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Review

Bacterial communities on the surface of oligotrophic (nutrient-poor) soils

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ABSTRACT

Oligotrophic (nutrient-poor) soil ecosystems have been found to contain a wide diversity of bacterial communities. These communities vary in composition according to the mineral content and the chemical and physical properties of their environment. This creates a challenge for microbiologists to identify population patterns based on ecosystem characteristics. Advances in new technologies, and in particular high-throughput DNA sequencing, have improved the identification of bacterial groups, thus aiding our understanding concerning the presence and role of microbial populations in different biomes. Here, we review the principal bacterial members on the surface layers of nutrient-poor soil ecosystems, as well as the bacterial groups present in various oligotrophic ecosystems. We also assess factors that may shape the bacterial communities in these ecosystems such as their involvement in mineral transformations in order to better understand their distribution and possible functions on oligotrophic soil surfaces.

KEYWORDS: oligotrophic, bacteria, surface, soil, DNA sequencing, minerals.

1. Introduction

Soil has been recognized as an ecosystem harboring one of the most diverse microbial populations on Earth [1, 2]. Soils are also complex physical and chemical environments, where heterogeneous mixtures of minerals and nutrients, water, organic matter and biological species interact [3]. Soil microorganisms play a fundamental role as the principal drivers of biogeochemical cycles through activities such as nutrient acquisition and cycling of nitrogen and carbon, and through their roles in soil formation and in soil plant and animal health [4, 5]. The development of new sequencing technologies has enabled researchers in microbial ecology to begin to identify and characterize these microbial ecosystem components and understand how they may interact. In turn, these results will be important for predicting future ecosystem dynamics and the consequences of global environmental changes [6-8].

The principal biological fluxes of the major elements of life (H, C, N, S, O and P) are often driven by microorganisms, although in the case of P, volcanic activities and rock weathering are also significant contributors. These elements are transformed by redox cycles, where a chemical element is reduced or oxidized in a series of biotic (and/or abiotic) steps [6]. The known principal bacteria that play preponderant roles in certain nutrient cycles are members of the genera *Nitrosomonas* and *Nitrobacter* (nitrification), *Thiobacillus* (sulfur and iron oxidation),

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Rhizobium and *Frankia* (N_2 fixation), *Bacillus* and *Clostridium* (carbon cycling) and *Caulobacter* and *Pseudomonas* (manganese oxidation) [9, 10].

Terrestrial soil ecosystems are of many types, such as deserts [11], forests [12], caves [13] and grasslands [14]. These ecosystems differ in nutrient availability and composition, soil structure and mineral composition and microbial species presence and distribution. They can be subject to interventions that change the original soil structure, such as agriculture and climate [15]. The subsequent alterations in soil physicochemical properties can influence microbial community composition and diversity [5, 16]. The main factors influencing soil structure are both abiotic, including pH, organic matter content, H_2O content, O_2 concentration, temperature, and biotic, including plant and animal presence and diversity, as well as microbe-microbe and microbe multicellular organism soil substrate interactions [17, 18].

Here, we review the communities of soil-associated bacteria and their potential functions in terrestrial ecosystems, with a special focus on oligotrophic and/or hostile habitats. The term “oligotrophy” (“poor food”) pertains to life in low-nutrient habitats, and describes a wide range of environments, including terrestrial, aquatic and aerial ecosystems [19, 20]. Oligotrophic environments are characterized by a limited supply of nutrients (carbon, nitrogen and phosphorus) and H_2O [19, 21] and are distributed all over the Earth’s surface.

2. Advances in microbial identification

Microbiology as a discipline really began in the 17th century with the development, by Antonie Van Leuwenhoek, of his powerful microscope. It allowed him to observe single-celled organisms, which he named “animalcules”. His contributions were essential for the later identification and classification of microorganisms, and thus crucial for research in microbiology [22].

The Earth is estimated to contain approximately 4-6 x 10^{30} prokaryotic cells [23]. Microorganisms constitute approximately 60% of the Earth’s biomass, with microbial cell numbers estimated to be approximately 1.2 x 10^{29} in aquatic environments and 4-5 x 10^{30} in terrestrial ecosystems [24]. In nature, prokaryotes are key players in most ecological processes and require sources of energy, nutrients and proper physicochemical conditions for survival and growth [25].

2.1. Culture-based methods

Culture-based approaches for identifying microorganisms are indispensable for the study of microbial ecology, but it is now known that this leads to an enormous bias in the estimation of microbial biodiversity, as different microorganisms require different concentrations and types of nutrients and growth conditions, and most are not cultivable under laboratory conditions [26]. Over the course of the 20th century, microbiologists designed a wide variety of selective laboratory growth conditions by varying the pH, nutrient concentration and composition, oxygen gradients and temperature, among others, in an effort to expand the cultivable fraction of microbes. These included *in vitro* reproduction of natural environments such as sea water and soil [27]. However, studies of the taxonomic relationships among cultivated microorganisms based on DNA-DNA hybridization [28] led to the realization that it is difficult to culture the vast majority (>95%) of microorganisms under laboratory conditions [29, 30], owing to ignorance of the factors required for their growth [25].

2.2. Culture-independent methods

Advances in DNA, RNA and protein sequencing techniques have greatly aided the ability to discern phylogenetic relationships among microbes. In the 1970’s, Carl Woese pioneered the study of molecular phylogenetics based on 16S rRNA sequences, with the purpose of reconstructing the tree of life. On this basis, he proposed that life comprises three primary evolutionary domains: Eucarya, Bacteria and Archaea [31, 32].

Norman Pace used recombinant DNA techniques to reveal that the Bacteria domain contains over 40 different divisions [28, 33]. Research on the Archaea revealed that this group can comprise most of the microbial inhabitants (“extremophiles”) of environments generally considered to be too hostile for Eucarya and Bacteria, and thus enlarged our view of habitats compatible with life [34].

2.3. Metagenomics and the 16S rRNA gene as a molecular marker

The earliest sequencing methods, based on chemical cleavage or chain synthesis termination [35, 36], were augmented by techniques based on hybridization and on ligation and cleavage [37]. These, and other, high-throughput sequencing techniques have enabled the development of metagenomics, the derivation of microbial genome sequences from mass sequencing of DNA from environmental samples [38]. The genomes of coexisting microbes (both cultivable and non-cultivable) is sampled from an environment and subsequently sequenced [39, 40]. Metagenomics makes possible the identification of functional gene comparisons, genetic diversity, species composition and putative interactions with the environment [41-45], and can lead to the discovery of new taxa and genes [46, 47]. Metagenomic surveys have been performed with the aim of understanding the functioning of ecosystems, such as oceans [48-50], cold and hot deserts [5], soils in France [12], permafrost soils in Alaska [51] and submerged sediments in Brazil [52], to name but a few. Most studies of bacterial and archaeal diversity in environmental samples have used the 16S rRNA gene, a component of the 30S small subunit of prokaryotic ribosomes, to identify the prokaryotes that are present. This gene is present in all prokaryotic cells and is very important in the study of microbial ecology and evolution owing to its universality, its extreme sequence conservation, coupled with distinct regions of genetic variability, and the rarity of its transfer among taxa [32, 53-55]. However, the 16S rRNA gene also has limits in taxonomy studies, especially when low sequence divergence restricts distinction between closely-related organisms [56] and when variations in 16S rRNA gene copy number per cell can distort relative and absolute abundance estimates [57].

2.4. Next-Generation DNA Sequencing (NGS) and bioinformatic tools for microbial characterization

Next generation sequencing platforms can allow the analysis of hundreds of environmental samples in a single sequencing run [58]. Various DNA sequencing platforms have been developed in the past decade. They share three steps: template preparation, sequencing, and data analyses. The different platforms produce different types of data [59, 60]. GS FLX pyrosequencing (454 by Roche) can generate up to one million reads of >500 nucleotides (nt). HiSeq 2000/2500 and MiSeq (Illumina/Solexa), also using sequencing by synthesis, can reach approximately 180 million reads, yielding about 600 Gb of data [61]. SOLiD (Life Technologies) can generate more reads than 454, but of only 35 nt in length [62]. Newer technology being incorporated by Ion Torrent does not rely on the optical detection of incorporated nucleotides using fluorescence and camera scanning. This platform has lower cost, is smaller and has higher throughput than 454 but, as in 454, the sequence templates are generated on a bead or sphere *via* emulsion polymerase chain reaction (emPCR). Other NGS technologies have been established, such as Helicos BioSciences, using a single molecule detection system, and PacBIO (Pacific Biosciences), released in 2010, and these may be ideal for *de novo* genome assemblies, based on the detection of DNA synthesis by a single DNA polymerase [63].

Interpretation of the data generated by NGS technologies requires complex bioinformatic analyses. A typical pipeline process includes sequence cleaning steps, followed by alignment to database reference sequences. The cleaning steps, essential for accurate downstream analyses, involve filtering to remove low quality reads, contaminating sequences and primer sequences [64]. Several open source pipeline algorithms are available for these procedures, including Qiime [65] and Mothur [66]. The alignment to a known 16S rRNA reference database is extremely important, as this step enables identification of taxa found in each sample from different environments. The databases SILVA [67], GreenGenes [68] and RDP [69], are the most frequently used for 16S rRNA gene annotation.

The 16S rRNA gene can be clustered into Operational Taxonomic Units (OTUs) using a cut-off, generally of 97% (species level of taxonomy identification) sequence identity, with algorithms such as UCLUST [70] or UPARSE [71]. This step delineates operational species that then allows calculations of alpha and beta diversity, respectively, the number of species in each sample and the degree of dissimilarity among samples [72].

3. Bacterial biogeography: Are bacteria distributed ubiquitously?

Biogeography, as applied to microbial ecology, comprises the study of microorganism distribution in space and time and attempts to discern the mechanisms responsible, including selection, drift, dispersal and mutation, for the richness and composition of microbial communities [73]. Endemic taxa are restricted to particular habitats, and microorganisms living in extreme or oligotrophic environments appear to be endemic to distinct types of environments [74, 75], and non-randomly distributed in space [73]. Taking into account the bacterial diversity at the micro-scale, studies based on the 16S rRNA gene show a large diversity of taxa in just a few cm^3 of soil. However, many of these taxa may not be metabolically active. Thus, the use of the 16S rRNA genes for microbial identification may overestimate active bacterial diversity. Under unfavorable environmental conditions, some elements of bacterial communities may be in a dormant state, and then revive when conditions change in their favor [76, 77]. Different mechanisms can influence the distribution of bacteria, such as the colonization of new environments, in particular in soils where passive transport is limited by physical influences such as pore size and surface particle interactions [73, 78]. In oligotrophic soil environments, diverse physical and chemical characteristics can play a role in the profile of native bacterial populations [79, 80] and are discussed in the next section.

4. Principal factors affecting bacterial diversity in surface soils

Microorganisms living in the surface soil of oligotrophic environments are exposed to various abiotic and biotic factors that can selectively influence the survival and resistance of particular groups [12]. The factors known to influence bacterial composition in oligotrophic ecosystems include pH, salinity, temperature, plant and animal presence, soil moisture, and water and nutrient availability. The structure of soils, in particular the size of aggregates, plays an important role in the distribution of bacterial communities [3, 81]. For example, a study of the mineral composition in artificial soils suggested that quartz, montmorillillonite and charcoal particles can affect the abundance and functional diversity of soil bacterial communities, notably members belonging to the Proteobacteria, Actinobacteria, Firmicutes and Bacteroidetes phyla [82].

Soils can be characterized by different physical and chemical properties, and can contain a unique microbial community in a specific geographical location [11]. The most important known physical factors shaping microbial communities in soils are pH [83] and salinity [84]. The pH is commonly lower on the surface than deeper in the soil, as a result of interactions with organic matter [85]. However, in hot desert surface soils, the pH is commonly alkaline, with pH values > 8.5 being observed [83, 86]. It has been previously shown that microbial phylum composition is influenced by changes in soil pH, particularly for members of the Acidobacteria, which are commonly found in, though not restricted to, low pH soils, and for members of the Actinobacteria phyla that are found in soils with high pH in arid or semiarid ecosystems. In contrast, diversity has been reported to be higher in neutral pH value soils [87]. Salinity may decrease bacterial biomass and enzyme activity [88], though some groups, such as halophilic bacteria, can resist osmotic stress and desiccation [84, 89]. Other factors, such as temperature, UV radiation, wind, altitude, and nutrients also affect bacterial community composition. Bacteria can confront these challenges through different tolerance strategies such as biofilm formation, stress responses or dormancy [90-92]. Oligotrophic soils present further challenges to microbial life as these are generally low-nutrient/highly mineralized soils.

5. Biogeochemistry: How soils get mineralized?

5.1. Definition

Mineralization in soils is the effect of the dissolution of minerals, which can influence the physicochemical structure of the soils and, as a consequence, soil fertility [93]. Mineralization occurs by the generation of new rock material, generally by tectonics, by sedimentation of organic and inorganic particles, and by rock erosion [94] (Figure 1).

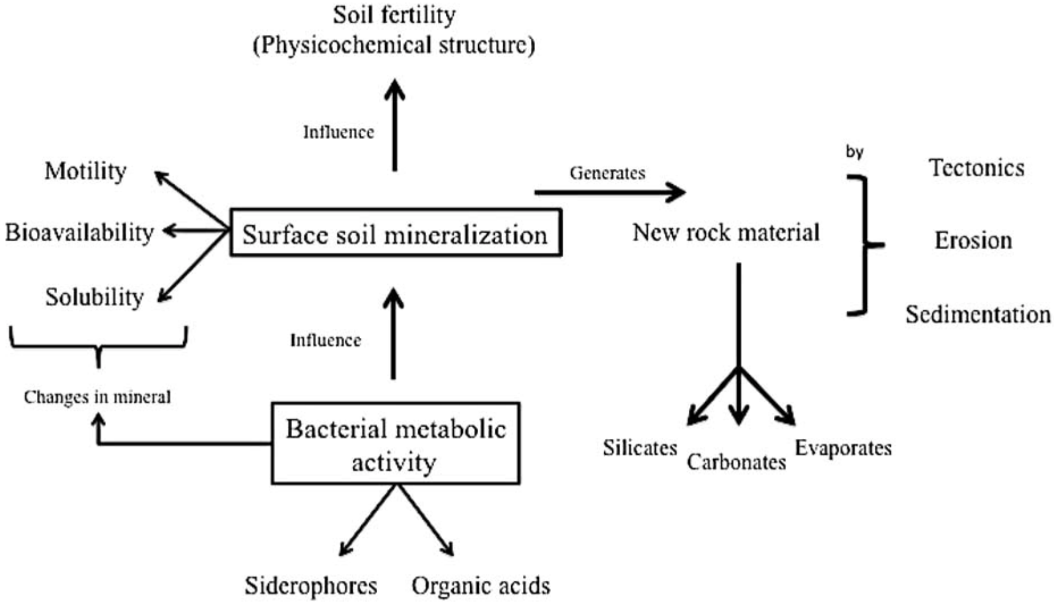

Figure 1. Diagram showing bacterial activity and mechanical processes involved in surface soil mineralization.

5.2. Composition and processes

The minerals in surface soils are the result of weathering and erosion of rocks exposed on the Earth's surface. These minerals are classified into three primary types: silicates (granite, basalt and shale), carbonates (limestone and dolomite) and evaporates (halite and gypsum) [95] (Figure 1). Silicates comprise 90% of the Earth's land surface [96]. The chemical weathering of rock is an irreversible process brought about by temperature and pressure changes, precipitation, erosion and runoff [96]. Weathering of continental rocks is a major cause of soil mineralization. It determines the formation, evolution, chemical and physical properties and fertility of soil. Weathering of silicate rocks (which increases with temperature and runoff) consumes CO_2, an important factor in climate regulation, and produces chemically mobile elements such as Na and Ca and immobile elements such as Al or Fe that are constituents of clays (e.g., kaolinite) and metallic oxyhydroxides (e.g., goethite) [95]. The dissolved material is derived from rock by chemical (i.e., production of secondary minerals) and physical (i.e., breakdown of the rocks) weathering [94, 95]. Biotic factors that contribute to soil weathering include plant roots and microorganisms, which, by releasing CO_2 and organic acids, produce an acid environment that improves nutrient uptake and mineral dissolution [97]. The principal parameters controlling chemical weathering in soils are lithology (nature of the rocks), climate, mechanical erosion, biotic activity and organic material [96-98].

5.3. Lithology

The major elements present on the Earth's surface resulting from soil weathering processes are SiO_2, cations (Na, K, Ca and Mg) and anions (HCO_3, SO_4 and Cl) [99]. Rock properties such as mineralogy, crystal sizes, surface and fracture density can influence the lithology and, as a consequence, chemical weathering [98]. The dissolution rates vary among the different mineral types and depend on the soil matrix and specific environmental factors at different locations, and are essential for specific microbial group colonization [100, 101].

5.4. Climate and mechanical erosion

Local climate effects can affect temperature and runoff. Depending on the ecosystem (i.e., tropical, mountainous, etc.), temperature may influence weathering, and its fluctuations may do so through effects on activation energies [102].

However, runoff will produce a direct interaction with the rock and, depending on soil characteristics (nature, thickness, porosity and plant root systems) and rain intensity, will induce soil weathering. Soils are often thick at low elevation and thin at high elevation [95]. The role of physical erosion in mineral weathering is also related to the aging of the mineral surface and present-day climatic conditions [103, 104] that may contribute to clay mineralogy and thus the microorganism populations present in these soils. It has been reported that the basalt age is also a factor that can influence the bacterial communities associated with basaltic rock [105].

5.5. Organisms and organic matter

From a physical perspective, vegetation and, in particular, plant root systems can decrease the mechanical erosion of soils because they facilitate the production of organic material and soil microbial colonization which act as adhesive factors for soil particles [106]. Vegetation also induces evapotranspiration that can decrease runoff but also generate local rainfall [98]. Chemically, plants produce organic acids in their root exudates, which can promote the solubilization of insoluble and immobilized minerals from the deep soil layers [95, 97]. Bacteria also help accelerate mineral weathering directly by oxidation/reduction of minerals and through the decomposition of litterfall that acidifies the upper soil [106].

6. Bacterial adaptations and roles in mineral soil surfaces

Bacterial communities in soils may cause complex mineral transformations such as biological weathering [94]. However, determining whether such a process results from the activity of specific microbes [107] can be difficult, owing to the low cultivability of most microorganisms [108]. Bacteria interact with minerals by various mechanisms, depending on the mineral type, organism and environmental conditions, while mineral composition and bacterial metabolic activity can influence mineral solubility, mobility and bioavailability [109] (Figure 1). Bacteria promote mineral release from silicates by colonizing the mineral surfaces, where they release hydrogen ions, low molecular-weight organic molecules such as siderophores, and organic acids [110]. Abiotic and biotic factors can modify the original chemical structure of the soil surface and, as a consequence, influence changes in the taxonomic distribution of bacterial groups present on mineral surfaces [94]. The products of dissolution, from mineral complexes, by bacterial activity depends on bacterial cell wall structure, their outer layers, and to products of secondary metabolism, such as exopolymers that can adsorb to minerals such as clays, colloids or oxides [109]. Several studies of bacteria associated with minerals report that, in silicate mineral weathering processes, the principal dynamics are associated with the production of hydrogen ions, hydroxyl ions or metal chelating metabolic products [100]. Different mineral types may be associated with a wide variety of bacterial types, as described by Glesson *et al.* [111], who demonstrated that distinct bacterial communities present on the surfaces of mineral types are determined principally by the chemical composition of the mineral substrate, suggesting that chemically different substrates are colonized by different bacterial communities, as are different-sized soil particles [112]. Ding *et al.* [82], suggested that bacterial dissemination in artificial soils is not a stochastic process, and that the abundance of bacterial populations is determined by the type of clay mineral, metal oxides and the presence of carbon. Under aerobic conditions, bacteria-mineral interactions generate hydrogen ions and ligands that contribute to acidolysis, complexolysis and iron immobilization [113]. Microbes can also contribute to biomineralization, forming minerals such as calcium carbonates, silicates, iron oxides and sulfides. Bacteria-mineral interactions can also affect bacterial growth and metabolic activity. The principal mechanisms of bacterial survival in the presence of minerals are redox transformations, production of proteins and peptides for mineral binding, precipitation and active mineral transport [114]. Energy generation, nutrient acquisition, cell adhesion and biofilm formation can all respond to the relative toxicity of minerals. Micro-topography, surface composition, surface charge and hydrophobicity can also play a role in the ecology of bacterial communities associated with mineral surfaces [115]. This is particularly true for Al and Fe oxides, which are among the most reactive components on the surface of acidic and neutral soils, and also play a role in the mineral catalysis of humic substances [116]. The principal elements forming inorganic mineral complexes under the influence of bacterial activity are Al, Fe, Si, Mg, Mn, S and P [109]. Specific bacterial groups are involved in these geochemical transformations, mainly those that oxidize and reduce iron and manganese and that reduce sulfur and sulfate [109]. One of the common minerals transformed by bacteria is bauxite, whose major constituents are Al_2O_3, Fe_2O_3 and SiO_2. Here, weathering is promoted by bacteria that can mobilize oxides of aluminum, iron and silicates, and that reduce iron under anaerobic conditions [117]. Carbonates, which represent a significant portion of insoluble minerals, are also mineralized by bacterial biofilms. *Cyanobacteria* participate in global carbon cycling and photosynthesis [118]. Sulfate-reducing bacterial groups play a role in carbonate deposition due to the production of extracellular polymeric substances, which can nucleate carbonate [118, 119]. Phosphates can also be found on the surface of mineral soils, and bacteria can solubilize inorganic phosphate complexes ($FePO_4$, $AlPO_4$) by producing organic or mineral acids, or by chelation [97]. Silicates comprise up to 90% of the Earth's surface, and are subject to environmental change [117, 120], where their bond structures may be altered by bacteria through the release of organic acid products, the ligands of cations, and acidic polysaccharides [117].

7. Bacteria living in mineralized surface soil ecosystems: Which genera are perceived to be the most abundant?

Bacteria can transform mineral complexes by various mechanisms *via* interactions with mineral complexes on soil surfaces. Ecosystems, such as deserts or caves, generally have low levels of nutrients [91, 121]. Others, such as forest soils, can have high levels of nutrients and also surface layers composed of a variety of mineral complexes, creating oligotrophic niches for bacterial communities which depend on mineral weathering for their growth and survival [107]. In this section, we describe the bacteria that can play important roles in mineral soil surfaces. In general, the principal elements released by microorganisms from the mineral complex of biotite and granite are Al, Fe, Ni and Si [94, 122]. Different bacteria colonize rock and sand surfaces [123], and endolithic and epilithic bacterial communities are usually different [124]. In deep mineral soils, bacteria are principally involved in complexolysis, whereas on the surface they weather minerals by acidolysis [113]. Table 1 presents a list of the principal bacterial genera known to play a role in mineral transformation and in particular, mineral weathering. Surface soils mostly harbor members of the *Burkholderia, Collimonas, Pseudomonas, Bacillus* and *Arthrobacter* genera (see Table 1). Wang *et al*. [125] studied the differences in weathering ability of bacteria in upper and deeper soils from red soil in China. Their results suggest that the elements released from mineral surfaces are Fe, Si and Al, and that bacterial diversity was higher in upper soils than in deeper soils. Some *Burkholderia*, *Bacillus* and *Lysinibacillus* species are highly efficient weathering bacteria, while some *Burkholderia* species were found to be the most abundant in mineral transformations (Table 1). It is interesting to note that the latter association was also seen in the surface soils of forests [12, 126].

8. Bacterial communities of oligotrophic ecosystems: Which bacterial groups predominate?

Many different ecosystems are oligotrophic on the basis of low nutrient availability. These ecosystems are often represented by soils composed of a complex of mineral elements, for example desert sand, caves, ice and rocks. However, ecosystems can contain specific niches (where nutrient availability is low) that can be considered as oligotrophic, such as, for example, acid forest soils, grasslands, and other mineralized surface soils. Bacteria living in oligotrophic soil ecosystems adapted to drastic climatic changes are likely to be also adapted to conditions of carbon scarcity, suggesting that the study of these ecosystems may offer an opportunity to discover novel metabolic products, such as proteases [127]. Desert-like ecosystems make up > 30% of the Earth's land mass [91]. Because of interest in the impact of

Table 1. Bacterial members associated with inorganic mineral transformations.

Bacterial members associated with inorganic mineral transformation in surface soils		
Bacteria	**Mineral dissolution (or released)**	**Referente**
Sphingomonas spp.	Biotite, phosphate	[113]
Burkholderia spp.	Biotite, phosphate, granite, apatite	[113, 125, 148-150]
Collimonas spp.	Apatite; Biotite	[113, 148-150]
Janthinobacterium spp.	Biotite	[149]
Geobacter spp.	Iron	[151]
Gallionella spp.	Iron	[117]
Leptothrix spp.	Iron	[117]
Acidithiobacillus spp.	Sulfides oxidation	[109]
Leptospirillum spp.		
Sulfolobus spp.		
Acidianus spp.		
Pseudomonas spp.	Biotite, phosphate, kaolinite, vermiculite	[122]
Arthrobacter spp.	Apatite, biotite	[125, 149]
Paenibacillus spp.	Biotite, bauxite	[152]
Bacillus spp.	Granite, apatite, bentonite	[149, 153]
Erwinia spp.	Biotite	[122]
Pedobacter spp.	Apatite	[149]
Chinitophaga spp.	Apatite	[149]
Shewanella spp.	Nontronite	[154]

microorganisms on desertification, they are now one of the most studied oligotrophic ecosystems in relation to their bacterial communities [11, 80, 128]. In deserts, surface soils are composed of complex mineral structures formed principally by sandy loam and load sand, which themselves are formed by weathering of the surface soils, and have a very low percentage of water retention and thus less vegetation. Sandy structures are formed principally of rocks such as granite, quartz and limestone, as also observed in soils from coastal forests and grasslands [129] where bacterial populations able to weather rock have been described [130]. Biological soil crusts (BSC) are complex microbial communities which colonize interstitial soil surfaces and can be distributed in arid and cold soil ecosystems, representing a niche for various microbes, including both photosynthetic and heterotrophic bacteria [91]. BSC's also exist in other biomes, such as grasslands, forest soils, permafrost soils and polar regions [131], where *Cyanobacteria*, plus phototrophic microorganisms of high radiation and salt resistance, are the first colonizers, thus creating unique niches in which other microorganisms can be integrated [132]. Certain *Cyanobacteria* are able to fix atmospheric nitrogen in the presence of CO_2 [80]. A study of BSC's on the surface of pasture soils [133] showed that the soil surface (0-3mm) and bulk soil (3-12mm) are exposed to different light conditions. It was also observed that the influence of light on microbial communities was restricted to the soil surface, and that nutrients, such as extractable P and K, were altered at the soil surface as a result of growth of phototrophic communities. Numerous studies of bacterial diversity in arid ecosystems (e.g. hot deserts) have been performed. The most abundant groups observed are members belonging to the Actinobacteria, Proteobacteria and Bacteroidetes phyla [134] while, in lower proportions, members belonging to the Firmicutes, Acidobacteria, Gemmatimonadetes and Cyanobacteria phyla [11, 135] were also found. However, the bacterial diversity in surface hot desert soils differs significantly from that of other terrestrial biomes [5]. Bacterial association with minerals from sandy soils have been studied, revealing that members of the Proteobacteria, Actinobacteria and Acidobacteria phyla displayed strong associations with quartz, magnetite and pyroxene, though differences were observed between the types of minerals present and bacterial types [130]. Microbial abundance has been explored, for other non arid-desert oligotrophic ecosystems, such as polar deserts (McMurdo Dry Valley, Antarctica) [136]. Here, members belonging to the Acidobacteria and Actinobacteria phyla were present in higher proportions in high pH soils, while Acidobacteria phyla are commonly found in acidic soils [87, 137].

Ganzert *et al*. [138] studied bacterial diversity of permafrost soils in Greenland, and showed that soil bacterial communities depend significantly on soil pH. Members of the Acidobacteria, Bacteroidetes and Proteobacteria phyla were found to predominate in the soils, while the relatively low pH supported Acidobacteria and Proteobacteria but not Bacteroidetes phyla, whose members predominate at higher soil pH [85]. Members belonging to the Proteobacteria phyla were found principally in soils with high nitrogen and carbon availability [139].

Other terrestrial oligotrophic soil ecosystems, such as grassland soils [140], have been studied, revealing that oligotrophic and acidophilic organisms, such as Acidobacteria and Proteobacteria, decrease in abundance with high pH, total C and N, while copiotrophic and alkaplophilic bacteria (Firmicutes, Chloroflexi, Actinobacteria and Bacteroidetes) are more abundant in soils rich in organic matter and nutrients. In the surface soil of an acid forest ecosystem, similar results were found. Members belonging to the Proteobacteria and Acidobacteria phyla were found in low pH soils, suggesting that these bacteria could be a microbial indicator of soil quality improvement [141].

9. Conclusions and perspectives

A variety of modern metagenomic studies have begun to provide new insights into the bacterial communities present in oligotrophic or hostile soil conditions, such as those of arid hot deserts [142], rock surfaces [143], shallow biofilms in mountains [144] and coastal saline sandy soils [145]. One response of bacteria in oligotrophic surface environments is the formation of biofilm complexes, which protects the embedded microorganisms from environmental fluctuations and UV exposure [146]. Such ecosystems may provide keys for understanding the evolution of these microorganisms under harsh environmental conditions [147].

The study of bacterial communities living in terrestrial surface soil ecosystems is a challenge, owing to the fact that fewer than 5% of the bacterial species present are cultivable under laboratory conditions [30]. Oligotrophic ecosystems are not well characterized, and new technological approaches to bacterial identification and function will facilitate the study of bacterial communities inhabiting different terrestrial ecosystems.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest

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