



Review Article

Soil is alive – How does soil biota influence soil mechanical properties? A perspective review

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ABSTRACT

There is a growing need for sustainable ground improvement, stabilization and remediation, as well as ways to maintain infrastructure. This is resulting in a rise of nature-based solutions, bio-based ground improvement techniques, bio-inspired methods, a “build-with-nature” approach. Shallow soil layers have historically been disregarded by geotechnical engineers due to unwanted characteristics, an overall lack of familiarity with the evolution of their properties in time, and/or theoretical framework for interpretation. Recent research in unsaturated soil mechanics, the characterization of organic soils, and understanding of organic matter transformation processes has improved understanding and modelling capabilities of shallow soil layers. However, soil biota (bacteria, fungi, algae, protists, soil fauna and plants) must also be considered. In this perspective, we summarize the effects of soil biota presence and activity on soil mechanical and hydraulic properties, explore their underlying mechanisms, and discuss how they can be utilized in implementing bio-based solutions. Additionally, we examine the applications and limitations of these bio-based solutions.

1. Introduction

Common ground engineering practices are being challenged by the growing demand for sustainable use of resources and the need to limit CO₂ emissions. Several researchers have advocated for the development of nature-based solutions to reach these goals, i.e. technologies that rely on biological processes or mimic biosystems (DeJong et al., 2011; El Mountassir et al., 2018; Jain et al., 2023; Martinez et al., 2022). While biogeotechnical solutions can complement or replace traditional engineering techniques for ground improvement, remediation and stabilization, their adoption requires a shift in design that incorporates landscaping and ecology throughout the process. One key challenge is that many geotechnical engineers lack familiarity with soil ecosystems and the biological processes within them. The lack of theoretical background about topsoil behavior stems from the fact that it is removed in most geotechnical applications due to unwanted characteristics.

Classic theories describing the fundamentals of soil behaviour (e.g., Schofield and Wroth, 1968) were developed based on water-saturated, unstructured soils. In contrast, terrestrial shallow soil layers up to depths of 1–3 m, are typically unsaturated, structured/aggregated and their properties are profoundly influenced by biota and climate (Berli and Hallett, 2023). Not only partial saturation represents the most

general state for shallow soil layers on land, but the presence of air is key for life in soil, while aggregate formation, persistence and disintegration is influenced by biological as well as chemical and physical processes (Six et al., 2004; Lehmann et al., 2017; Mueller et al., 2024). A better geotechnical characterization of these layers requires knowledge of: 1) unsaturated soil mechanics; 2) strength and hydrological parameters of organic soils; and 3) temporal and spatial changes in soil biota activity and biomass.

Unsaturated soil mechanics is nowadays a well-established field and some of its principles are starting to be applied routinely in design (Sheng, 2011; Rahardjo et al., 2019; Lu, 2020). Similarly fundamental research into the mechanical properties of organic matter-enriched soils has been ongoing for decades (Long, 2005; Mesri & Ajlouni, 2007) and in recent years it has experienced a renewed interest with focus on multiphysics characterization (Jommi et al., 2019; Ponzoni et al., 2024; Siddiqua et al., 2024). However, the ecological role of upper soil layers – which serve as habitat for thousands of millions of organisms essential to ecosystem services – receives far less attention within geotechnical engineering. It should be noted that the presence of various forms of organic matter in soils and sediments is due to recent and relict biological processes. These processes typically involve many different organisms that are connected through complicated food webs and long-term interactions. Furthermore, while soil properties define the living

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conditions for various soil-inhabiting organisms, these organisms, in turn, can alter both mechanical and chemical soil properties by acting as ecosystem engineers (Jones et al., 1994; DeJong et al., 2015).

Creation and consumption of organic matter on a small-scale, and vegetation establishment on a large-scale follow specific successional patterns, i.e. a sequence of species populations change over time (Odum, 1969). For example, a typical revegetation succession on a barren substrate begins with increase of biomass of fast-growing and less resource-demanding pioneer species (microorganisms, lichens, algae, pioneer plants), and continues with the increase of biomass of slow-growing species (soil fauna, longer-lived woody plants, associated symbiotic fungi, e.g. mycorrhizal fungi) that are in a higher need of available nutrients (Poorter et al., 2023). Successional patterns vary among biomes and are studied by ecologists, soil scientists and microbiologists. These successional patterns should be considered while researching and implementing nature-based solutions.

This perspective review summarizes the effects of soil-inhabiting biota on soil mechanical properties, analyzing how different organisms, their presence and activity contribute to these properties across various spatial and temporal scales for terrestrial soils, which however were often deposited by water. The research gaps, geotechnical potential of bio-based technologies, and their limitations are discussed.

2. Bacteria

Bacteria are prokaryotic unicellular organisms that are abundant in soil, their biomass may reach 300 µg/g (i.e. mg/kg/g) of soil in the upper 50 cm of soil, and their number can be up to 10¹⁰-10¹¹/g of soil (Semenov, 2023). Their biomass and activity typically reduce with depth, but they can be found in significant quantities (10⁵-10⁶/g of soil) at 2-4 m depth and lower. However, their distribution is uneven and bacterial hot spots are commonly associated with organic matter inputs around roots (rhizosphere), around dead plant parts

(detritosphere) and soil fauna burrows (drillosphere) (Kuzyakov and Blagodatskaya, 2015). Bacteria are characterized by a relatively high duplication rate and a wide variety of metabolism types and metabolic pathways are involved in many biogeochemical cycles of elements (carbon, nitrogen, phosphorus, sulphur and others). In particular, they can be either primary producers of organic matter (autotrophs in the first line of Fig. 1A) or primary and secondary consumers of organic matter produced by autotrophs (heterotrophs in the second line of Fig. 1A). Their metabolic products may provide plants with nutrients (freshly-fixed ammonia, water-soluble P-containing salts) and growth-promoting substances (organic molecules like vitamins) (Van Der Heijden et al., 2008). Various bacteria may be present in the soil as biofilms attached to particles, where different parts of a colony have distinct functions (e.g. food mining at the interface with the substrate and protection at the interface with the environment), or as individual cells floating in the soil pore-water. Despite their relatively small size and amount, they may have significant effects on geotechnical properties due to their ability to interact with minerals causing either weathering or precipitation, form biofilms, transform different organic substances, and most importantly they are the starting stepstone in many successional patterns.

Because of their individual extremely small dimensions, the physical presence of bacteria primarily manifests as a biofilm. However, some Actinobacteria (referred to as actinomycetes), have the ability to form filamentous, mycelium-like structures with diameters of 1-5 µm (i.e. mkm). Actinomycetes can be involved in biocrusts formation as they are capable to grow in water-limited conditions (DeGroot et al., 2005). Some actinomycetes are in symbiotic or mutualistic relationships with plants, providing them with nutrients in available forms (N fixation in symbiosis with some plants, P mined from organic matter) (Zhang et al., 2023). Furthermore, they have the potential for geoenvironmental applications, because they can live in heavy-metal polluted environments (DeGroot et al., 2005), and degrade complex organic materials such as

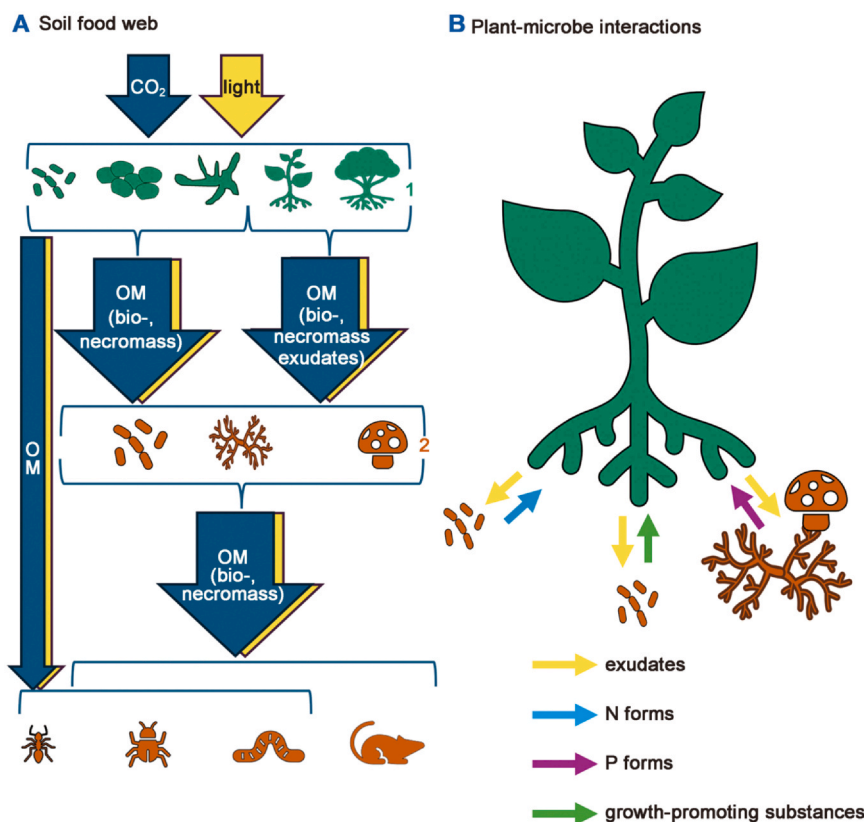


Fig. 1. Interactions between soil biota groups. 1 Producers (autotrophs): some bacteria (Cyanobacteria), unicellular and multicellular algae, herbaceous and woody plants. 2 Primary and secondary consumers (heterotrophs): most bacteria, fungi, protists, different groups of soil fauna. See first line of Table 1 for icons legend.

polysaccharides and pesticides (Castillo et al., 2006; Manucharova, 2009).

One of the most researched bacterial-mediated processes in geotechnical engineering is urease induced biocementation (Microbial Induced Carbonate Precipitation, MICP, or Enzyme Induced Carbonate Precipitation, EICP) (Zhang et al., 2023). Both MICP and EICP are based on the urease enzyme activity, when a urea-containing substrate and Ca^{2+} -containing soluble salts are present in the soil, urea is hydrolysed to ammonia (NH_3) and CO_2 . As a result, pH increases and calcium carbonate (CaCO_3) precipitates bonding or coating particles according to the fluid kinematics (Terzis and Laloui, 2019). MICP treatment can be performed either by adding the urease-producing strain together with the substrates (bioaugmentation) or relying on native/indigenous soil bacteria (biostimulation) for urease production. Substrates consisting of nutrients and most commonly CaCl_2 are added in both cases (Zhang et al., 2023). According to past and more recent research, up to 17%–30% of all soil bacteria have urease activity (Lloyd and Sheaffe, 1973; Burbank et al., 2012). Because indigenous bacterial strains are more adapted to local environmental conditions in terms of physiochemical parameters and competitive interactions with other microbes (Devrani et al., 2024), biostimulation is likely underutilized. The potential of indigenous soil bacteria for urease enzyme activity can be measured and estimated by the number of genes encoding urease enzyme (Fisher et al., 2017). It should be noted that up to 50% of urease in soil is extracellular, i.e. not bound to microbial cells; and that microbial urease activity can be limited by the presence of other available forms of nitrogen (Geisseler et al., 2010).

Biocementation leads to improved mechanical parameters (Bhurtel et al. 2024; Xiao et al., 2022), and it has been extensively investigated for a range of applications (Mujah et al., 2017) including erosion control (Dubey et al., 2023), and the creation of self-healing materials (Fan et al., 2024). However, this treatment tends to be more effective in predominantly coarse-grained soils because in situ treatment requires injection and therefore relatively high hydraulic conductivity. In addition, larger pores enhance conditions for bacterial growth (Rong et al., 2011).

Calcium carbonate precipitation is not the only mineral transformation process to which bacteria contribute. In general, minerals are required for biochemical processes in bacteria as sources of energy and essential elements for enzyme functioning (Dong et al., 2022). Studies by Finlay et al. (2020) and Uroz et al. (2009) investigated how bacteria use minerals as a donor or acceptor of electrons using inorganic and organic acids and iron-chelating siderophores leading to mineral dissolution and transformation, contributing to the biogeochemical cycles of P, S, K, Fe, Ca, Na, Mn and other metals (Kertesz and Frossard, 2015; Ortiz-Castillo et al., 2021). Even though mineral weathering by bacteria can profoundly affect soil mineral composition, the resulting changes can be observed in years, as these processes are slower compared to organic matter transformation processes in upper soil layers. The enhancement of mineral weathering by bacteria is dependent on many factors, such as mineral type, bacterial taxon or community composition, available sources of organic matter, and environmental conditions (Uroz et al., 2022; Wild et al., 2022). While Ortiz-Castillo et al. (2021) suggested bacterial-induced mineral transformation for bioremediation of mine waste and former ground cover formation of mine tailings, effects of bacterial mineral weathering on the mechanical properties are not extensively studied.

Another feature of the metabolism of some bacteria is the production of Extracellular Polymeric Substances (EPS). These metabolites are various exo- and lipopolysaccharides, proteins, and nucleic acids. EPS provides better adsorption of bacteria to the solid fraction of soils, which allows biofilm formation (Costa et al., 2018). Their production by bacterial community depends both on species composition and the activity of several taxa in given conditions (Cania et al., 2020). Various abiotic stresses (e.g. drought, high salinity) may cause an increase in EPS production by bacteria as a measure for stress protection. These

substances may act as a glue for soil particles and promote soil aggregate stability (Zethof et al., 2020; Guhra et al., 2022; Amelung et al., 2023). Therefore, bacterial biopolymers can increase critical shear stress and soil erosion resistance (Ham et al., 2018). Biofilms containing bacterial EPS, biomass and necromass can induce pore clogging and reduce soil permeability by one or more orders of magnitude (Baveye et al., 1998; Dennis and Turner, 1998; Mitchell and Santamarina, 2005; Ivanov and Chu, 2008), and increase soil water holding capacity. In particular, Kästner et al. (2021) showed that necromass (i.e. fragmented components of bacterial cell walls) is key to determining the effects of bacterial biofilms on soil hydrological properties. Even though previously bioclogging was considered as a negative effect that may lead to poor performance of water wells, reduced filtering capacity of geotextiles, or even structural failures (Mitchell and Santamarina, 2005), it is now being used more frequently.

Bacterial respiration and any other gaseous metabolic product entering the atmosphere, as well as the environmental impact of certain compounds generated (e.g. ammonia NH_3), should be considered as negative side effects when trying to replace conventional soil stabilizers (Alotaibi et al., 2022). However, the gases formed during calcium carbonate precipitation induce partial saturation and therefore have the potential to limit pore-water pressure buildup during seismic events. Therefore, MICP has been rather extensively studied for liquefaction prevention (Burbank et al., 2011; He et al., 2013; Rebata-Landa & Santamarina, 2012; Terzis & Laloui, 2019). Furthermore, inert nitrogen and nitrogen oxides are formed during several steps of denitrification. Biomediated gas production by denitrifying bacterial strains was investigated by Moug et al. (2022), Kwon et al. (2024) and Lv et al. (2024), while O'Donnell et al. (2019) and Faruqi et al. (2023) used urease-producing bacterial strains.

3. Fungi

Fungi are eukaryotic multicellular organisms that consume organic matter produced by others (heterotrophs as seen in the second line of Fig. 1A) and therefore can be in competition with some bacteria or feed on them, as well as algae and plants or their exudates. In particular, many fungi produce enzymes that can degrade recalcitrant organic matter like lignin (Chapin et al., 2011). 1 g of soil may contain up to several hundred meters of fungal mycelium, or hyphae with a diameter from 2 to 20 μm (Susyan et al., 2008; Blagodatskaya and Kuzyakov, 2013). Fungi can be found up to the rooting depth of plants, i.e. 8 m or more. However, their growth reduces with depth due to low gas exchange with the atmosphere and scarce organic matter sources (de Araujo Pereira et al., 2018). According to Lew (2011), fungal hyphae turgor (i.e. the internal pressure on the cell wall) is commonly in the range of 430–570 kPa. Turgor defines hyphal penetration and elongation through the soil. Several studies showed that fungal spores can stay dormant for years and this enables them to survive and remain viable until conditions become favorable (Nagtzaam and Bollen, 1994; Wyatt et al., 2013). For example, pyrophilous fungi's growth is activated by forest fires, and for this reason Filialuna and Cripps (2021) identified their presence as key in contributing to soil aggregation and erosion reduction post-fire. Fungi have the potential to influence geotechnical properties of shallow soil layers by taking part in aggregation processes, by weathering minerals and by interaction with plant roots.

Fungal hyphae contribute to soil aggregation through several mechanisms including direct physical bonding between particles, adhesion of biopolymers to hyphae and production of extracellular polymeric substances, the creation of water-repellent surfaces (i.e. hydrophobic), particle entanglement and compression, and tunnelling through existing aggregates (Lehmann and Rillig, 2015; Li et al., 2023).

Lehmann et al. (2020) found that colony biomass density was the most influential parameter in soil aggregation among a range of chemical and biological traits. Furthermore, Li et al. (2023) showed that single fungal species are more successful in aggregate formation

comparing to the consortia, presumably, due to lack of competition. Mycelium-based materials have density in a range from 100 to 1000 kg/m³, and [Bitting et al. \(2022\)](#) measured corresponding Young moduli in a range from 10⁻³ to 1 GPa. [Tisdall et al. \(2012\)](#) attributed an increase in soil tensile strength and abrasion resistance to the presence of fungal hyphae and their metabolites, while [Lim et al. \(2023\)](#) found increased unconfined compressive strength. At the same time, fungi may disrupt ground improvement obtained by the addition of lignin powder ([Liu et al., 2020](#)), even though the aggregation they cause may provide greater improvement in overall strength. With respect to hydraulic properties, [Lim et al. \(2023\)](#) found a decrease in permeability for sedimentary sands due to hyphae growing into the soil pores, while [Salifu and El Mountassir \(2021\)](#) and [Salifu et al. \(2024\)](#) showed water repellence being established in sands by employing *Pleurotus ostreatus*. Therefore, fungal remediation has been suggested to treat coarse grained soils, where water infiltration and consequent loss of suction can induce failure ([Balzano et al., 2019](#)).

With regards to mineral weathering, fungi act by producing organic acids and siderophores ([Gorbushina, 2007](#); [Lybrand et al., 2019](#)), which reduce the pH of pore-water. Fungal capability for mineral weathering is a necessary feature for colonization of barren rock surfaces ([Gorbushina, 2007](#)) and for symbiotic relationships with plants ([Wu et al., 2024](#)). According to a study by [Lybrand et al. \(2022\)](#), the effects of fungal weathering on the surface of mineral grains are visible within 1–3 years. This and the change in pH they cause can lead to a general weakening in mechanical properties and an increase in permeability during pedogenesis (i.e. soil formation), contrary to the effect observed on hydraulic conductivity in sedimentary sands.

Even though fungi are primarily responsible for mineral weathering, [Fang et al. \(2018\)](#) and [Masaphy et al. \(2009\)](#) documented formation of calcite concretions around the hyphae of *Penicillium chrysogenum* and *Morchella sp.*, respectively.

4. Algae and soil protists

Soil algae are uni- and multicellular organisms that are mostly concentrated in a few millimeters of topsoil, due to their need for sunlight as an energy source. As plants, they are primary producers of organic matter (autotrophs in the first line in [Fig. 1A](#)). Algae are especially important in water-limited soils of extreme environments and as first colonizers of barren substrates; they are involved in a biocrust formation ([Ciccazzo et al., 2016](#)), which may occur through fibrous structures ([Ramakrishnan et al., 2023](#)), and extracellular polymeric substances. [Crouzet et al. \(2019\)](#) showed that photosynthetic algae contribute to the stability of aggregates larger than 2 mm by comparing two types of agricultural treatments in dark and light conditions. Furthermore, [Weber et al. \(2022\)](#) provided experimental evidence that natural biocrusts reduce wind and rain erosion, while [Rodríguez-Caballero et al. \(2022\)](#) attributed reduction in dust and dune stability to their presence. From a geotechnical point of view, some researchers have investigated algal biopolymers (e.g. agar gum, sodium alginate) for carbonate precipitation ([Ivanov, 2020](#); [Huynh et al., 2023](#)), while others investigated algal biopolymers as soil additives to increase the compressive strength of soil ([Fatehi et al., 2021](#); [Kidron and Drahorad, 2022](#)) and to control erosion ([Chang et al., 2015](#); [Lemboye et al., 2021](#)). Compared to barren soils, a biocrust has higher water-holding capacity, which affects infiltration and evaporation rates ([Lichner et al., 2018](#); [Kidron et al., 2022](#)). Due to the potential of algae to form biocrusts, they have been suggested for post-fire soil restoration ([Muñoz-Rojas et al., 2021](#)), desert ecosystem recovery ([Xu et al., 2024](#)), and sand fixation. However, it should be noted that once a biocrust is formed, its presence may impede the growth of other plants.

[Geisen et al. \(2018\)](#) provide an overview of soil protists, which are unicellular organisms ranging from a few micrometers to over a millimeter in size. Based on recent taxonomy, unicellular soil algae are currently referred to as autotrophic protists. The majority of soil protists

are however heterotrophic with immense morphological and functional diversity ([Geisen et al., 2017, 2018](#)). Protists play an indirect role in influencing soil aggregation by participating in the food webs and feeding on populations of either one or more (mixotrophic) soil biota groups ([Bonkowski, 2004](#); [Clarholm, 1985](#); [Geisen et al., 2017](#); [Jassey et al., 2015](#)). Furthermore, protists can have mutualistic or parasitic symbioses with various organisms and can be a host for ectosymbiotic or endosymbiotic soil bacteria ([de Vargas et al., 2015](#)). For example, mixotrophic protists in carbon-rich peatland soils play a crucial role in sequestration and carbon storage ([Jassey et al., 2015](#)). Even though the overall impact of protists may not yet be fully understood ([Geisen et al., 2018](#)), and the effects of their presence and activity on soil mechanical properties have not been investigated yet, they may contribute to the improvement of soil aggregation ([Panakoulia et al., 2017](#)).

5. Soil fauna

Soil fauna varies widely in size and taxonomy, from tiny 10 µm wide nematodes up to 10 cm moles. Various species of soil fauna are primary and secondary consumers ([Fig. 1A](#)) that transform soil organic matter by feeding on fungal and bacterial biomass, living plants, or plant residues ([Potapov et al., 2023](#)). Soil fauna feeding patterns influence soil aggregation processes, either breaking down aggregates and making organic matter available or feeding on microbes ([Hannula et al., 2023](#)). Typically, most groups of soil fauna are concentrated in the upper few centimeters, except for some geobionts. Geobionts are taxa of soil fauna that spend most of their life cycle in the soil (such as earthworms, ants and termites, some nematodes and some beetles), and they may live up to several meters deep ([Coleman and Wall, 2015](#)). Among the diverse soil fauna, large geobionts are known as soil engineers due to their important role in soil structure formation ([Bottinelli et al., 2015](#); [Briones, 2023](#)). Their burrowing activities can profoundly influence the soil hydrological regime by altering pore size and distribution, creating new pores that serve as preferential pathways for water flow and thereby increasing water infiltration ([Barbosa and Gerke, 2023](#); [Chen et al., 2022](#)). For this reason, according to [Freeman et al. \(2023\)](#) soil acidification may increase the risk of floods because it results in a significant decrease in earthworm quantity.

The fauna burrowing enhances soil aeration and reduces soil compaction ([Müller-Inkmann and Fründ, 2021](#)), providing more favorable conditions for the growth of plants and other microorganisms. These conditions will result in increased infiltration rates and consequently water drainage ([Bardgett, 2005](#)). The presence of fauna is also responsible for variation in pH and pore-water chemistry that may affect electro-chemical properties of clay sediments, as well as other soil microorganisms ([Harvey et al., 2019](#)). However, [Harvey et al. \(2019\)](#) also suggested that fauna burrows may limit or contrast the growth of plants that would otherwise have a stabilizing effect. Furthermore, they investigated the detrimental effect of larger fauna burrows and/or that of invasive species on slope stability of water embankments. The general consensus is that these burrows are (co-)responsible to river embankments failure (e.g., [Gottardi et al., 2020](#)), and therefore strict control is applied in the management of these infrastructure to limit their presence.

From a geoenvironmental point of view, earthworm bioturbation has been suggested by [Rodríguez-Campos et al. \(2014\)](#) to be employed for soil remediation from low concentrations of organic contaminants. Removal of contaminants happens due to the improvement of soil aeration and, consequently, better growth of various bacteria with the potential to degrade specific contaminants. Finally, the burrow mechanisms of earthworms, termites, clams and crayfish have been studied to gain insights for the development of bio-inspired equipment that requires less energy for soil penetration ([Ruiz et al., 2015](#); [Chen et al., 2022](#)).

6. Plants

Plants are multicellular eukaryotic organisms and the main producers of organic matter due to their capability to perform photosynthesis (autotrophs as seen in the first line in Fig. 1A). Depending on the biome type, as well as water and nutrients availability, plant roots can proliferate to depths ranging from 1 to 7 m to as much as 40–70 m, with these factors also influencing root architecture (Lambers et al., 2008; Fan et al., 2017; Jørgensen et al., 2022). Root penetration resistance is defined by cell turgor, which rarely exceeds 1 MPa (Martins et al., 2020). Roots provide plants with water, nutrient uptake and anchorage. Furthermore, some roots act as a storage of resources and for vegetative propagation.

The anchoring properties of plant roots and soil reinforcement with roots are relatively well studied. It is known that root presence increases soils' shear strength in both drained and undrained conditions (D'Souza et al., 2019; Alam et al., 2022; Li et al., 2023). Plant potential for improvement of soil mechanical properties is employed for slope engineering, coastal protection, and beach nourishment (Assadi-Langroudi et al., 2022; Bordoloi & Ng, 2020; Capobianco et al., 2021; Kindeberg et al., 2023). Root influence on slope stability has not only mechanical but also hydrological components (Capobianco et al., 2021; Ni et al., 2018; Vergani et al., 2017; Wang et al., 2023). Plant roots influence soil hydrology by increasing evapotranspiration (when alive) and forming main "tunnels" for water flow (when dead and decaying) (Jørgensen et al., 2022; Xiao et al., 2024). Overall, their effect on hydraulic conductivity varies based on the pore size, reducing it by filling pores for coarse grained soils and increasing it by creating preferential channels in fine grained soils. Furthermore, roots have been demonstrated to reduce air conductivity (Chen et al., 2023). However, it should be noted that environmental boundary conditions also play a role, for example a rise in temperature or draughts can shrink roots giving rise to an increase in hydraulic conductivity (Wang et al., 2023).

Although the role of roots in the physical reinforcement of soil and its evapo-transpiration has been extensively investigated, less is known about bio-geo-chemical interactions. Roots release exudates as a part of interaction with soil bacteria and fungi, either promoting or inhibiting growth of different taxa, and thereby forming the rhizosphere (the part of soil along the root surface influenced by exudates). Up to 3% of CO₂ fixed by the plant is transported to soil in the form of root exudates (Kuzyakov and Domanski, 2000). They consist of light-weight organic molecules like sugars, amino and organic acids (up to 80%), proteins (up to 6%) and polysaccharides. However, their exact chemical content depends on plant species, age and its growing conditions: temperature and water regime, as well as soil density (Granssee and Wittenmayer, 2000; Naveed et al., 2017; Dietz et al., 2020; McLaughlin et al., 2023; Nazari et al., 2023; Rathore et al., 2023).

A comprehensive review by Xiao et al. (2024) indicates that root exudates increase the soil water-holding capacity and decrease the saturated hydraulic conductivity. However, there is no consistent opinion on whether root exudates act as lubricant or a glueing agent. In Jiang et al. (2023) it was mentioned that hydrated root mucilage acts as a protective barrier and a lubricant for root tips during soil propagation. The same conclusions were reported by Traoré et al. (2000): when hydrated, root exudates destabilize soil aggregates, whereas in dry conditions, the effect is the opposite. A higher amount of root mucilage is one of several adaptations for plant growth in compacted soil, together with thick and more branchy roots with sharper tips and more dense root hair (Pandey and Bennett, 2024). Most other studies consider that root exudates impact positively on soil aggregate stability by enhancing microbial growth and biofilm formation, e.g. Naveed et al. (2018), or Xiao et al. (2024). According to Vives-Peris et al. (2020), it is likely that root-secreted exudates can serve as both a lubricant and a glueing agent, though not simultaneously. During early growth or when penetrating soil, lubrication is more pronounced to facilitate root movement, while in the established stage, the glueing action may be more significant for soil aggregation.

7. Soil as a community

The effects of different soil inhabitants' groups were discussed separately for simplicity, and this also reflects the engineering approach when considering utilizing soil microbiology for ground improvement and stabilization. However, as just described in some of the examples above, all groups are connected in complicated food webs and various kinds of interactions, either mutualistic or competitive. Fig. 1 shows its simplest representation, where some bacteria, algae and plants are primary producers of organic matter, while most bacteria, fungi, and soil fauna either feed on this organic matter (primary consumers) or on each other (secondary consumers) (Potapov et al., 2023). Sources of organic matter in soils include biomass of primary producers, exudates, necromass, mineral-bound fractions, which are not equally easy to transform; some degrade more easily like sugars and others are recalcitrant like lignin. Heterotrophs transform this organic matter either by consuming it or by extracellular enzyme activity. Furthermore, soil fauna enhances the organic matter transformation by physical grinding of substrates. For each group there can be competition, synergy or no interaction, either inside or across groups, as well as predation. For example, bacteria and fungi might compete for organic matter formed by autotrophs, while many plants are in mutualistic interactions with soil bacteria and mycorrhizal fungi (Fig. 1B). This means an ongoing exchange between plants and microbes: readily available organic matter in the form of root exudates is transferred to the rhizosphere, while nutrients, vitamins, growth promoting factors are transferred back to plants. Fungi-plant symbioses rely on fungi delivering otherwise unavailable forms of nutrients in exchange for organic matter from root exudates (Marschner and Dell, 1994). Selective "mining" of essential nutrients like phosphorous and potassium by fungi is an important factor of plant symbiosis with ectomycorrhizal fungi in boreal forests (Smits et al., 2008) and with arbuscular mycorrhizal fungi in agricultural soils (Arocena et al., 2012). Mycorrhizal fungi not only provide plants with available nutrients, but also help mitigate various abiotic stresses like drought, salinity increase, heavy metal presence (Begum et al., 2019; Evelin et al., 2019; Kuyper and Jansa, 2023). In the early stages of plant growth, the effect of mycorrhizal fungi presence can profoundly affect root properties and improve biomechanical parameters in the later stages. For example, Chen et al. (2023) showed that after 12th month growth, Vetiver (*Chrysopogon zizanioides*) roots exhibited higher tensile strength and strain at break point (i.e. ultimate strength), if incubated with arbuscular mycorrhizal fungi compared to incubation with non-mycorrhizal fungi. Similarly, Kamchoom et al. (2023) showed that Bermuda grass (*Cynodon dactylon*), which is commonly used for erosion control and slope stabilization, had higher biomass and increased cellulose content in roots when grown after inoculation with arbuscular mycorrhizal fungi (compared to non-inoculated grass). Furthermore, root exudates may boost the formation of microaggregates by stimulation of fungal growth (Baumert et al., 2021).

Certain soil bacteria inhabiting the zone around plant root (rhizosphere) and feeding on root exudates have also been shown to promote plant growth and influence successful plant establishment (Van Loon, 2007; Lugtenberg and Kamilova, 2009; Bakker et al., 2018). These Plant-Growth Promoting Rhizobacteria (PGPR) have several modes of action, including production of chemicals stimulating growth and bio-control of plant pathogens. At the moment, the PGPR potential was mostly employed for crop production improvement (Rillig et al., 2018; George et al., 2024). Other emerging applications could be enhanced phytoremediation, which requires better understanding of the PGPR effects on plant development on barren soils (Hassan et al., 2024).

On the other hand, the activity of different soil biota groups can also be affected by soil viruses, and their influence on biochemical processes in soil is an emerging field of research (Kuzyakov and Mason-Jones, 2018). Viruses are smaller than bacteria (0.00003–0.0005 μm³ in volume), do not have an independent metabolism and rely solely on

cellular structures of host organisms (Jansson and Wu, 2023). The host organisms can be various species of bacteria, fungi or soil fauna (Carreira et al., 2024; Emerson, 2019). Liang et al. (2024) suggest that soil viruses may be responsible for large part of bacterial necromass found in soil and bacterial dormancy, i.e. that they tend to enter an inactive state when attacked by viruses. Therefore, viruses contribute to the biochemical cycle by regulating the quantity and activity of their hosts. While they may indirectly affect the soil mechanical properties, this is yet to be studied.

8. Bio-based ground improvement technologies: applicability and limitations

Table 1 summarizes how each soil biota group modifies soil, either from a physical or chemical point of view, including the soil water interaction. These effects on physical and chemical properties are, in turn, responsible for modifying soil hydraulic and mechanical properties, and these are the changes that bioinspired solutions can leverage on (Table 2). Reduction in hydraulic conductivity can for example be obtained by the formation of biofilms, mineralization processes, or growth of hyphae and root hairs due to the reduction in pore size. Furthermore, biofilms and more generally the presence of organic matter can increase water holding capacity and slow down infiltration and/or water flow by changing the hydrophobicity of the material, which is also the main mechanism behind the effects of biocrusts. The presence of biofilms and organic matter also changes pH and modifies surface charge of clay minerals, leading to changes in soil water interaction. Finally, metabolic gas formation resulting in unsaturated conditions also leads to a reduction in water flow. On the contrary, soil fauna and plants are responsible for a general increase in hydraulic conductivity by providing preferential paths and introducing secondary porosity that is most often larger in size than that of the barren soil.

From a mechanical point of view, the greatest contribution results from mineralization processes (bacteria and some fungi and algae), particle binding (bacterial necromass and organic matter), fiber reinforcement (fungi and plant roots), which combined lead to soil aggregation. These generally make a positive contribution in terms of strength and stiffness, as well as limiting surface and internal erosion. Gas formation can furthermore be used to limit pore pressure buildup in dynamic conditions. However, some natural processes lead to weakening, namely bioweathering (fungi and certain bacteria) and burrowings (fauna and plant roots).

In the context of slope stability, plants have gained the most attention because their presence is the most influential due to their larger biomass and size compared to other soil biota. However, as mentioned the effects of plant roots are complemented by bacterial and fungal presence (Fig. 1B), and different species of soil fauna affect plant growth by change in soil hydrology and by feeding patterns targeting groups of bacteria and fungi. The scarcity and lack of systematic studies investigating such interactions provides a significant research opportunity. Furthermore, fungi and algae provide a major contribution against wind and water erosion for barren slopes. For example, bio-mediated solutions have been used as a restoration measure for mine tailings (Li et al., 2023), where fungi can be used in combination with plants for enhanced pedogenesis. While their role in geoenvironmental applications is widely acknowledged, further research on mechanical and hydraulic properties is needed.

It is important to remember that the biomass and species richness of soil biota groups change along with succession, for example at the time of plant establishment on barren soil (Morriën et al., 2017). When applying multi-functional geotechnical nature-based solutions, the connectivity between groups should be considered for estimation of soil-inhabiting organisms' effect on soil mechanical properties (DeJong et al., 2011). A useful principle developed for agricultural science that should be taken into account is the Liebig law of the minimum, by

which the yield achievable is dictated by the most limiting nutrient, as the root biomass is linked to the overall plant health. Additionally, there are many stress factors limiting growth and, therefore, sufficient root development of plants: droughts, saline water ingress, frost periods, high temperatures, or wind.

The conditions required for the thriving and survival of soil bacteria and fungi are: energy, carbon and electron source availability, available water, presence of macro- and micronutrients (Kästner et al., 2021). Other important factors that must be considered when applying bio-inspired or bio-based methods of soil improvement are temperature, pH, redox potential, soil density, and pressure in a species-specific range (Tecon and Or, 2017; Jin and Kirk, 2018; Chernov and Zhelezova, 2020; Juyal et al., 2021). Even though different bacterial taxa can be active in a wide range of temperatures, from $-15\text{ }^{\circ}\text{C}$ to $110\text{ }^{\circ}\text{C}$, temperature optimums for respiration and growth of most soil bacteria are in a range between $20\text{ }^{\circ}\text{C}$ to $40\text{ }^{\circ}\text{C}$, and in temperatures below $5\text{ }^{\circ}\text{C}$, biological and enzyme activities are hampered (Cockell and Nixon, 2013; Liu et al., 2018). Moreover, temperature affects gas permeability that can be another important factor in influencing microbial activity (Wang et al., 2024). Another limiting factor is pore size distribution compared to the size of microorganism that is suggested to be used, which may be critical in clayey soils (Mitchell and Santamarina, 2005; DeJong et al., 2010). Since various organisms adapt to environmental stresses in distinct ways, specific studies tailored to particular conditions are required. For instance, the branching patterns and internal volume of arbuscular mycorrhizal fungi mycelium vary according to the available pore space (Hammer et al., 2024). This variability underscores the challenge of establishing general rules, as the response of these organisms to environmental factors can be highly context-dependent and may require detailed, condition-specific research to fully understand and predict their behavior.

With regard to bio-mediated processes such as MICP and EICP, the interaction with native soil biota groups may hamper the efficacy of bio-based ground improvement solutions. Fig. 2 illustrates an example where indigenous soil bacteria compete for substrates with added strains in case of MICP, which may result in unsatisfactory level of cementation and in formation of undesired side products if their metabolism is different. Unwanted outcomes may result not only from competition of autochthonous strains, but also due to predation, or unintended synergies.

Therefore, although bio-inspired engineering is an emerging multi-disciplinary approach with enormous potential to solve complex problems across various fields, its application still faces certain limitations, such as: 1) limited range of conditions suitable for the life of soil-inhabiting organisms; 2) lower strength and higher variability of biological materials compared to traditional engineered materials; and 3) different ecological strategies of soil-inhabiting organisms in terms of substrate consumption and growth speed, which results in pronounced spatial and temporal variability of their distribution.

9. Case study

To place this information into context, the case study of coastal sand dunes is presented. These are encountered in several parts of the world including coastal areas in Northern Europe. While they tend to naturally form in sandy beaches, in the recent past they have often been removed to give way to urban space. However, they are currently being re-established in a push for sustainability because this practice reduces renourishment needs since sediments tend to accumulate over time. At the same time, it provides some protection from water surges and in this context, the public increasingly prefers them to traditional embankments because it perceives them as a natural solution even when anthropogenic (van der Meulen et al., 2023; Van Well et al., 2023; Geukes et al., 2024). There are many ongoing research projects aiming to improve coastal and flood protection together

Table 1
Summary of soil biota effects on mechanical properties.

	Bacteria	Fungi	Algae	Soil fauna	Plants
Physics	Through extracellular polymeric substances Only for actinobacteria through hyphae-like structure	Through hyphae Through weathering	-	-	Through roots
Chemistry	Through metabolic products For several indigenous communities and pure strains Limited to certain iron oxidizing bacteria (reduction and/or oxidation processes) Limited to autotrophs (Cyanobacteria) Most soil bacteria (organic heterotrophs) Through changes in pH	Mostly for yeasts, through metabolic products For some fungi Through pH reduction	Limited to certain algal species	Through burrows	Through decay of dead roots
Water interaction	Organic matter production Organic matter consumption/transformation/degradation Changes in electrical charge of clay minerals Hydrophobic surface formation (biofilm)	- Through intracellular and extracellular enzyme activity	Through photosynthesis, mostly in upper few cm of soil	Through grinding and digestion	Through photosynthesis

Table 2
Engineering properties changes due to soil biota presence and activity.

	Bacteria	Fungi	Algae	Soil fauna	Plants
Hydraulic properties	Changes in porosity and/or density	Bioclogging: either from necromass filling up pores (especially around rhizosphere, drilosphere and detritosphere), or MICP	Bioclogging: hyphae filling up pores in coarse grained soils. In some limited cases as a result of MICP	Biopores: through burrowing activity creates macropores	Biopores: preferential flow along roots or cavities left by decomposed dead roots. Penetration and creation of larger pores in fine grained soils. Bioclogging: Pore filling by smaller roots and root hair in coarse grained soils. Increase of evapotranspiration.
Mechanical properties	Fluid properties and interaction Shear strength Deformability Erodibility	Through biofilm formation Through biocementation, particle binding Through biocementation and fibre reinforcement for actinomycetes Through aggregate formation (particle binding and fibre reinforcement)	Through biofilm formation and changes in pH Through fibre reinforcement, particle binding, biocementation Adverse effect through weathering Adverse effect through weathering Through aggregate formation	Through biofilm formation Limited to a thin layer as a result of EICP	Through fibre reinforcement Through fibre reinforcement Through fibre reinforcement and vegetation cover

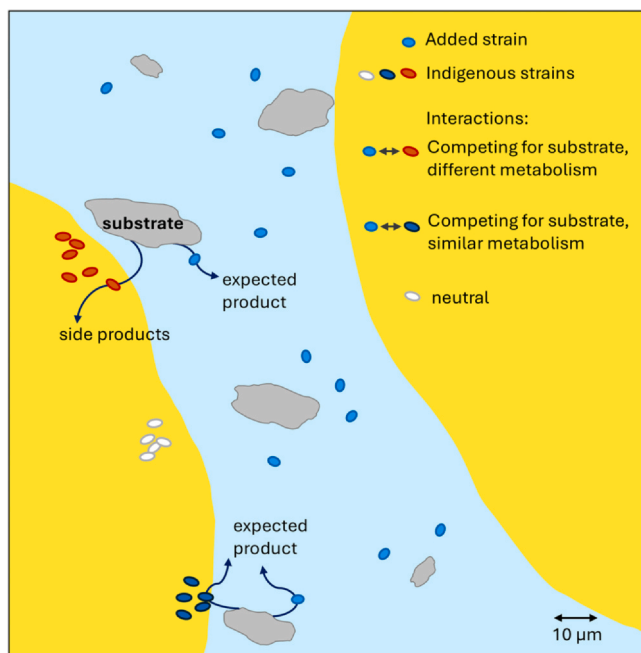


Fig. 2. Interaction between added bacterial strain and indigenous (local) strains in case of hypothetical bio-based ground improvement technology aiming to use exact enzyme activity of added strain. Added substrate is modified by added strain to an expected product, while indigenous strain may compete for the added substrate and transform into some others, side products.

with creation of biodiverse habitats: MANABAS COAST (<https://www.interregnorthsea.eu/manabas-coast>), DuneFront (<https://www.dunefront.eu/>), LIFECAPEable (<https://webgate.ec.europa.eu/life/publicWebsite/project/LIFE22-CCA-SE-LIFECAPEable-101113673/nature-based-solutions-for-flood-protection-of-low-lying-capes-to-strengthen-physical-safety-biodiversity-and-social-and-economic-benefits>).

Even though so-called natural coastal dunes cannot be entirely considered pristine from human intervention, it is important to highlight that they differ in several aspects from newly established coastal dunes because of the natural processes they underwent during their lifetime, which are mostly of biogenic nature. Some differences may be inherent and stem from the genesis of the deposit. For example, Garcia et al. (2024) recently found that naturally deposited particles align the axis of their main dimension in a same direction by comparing computed tomography imaging of a natural sand in its undisturbed state and that of a specimen prepared in the laboratory by pluviation. The orientation was postulated to be caused by the action of sea currents during deposition. It can therefore be assumed that aeolian deposits, consisting of fine silica sands like those found in the West Danish peninsula, are also likely to have particle arrangements dictated by wind direction making them more anisotropic compared to the same sand placed by heavy machinery and compacted, or even one placed hydraulically. Anisotropy in the particle arrangement would impact hydraulic as well as deformation properties, which in turn may influence the water regime, plant growth, slope stability and erosion.

A key difference between natural and anthropogenic dunes is in the jump in succession that the latter typically experience. As mentioned, the colonization of a barren dune would naturally follow a certain sequence. Firstly, primary producers like Cyanobacteria and algae start to live in barren sand with low concentration of organic matter and limited N and P, followed by undemanding pioneer plant species, mosses or lichens (Schaub et al., 2018; Zhelezova et al., 2019; Chowaniec et al., 2024). Over time, the accumulation of organic matter occurs, promoting the establishment of more diverse plant, fungal and soil fauna communities with higher nutrients demand (Poorter et al., 2023; Gao et al., 2024). Stress factors like drying, sand burial, salt water

ingression, salt spray, or pathogens may hamper the succession progress (Hesp, 1991). Bardgett (2005) also highlighted the key role of soil-borne pathogens in driving ecological succession via negative feedback mechanisms on host plants. A notable example comes from a sand dune system in the Netherlands, where the presence of root pathogens and root-feeding nematodes contributed to the decline of marram grass (*Ammophila arenaria*). This led to a more resilient species (*Festuca rubra*) becoming established in the ecosystem (Putten et al., 1993).

In newly established artificial dunes, sediments with low organic matter content are relocated to form the body of the dunes with vegetation placed on top either by hydroseeding on an organic mat (e.g. coconets), or by direct placing of an organic topsoil. The roots in the topsoil layer typically placed as a vegetation cover are significantly different compared to natural ones. This vegetated layer is only a few tens of cm thick to ease its relocation and has experienced optimal growth conditions. In the process of natural root development, primary roots emerging from seedlings or adventitious roots originating from non-root tissues, such as cuttings, contribute to the formation of lateral roots. Following their growth higher-order lateral roots emerge, which grow randomly at an angle or even at a right angle to gravity (i.e. plagiotropism and diagravitropism, respectively). This is advantageous in maximizing the plant's ability to acquire water and nutrients effectively (Lynch & Brown, 2001; Ma & Hasenstein, 2006; Mullen & Hangarter, 2003). On the contrary, the root network in artificial topsoils spread almost exclusively horizontally. Because newly established dunes have a higher soil bulk density compared to wind-deposited dunes that formed over a much longer period, water tends to infiltrate and flow through the top layer. As a result, roots not only find it difficult to penetrate the underlying ground, but they also lack the incentive to do so. The difficulty to penetrate the underlying ground is equally applicable when plants grow from seeds, so that the root anchoring effect observed in nature can be hardly achieved and blanket failure of the top layer ensues. Furthermore, the contribution that rooted soil make towards slope stability is based on pot experiments whose growth conditions are not entirely representative of those in nature, for example because they are not grown on a sloping ground. Furthermore, Karimzadeh et al. (2024) showed that strength of rooted soil is anisotropic and therefore results obtained from direct shear tests may not be representative.

This highlights how to improve the existing nature-based coastal protection measures and beach nourishment practices; it is important to consider successional patterns. Dune revegetation efficacy may be increased by 1) picking local plant species with high tolerance to stress factors, 2) adding microbial inoculants and/or organic matter (Farrer et al., 2022). Knowledge of factors contributing to form a stable natural state of coastal vegetation, is key to create a self-maintaining infrastructural element. Thus, resource-saving coastal protection together with ecological restoration could be achieved simultaneously.

10. Conclusions

Interdisciplinary approaches are required to tackle modern challenges: using biogeotechnical solutions to create sustainable infrastructure requires considering soil science, soil biology, plant physiology and ecology. This article describes how various groups of soil biota can influence soil mechanical properties. This influence is due to: 1) organic matter formation (plants, algae) and transformation (bacteria, fungi, soil fauna) that can affect soil pore-water viscosity and soil hydraulic properties, 2) physical binding and/or interparticle bonding (bacterial and algal biofilms, fungal hyphae, plant roots) that results in soil reinforcement, 3) change in size and distribution of pores (roots' growth and decay, soil fauna burrowing) that influence the hydrogeological regime, 4) mineral weathering by root-associated and free-living bacteria and fungi that can lead to a reduction in strength parameters, and 5) biological processes resulting in gas production and consequent desaturation. Soil biota presence and influence should be

considered for developing, improving and applying nature-based solutions in ground engineering, being mindful that the requirements for survival, activity and thriving vary for different soil biota groups. Furthermore, when adopting ground improvement techniques that rely on adding a substrate in the soil, care should be taken of the possible ecosystem dynamics. This is especially important when considering bioaugmentation as opposed to biostimulation.

CRedit authorship contribution statement

Alena Zhelezova: Writing – original draft, Visualization, Data curation, Conceptualization. **Gianmario Sorrentino:** Writing – review & editing, Conceptualization. **Gerald Innocent Otim:** Writing – review & editing, Conceptualization. **Irene Rocchi:** Writing – review & editing, Supervision, Project administration, Funding acquisition, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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