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Review article

The interplay between microbial communities and soil properties

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Abstract

In recent years, there has been considerable progress in determining the soil properties that influence the structure of the soil microbiome. By contrast, the effects of microorganisms on their soil habitat have received less attention with most previous studies focusing on microbial contributions to soil carbon and nitrogen dynamics. However, soil microorganisms are not only involved in nutrient cycling and organic matter transformations but also alter the soil habitat through various biochemical and biophysical mechanisms. Such microbially mediated modifications of soil properties can have local impacts on microbiome assembly with pronounced ecological ramifications. In this Review, we describe the processes by which microorganisms modify the soil environment, considering soil physics, hydrology and chemistry. We explore how microorganism–soil interactions can generate feedback loops and discuss how microbially mediated modifications of soil properties can serve as an alternative avenue for the management and manipulation of microbiomes to combat soil threats and global change.

Sections

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Introduction

Soils harbour some of the most diverse microbiomes on Earth[1] (Box 1). This staggering microbial diversity is intrinsically linked to the breadth of environmental conditions found within soil. The remarkable spatiotemporal variability in soil physico-chemical properties has promoted microorganisms to evolve a wealth of different strategies to cope with the most extreme conditions. Since the pioneering work of Beijerinck and Winogradsky, soil microbial ecologists have been seeking to unravel the interrelationships between microbial communities and their environment. In recent decades, considerable effort in the field has been dedicated to determining which soil properties are shaping the soil microbiome. With methodological advances that enable more comprehensive investigations of soil microbial diversity, we know that soil properties such as pH, soil organic carbon and oxygen partial pressure emerge as key drivers of microbiome structure and microbial activities[2]. For example, metabarcoding of topsoil samples at a global scale showed the key role of soil pH in explaining the diversity and composition of soil bacterial communities[3]. Likewise, anoxic microsites in soil can effectively inhibit rates of microbial mineralization and selectively protect certain reduced organic compounds from decomposition[4]. By contrast, endeavours to unravel the effects of soil microorganisms on their habitat have been more limited and have mostly focused on the turnover of the carbon and nitrogen pools[5–7]. However, soil microorganisms are not only involved in nutrient and carbon transformations but also shape the soil habitat through various biogeochemical and biophysical mechanisms (Fig. 1).

Recent studies have shown that a range of novel microbial processes can affect the availability of elements in soil. Studies during the past few decades have revealed that microorganisms not only actively accelerate the weathering of rocks and minerals but can also build mineral structures by bio-precipitation[8–10]. Evidence is growing that these microbially mediated modifications of soil properties can have ecological ramifications and locally shape microbiome assembly and microbial activities. In particular, bio-weathering can increase nutrient availability in soil, thereby not only improving the fitness of microorganisms that have developed strategies to solubilize minerals but also of those present in the surrounding environment[11]. Yet, the broader biotic and abiotic relevance of such impacts that microorganisms can have on the soil habitat often remains overlooked.

The objective of this Review is to highlight that the relationships between soil properties and soil microorganisms are reciprocal owing to complex networks of causation and feedback effects that can have eco-evolutionary consequences. First, we illustrate how soil microorganisms can affect the physical and chemical properties of soil. Next, we discuss the ecological and evolutionary consequences of these microbially driven shifts in soil properties. Finally, we explore potentially fruitful research avenues for the management and manipulation of microbiomes to combat soil threats and climate change. Given that the influences of microorganisms on soil nitrogen and carbon pools have been covered in previous Reviews[12–15], we primarily focus on other soil properties, although we highlight some prominent examples that pertain to nitrogen and carbon pools.

Box 1

Diversity and functions of the soil microbiome

In soils, microorganisms are key drivers of organic carbon and nutrient cycling[174]. Thousands of microbial taxa, including viruses and members of all three domains of life, most notably bacteria, archaea, protists and fungi, can be found in a single gram of soil with an overall soil microbial biomass rivalling (at the global scale) aboveground plant biomass[2]. Microbial activities affect soil biogeochemistry[193] as well as atmospheric chemistry by producing and consuming greenhouse gases (for example, CO_2, CH_4 and N_2O)[194]. Microorganisms that metabolize organic carbon, usually releasing CO_2, are termed heterotrophs and are largely responsible for controlling the organic carbon budget in soils. Under anoxic (O_2-limited) conditions, anaerobic microorganisms can use electron acceptors other than O_2, including nitrate, oxidized iron (Fe(III)) and manganese (Mn(IV)), sulfate or even CO_2. Some bacteria can also convert atmospheric nitrogen into ammonia. This process of biological nitrogen fixation can be performed by free-living bacteria or by bacteria living symbiotically with plants and is responsible for adding more than 100 Tg N per year to soils globally[7]. The enormous diversity of microorganisms in soils and their extremely large range of metabolic activities continue to be discovered with meta-omics techniques[2]. The large amount of microbial diversity found in soil is a product of many interrelated factors, including the complexity of soil organic matter resources[195], the wide range of inorganic and organic electron donors and acceptors found in soil and the physical structure of soils, which can lead to pronounced microscale heterogeneity in environmental conditions (including pH, O_2 concentration, moisture conditions and resource availability)[196].

Soil properties and microorganisms

Soil pH

pH is often described as the master soil variable as it influences a wide range of soil chemical and biological processes[16]. Microbial activities related to biogeochemical cycling of carbon, nitrogen and sulfur are the most notable microbial processes that generate protons and hydroxyl ions, therefore affecting soil pH[17] (Fig. 1). In the carbon cycle, the dissolution of the CO_2 produced by microbial respiration to form carbonic acid (H_2CO_3) in the soil solution is a source of protons, which leads to soil acidification. Recent work suggests that only one-third of the CO_2 produced by soil respiration is directly emitted to the atmosphere, whereas the remaining CO_2 is consumed by dissolution in the soil solution, biological activities and chemical reactions (for example, chemical carbonate weathering)[18]. Cyanobacteria, similar to other photosynthetic autotrophs, alkalinize their microenvironment owing to their CO_2 fixation activity, which requires proton pumping[19]. Both free-living and symbiotic fungi as well as bacteria can produce and secrete organic acids (for example, oxalate or citrate), which can contribute to soil acidification[20]. In a recent study[21], researchers have estimated that most of the organic acids that enter the soil solution are likely to be produced by microorganisms, not plants. Conversely, oxalate catabolism by bacteria is associated with a strong soil pH increase of up to 2.5 units[22,23]. In the nitrogen cycle, the oxidation of ammonium to nitrate by bacteria and archaea during nitrification produces protons and is a well-known soil-acidifying process, especially in arable soils with nitrogen fertilization[24]. For example, a study[10] showed that nitrification resulted in a soil pH decrease from 7.5 to 6.4 within a

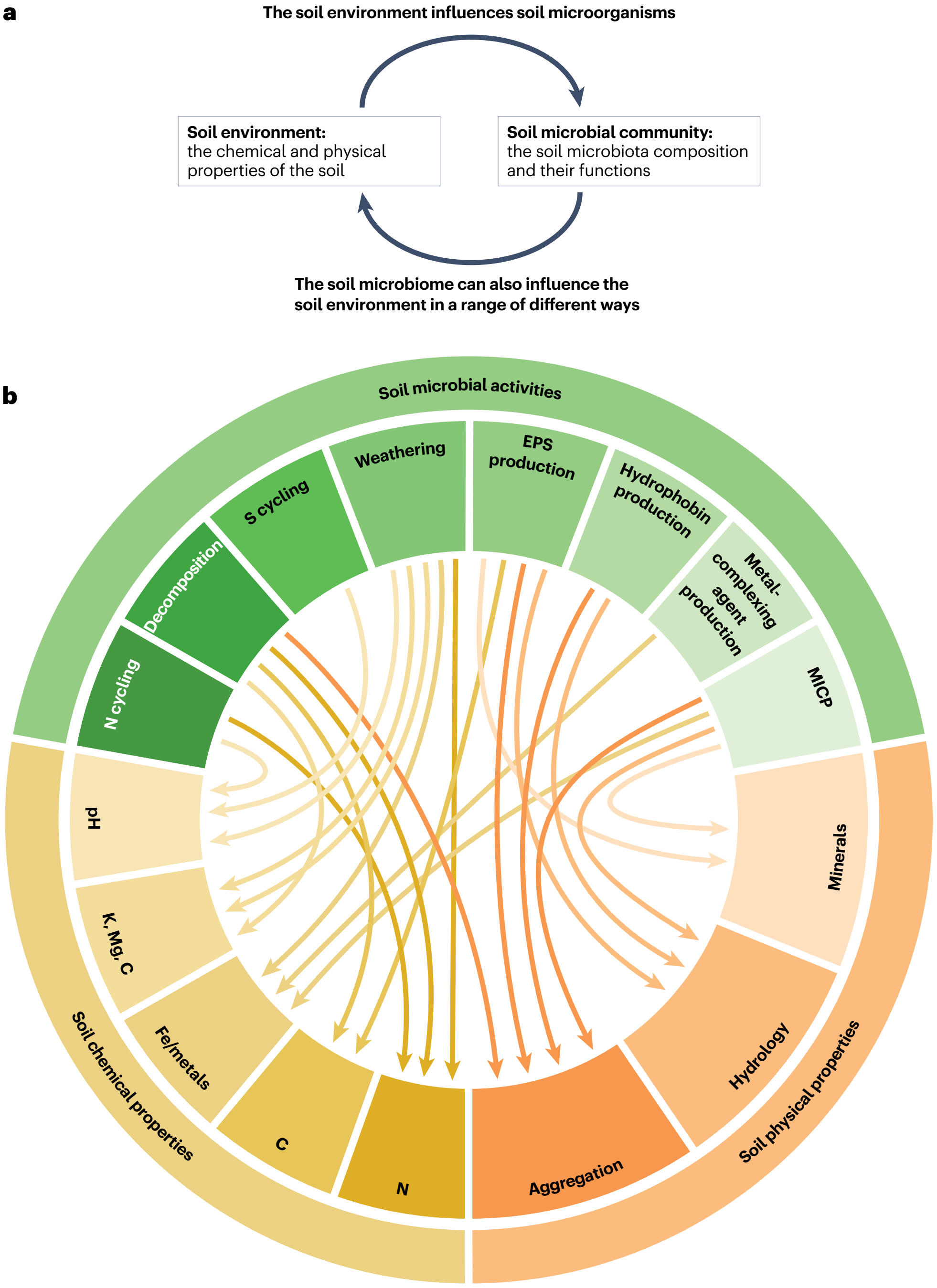

Fig. 1 | The interplay between soil environmental conditions and the soil microbiome. a, Soil properties, such as pH, soil organic carbon and oxygen partial pressure, are shaping the soil microbiome composition and function. Soil microorganisms also exert an effect on their habitat through various biogeochemical and biophysical mechanisms. The latter has received less attention with most previous studies focusing on microbial contributions to soil carbon and nitrogen dynamics. **b**, This schematic summarizes the various microbial processes (in green) affecting soil chemical (in yellow) and physical properties (in orange). The colour of the arrow indicates the affected soil properties. EPS, extracellular polymeric substance; MICP, microbially induced carbonate precipitation.

month, whereas depletion of the soil nitrifier *Nitrosospira* sp. through community manipulation led to an increased pH of 1 unit compared with the control soil[25]. By contrast, ammonification and denitrification are proton-consuming processes and consume only half the amount produced by nitrification per mole of nitrogen. Environmental alkalinization by fungi is a frequently observed, yet not well-understood, phenomenon[26,27]. Often, this process is mediated by ammonia, a highly basic compound, which is generated as a by-product of protein and amino acid catabolism and secreted or exported from hyphae[28]. As the nitrogen:sulfur ratio in surface soils is in the range of 8–12:1, the contribution of the sulfur cycle to the generation of protons and hydroxide ions is roughly one-tenth of that of the nitrogen cycle. In well-aerated soils, more than 90% of the sulfur is usually present in organic forms[29], with the mineralization of organic sulfur generating acidity. Likewise, oxidation of inorganic sulfur compounds by bacteria and fungi can also lead to soil acidification[30–32]. A number of other biogeochemical cycles can also generate proton and hydroxide ions, such as redox reactions that involve iron and manganese as well as weathering reactions involving calcium, magnesium, potassium and phosphorus. Bacteria and fungi can thus actively alter soil pH, which, in turn, is a primary factor often structuring soil microbial communities[2].

Soil minerals and metals

Bacteria and archaea have evolved enzymatic pathways that enable them to use various metal ions to harvest reducing equivalents and generate energy. Iron, as the fourth most abundant element in the earth crust, has a prominent role in this regard. Although oxidized iron, that is, Fe(III), can be used as an alternative electron acceptor to O_2 for respiration under anoxic conditions, the reduced Fe species, that is, Fe(II), can be used as electron donor coupled to the enzymatic reduction of O_2, nitrate or even CO_2 in anoxygenic photosynthesis[33]. For example, anaerobic oxidation of methane by archaea with Fe(III) acting as electron acceptor and subsequent Fe(II) accumulation has been reported in paddy soils and flooded forests[34,35]. As the solubility of iron at circumneutral pH conditions varies with the redox state, Fe(II) generally being more soluble than Fe(III), the redox transformation of iron is often associated with mineral precipitation or mineral dissolution with consequences for soil redox and sorption properties (see the next section). Likewise, manganese, and even toxic metals such as uranium and chromate, can be oxidized and reduced. As their solubility varies depending on their redox state (dissolved Mn(II), Cr(VI), U(VI) versus precipitated MnO_2, Cr_2O_3, UO_2), microbial redox transformations of these metals also determine their solubility and bioavailability, and as a consequence, their toxicity or their availability as electron acceptors or donors thus influences the ecological responses of soil microorganisms[36]. Fe(II)-oxidizing and Fe(III)-reducing bacteria are also known to produce mixed-valent redox-active minerals such as magnetite (Fe_3O_4 with an ideal stoichiometry of Fe(II):Fe(III) of 1:2) or green rust phases; that is, sulfate-bearing, chloride-bearing or carbonate-bearing layered Fe(II)–Fe(III)-containing minerals. These minerals are reactive and further transform into other phases such as goethite over time[23]. Because they can contain varying ranges of Fe(II)/Fe(III) ratios, they also possess a broad range of redox potentials (from reducing to oxidizing), which enables a diverse community of soil microorganisms to use these minerals either as electron donors or as acceptors[37]. As a consequence, the microbial formation of such reactive, meta-stable minerals can affect soil redox and sorption processes.

In addition to serving energy-generating purposes, metal ion constituents of minerals or mineral-associated elements such as phosphorus or trace elements such as zinc (Zn), molybdenum (Mo) or cobalt (Co) are also needed as nutrients by soil microorganisms and plants (for example, metal ions as catalytic centres in enzymes). Because most of these essential metal ions are present either in the form of poorly soluble minerals (Fe(III) (oxyhydr)oxides and Mn oxides), adsorbed to surfaces or co-precipitated with minerals, soil microorganisms have developed weathering strategies to increase the solubility, and thus the bioavailability, of these metals (Fig. 2a). This is achieved either by acidification of the soil environment, thus increasing metal solubility[20,21], or by synthesis and excretion of metal-complexing agents (for example, organic ligands complexing Fe and also other metal ions such as Zn, Cu and manganese[38,39]). In particular, the microbial release of protons, organic acids (such as citrate or oxalate) or metal-complexing siderophores can contribute to biological weathering of minerals including granitic bedrock and silicates[10,40–43]. This release of elements from the alteration of rocks and minerals can further change the geochemical and mineralogical conditions in the surrounding soil environment[44]. We also know that some protists, including testate amoeba, can take up silicic acid from the soil to build skeletons composed of amorphous silica, a process called biosilicification. In forest soils, biosilicification from testate amoebae was comparable in magnitude to the silica released by trees through litter fall, which highlights the relevance of protists to soil silica dynamics[45,46].

Bacteria and fungi are not only involved in mineral dissolution and mineral formation via redox transformations of metal ions but they can also induce the precipitation of carbonate minerals by changing the CO_2 and bicarbonate concentrations (metabolic by-products) and soil pH (Fig. 2). Microbially induced carbonate precipitation (MICP) can affect many physical and mechanical properties of soils, which results in reduced hydraulic conductivity and increased shear strength[34]. Some of the relevant microbial metabolisms involved in MICP are ureolysis, denitrification and photosynthesis[47]. For example, in the urea hydrolysis process, urea is hydrolysed by microbial ureases, forming ammonia and carbamic acid. Carbamic acid is then hydrolysed to produce ammonia and carbonic acid, which in turn generate bicarbonate ions (Fig. 2b).

Soil structure

Soil structure, the 3D arrangement of soil particles and corresponding pore spaces, is likely to be one of the most far-reaching soil parameters modified by the soil microbiome[48,49]. This microbial influence is dynamic, counter to the intuition that 'structure' is a static soil property. Soil aggregates, that is, groups of primary soil particles that cohere to each other more strongly than to other surrounding particles, are building blocks of soil structure, continuously formed, stabilized and disintegrated again. These processes are under the influence of the microbiome, among other drivers, as microorganisms can affect the spatial arrangement of soil particles, stabilize this architecture via their cells and metabolic products and lead to aggregate disintegration as they catabolize the binding agents that hold soil particles together[50]. The soil microbiome can also have indirect effects on soil aggregation, for example, via the effects of mycorrhizal fungi or other root-associated fungi, viruses or bacteria on plants and plant communities[51].

A number of experimental studies have identified a clear role for soil microorganisms in soil aggregation[52], with bacteria and fungi typically having a larger influence than soil fauna. Bacteria are important for the formation of macroaggregates and microaggregates (those smaller than 250 µm), whereas fungi are most important for macroaggregate formation[53]. Fungi have been the focus of much of the work on soil aggregation, as their filamentous nature makes them effective agents for particle enmeshment and physical entanglement, together with the production of binding agents, and the production of amphiphilic proteins that can modulate surface polarity, that is, hydrophobins (Fig. 3). In particular, a meta-analysis has revealed strong positive effects of arbuscular mycorrhizal fungi, which are symbionts of most land plants, on soil aggregation[54]. Contributions of microorganisms to soil aggregation have recently been examined using trait-based approaches[55], whereby functional characteristics are used to predict the importance of particular taxa to soil aggregation. As an example, for saprobic fungi, important mycelial traits included mycelium density (that is, mycelium biomass per area) and a lack of lytic enzymes[52] that break down aggregate binding agents. Extracellular polymeric substances (EPSs), including polysaccharides, proteins and lipids, also have a role as binding agents for aggregates, which also applies to bacteria[56,57]. Cyanobacteria, as part of biocrust communities near the soil surface, can contribute to soil stabilization via production of EPSs[58]. Moving beyond the scale of soil aggregates to smaller scales,

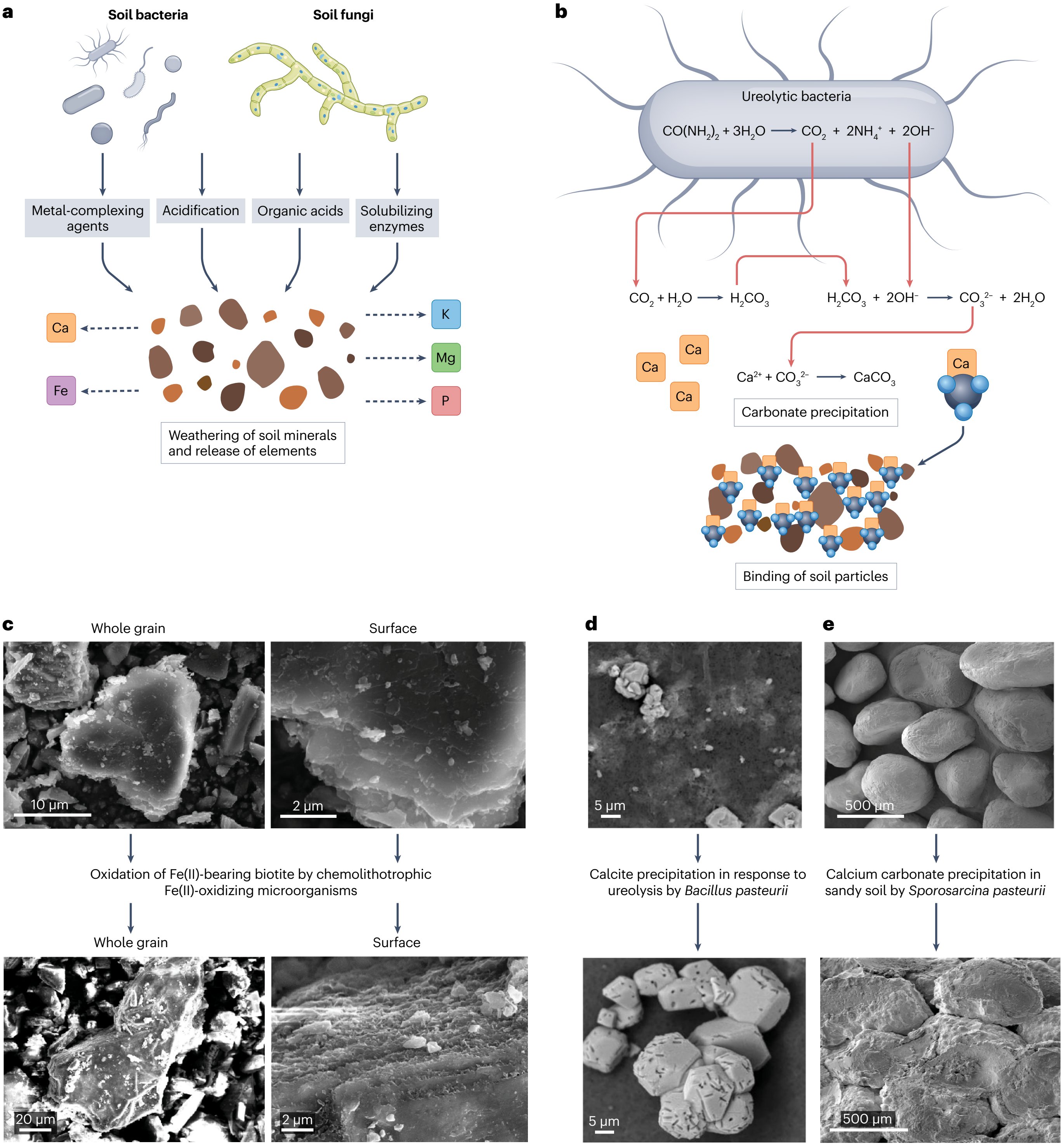

Fig. 2 | Microorganisms break down minerals and build mineral structures. **a**, Microbial processes involved in mineral weathering. The release of protons and/or organic acids by microorganisms is decreasing the pH, resulting in enhanced mineral dissolution rates. Metals can also be released from the minerals by solubilizing enzymes or by complexing agents that are chelating to metal ions at the mineral surface. **b**, Calcium carbonate precipitation induced by ureolytic bacteria results in the binding of soil particles. **c**, Scanning electron microscopy images of biotite at the whole-grain scale (left) and basal plane (right) showing substantial alteration of the basal plane of biotite after microbial inoculation. **d**, Scanning electron microscopy images of calcite precipitates generated by microbially induced carbonate precipitation 7 days after inoculation with *Bacillus pasteurii*. **e**, Scanning electron microscopy images of untreated sand and fracture surfaces of processed sand after microbially induced carbonate precipitation by *Sporosarcina pasteurii*. Part **c** adapted with permission from ref. 10, PNAS. Part **d** adapted with permission from ref. 188, Taylor and Francis. Part **e** adapted with permission from ref. 189, Oxford University Press.

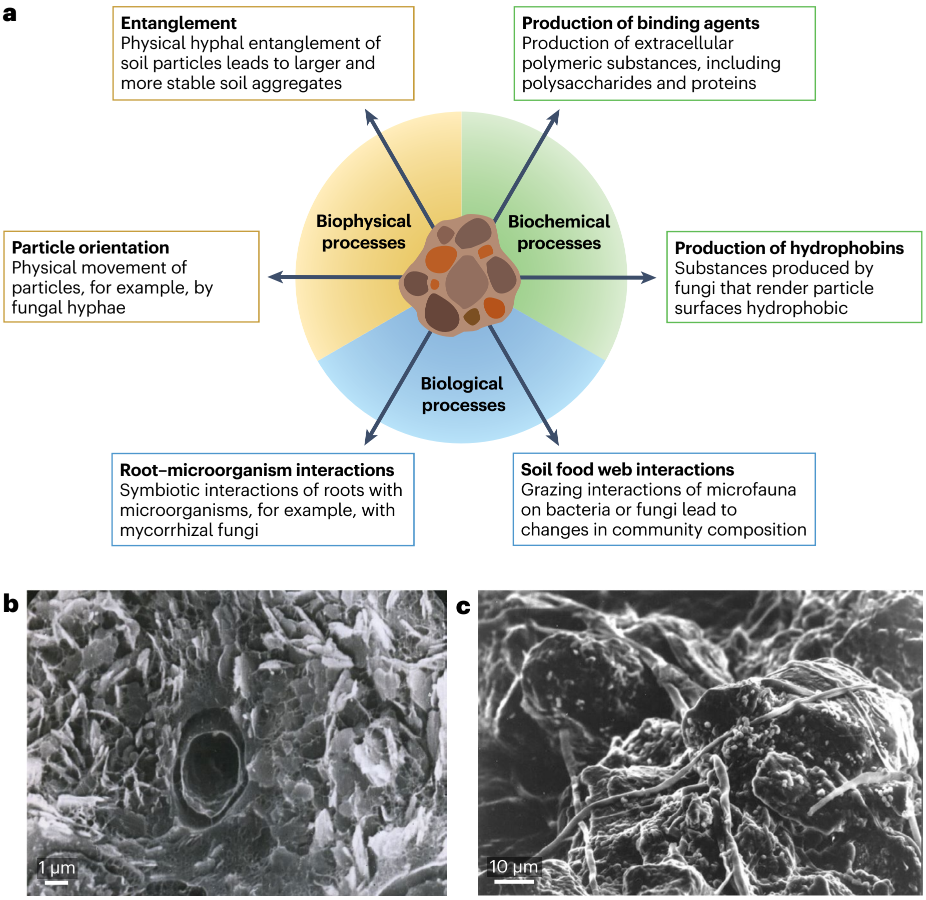

Fig. 3 | Microbial processes that affect soil aggregation. a, Soil bacteria and fungi are affecting soil aggregation in many ways including biophysical, biochemical and biological processes. **b**, Electron microscopy image of fungal hyphae aligning clay (kaolinite) particles and exuding extracellular polymeric substances that aggregate clay particles. **c**, Electron microscopy image detailing the entanglement by fungal hyphae. Bacteria can also be observed at the surface of aggregates. Part **a** adapted with permission from ref. 190, Elsevier. Part **b** adapted with permission from ref. 191, Elsevier. Part **c** adapted with permission from ref. 192, Taylor and Francis.

microbial interactions with clay minerals also become important[59]. Bacteria and fungi form biofilms on mineral and organic surfaces and change properties of minerals by weathering, and microbial cells or cell products adhering and adsorbing to these particles can create conditions conducive to the formation of microaggregates[60]. Thus, various microbial groups affect soil aggregation from the smallest scales (for example, mineral modification and interaction), to intermediate scales (for example, soil aggregate stabilization via fungal hypha) and to the largest scale (for example, changes in plant community composition by arbuscular mycorrhizal fungi translating into effects on soil structure).

Soil water

Microorganisms are not just passively responding to soil moisture levels[61], but can also actively alter soil water-related properties, such as the infiltration of water into soil, water retention and evaporation (Fig. 4). There are at least three broadly defined mechanisms by which microorganisms can alter soil hydrology. First, bacteria and fungi can secrete compounds that directly alter soil water dynamics. These compounds include EPSs that increase the water retention of soils and sands[62–64], decrease the hydraulic conductivity by clogging macropores[65–67], slow down the rate of evaporation from soil[64,68,69], attenuate rewetting rates owing to the development of hydrophobicity[62,66,70] and maintain the continuity of the liquid phase in dry conditions owing to smaller pore sizes that do not desaturate easily, therefore enabling the diffusion of nutrients and metabolic products to take place[71,72]. The mechanical and hydrological properties of these microhydrological niches were demonstrated to be emergent properties of the interactions between the EPS hydrogels and the soil particles[73–75]. Likewise, fungi can produce compounds coating soil particle surfaces, which alter the magnitude and direction of soil water repellency[76]. Such compounds include a wide range of amphiphilic compounds (for example, hydrophobins) that can be either hydrophobic or hydrophilic depending on the conditions.

Second, as detailed earlier, microorganisms can alter soil particles, pore organization and cohesion of the soil structure, thus affecting soil water retention and infiltration rates[77] (Fig. 4). In the past 15 years, the rapid development of X-ray microcomputed tomography has made it possible to obtain unprecedented 3D images of the pore system of undisturbed and moist soil samples, as well as quantitative information on the size, shape, volume and connectivity of soil pores. A comparison of the pore system of soils incubated with organic compounds to stimulate microbial growth, versus a sterile reference soil, has shown that microbial activity generally increases the volume of soil micropores[78–81], which are those pores that are capable of holding available water through capillary forces, thereby increasing water retention (Fig. 5).

Third, there is some evidence that microorganisms can facilitate the movement of water through soil. This phenomenon is best studied for mycorrhizal fungi, which can, under certain conditions, effectively increase root water uptake, passively facilitating movement of water between plants along their hyphae, and alter the distribution of water through the soil profile[82,83]. These effects of mycorrhizal fungi on soil water availability can be large enough to mitigate the effects of drought on plant productivity[84–86]. The magnitude of mycorrhizal contributions to water movement can be high, with a recent study demonstrating that water transported along mycorrhizal hyphae accounts for nearly 35% of the water transpired by host plants[87]. Although there are other microorganisms in soil, including filamentous bacteria and saprophytic fungi, that may also be capable of re-distributing water through soil, the contributions of non-mycorrhizal microorganisms to water transport in soil have not been well studied.

These three mechanisms by which microorganisms can alter water availability are not necessarily independent. Given the broad diversity of microbial taxa found in soil, even within individual aggregates[88], these processes could occur simultaneously or be stratified across different locations within a given soil profile. Likewise, any effects of microorganisms on soil hydrology are not static over time. This complexity of microbial contributions to soil hydrology, and the corresponding complexity in soil hydrology (even in the absence of microbial activity), makes it challenging to predict a priori the magnitude by which microorganisms may alter available water in a given soil.

Ecological consequences

Microbially mediated modifications of soil properties generate ecological feedbacks

Owing to the large range of soil properties that can be modified by microorganisms, one could expect that some of these microbially driven shifts in soil properties will affect the fitness of the modifying microorganisms. If these modifications are persistent in time, microorganisms can affect selective pressures across generations with possible adaptive evolution in response to the changes in the environment. Such processes, whereby organisms actively modify their own selective environment, were central to the development of the niche construction theory[89,90]. Typically, niche construction theory embraces the concepts of evolutionary niches and ecological inheritance to predict that organismal modifications of the environment can have ecological consequences on the contemporary biota that initiate an evolutionary response. As such, the basic premise of the niche construction theory is that organisms can act as potent agents of natural selection by modifying biotic and abiotic environmental conditions. Although it has been suggested that niche construction may be a general phenomenon, the eco-evolutionary feedbacks of microbial modifications to the soil remain understudied. Yet, laboratory studies have demonstrated the large potential of niche construction by microorganisms[91] with adaptive niche construction emerging within approximately 100 generations, which was evidenced by a lower fitness of evolved *Pseudomonas* strains in the ancestral environment[92]. An emblematic example of microbial niche construction is the release of oxygen by cyanobacteria triggering the great oxidation event (GOE), a period that lasted more than 200 Myr (ref. 93) during which the transformation of the atmosphere of the entire planet provided a competitive advantage to aerobic organisms[94–96]. The GOE also irreversibly transformed the surface mineralogy of the Earth and may be directly or indirectly responsible for most of the known mineral species of Earth[97,98]. There is also increasing evidence that mineral type, in combination with the identity of the organic carbon substrate, can have an impact on soil microbial community assembly and composition over relatively short time spans of 6–18 months[99–102], therefore indicating that mineral transformation can modify the selective pressure on microorganisms. For example, researchers[102] have shown that changes in Fe(III) (oxyhydr)oxide identity (ferrihydrite, goethite or hematite) and resource availability could shift Fe(III)-reducing communities from dominantly metal-respiring organisms (*Geobacter* sp.) to fermenting (*Enterobacter* sp.) and/or sulfate-reducing organisms (*Desulfovibrio* sp.), which can reduce more recalcitrant Fe pools. Soil minerals are also transformed through microbial weathering, which may also confer a direct fitness advantage by providing access to limiting elements[11,103,104]. In fact, transcriptional analyses have shown that some soil fungi, such as the ectomycorrhiza *Amanita pantherina*, upregulate both the expression of enzymes that accelerate weathering and the expression of high-affinity

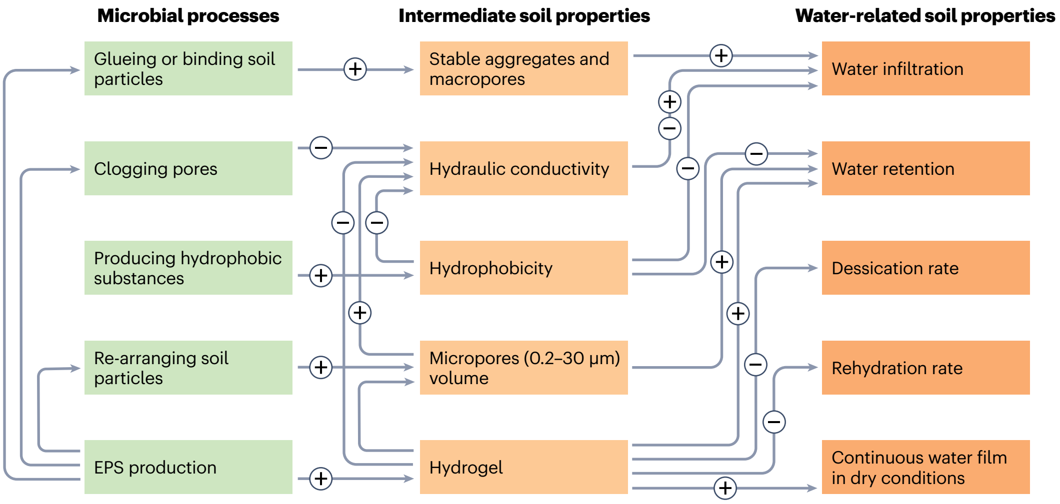

Fig. 4 | Microbial processes with varying impacts on water-related soil properties. Microbial processes are shown in green in the left panel, and the modified soil properties and consequences for soil hydrology are represented in the middle and right panels, respectively. For example, microbial production of extracellular polymeric substance (EPS) is also linked to the re-organization and binding of soil particles as well as to the clogging of pores. All these processes can directly or indirectly alter hydrogel formation, micropore sizes, aggregate stability and hydraulic conductivity with consequences for soil hydrological dynamics.

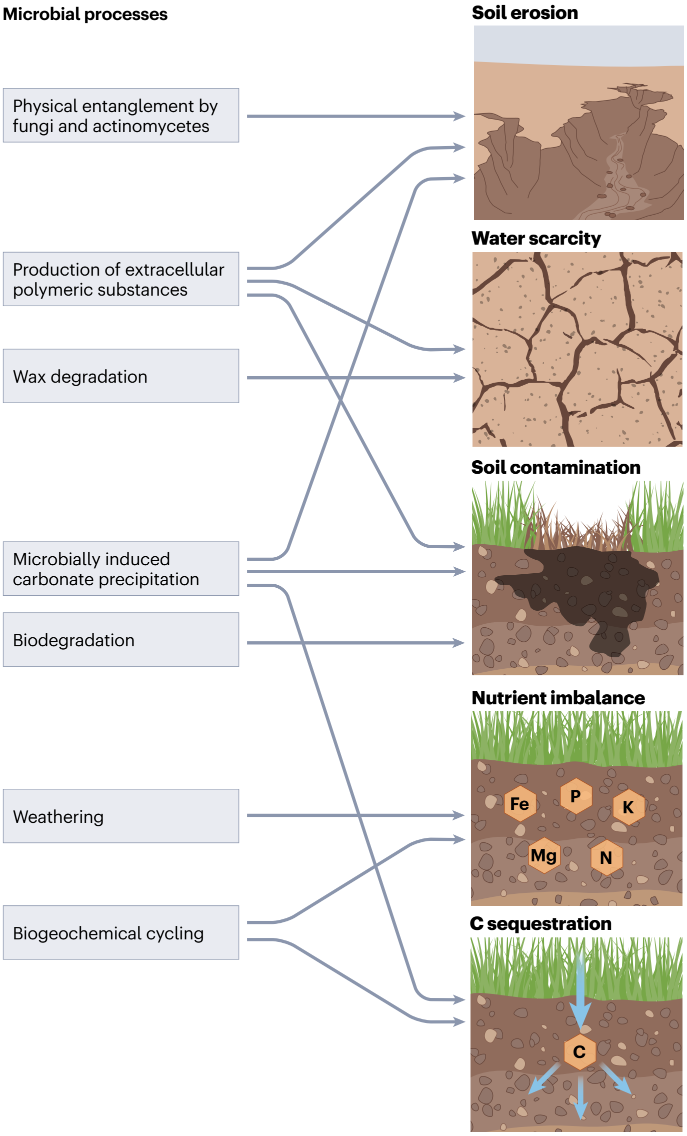

Fig. 5 | Harnessing microbial communities to combat soil threats and global change. Examples of microbial processes (that is, physical entanglement, production of extracellular polymeric substances, wax degradation, carbonate precipitation, biodegradation, weathering and biogeochemical cycling) that can be used to mitigate soil erosion, reduce soil contamination and drought as well as to improve nutrient imbalance and carbon sequestration.

potassium-transporter systems when exposed to potassium-bearing minerals[105]. This observation supports the hypothesis that weathering has led to adaptations for enhancing the release and the uptake of mineral nutrients. Changes in soil properties through EPS production are also candidates for positive microbial niche construction as EPS production can mitigate selective pressures by offering protection against biotic and abiotic stressors such as salinity and drought[57,106,107], thereby maintaining environmental conditions conducive to growth. As an example, researchers[108] showed that soil *Pseudomonas* sp. subjected to desiccation produced more EPS, which served to effectively slow water loss from soil and maintained the continuity of the water phase in soil even in dry conditions, thereby enabling diffusion of nutrients to bacteria to still take place in such conditions.

However, microorganisms may also alter their local environment in a manner that could reduce their overall fitness[95]. Such negative feedbacks have been reported in a laboratory experiment whereby soil bacteria acidified a glucose medium to the point that led to their extinction[109]. The alteration of soil hydrology over time by EPS production can also lead to negative feedbacks. For example, an increase in water retention owing to microbial production of EPS can eventually lead to the clogging of soil pores, inhibiting microbial activity over time as EPSs accumulate and preferential flow paths are reduced[71]. However, the extent to which direct negative feedbacks caused by niche alteration may occur in the complex microbial communities found in natural environments remains unclear.

Indirect positive and negative feedback loops

Organisms living in soil form diverse and complex communities with a myriad of interactions (Box 2). As such, niche construction by some community members can modify the local environmental conditions sufficiently to alter the fitness of the other organisms present in their surroundings. Microbial niche construction can also translate into fitness changes of the species that are competing or cooperating with those affected by the modified environmental conditions[110]. Such indirect feedback loops caused by microbially mediated shifts in environmental conditions through changes in microbial interactions have been reported in soil aggregates. For example, a shift from oxic to anoxic conditions in aggregate interiors owing to microbial respiration when oxygen diffusion is limited provides a competitive advantage to bacteria able to use oxidized forms of nitrogen as alternate electron acceptors and leads to increased denitrification activity[111–113]. Similarly, researchers[114] have shown that manipulation of oxygen concentrations as well as of the metabolism of a *Pseudomonas* strain to reduce its ability to modify the oxygen environment can change adaptative radiation dynamics, therefore providing experimental evidence of microbial evolution by niche construction. As fungi are often considered less sensitive to drought than bacteria[115–117], the fungal production of hydrophobic compounds that reduce water infiltration in soil may provide them with fitness advantages over bacteria[118]. Many soil microorganisms influence metal bioavailability by producing siderophores, which are complex organic molecules chelating solid-phase ferric iron, thereby enabling iron to be solubilized and taken up via siderophore receptors[38]. As such, sequestration of soil iron mediated by siderophore production provides a fitness advantage by making iron unavailable to competitors[119–121]. Conversely, some siderophore–iron complexes can be taken up by siderophore 'cheaters', which scavenge siderophores but do not produce their own siderophores, thus being able to outcompete non-exclusive siderophore producers[122,123].

Biological soil crusts, which are widespread and cover about 12% of the terrestrial surface of the Earth[124], can also generate ecologically relevant feedback loops. Biocrust formation is typically initiated by pioneering filamentous, bundle-forming cyanobacteria, such as *Microcoleus vaginatus* and *Microcoleus steenstrupii*, which aggregate soil particles and stabilize the surface of loose soils[125,126]. It is well established that biocrusts can influence the diversity and composition of microbial communities through shifts in key soil properties such as nutrient availability, water retention, pH, silt and clay content[127–129]. For example, the biocrust microbiome associated with *M. vaginatus* differs from the microbiome found in bulk soil by selecting for diazotrophic bacteria[130]. Thus, by creating habitat and resources that can be exploited by other organisms, microorganisms living in biocrusts can alter selection pressures and influence successional dynamics involving other cyanobacteria, bacteria, fungi as well as the lichens and bryophytes at the later stages of crust development[131].

Many questions about the ecological and evolutionary consequences of microbially mediated modifications of soil properties remain open. For example, what is the relative importance of such modifications of the local habitat compared with other environmental factors known to affect microbial fitness? To what extent are microbially mediated modifications of soil properties followed by evolutionary effects beyond changes in selection pressures? Soils are extremely heterogenous in their characteristics at the microscale and can be viewed as a mosaic of contrasted microbial habitats. Methodological challenges related to the analysis of microscale soil habitats and their inhabitants[132,133] have clearly been a bottleneck to addressing these and other questions. In addition, the ecological ramifications of microbial modifications of their habitat have also been underappreciated. Niche construction theory can provide a useful conceptual framework to deepen our understanding of these feedback loops between soil microorganisms and their physico-chemical environment.

Changing land use and climate

Importance of land management practices for microbially mediated shifts in soil properties

Decades of research have shown that many anthropogenic activities can fundamentally alter both soil properties and composition of the soil microbiome[134,135]. However, the extent to which the impact of land management practices on the soil microbiome can also indirectly contribute to changes in soil properties through niche construction has rarely been investigated. Indeed, despite numerous methodological advances in the field, it remains challenging to disentangle the direct effects of changes in land management practices on soil properties from the indirect effects mediated by the altered soil biota. For example, tilling and plowing practices whereby surface soil layers are mechanically mixed before planting can have detrimental effects on fungal hyphal networks and bacterial exopolysaccharide production[48,136,137], both of which can lead to a reduction in soil aggregate stability as described earlier. Likewise, tilling can promote soil erosion, particularly when high intensity rain or wind events occur when bare soils are exposed before crop planting[138]. This erosion can be further exacerbated by the disruption of biocrusts and filamentous microbial growth that stabilize aggregates. Combatting erosion is one reason for the increased adoption of no-till agriculture worldwide, as the structure of surface soils is often improved over time by promoting the maintenance and recovery of microorganisms, which enhance aggregation[139].

Croplands as well as managed grasslands and forests also typically receive increased inputs of nutrients via the addition of organic or inorganic fertilizers. Such fertilizer inputs can have persistent impacts on the soil microbiome[140–142]. Most notably, application of ammonium or urea-based fertilizers can promote the activity of nitrifiers[143–145], which can substantially increase soil acidity (as noted earlier). Such nitrification-associated increases in soil acidity can be sufficiently large to necessitate the application of lime to agricultural fields, an additional expense for farmers. Similar microbially mediated acidification can

Box 2

The interactions of microorganisms with plants and fauna mediate shifts in soil properties

Microorganisms are not the only organisms with strong potential impacts on soil properties. Plants, as well as earthworms, microarthropods, nematodes, protists and other organisms, are also well known to affect, and to be affected by, soil properties, therefore resulting in a complex interplay between organismal-mediated modifications of soil properties. For example, the acidification caused by nitrification occurs mostly in the uppermost soil horizons, where most plant-accessible nutrients are found. By taking up the nitrate produced by nitrification, plant roots can buffer the acidifying effect of nitrification by releasing OH^- or HCO^- into the rhizosphere to counterbalance the corresponding excess of negative charges[197]. Plants can not only produce phytosiderophores, which scavenge Fe^{3+}, but can also take up microbial siderophores for their nutrition in iron-limiting conditions[198,199], therefore affecting iron availability in soil. In anoxic soils, the oxygen leaking from root aerenchyma can react with the Fe^{2+} produced by iron(III)-reducing bacteria, causing the formation of an iron plaque consisting of orange-brownish Fe(III) (oxyhydr)oxide minerals and biological cementation[200]. By enhancing their allocation of photosynthates to ectomycorrhizal fungi under phosphorus-limited conditions, *Pinus* trees increased apatite dissolution by the fungal partner, highlighting the importance of plant–fungi interactions in biological weathering[201]. Some plants, as well as fungi and termites, can produce oxalic acid and oxalate minerals as secondary compounds that can be used by oxalotrophic bacteria as energy and carbon sources[202,203]. This microbial oxidation of oxalate to CO_2 leads to bicarbonate ion excretion and soil alkalinization, and eventually to $CaCO_3$ precipitation, which can alter soil structure by binding loose particles and filling pores.

Our understanding of the interactions between soil organisms is still in its infancy. For example, it is now accepted that soil protists have a substantial role in nutrient cycling mostly by releasing nutrients via predation of soil bacteria and fungi[204]. However, a few studies have shown that microbial predation by protists can also affect soil physical properties. For example, additions of the bacterivorous protist *Acanthamoeba castellanii* increased the formation of soil aggregates, which may be a consequence of bacteria increasing the production of extracellular polymeric substances in response to predation[205]. Clearly, organisms living in soils are intertwined in a complex web of trophic and non-trophic interactions, and their effects on soil properties cannot be understood by studying individual taxa in isolation.

Glossary

Adaptative radiation
The rapid diversification of species as a consequence of adaption to different environmental conditions.

Ammonification
The respiratory reduction of nitrate to ammonium when oxygen is limiting.

Arbuscular mycorrhizal fungi
Fungi that form a symbiosis with plants by penetrating the cortical cells of the roots of a vascular plant.

Denitrification
The respiratory reduction of nitrogen oxides to N_2O and N_2 when oxygen is limiting.

Extracellular polymeric substances
(EPSs). Polymeric organic compounds (mainly polysaccharides, proteins and nucleic acids) that are produced and released by microorganisms.

Hydrophobins
Small proteins produced by filamentous fungi that can spontaneously self-assemble and change the polarity of a surface.

Niche construction theory
The concept that organisms can modify their environment and that, in turn, these changes influence the organisms.

Nitrification
Aerobic oxidation of ammonium to nitrite and then to nitrate to generate energy.

Photosynthetic autotrophs
An organism that uses light energy to fix CO_2.

Siderophores
Organic compounds that are produced and released by microorganisms to make otherwise poorly soluble Fe(III) ions bioavailable for the cells and to facilitate their uptake.

Soil micropores
Pores in which water is essentially held by capillary forces (≤0.08 mm), nearly immobile and in which solute movement is limited to diffusion.

Weathering
The process of breaking down or dissolving solids (minerals and rocks) by biological, chemical or physical processes.

occur with the frequent application of sulfur as a fungicide or fertilizer, particularly in systems in which alfalfa, tomato or wine grapes are grown as these crops often receive high inputs of sulfur compounds[146]. Such sulfur applications can promote the activity of sulfur oxidizers and soil acidification via the generation of sulfuric acid[31,147]. Applications of pesticides to agricultural fields have also been shown to directly or indirectly affect microbial communities with consequences for soil properties. For example, harmful effects of herbicides were reported on soil photosynthetic algal and cyanobacterial communities that promote aggregate stability, which resulted in a reduction of up to 42% in the size of soil aggregates[148]. Large-scale conversion of natural ecosystems to agricultural lands has contributed to increased food production, but has pronounced impacts on soil biodiversity and biotic influences on soil properties. For example, conversion of rainforest into rubber and palm oil plantations led to a 50% reduction in the numbers of testate amoebae in soil, a shift that can alter biogenic silicon pools and increase silicon losses over time[149]. Plant–microorganism interactions can also have an impact on soil properties that is likely to vary as a function of the crop species[150]. For example, a $^{13}CO_2$ greenhouse tracer experiment showed that switchgrass cultivation enhanced microbial production of extracellular polysaccharides and soil aggregate stability[151]. Comparison of long-term switchgrass fields with adjacent annual crops fields also revealed larger amount of extracellular polysaccharides under switchgrass cultivation, which could explain the increased soil aggregation and the greater persistence of soil organic carbon[151].

Harnessing microbial communities to combat soil threats and global change

Given the many ways whereby microorganisms can affect soil properties, it is reasonable to ask how the soil microbiome could be modified, directly or indirectly, to combat soil threats and global change. Before answering this question, it is important to emphasize that there is already a long history in agriculture of efforts to control soil microbial communities and their activities using, for example, antimicrobial compounds and organic fertilizers. However, there are new opportunities to use microorganisms as an innovative approach to address soil threats, such as erosion, contamination and nutrient imbalances. For example, it has been proposed that MICP, which leads to the cementation of loose soil particles, could be used to limit the loss of organic matter and nutrient-rich surface soil horizons by erosion. However, further research is warranted before MICP application can be upscaled from laboratory-scale or small-scale experiments to large-scale engineering practices[152–154]. MICP can be achieved by many different processes[155,156], and both biostimulation (that is, the stimulation of indigenous urea-hydrolysing bacteria by providing the appropriate nutrient medium)[157] and bioaugmentation (that is, the inoculation of exogenous bacteria together with the precipitation medium) are being investigated to promote MICP[158]. In a laboratory-scale experiment, treating a sandy soil with *Sporosarcina pasteurii*, $CaCl_2$ and urea led to a calcite production by MICP of 120 kg m^{-3}, filling nearly 10% of pore space[159]. Likewise, a field test of MICP for mitigating wind erosion in a desert soil led to a decrease of the erosion depth by 95% compared with the untreated plots[160]. However, MICP can also affect soil hydrology by improving water retention capacity and lowering desiccation cracking in clayey soils[117,161,162]. Several laboratory and field studies have also highlighted the potential of using filamentous cyanobacteria as inoculants to stabilize soil aggregates and limit both water and wind erosion[58,163–165]. For example, field inoculation of cyanobacteria alone, or in combination with other bacterial taxa, led to a 77–89% decrease in soil loss from erosion when compared with uninoculated control plots[166]. Soil contamination is caused by the presence of organic or inorganic pollutants, such as pesticides and heavy metals. Owing to their vast metabolic capabilities, microorganisms have a great potential for degrading pollutants such as pesticides[167,168] or immobilizing pollutants such as heavy metals (for example, uranium, copper, chromium or arsenic)[36]. Several studies have highlighted the potential of microbially based solutions, and the combined use of microorganisms and plants, for the bioremediation of contaminated soils[169–171]. MICP has also been investigated as a strategy for heavy metal bioremediation as toxic metals such as lead (Pb) are immobilized after co-precipitation with carbonates[172,173]. The role of soil microorganisms in nutrient availability is well recognized as they are key players in the biogeochemical cycling of many elements such as nitrogen, phosphorus and potassium[174]. Recent studies have suggested that microbial weathering could be used to increase soil fertility in arable soil by releasing macronutrients and micronutrients from soil minerals or crushed rocks applied to soil[175]. For example, inoculation of a potassium-solubilizing *Bacillus* strain together with mica resulted in enhanced potassium uptake by plants and potassium availability in soil[176]. Nitrification inhibitors are now widely used to minimize the loss of nitrogen from arable soil. Thus, inhibition of the ammonia-monooxygenase enzyme prevents the transformation of ammonium into nitrate, which is not only highly susceptible to leaching but also leads to the emissions of the greenhouse gas N_2O by denitrification. As such, the use of nitrification inhibitors has also been recommended by the Intergovernmental Panel on Climate Change to reduce agricultural greenhouse gas emissions[177].

Soil microorganisms can also help mitigate climate change through a wide range of processes other than those directly involved in the production and consumption of greenhouse gas. As carbon in carbonates is rather stable (10^2–10^6 years), microbial processes that lead to the precipitation of CO_2 into carbonates can be leveraged to sequester carbon to mitigate greenhouse gas emissions[23]. For example, it has been estimated that inoculation of a cyanobacteria-dominated consortium to serpentinite mine tailings can lead to the sequestration of more than 2,600 tonnes of CO_2 as carbonate precipitates (mostly dypingite and hydromagnesite) within a few weeks[178]. Another expected consequence of climate change is that many regions will experience larger and more frequent droughts[179]. As soil microorganisms can influence soil hydrology, addition of particular microorganisms with pronounced effects on soil moisture (via any of the mechanisms described earlier) holds promise for the promotion of more effective water retention or infiltration, therefore alleviating the effects of plant drought stress. For example, because water repellency can increase from the hydrophobic coatings on soil particles, researchers[180] have successfully demonstrated that the field inoculation of the wax-degrading bacteria *Mycobacterium* sp. resulted in substantial improvements in water infiltration. Similarly, inoculation of a *Bacillus subtilis* strain that can degrade hydrophobic compounds and produce biosurfactants in an agricultural soil increased water infiltration and water content while reducing water repellency[181].

To date, many of the proposed approaches to combat soil threats using microorganisms rely on soil inoculation, which remains challenging. First, it requires cost-effective production of large volume of inoculum and transfer to the field. Second, biotic and abiotic stresses are known to affect the establishment and effectiveness of microbial inoculants, which lead to inconsistent performance in field conditions[182,183]. Besides, there is a growing concern regarding the possible legacies of microbial inoculants on the indigenous soil microbiome with unexpected consequences for other vital soil processes required to maintain soil health[184,185]. Nevertheless, microbial inoculants are already widely used in agriculture for their plant beneficial activities. For example, in Brazil, 36.8 million hectares of soybean fields were inoculated in 2018 with commercial rhizobial inoculants[186]. As microorganisms are increasingly seen as an alternative to mineral fertilizers and pesticides, the largest agricultural companies are now investing heavily in microbial inoculants[187].

Conclusions

In this Review, we highlighted the many ways by which soil microorganisms can modify their environment, by altering soil properties in their surroundings or by building mineral structures. These environmental changes include shifts in pH, metal availability, mineral composition, aggregation and soil hydrology that profoundly alter soil physics and chemistry. As soil properties are also well known to affect soil microbial communities and composition, the relationships between soil properties and soil microorganisms are reciprocal. Thus, microorganism–soil interactions entail networks of causation and feedback in which previously selected microorganisms drive environmental changes and, as a consequence, microbially driven shifts in soil properties subsequently shape microbial community composition and activity, and possibly evolutionary trajectories. However, these feedback loops generated by microorganism–soil interactions are often overlooked in contemporary soil microbial ecology.

To advance the field, integrative studies bridging soil science, ecology, biogeochemistry, evolution and microbiology are needed. Owing to the interconnected nature of microbial communities and soil properties, identifying the underlying mechanisms using reductionist approaches in which individual factors are studied in isolation remains challenging. Given the pressing need to protect and restore soil, future approaches should leverage insights gained from studying natural systems and the interkingdom interactions between soil dwelling organisms. Progress towards understanding the functional roles of the microbiome in shaping soil properties can also come from using more proactive approaches whereby microbial communities are directly manipulated in controlled experiments. Such research should include examining the evolutionary consequences of niche construction by soil microorganisms.

From evidence outlined in this Review, microbially driven shifts in soil properties can also have practical applications such as limiting soil erosion, promoting carbon sequestration or restoring contaminated soil through bioremediation. The directed modification of the soil microbiome is an emerging research area that requires a better understanding of how microbially mediated shifts in soil properties can be used to combat threats to soil health and other environmental challenges.

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    This study is a comprehensive analysis of the complex interactions among soil structure, soil organic matter and soil organisms within trophic networks.

Author contributions

The authors contributed equally to all aspects of the article.

Competing interests

The authors declare no competing interests.

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