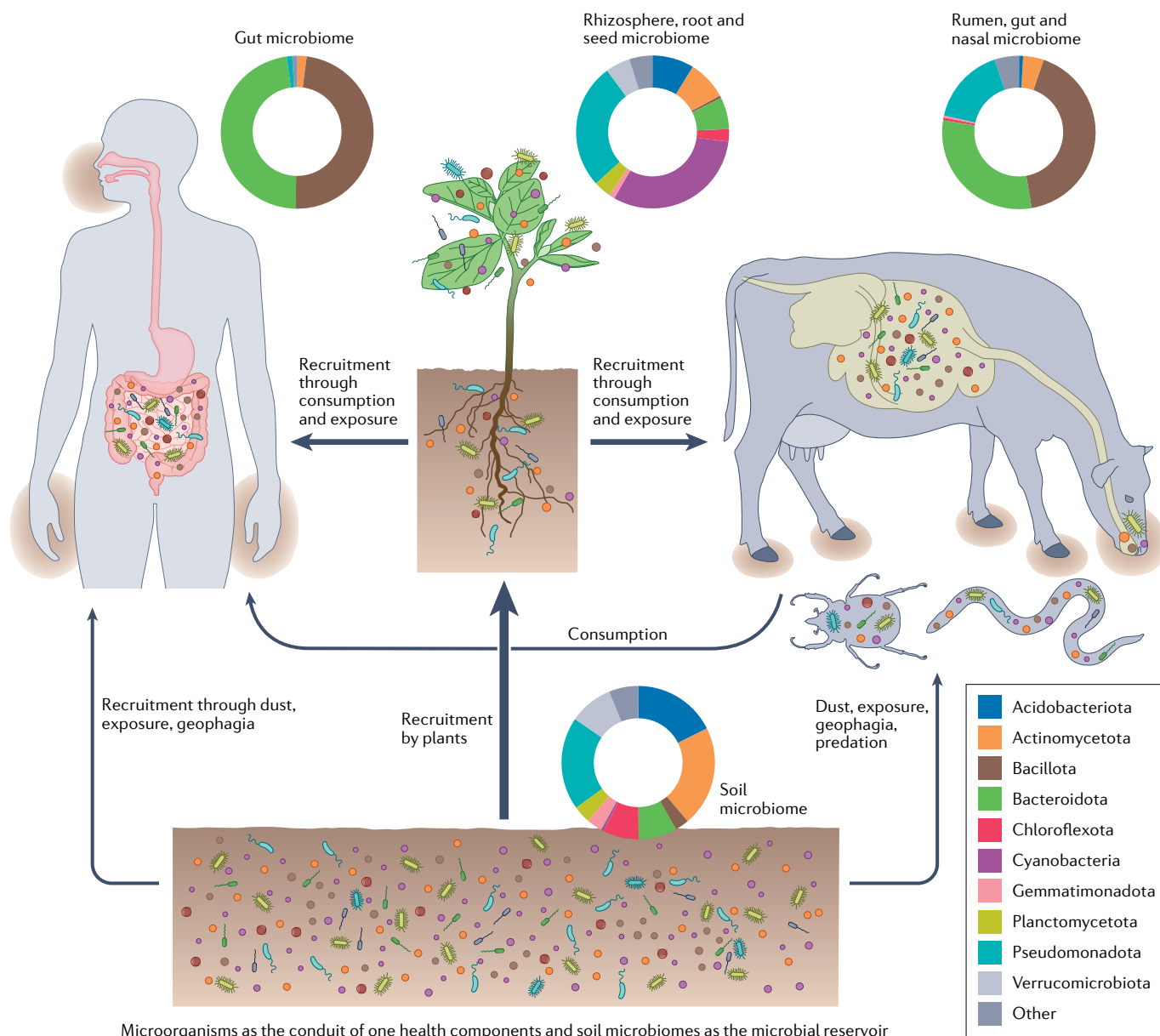
Human geophagy has also been reported in many parts of the world including Asia, sub-Saharan Africa, Latin America and the Pacific Islands<sup>34,35</sup>. It is an epiphenomenon of nutrient deficiency whereby pregnant women consume mineral and trace element-rich soils as a prenatal dietary supplement<sup>34</sup>. Interestingly, a study

### Dysbiosis

An imbalance of microbiome structure and composition that is caused by host/environmental perturbations. It is usually associated with loss of taxonomic and/or functional diversity.

comparing environmental characteristics with human microbiomes found that soil types (for example, clay loam soil versus loam soil) were correlated with the nasal and oral microbiomes<sup>36</sup>. 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<sup>37</sup>. A possible

explanation for this observation is that higher microbial diversity in the environment buffers against diseases by occupying niches that otherwise are taken by pathogens or through direct inhibition (see below). Pet dogs and cats can regularly bring soil-associated microorganisms to built environments, resulting in microbial exposures of their owners and other inhabitants<sup>31</sup>. Furthermore, the oral, nasal and skin microbiomes of farmworkers are



**Fig. 1 | The link between soil, plant, animal and human microbiomes.** Microorganisms link soil, plant, animal and human health, and microbial communities connect the different ecosystems. Soil harbours 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 more than two-thirds of the bacterial and fungal diversity. Diets play a major role in shaping the gut microbiome composition of both humans and animals. Plant microbiota, including microorganisms originally derived from soil, can also make their way into human and animal gut microbiota. Farmers or farm animals are regularly exposed to soils, and we also inhale soil particles, including soil microorganisms, through dust. Geophagia is the deliberate consumption

of soil or clay. Sheep, gorillas, bats and parrots are a few animals that carry out geophagia. Human geophagia is also not uncommon. 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 and human). We conducted a literature search to identify the compositional overlap among the microbiomes of soils, plants, animals and humans. We only selected studies from the Midwest region of the United States that had sequences deposited in the Sequence Read Archive repository of the National Center for Biotechnology Information (NCBI). In total, we processed sequences available from 431 independent biological samples from soils (177 samples), plants (112 samples), animals (24 samples) and humans (118 samples).

**Microbial diversity**

The number, relative abundance and composition of different microbial taxa present at a particular location. Thus, microbial diversity is a measure of microbial variation at the taxonomic, genetic, phylogenetic, functional and ecosystem levels. An optimal index should incorporate both richness and evenness.

**Resistance**

The ability of a microbiome to withstand a perturbation and remain unchanged in terms of community structure and composition.

associated with the soil microbiome composition of their farms<sup>38,39</sup>. Overall, the soil microbiome can be a major contributor to microbial communities in other organisms and act as the foundation 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 well-being.

**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<sup>40</sup>. The quality and health of soils are linked to global food and water security, and have important implications for energy security and mitigating climate change<sup>41,42</sup>. In recent years, the degradation of soils owing to land-use change, erosion, compaction and pesticide contamination has highlighted the urgent need for sustaining the ecosystem services of soils<sup>43</sup>. Consequently, researchers are increasingly realizing that the role of microbial communities must be understood and incorporated to safeguard and enhance soil health<sup>44</sup> and there is growing interest in the practices that can maintain healthy soils. For example, several studies have shown that crop diversification<sup>45,46</sup> and reductions of synthetic pesticides<sup>47,48</sup>, mineral fertilizers<sup>40</sup> and intensive tillage<sup>49</sup> can improve soil biodiversity and soil health.

Soil microbial communities 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 largest terrestrial pool of carbon, and a growing body of research suggests that microbial communities play an important role in soil carbon stability<sup>50,51</sup>. Microbial biomass is not as labile as previously thought, and fine-fraction stable organic matter can be of microbial origin<sup>52,53</sup>. Microbial biomass, complexity and the 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<sup>53,54</sup>. Soil microorganisms also determine biogeochemical cycling of other elements, including nitrogen, phosphorus, sulfur and iron, which have direct implications for all of the components of one health<sup>12,13,55–57</sup>. However, whereas the physical and chemical indicators of soil health have been emphasized in the literature, the soil biological indicators have received little recognition<sup>40,42</sup>. Furthermore, the current perception of microbial contribution to soil health is overly simplistic as studies often considered broad indices such as the overall microbial biomass, fungi to bacteria ratio or soil enzymes. Two recent articles have provided several recommendations and examples of microbial indices that can be used to assess soil health<sup>42,44</sup>. These indices include pathogen occurrence, the abundance of pathogenicity genes, overall microbial diversity and specific soil functional groups.

**Plant health**

The contribution of soil microorganisms to plant health is indisputable and is 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<sup>58</sup>. Plants preferentially recruit microorganisms from the rhizosphere that are essential for their growth and development. Soil microorganisms can shape 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<sup>2,24,59,60</sup> (TABLE 1 and FIG. 2). Microorganisms acquire up to 80% of plant nitrogen and 90% of plant phosphorus<sup>11</sup>. Even in intensively managed ecosystems, soil microorganisms can have a large impact on plants. For example, legumes associate with soil-inhabiting nitrogen-fixing bacteria, providing more than 300 kg of nitrogen per hectare per year<sup>12,13,61</sup>. Indirectly as well, microorganisms in the rhizosphere can influence important functional traits including leaf area, leaf longevity, leaf nutrient levels and the shoot to root ratio<sup>62</sup>. Bacteria such as *Rhizobium*, *Arthrobacter*, *Bacillus*, *Alcaligenes*, *Rhodococcus*, *Methylobacterium*, *Pseudomonas* and *Azospirillum* spp. 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 microorganisms are the mycorrhizal fungi, which form symbiotic associations with nearly 90% of land plants, including many crops<sup>60</sup>. 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<sup>63</sup>. For example, plants obtain water and essential micronutrients and macronutrients from mycorrhizal fungi and supply up to one-quarter of their photosynthates in return<sup>64</sup>. The growth of a wide range of crops can be enhanced by mycorrhizal fungi, with growth increases of up to 50%<sup>65</sup>. Field inoculation with mycorrhizal fungi can substantially promote plant yield, although effects are highly variable<sup>66</sup> and many commercial inoculants are of insufficient quality<sup>67</sup>. Fungi such as *Trichoderma* spp. or the endophytic fungus *Piriformospora indica* are other examples of beneficial microorganisms that can promote plant growth and stress tolerance, and/or induce local and systemic resistance to pathogens<sup>46,68</sup>. Soil protists can also have a strong impact on plant nutrient availability and plant health by grazing on pathogenic microorganisms and stimulating mineralization<sup>69</sup>. However, not all soil microorganisms promote plant health and there are numerous soil-borne plant pathogens, such as *Ralstonia*, *Rhizoctonia*, *Fusarium*, *Phytophthora* and *Gaeumannomyces* spp.<sup>70–72</sup>. Numerous in-depth reviews are available on both beneficial and pathogenic microorganisms in the rhizosphere<sup>2,62,73–75</sup>. By promoting plant growth and seedling survival, microorganisms also contribute to the establishment and maintenance

Table 1 | Soil microbial contributions to one health

Effects	Types of function	Examples of involved groups <sup>a</sup>	Refs.
<b>Direct effects on soil health</b>			
Nutrient uptake and cycling	Nitrogen fixation	<i>Rhizobium</i> , <i>Bradyrhizobium</i>	13
	Nitrification	<i>Nitrosomonas</i> , <i>Nitrobacter</i> , <i>Nitrospina</i> , <i>Thaumarchaeota</i>	
	Denitrification	<i>Alcaligenes</i> , <i>Pseudomonas</i> , <i>Trichoderma</i> , <i>Fusarium</i>	
	Phosphate solubilization	<i>Burkholderia</i> , <i>Pseudomonas</i> , <i>Bacillus</i> , <i>Serratia</i> , <i>Arthrobacter</i> , <i>Penicillium</i>	
	Siderophore formation	<i>Streptomyces</i> , <i>Azotobacter</i> , <i>Bacillus</i> , <i>Fusarium</i> , <i>Pseudomonas</i> , <i>Serratia</i>	
Greenhouse gas fluxes	Incomplete denitrification (N <sub>2</sub> O production), methanogenesis, microbial respiration	<i>Pseudomonas</i> , <i>Metahnosarcina</i> , <i>Methanobacterium</i> , wide range of microorganisms	13,118,160–162
Water purification	Uptake of nutrients, amino acids and chemical compounds from percolating water	Wide array of microorganisms	43,70
Soil structure and prevention of soil erosion	Soil aggregation and gluing of soil particles	Wide array of microorganisms	163
Soil carbon transformations and sequestration	SOM stabilization	Wide array of microorganisms	52,161
SOM dynamics	Decomposition	Wide array of microorganisms	164
	Detoxification of pesticides and contaminants	<i>Arthrobacter</i> , <i>Bacillus</i> , <i>Pseudomonas</i> , <i>Achromobacter</i>	
<b>Indirect effects on soil health</b>			
Control of biological communities	Disease suppressive soils	<i>Pseudomonas</i> , <i>Streptomyces</i> , <i>Paenibacillus</i> , <i>Penicillium</i>	82,83
Transfer of antibiotic resistance genes	Microbial exchange of genetic material (for example, plasmid transfer)	Wide array of microorganisms	129,131
Microbial reservoir and source of beneficial and pathogenic microorganisms	‘Seed bank’ of beneficial and pathogenic microorganisms	Wide array of microorganisms	Numerous
<b>Direct effects on plant health</b>			
Source of microorganisms	Soil harbours incredible diversity of microorganisms that plants can recruit	Beneficials: <i>Arthrobacter</i> , <i>Bacillus</i> , <i>Trichoderma</i> , <i>Fusarium</i> , <i>Glomus</i> Pathogens: <i>Fusarium</i> , <i>Phytophthora</i>	11,12
Plant yield and plant nutrition	Nitrogen-fixing bacteria, mycorrhizal fungi, endophytes	<i>Rhizobium</i> , <i>Bradyrhizobium</i> , Glomeraceae, Gigasporaceae	24,61
Plant growth promotion	Hydrogen cyanide production, hormone production, micronutrients	<i>Azospirillum</i> , <i>Burkholderia</i> , <i>Bacillus</i> , <i>Trichoderma</i>	59
Soil-borne plant pathogens	Harmful effects on plants	<i>Ralstonia</i> , <i>Rhizoctonia</i> , <i>Fusarium</i>	165
Pathogen suppression	Antagonistic to pathogens, induced systemic resistance	<i>Trichoderma</i> , <i>Pseudomonas</i> , <i>Burkholderia</i> , <i>Bacillus</i>	2,166
Disease suppressive soils	Prevent establishment of pathogens or disease development	<i>Pseudomonas</i> , <i>Streptomyces</i> , <i>Paenibacillus</i> , <i>Penicillium</i>	82,83
Stress control	1-Aminocyclopropane-1-carboxylate deaminase	<i>Alcaligenes</i> , <i>Rhizobium</i> , <i>Rhodococcus</i> , <i>Methylobacterium</i>	59,167
Seed germination	Regulation of dormancy and germination	<i>Pseudomonas</i> , <i>Azospirillum</i> , <i>Cellulosimicrobium</i> , <i>Bacillus</i>	59
Hormone regulation	Indole-3-acetic acid, cytokinins, gibberellins, ethylene regulation	<i>Pseudomonas</i> , <i>Enterobacter</i> , <i>Bacillus</i> , <i>Azotobacter</i>	71
Enhanced water uptake	Mycorrhizae can access water from micropores in soil	<i>Glomus</i> , <i>Paraglomus</i> , <i>Diversispora</i>	11
Delivery of amino acids	Metabolite exchange	Mycorrhizae	60
<b>Indirect effects on plant health</b>			
Signal interference	Degradation of homoserine lactones	<i>Bacillus thuringiensis</i>	59
Leaf area and nutrient levels	Microbial growth and metabolism	Wide range of microorganisms	59
Source of microorganisms	‘Seed bank’ of beneficial and pathogenic microorganisms	Wide range of microorganisms	Numerous



Table 1 (cont.) | Soil microbial contributions to one health

Effects	Types of function	Examples of involved groups <sup>a</sup>	Refs.
<b>Direct effects on animal health</b>			
Source of pathogens	Nocardiosis, anthrax, malignant oedema, blackleg disease	<i>Nocardia</i> , <i>Bacillus</i> , <i>Clostridium</i> , <i>Burkholderia</i> , <i>Chlamydia</i>	94,168
Source of food	Some vertebrates, but also nematodes and other groups feed on bacteria and fungi (fruiting bodies)	<i>Aphelenchus</i> , <i>Aphelenchoides</i> , <i>Rhabditis</i> , <i>Protorhabditis</i>	90,169
Social behaviour	Reduction of anxiety in mice upon exposure to soils with high microbial diversity	Reptiles, insects, mice and chimpanzees	26,27
<b>Indirect effects on animal health</b>			
Geophagia	Ingestion of soil	Wide range of microorganisms	25,170
Source of microorganisms	Soil harbours an incredible diversity of microorganisms that may be taken up directly or indirectly	Wide range of microorganisms	
Alleviation of toxic compounds	Animals including cows	Toxin-degrading microorganisms	92
Adaptation to environmental shifts	Wild animals such as baboons and chimpanzees	Wide range of microorganisms	92
<b>Direct effects on human health</b>			
Source of food	Truffles, root crops	Ectomycorrhizal fungi	11
Source of pathogens	Fungal meningitis	<i>Exserohilum rostratum</i>	70,103,104
	Ringworm infection	<i>Trichophyton rubrum</i>	
	Diarrhoea and dysentery	Protists	
	Gastroenteritis	<i>Campylobacter</i> , <i>Escherichia coli</i>	
	Conjunctivitis, polio	Soil viruses	
	Anthrax	<i>Bacillus anthracis</i>	
Source of allergies	Prevalence of allergens in soil	Wide array of microorganisms	70
<b>Indirect effects on human health</b>			
Geophagia	Deliberate intake of soil	NA	96
Protection against teratogens	Clay can confer protection against teratogens	NA	96
Source of microorganisms	Soil harbours incredible diversity of microorganisms that may be taken up directly or indirectly	NA	12
Source of antibiotic-resistant bacteria	Direct or indirect source	NA	70
Detoxification and suppression of pathogens and viruses	Reducing exposure	NA	79
Airborne dust	Coccidioidomycosis	<i>Coccidioides</i> spp.	58,104

NA, not assessed or applicable; SOM, soil organic matter. <sup>a</sup>Examples are given for specific groups and processes. Major microbial groups are indicated, but often there are other microorganisms, even clades acting alone or as microbial consortia that can also contribute to the functions listed. General processes such as soil structure or SOM decomposition involve a wide range of microorganisms.

of green roofs and urban agriculture, creating a pleasant and healthy environment<sup>76</sup>. It is important to note that microorganisms do not function in isolation and an increasing number of studies demonstrate that a systems approach is required to understand microbiome functioning. For example, microbial consortia, rather than individual microorganisms, may better explain the impact of microbiomes on plant growth and nutrient uptake<sup>77</sup>, nitrogen use efficiency<sup>78</sup>, pathogen suppression success<sup>79</sup> and, overall, ecosystem multifunctionality<sup>80</sup>. In line with this, selective soil microbiome recruitment by plants is key for plant survival<sup>62</sup>, nitrogen use efficiency<sup>78</sup> and plant fitness<sup>81</sup>.

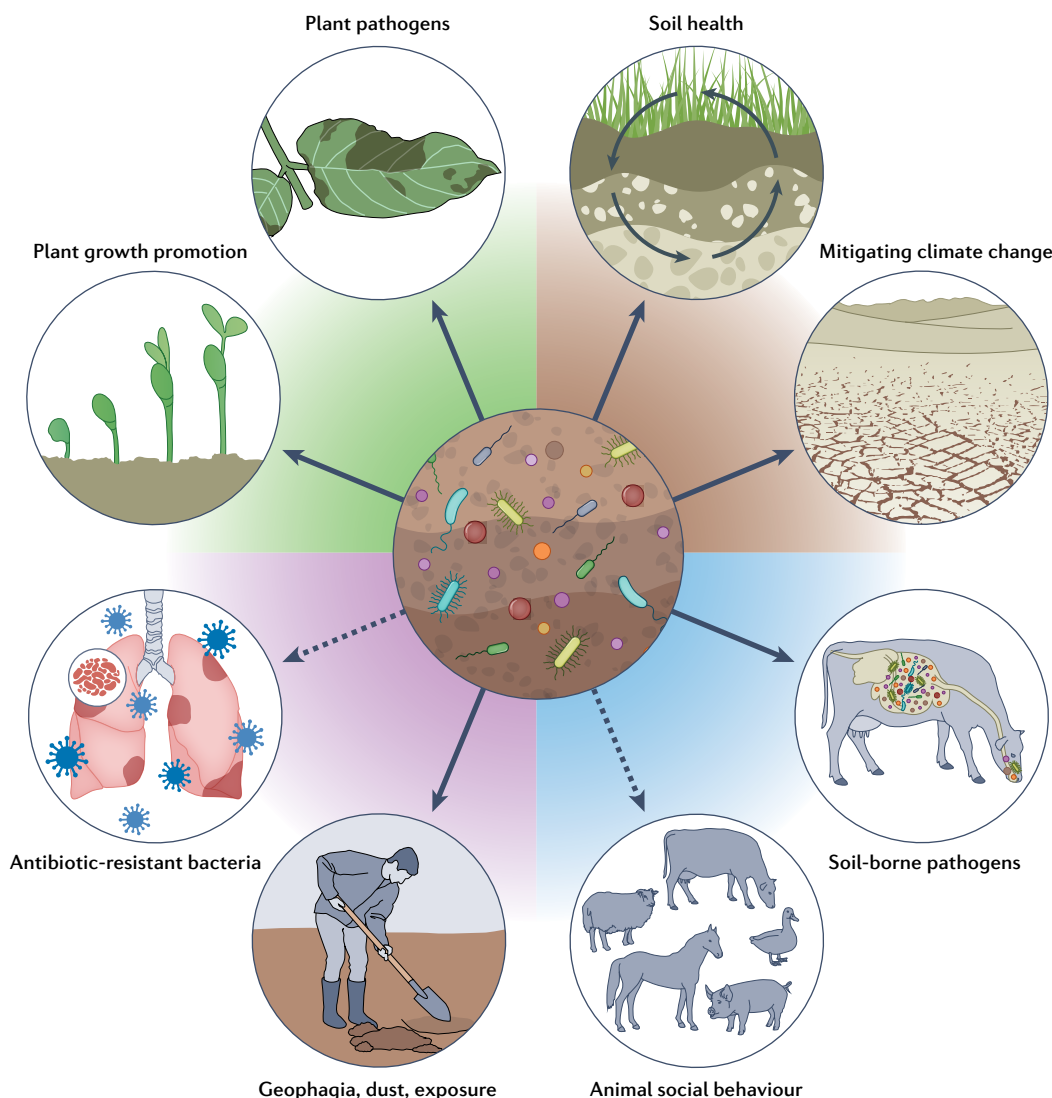
**Disease suppressive soils.** Disease suppressive soils are one of the finest examples of soil microbiome-conferred protection of plants against soil-borne pathogens<sup>82</sup>. Disease suppressive soils are soils that, owing to their microbiome composition and activities, prohibit pathogens from establishing or greatly reduce pathogen damage<sup>82,83</sup>. Disease suppressiveness can persist in soil for more than 40 years even in the presence of soil-borne pathogens<sup>83</sup>. Specific microorganisms can also confer disease suppressiveness; for example, siderophore-producing *Pseudomonas* spp. can suppress the pathogens *Gaeumannomyces graminis* var. *tritici* and *Fusarium* spp.<sup>84</sup>. Interestingly, parasitic fungi, such as *Trichoderma*

and *Verticillium* spp., can suppress potent fungal pathogens, such as *Sclerotinia sclerotiorum* and *Rhizoctonia solani*<sup>85</sup>. 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 microorganisms or altering soil management. Although disease suppressive soils have been assessed for agricultural systems, we

have limited knowledge about the prevalence of disease suppressiveness in native ecosystems.

#### Animal and insect health

**Beneficial roles of soils.** Soil microorganisms also have beneficial roles for animals and insects (TABLE 1 and FIG. 2). The soil environment can be a source of animal microbiomes, and microorganisms that animals ingest through



**Fig. 2 | How the soil microbiome influences one health.** Soil microbiota 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 microorganisms determine biogeochemical cycling processes on Earth, which have direct implications for climate change mitigation. Soil microorganisms such as mycorrhizal fungi, *Trichoderma* spp. and *Piriformospora* spp. are also known for their roles in plant nutrition, growth promotion, hormone regulation and stress control. However, not all soil microorganisms promote plant health and there are numerous soil-borne plant pathogens, including from the genera *Ralstonia*, *Rhizoctonia*, *Fusarium*, *Phytophthora* and *Gaeumannomyces*. Many soil-borne pathogens cause deadly diseases in animals, including nocardiosis, anthrax, malignant oedema and blackleg. Soil microbiota might even influence the social behaviour of animals. For example, a diverse soil microbiome may contain important bacteria capable of resupplying the mammalian gut microbiota, 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, and even use soils as detoxifying agents for making some food products edible and for medicinal reasons. People with more exposure to soils are less likely to suffer from allergic reactions. Coccidioidomycosis, fungal meningitis, diarrhoea, amoebic dysentery and helminthiasis are some examples of soil-borne diseases in humans.

food often originate from the soil. Many insects require endosymbionts such as various *Burkholderia* spp. clades for their growth and survival<sup>86</sup>. These endosymbionts are not only transmitted vertically from parents to offspring, but an increasing number of studies show that insects acquire these microorganisms by feeding on plants and being exposed to microorganisms originating from soil. For example, a recent study has demonstrated that foliar-feeding insects acquired microorganisms from the soil rather than the host plant, indicating that microbiome transmission in soil–plant–herbivore food webs may be widespread<sup>87</sup>. Insects can also acquire soil microorganisms that depolymerize insecticides, making themselves insecticide-resistant<sup>88</sup>. Such findings indicate that there is an evolutionary benefit for imprecise vertical transmission and microbiome fidelity to acquire new microorganisms and enable adaptation to changing environmental conditions<sup>89</sup>. Soil microorganisms can also be food; for example, nematodes, one of the most abundant groups of soil animals, thrive on their bacterial and fungal preys<sup>90</sup>. Soil microbiomes can even influence the health and social behaviour of soil-dwelling macroorganisms. For example, a recent study found that the abundance of the butyrate-producing bacterium *Kineothrix alysoides* in soil microbiomes was correlated to reduced anxiety in mice exposed through dust<sup>26</sup>. Similarly, exposure to soil can reduce allergic inflammation and have a positive influence on the gut–lung axis in mice<sup>27</sup>. Thus, a diverse soil microbiome can have positive implications for the gut health and mental health of soil-dwelling mammals. However, to what extent 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<sup>91</sup>, but which fraction of this finally ends up in herbivores or carnivores is less clear. Also, although it is well known that microbiome composition influences animal health both directly and indirectly<sup>92</sup>, it is still unclear how animal health might change in response to changes in the soil microbiome, that is, when animals are fed with more diverse food or when they are grazing in more diverse environments inhabited by a more diverse soil microbiome.

**Soil-borne animal pathogens.** Animal diseases can also directly develop from pathogen sources in soil and some of these pathogens can also directly or indirectly (as a zoonotic disease) infect humans. Transmission may occur through the disintegration of infected carcasses, infecting animals grazing nearby<sup>93</sup>. Soil-borne diseases in animals include nocardiosis, anthrax, malignant oedema and blackleg<sup>94,95</sup>. Nocardiosis is caused by the soil-borne actinomycetes *Nocardia* spp. and leads to localized or disseminated infection of mainly the lungs in a range of animals, including cats, dogs, guinea pigs and cattle<sup>94</sup>. Although nocardiosis is usually a self-limited and transient infection, in severe cases it can lead to tuberculosis or mastitis followed by anorexia, depression, fever, paralysis and cessation of milk flow. Similarly, soil-borne *Clostridium* spp. cause malignant oedema in sheep and other animals<sup>95</sup>. The soil-borne *Chlamydia psittaci* causes psittacosis (also known as ornithosis) in birds<sup>58</sup>.

### 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 and FIG. 2). Humans deliberately ingest soil to supplement a nutrient-poor diet<sup>35,96</sup>. Soils are also used as detoxifying agents for making some food products edible, as well as for medicinal reasons such as gastrointestinal treatments<sup>97</sup>. Furthermore, people with more exposure to natural environments are less likely to suffer from allergic reactions, which may be linked to soil microbiomes<sup>98</sup> and inhalation of soil particles. The western lifestyle accompanying small family size, intense 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<sup>99</sup>. The increase in allergic responses has been explained by the hygiene hypothesis, which predicts that greater hygiene leads to allergy due to insufficient stimulation of immuno-regulatory circuits in people<sup>98</sup>. On the other hand, the biodiversity hypothesis predicts that children growing up in farming environments have reduced allergic sensitivity as they are already exposed to a higher microbial diversity<sup>100</sup>. Together, these hypotheses highlight the importance of natural environmental microbiomes for human health. Whether specific microbial groups are responsible for this effect remains unclear and this is an area that deserves more research attention. For example, identification or isolation of microorganisms or microbial consortia that are potentially responsible for increased resistance to allergies and disease is highly relevant. Members of soil microbiomes can also directly act as food. For example, truffles, a fruiting body of some subterranean ascomycetes fungi, are 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 kilogram value three times higher than gold<sup>101</sup>.

Humans also obtain several essential elements from plant-based foods, and soil microbiomes regulate not only the cycling of those elements but also the health of all plants. For example, arbuscular mycorrhizal fungi deliver trace elements to plants, including zinc and selenium, which are important for human health<sup>64</sup>. 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 for essential vitamins<sup>102</sup>. Plants only produce small amounts of secondary metabolites, but beneficial microorganisms associated with them can enhance their production, including omega-3 (n-3) polyunsaturated fatty acids, linoleic acid, L-carnitine, choline or sphingomyelin, which can subsequently benefit animal and human health<sup>102</sup>. Furthermore, soil microbiomes are essential for food security. Healthy soils are linked to good soil structure, optimum nutrients and organic matter levels. Soil microorganisms mediate a wide range of environmental processes and soil ecosystem services, including purification of drinking water, stabilization of soil aggregates, carbon storage and the production of greenhouse gases



(for example, nitrous oxide and methane)<sup>41</sup>. 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 numerous soil-borne pathogens that can be harmful to human health. More than 300 soil fungal species are known to cause human disease<sup>103</sup>. *Coccidioidomycosis*, also known as valley fever, is caused by *Coccidioides* spp. commonly found in soils of the southwestern United States and Mexico<sup>104</sup>. *Exserohilum rostratum* caused a fungal meningitis outbreak in the United States in 2012 (REF.<sup>103</sup>). 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 worm larvae from soil<sup>70</sup>. For example, hookworm infection affects millions of people and causes more than 10,000 annual deaths worldwide<sup>105</sup>. Soil can also be a source of *Bacillus anthracis*, the causal agent of anthrax in humans<sup>70</sup>. Podoconiosis or chronic debilitating non-filarial elephantiasis is caused by nematodes and affects 1–2 million people. Tetanus can occur due to wound contamination with soils containing spores of *Clostridium tetani*<sup>58</sup>. *Escherichia coli* O157:H7 causes 73,000 infections per year in the United States<sup>106</sup> and it can persist for more than 90 days in soil<sup>107</sup>. Indeed, many facultative and opportunistic human pathogens can thrive in soils<sup>108</sup>. It is concerning that many pathogens in soils can be multiresistant, including a range of enterobacteria<sup>109</sup>. Although 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<sup>110</sup>. Whether this is also the case for members of the human microbiome remains speculation.

### Influencing factors

#### Edaphic factors

Soil habitat properties control the composition and function of the soil microbiome (FIG. 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 of their contributions to ecosystem processes and one health<sup>12,13</sup>. Soil moisture and temperature exert overarching effects on microbial communities 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<sup>111,112</sup>. Even when a wide range of soil properties were studied, pH emerged as the strongest predictor of microbiome composition. Important microbial groups such as Acidobacteria, Bacteroidetes and Actinobacteria display predictable patterns across pH gradients in soil<sup>111</sup>. A range of recent microbiome studies have shown that soil pH drives, directly and indirectly, the effects of soil microbial communities on plant

growth and ecosystem or soil multifunctionality<sup>113</sup>. For example, the ability of mycorrhizal fungi to forage for nutrients and deliver them to plants is directly linked to soil pH<sup>47,114</sup>. Interestingly, the reduced ability of mycorrhizal fungi to acquire nutrients at low soil pH is not only determined by soil pH but is also linked to the dominance of specific bacteria such as members of the Acidobacteriota with putative antifungal properties that are more dominant at low soil pH<sup>114</sup>.

Soil organic matter (SOM) content is another important driver of soil functioning. SOM has an overall positive effect on soil microbial diversity and community composition (for example, soil microbial biomass is strongly correlated to soil organic carbon content<sup>53</sup>). SOM offers carbon resources for microbial populations and is linked to the cycling and availability of other nutrients<sup>115</sup>. Needless to mention, SOM also has a direct effect on soil structure, oxygen and water availability<sup>116</sup>.

#### Global change factors

Global change factors directly threaten microbial contributions to ecosystem services<sup>17</sup> and one health (FIG. 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<sup>118</sup>. One of the strongest consequences of global climate change is increasing occurrences of drought. The decline of ecto-mycorrhizal fungal symbionts of trees owing to warming and drought can cascade below ground and accelerate SOM decomposition, reduce soil organic carbon content and alter ecosystem biogeochemistry<sup>119</sup>. Unlike drought, the effect of elevated CO<sub>2</sub> can be more complex and rising CO<sub>2</sub> can differentially alter microbial ecophysiological strategies with divergent effects on different functional groups<sup>120</sup>. Another potent global change factor is rising temperature. For example, the proportional abundance of soil-borne pathogens may increase with rising temperature<sup>121</sup>, altered humidity and precipitation<sup>122</sup>. Consequently, warming and altered humidity may enhance plant disease owing to a 'microbial loop'. However, context dependency is a major factor here as some soil ecosystems (for example, 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 whereas others may weaken<sup>123</sup>. A recent meta-analysis of 1,235 global change experiments found that the net effects of global change factors (warming, elevated CO<sub>2</sub>, drought, fertilization and land-use change) on microbial alpha diversity are highly variable, with rare microorganisms more strongly affected by global change than the dominant taxa<sup>124</sup>. These findings are important because several studies have shown that rare microorganisms drive pivotal ecosystem functions<sup>125</sup> and contribute to ecosystem multifunctionality<sup>126</sup>.

#### Antimicrobial resistance

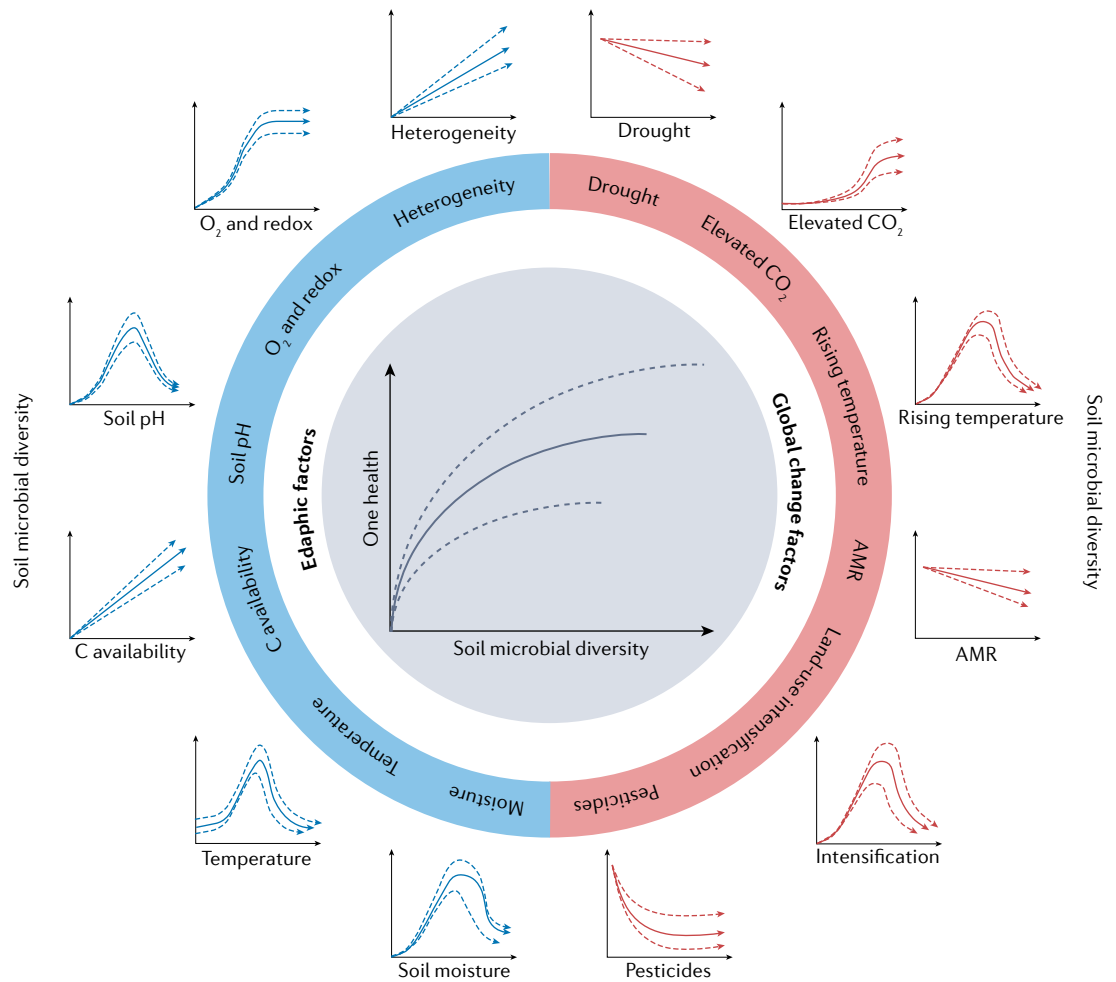
Soil microbial communities and their contributions to one health are further threatened by chemical pollution, including microplastics<sup>127</sup>, antibiotics<sup>128</sup> and pesticides (see below). Although antibiotics are the

#### Edaphic factors

Factors related to soil properties.

#### Global change factors

Natural or anthropogenic factors that are affecting environments globally.



**Fig. 3 | Factors governing the soil microbial contributions to one health.** Inner circle shows the association between soil microbial diversity and one health. Dashed lines indicate that this association may be context-dependent. The nature and strength of this association will depend not only on the ecosystem, but also on a range of environmental factors. Outer circle shows edaphic and global change factors that can regulate the contribution of soil microbial diversity to one health. The outer graphs represent hypothetical relationships between different 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 microorganisms 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. AMR, antimicrobial resistance.

foundation of global health, more than 700,000 people die annually from antimicrobial-resistant infections with a projection of up to 10 million by 2050 (REFS.<sup>129,130</sup>). It is concerning that as much as 32 tons of third- and fourth-generation antibiotics are annually used in meat and dairy industries<sup>131</sup> and antibiotics are also widely used by humans. 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 example, AMR genes can be detected 90 days after application of AMR-contaminated manure in soils and can be transferred from manure-amended soils to vegetables<sup>132</sup>. However, soil is also a natural source of a wide range of AMR genes<sup>133</sup>, used by microorganisms for survival and chemical warfare against competing microorganisms. Thus, although 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 microorganisms does 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 twenty-first century that alters the local biodiversity and affects ecosystem processes<sup>134,135</sup>. The total area of cultivated land worldwide has increased by more than 500% in the past five decades with a 700% increase in fertilizer use and a several-fold increase in pesticide use<sup>136</sup>. Such intensive practices can reduce the diversity and complexity of microbiomes and negatively influence beneficial microorganisms in roots and soils<sup>49,137–139</sup>. Land-use intensification can cause homogenization of soil microbial communities with dominance of a few taxonomic and/or trophic groups and a decrease in the

**Homogenization**

A decline in the differences between ecosystems owing to external factors often resulting in reduced diversity and dominance of certain microbial groups.

**Tipping points**

Critical points that may occur owing to a single or a series of environmental perturbations and may either lead to dysbiosis or an alternative stable or healthy state.

**Eubiosis**

A healthy and stable state of microbiota with high diversity and abundance of commensals.

**Redundancy**

An important trait of microbiome stability whereby some taxa are functionally replaceable as other groups can continue their functions.

**Resilience**

The ability of a microbiome to endure a perturbation and return to a healthy state despite encountering initial changes in structure and composition.

overall diversity<sup>140,141</sup>. Fertilizer use and management type have 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<sup>142</sup>. 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 by more than 40% in recent years, with as much as 1.2 million tons of active pesticide ingredients used annually<sup>143</sup>. A recent comprehensive study found that synthetic pesticides are widespread in soils<sup>144</sup> and residues can be detected even after 20 years of organic management, which does not apply any synthetic pesticides<sup>145</sup>. Although the effects of pesticides on soil microorganisms can be variable, a recent study found that pesticide residues had negative associations with the overall microbial biomass<sup>136</sup> and impaired the nutrient uptake machinery of beneficial mycorrhizal fungi<sup>147</sup>. 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**

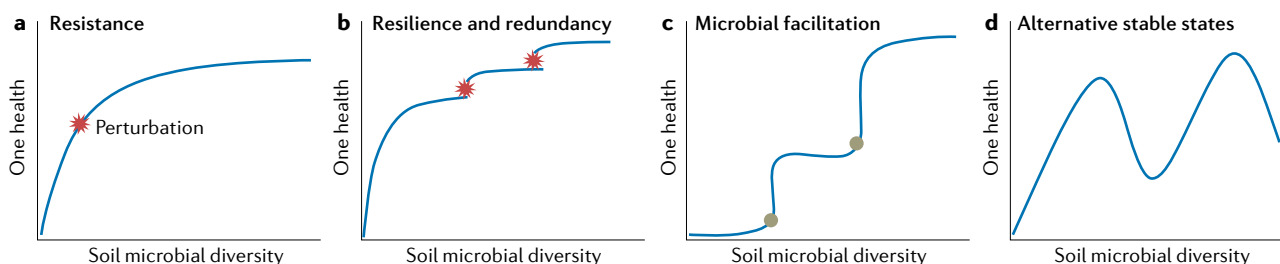
Soil microbial diversity can influence one health in various ways (BOX 2). A range of studies have revealed that soil microbial diversity is positively linked to various components of one health, including aspects of soil<sup>79</sup>,

plant<sup>20</sup> and ecosystem<sup>146</sup> health. The positive effects of soil microbial diversity are explained by the fact that different microorganisms provide different functions. Moreover, the resistance and resilience of soil microbiomes to disturbance is expected to increase with microbial diversity, that is, some groups that are susceptible to perturbations may be replaced by other 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 notion, the disruption of microbiome homeostasis (that is, dysbiosis) can cause impaired soil<sup>80</sup>, plant<sup>147</sup> and human<sup>148</sup> health and this is often linked to reduced microbial diversity, indicating the importance of biodiversity. 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<sup>149</sup>. 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<sup>150</sup>. 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).

**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 whether the conventional perception of health is sufficiently inclusive of defining and understanding microbial health. The World Health Organization (WHO) defines health as a state of complete physical, mental and social well-being and not merely the absence of disease or infirmity<sup>173</sup>. The importance of 'well-being' connects health to the one health premise. Maintaining a 'healthy' state requires 'eubiosis' of soil microbial communities, which is typically associated with high diversity and uniformity of representative microbiota<sup>1</sup>. 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<sup>174</sup>, and, as such, by definition, microbiomes are not stable. A range of experimental studies have demonstrated that although microbiome performance increases when diversity increases (see the figure, panel a), there is a saturation point of that promoting role of diversity<sup>175</sup>. Thus, a basic level of microbiome diversity seems 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 (see the figure, panel b). Moreover, the importance of soil microbial diversity for one health can also depend on the presence of specific taxa (for example, keystone taxa<sup>176</sup>) that play an important role (see the figure, panel c) in microbiome structuring and perform ecosystem functions such as

nitrogen fixation, detoxification, nitrification and pathogen suppression, facilitating one health. Thus, the establishment or disappearance of such taxa may lead to changes in one health. For example, the establishment of mycorrhizal fungi on small islands can facilitate tree growth and change ecosystem performance<sup>177</sup>. 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<sup>178</sup> (see the figure, panel d). The role of soil microorganisms as moderators of such alternative stable states is not well understood, but could be potentially strong considering the intimate association between soil microorganisms and other organisms and ecosystem processes. For example, 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<sup>179</sup>. Importantly, a healthy microbiome is not, by definition, diverse. Although 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 represent nearly 70% of the total microbiota<sup>180</sup>, 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.



## Insurance

In this hypothesis, biodiversity insures ecosystems against perturbations and decline in functioning, as a diverse community guarantees that some groups will maintain functioning in the event that other groups fail.

## Alternative stable state

A 'healthy' state that may occur owing to resilience in which the structure and composition of a microbiome are different from that of the original healthy state and yet the microbiome may continue to perform the same functions.

## Outlook

In this Review, we highlight that microbial health is woven into one health because the health of each of its components is determined by microorganisms. We propose that soil may be a reservoir of microorganisms that determines the plant, animal and human microbiomes. 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.

First, recent studies have shown that land-use intensification<sup>140</sup>, urbanization<sup>151</sup> and landscape simplification<sup>141</sup> 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 of pathogens or antibiotic-resistant bacteria requires further investigation. Recent observations that soil microbiomes in urban sites, compared with rural sites, contain more antibiotic resistance genes and genes associated with human pathogens<sup>151</sup> point in this direction. Moreover, animal livestock consumes the majority of the world's antibiotics<sup>152</sup>, 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.

Second, viruses may play a much more important role in soil communities than previously thought. A recent study measuring carbon flow with isotopically labelled plants demonstrated that the most heavily labelled organisms in the rhizosphere were two phages<sup>153</sup> and soils are reservoirs of substantial undescribed viral genetic diversity with viruses likely to be adapted to major microbial lineages<sup>154</sup>. How widespread viruses are in soils and to what extent they influence soil microbiome functions are still incompletely understood. Recent estimates suggest that viruses are highly abundant with  $10^7$ – $10^9$  virus particles per gram of soil<sup>155</sup>, but this number could be even higher considering the abundance of potential (microbial as well as invertebrate) hosts 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.

Third, chemical pollution is widespread<sup>127</sup> and it is not well understood how microbiomes are affected and whether this, in turn, affects human or ecosystem health<sup>156</sup>. Moreover, the soil microbiome is exposed to many chemical contaminants, including antibiotics, microplastics, 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<sup>117</sup>. 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<sup>157</sup>.

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<sup>158</sup>. Previous studies reported that pathogen invasion is hampered when soil microbial diversity is high<sup>79</sup>. Enhancing microbial diversity through targeted practices that are known to promote soil health and microbial diversity (for example, 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 microorganisms (for example, 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 through 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 microorganisms in one health should consider not only different groups of soil microbiota but also their associations with other groups including viruses, nematodes, earthworms and soil arthropods.

Finally, whereas the state of above-ground biodiversity is easy to monitor and already assessed in many countries, underground processes are more difficult to study and far less understood<sup>159</sup>. 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.

## Data availability

The data for microbiome composition in FIG. 1 are available in Dryad: <https://datadryad.org/stash/share/CPLkD5krQ1-Mgaai3T0eYgCTolnsN6tgK0sJ5GlQg>.

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**Competing interests**

The authors declare no competing interests.

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