The Mineralosphere concept: mineralogical control of the distribution and function of the mineral-associated bacterial communities

AUTHORS: Uroz, S.[1,2*], Kelly, L.C.[1,2,3,4], Turpault, M-P.[1], Lepleux, C.[1,2,5], Frey-Klett P. [1,2]

[1] INRA, Université de Lorraine, UMR 1136 “Interactions Arbres Micro-organismes”, Centre INRA de Nancy, 54280 Champenoux, France

[2] INRA UR 1138 “Biogéochimie des Ecosystèmes Forestiers”, Centre INRA de Nancy, 54280 Champenoux, France.

Present address:

[3] Division of Biology and Conservation Ecology, Manchester Metropolitan University, Oxford Road, Manchester, M1 5GD, UK.

[4] School of Biological Sciences, Bangor University, Deiniol Road, Bangor, LL57 2UW, UK.

[5] Leibniz-Institut DSMZ-Deutsche Sammlung von Mikroorganismen und Zellkulturen GmbH, 38124, Braunschweig, Germany.

* Corresponding author: Mailing address: INRA-Université de Lorraine, Interactions Arbres Micro-organismes, UMR 1136, 54280 Champenoux, France. Phone: +33 (0)3 83 39 40 81, Fax: +33 (0)3 83 39 40 69. E-mail: uroz@nancy.inra.fr

Highlights

- Minerals can be considered as a real microbial habitat, the mineralosphere
- Mineralogy drives the taxonomic and functional distribution of bacteria
- Mineral-associated bacteria are capable of weathering minerals
- Minerals can induce or repress bacterial functions

Abstract

Soil is composed of a mosaic of different rocks and minerals, usually considered as inert substrata for microbial colonization. However, recent findings suggest that minerals, in soils and elsewhere, favour the development of specific microbial communities according to their mineralogy, nutritive content and weatherability. Based upon recent studies, we highlight how bacterial communities are distributed on the surface of and in close proximity to minerals. We also consider the potential role of the mineral-associated bacterial communities in mineral weathering and nutrient cycling in soils, with a specific focus on nutrient-poor and acidic forest ecosystems. We propose to define this microbial habitat as the mineralosphere, where key drivers of the microbial communities are the physico-chemical properties of the minerals.

Key words: microbial habitat, bacteria, mineral weathering, mineral chemistry, mineral weatherability, nutrient cycling, forest soil

1. Rocks and Minerals: support of life

Earth conditions allow the continuous genesis of igneous, metamorphic, and sedimentary rocks. Such processes continue to shape landscapes, generating new rock material as a result of tectonics, sedimentation of organic and inorganic particles, or conversely rock erosion over geological timescales. Our planet can therefore be considered as a mosaic of different rocks and minerals (**Figure 1**), subjected to various degrees of environmental pressure and characterized by different physicochemical characteristics. Minerals are also differentiated according to their weatherability. Indeed, certain classes of mineral are easily weathered in acidic conditions, while others are quite recalcitrant [1]. Due to their nutritive content and their variable dissolution rates, mineral surfaces can be considered as reactive interfaces where nutritive cations are potentially accessible to the biosphere.

Whatever their location and their physical and chemical form, minerals play a central role in our environment. Regardless of their location and origins, from atmospheric dust, aquatic, terrestrial, deep-biosphere minerals or even human teeth, all mineral and rock environments have the potential for microbial colonization. Rocks and minerals serve as physical supports for attachment of microorganisms (bacteria, fungi) and plants, and as nutritive reserves participating in nutrient cycling, soil fertility and water quality. From an evolutionary perspective, microbial habitation of minerals seems to be an ancient strategy [2-4]. Interestingly, life on Earth itself may have originated within a mineral habitat [5]. Analyses of microbial interactions in the critical-zone have revealed the exceptional abilities of microorganisms, both prokaryotes and eukaryotes, to successfully colonize and interact with a diverse array of rocks and minerals [6-21].

Do these minerals drive the establishment and development of specific microorganisms adapted to colonize such environments? Or conversely, are these minerals merely inert supports for microbial opportunists? Answering this question is of major importance because nutrient-poor, rocky mineral environments represent one of the main sources of nutritive cations for ecosystem functioning. One way to answer this question is to determine whether mineral colonization is a random process, or controled by environmental conditions (extrinsic factors) and/or mineral characteristics (intrinsic factors). In this opinion paper, we argue that minerals represent specific microbial habitats, the intrinsic characteristics of which control microbial community establishment. We propose to call such a mineral-influenced habitats the mineralosphere [22]. We have chosen to focus on heterotrophic bacterial communities, the role of which in mineral weathering remains poorly understood compared to fungal communities. Analysing mainly *in situ* examples from aquatic and terrestrial environments, we will consider the extrinsic and intrinsic factors which make minerals suitable habitats for microbial colonisation. We will also discuss the links between mineral chemistry and weatherabililty, together with the composition, diversity and functional potentials of the mineral-inhabiting bacterial communities. A more thorough understanding of the factors driving mineral colonization by bacteria will allow enhanced appreciation of the potential roles of bacteria in mineral weathering, soil formation and nutrient cycling.

2. Is mineral colonization random or specific?

If the establishment, succession and/or persistence of mineral-colonizing microbial communities on minerals are driven by the minerals themselves, the factors driving this colonization are expected to vary among environments. Here, we examine potential extrinsic and intrinsic factors to offer a wider perspective of the subject.

2.1. Extrinsic factors: environmental factors

Surface and subsurface minerals are subjected to very different conditions that may influence microbial colonization on minerals. Surface minerals are exposed to ambient air conditions and the presence of more or less complex biofilms due to atmospheric deposition can be easily observed on any stone or monument. Notably, several studies have reported that microbial colonisation of mineral surfaces was strongly affected by the temperature, pH, light, UV irradiation, oxygen, water and nutrient availability, and aeolian erosion [7,15,23]. For example, Wierzchos et al. [15] reported that the microbial colonization of gypsum crust in the Atacama Desert was controlled by moisture, exhibiting higher colonization in a wet environment contrary to the drier one. In acid mine drainage where very acidic conditions (pH 2) occur, specific microorganisms such as *Thiobacillus* are enriched on pyrite surfaces, from which they use the ferric iron as electron acceptor [24]. These and other studies suggest that mineral colonization is strongly determined by environmental factors, especially in environments characterized by extreme temperatures, pH and water content, such as deserts. One may explain the presence of microorganisms in such locations by an adaptive strategy, where bacteria seek protection from the extrinsic parameters (i.e. irradiation, temperature, water content), or as the result of a passive accumulation [7,23,33,34]. Comparatively, subsurface minerals are exposed to quite different environmental conditions, whether it is in the critical-zone or aquatic environments, and few studies have evaluated *in situ* the environmental factors determining microbial colonization of such minerals [25-26]. Comparing minerals incubated in a petroleum-contaminated aquifer in three geochemically zones, Mauck and Roberts revealed that mineral colonization by microbes was strongly dependent on the carbon and oxygen availability [25]. In a batch experiment, Scholl et al [26] reported increased bacterial cell attachment on microcline and quartz surfaces according to the pH and ionic strength of the environment, highlighting the importance of the surface binding forces in the attachment of microbes to mineral surfaces. Although no direct demonstration of the effects of soil pH, organic matter, nutrient availability or land cover on mineral colonization have been shown on subsurface minerals or rocks *in situ*, these extrinsic factors are known to impact the composition and diversity of soil microbial communities at a larger scale [27-32]. Consequently, we expect that these factors will also impact the colonization as well as the functioning of the mineral-associated microbial communities at smaller scales.

2.2. Intrinsic factors: Do mineral characteristics influence bacterial colonization?

2.2.1. Physical attributes

By adopting an endolithic lifestyle, the presence of cracks, fissures, cavities and pores in minerals are expected to provide microbial protection against the extrinsic factors described previously [7,23,33,35]. Analysing the apparent heterogeneity of colonization of granites, sandstones and other minerals, several studies reported preferential microbial development according to porosity and size of the mineral particles, or on the edges formed during mineral dissolution [7,23,33,35]. Considering granitic rock fragments, Abdulla [33] demonstrated an increased Actinomycetes colonization of minerals with higher porosity. Analysing various size fractions of soil sandstones, Certini et al. [35] showed that the smallest sandstone fractions were more colonized than the largest fractions. Incubating model Gram negative and Gram positive bacterial strains in the presence of biotite and plagioclase feldspar, Barker et al. [36] showed that bacteria colonized all mineral surfaces, with preferential accumulation along the cleavage steps and edges of mineral particles. Altogether these *in situ* and *in labo* observations suggest that mineral colonization is not random but determined by the physical attributes of minerals. Among them, the preferential colonization of the smaller size fractions may be explained by the reactivity of mineral surfaces. Indeed, the smaller mineral fractions are characterized by higher reactive surfaces, giving them more available for microbial colonization. Due to their negative charge, bacterial cells could establish electrostatic interactions with the positive charges of these specific sites, interactions that may be reversible according to localised pH conditions [26, 39]. This preferential colonization of microbes on mineral surfaces, due to chemotactic processes can allow to the establishment of complex biofilms [40]. Such biofilms have been observed *in situ* on the surface of various stone monuments, aquatic or aquifer environments [40], *in labo* using pure-culture based experiments [41-42], but rarely *in situ* on soil minerals. Consequently, experiments analysing microbial colonization on soil mineral surfaces varying in size, porosity or charge are necessary to confirm the relative importance of these physical attributes.

2.2.2. Mineral chemistry and weatherability

Minerals are categorized according to their chemical composition and complexity [42]. Primary minerals (e.g. silicates) are formed during rock genesis, while secondary minerals (e.g. oxides, clay minerals) are precipitates of chemicals released from primary minerals during weathering, or formed during hydrothermal events. Although few contain carbon or nitrogen, rocks and minerals can contain key nutritive or toxic elements. Consequently, the chemical composition and dissolution rates of minerals may be considered as important drivers of the microbial communities.

a) Impact of mineral chemistry

Analysis of natural mineral inclusions such as muscovite, plagioclase, K-feldspar and quartz, extracted *in situ* from various rocks, revealed that bacterial community structure varied in relation to the inclusion type, with some phylotypes present only on certain inclusions [10, 43-46]. A detailed analysis revealed positive and negative correlations between the abundance of some phylotypes and the elemental composition of the inclusion. Surprisingly, elements such as sodium and silica were identified as key structuring elements. Similarly, Hutchens et al. [10] revealed a relative specificity of certain phylotypes only detected on quartz (SiO_2), considered as a nutrient-poor mineral. The impact of host rock chemistry was also investigated in cave environments. Comparing two distinct areas in Carlsbad Cavern, Barton et al. [47] revealed that the first area, composed mainly of $CaCO_3$, harboured a higher cell density but a lower bacterial diversity compared to the second area characterized by a more complex mineral composition (volcanic and metamorphic minerals). Based on a 16S rDNA cloning-sequencing approach, the authors showed an enrichment of *Actinobacteria* in the $CaCO_3$ environment and, on the contrary, a dominance of alpha-, beta- and gamma-proteobacteria on the complex minerals [47].

Experiments on pure minerals have been undertaken in various environments [22, 25-26, 48-52]. Using a mesh bag approach (**Box 1**) in acidic forest soils, we revealed a link between mineral geochemistry and the structure of the bacterial communities [22]. Similarly, several studies performed in petroleum-contaminated aquifers reported a higher bacterial colonization of P- and Fe-rich minerals compared to other minerals [16-17, 25, 45]. Authors suggested a preferential colonization of mineral surfaces containing nutritive elements that are limiting in the aquifers. These studies also reported a potential toxic effect of Al-containing minerals, resulting in reduced microbial biomass [43, 51]. Furthermore, the importance of the mineral geochemistry was evidenced in extreme aquatic environments such as in a hot thermal system [53] and subglacial environments [50]. Incubating small crystals of pyrite, hematite, magnetite, olivine, calcite and quartz in the glacial meltwater stream at Robertson Glacier (Canada), Mitchell et al. [43] showed that the bacterial communities were quantitatively (higher biomass) and qualitatively (structure and composition) affected by the mineral geochemistry, especially the Fe content. The authors explained this result by a preferential colonization of mineral surfaces acting as electron donors or acceptors (pyrite, hematite, magnetite). Similarly, Phillips-Lander et al. [53] showed that bacteria preferentially colonized minerals with higher Fe and P content.

The impact of mineral geochemistry on microbial colonisation has been investigated further using engineered minerals. Scholl et al. [26] tested the impact of iron by comparing bacterial colonization of natural and Fe-coated minerals (quartz and muscovite). These authors demonstrated that after a short-incubation (16h), the Fe-coated minerals were more colonized than non-coated minerals. Interestingly, Rogers and Bennett [46] used artificial borosilicate glasses containing additions of apatite, goethite or a mixture at 1% final concentration. After a 9-month incubation in aquifer conditions, apatite-goethite and apatite glasses appeared more colonized than goethite glasses and unamended borosilicate glasses.

All the observations obtained using natural or artificially coated minerals [10, 16, 25, 43-47] show that minerals are not just inert substrata on which microbial life can expand, but that strong relationships exist between the chemistry of these minerals and the distribution of the bacterial communities. Due to their reactivity with the environmental conditions, minerals can be considered as physicochemical interfaces releasing nutrients, adsorbing compounds on their surface and forming precipitates. Notably, many of the elements (e.g. Fe, Mn, Mg, P, Ca, Na) entrapped in minerals are physiologically required by bacteria as electron donors, terminal electron acceptors, co-factors or nutrients. The structuring effect of minerals and mineral chemistry presented above prompts us to propose that these factors strongly determine the distribution and functioning of the mineralosphere bacterial communities.

b) Mineral weatherability

As stated above, minerals vary in their recalcitrance to environmental pressures (e.g. pH), hence the nutrients contained within more recalcitrant minerals may be less accessible to biota than those of more easily weatherable minerals. Consequently, one could hypothesize that the colonization of mineral surfaces is largely determined by the weatherability of these minerals. To decipher such relationships, we used the dissolution rates presented by Palandri and Kharaka [55] for each class of mineral, to analyse the available quantitative and qualitative data from the literature related to mineral colonization by microorganisms.

Quantitatively, several studies performed in aquatic environments using pure minerals and/or rocks, reported a higher colonization of poorly weatherable minerals such as quartz and K/Na-feldspar [17, 53]. Notably, Mitchell et al. [50] reported a greater colonization of poorly weatherable minerals such as hematite and magnetite, and conversely a comparatively reduced colonization of highly weatherable minerals such as calcite and pyrite. On the contrary, higher colonization was reported on highly weatherable minerals such as calcite [26]. Using a real-time PCR approach, Santelli et al. [56] revealed a significant correlation between the age of marine basalt and the abundance of mineral-colonizing bacteria, showing that the oldest and most weathered basalts, were the most highly colonized. In terrestrial environments, higher cell densities were measured in the most weatherable zone of Carlsbad Cavern than in the less weatherable zone [47]. Finally, using a grain-per-grain strategy on desert sand samples, Gommaux *et al.* [57] highlighted that the density of culturable bacteria was the same on different mineral types.

Qualitatively, Gleeson et al. [43-44] were among the first to apply molecular techniques on independent minerals extracted from granitic outcrops, determining the impact of the different mineral particles contained in granite (kaolinite, pegmatitic granite, unweathered granite) on the structure of the mineral-associated microbial communities. A differentiation of mineral-associated communities was confirmed here and in other studies performed on inclusions (muscovite, plagioclase, K-feldspar, and quartz) extracted from granite [10, 44], suggesting that different communities inhabited weatherable and poorly weatherable minerals. Similarly, several studies performed on marine basalt described the phylogenetic diversity of the basalt-associated bacterial communities in relation with basalt age [56-59], revealing a clustering of the bacterial communities according to basalt age (level of alteration).

However, none of these studies directly measured the level of weathering of the minerals analysed. Examples combining mineral weathering and molecular analyses are presented in **Box 2**. From all these observations, one may ask if these taxa are enriched on minerals due to their ability to weather minerals or because they are attracted due to the higher nutrient availability occurring near weathered mineral surfaces.

2.3 Artificial soils: a tool to decipher the impact of minerals on the bacterial communities

In the last decade, several studies have tested how soil microbial communities are structured in artificial soils containing clay minerals, rock phosphate, silicate, or metal oxide [60-62]. A microcosm study by Carson *et al*. [60] revealed that bacterial communities from soil amended with mica did not cluster with those of other artificial soils. Additionally, the authors showed that the soil respiration was significantly higher in the soil amended with rock phosphate than in the soils amended with mica or basalt, suggesting that both the structure and function of the bacterial communities were modified in response to different amendments. Using a similar approach, Ding et al. [62] also reported significant differences in the relative abundance of Proteobacteria, Firmicutes, Actinobacteria and Bacteroidetes in relation to the mineral types present in the artificial soil. These taxa were significantly enriched in the artificial soil containing a mix of quartz, montmorillonite and charcoal. These first studies clearly confirm that mineralogy drives the composition and functioning of soil bacterial communities.

3. Mineral weathering ability and other functional abilities of the mineral-associated bacteria

Aside from some specific bacterial taxa, which use insoluble terminal electron acceptors contained within secondary minerals [24], few studies have focused on the mineral-associated bacterial communities and their functional abilities [49, 63-66]. If minerals support the development of specific bacterial communities, it is logical then that for certain functionalities mineral selection should operate, permitting the development of adapted bacteria. In this context, we thus wonder whether mineral-associated bacteria possess specific metabolic and physiological abilities adapted to the specific mineral environments, and whether they are capable of weathering their mineral substratum. Due to the absence of known functional genes specifically associated with the mineral weathering activity, culture-based approaches remain an essential tool to address such questions.

3.1. Are all mineral-associated bacteria capable of weathering minerals?

Such a question was addressed using microbial consortia and pure cultures isolated from various mineral environments. In aquifer systems, Bennett et al. [16] reported that the most intensively weathered minerals were the most colonized, suggesting a role of the mineral-associated microorganisms in the dissolution of minerals. Considering granite samples, Welch et al. [66] reported that granite-associated microbial consortia were able to weather both apatite and biotite in batch experiments through the production of organic acids during incubation. Other granite samples collected in front of the Damma glacier (Switzerland) were used to characterize the mineral weathering ability of a set of bacterial strains [63-64]. Mineral weathering assays revealed that around half of these Damma glacier bacterial strains were effective at weathering granite, with differences in the ability to release specific elements (Fe, Al, Ni). The highest mineral weathering potentials were obtained for bacterial strains belonging to the *Arthrobacter*, *Janthinobacterium*, *Leifsonia* and *Polaromonas* genera. Effective mineral weathering bacteria belonging to the *Arthrobacter* and *Burkholderia* genera were also isolated from apatite particles incubated for several years in an acidic forest soil [49]. In the context of patrimony conservation, Qi-Wang et al. [59] revealed that bricks of the Nanjing Ming city walls (China) were inhabited by effective mineral weathering bacteria. Lastly, effective mineral weathering bacteria were found in the buccal cavity on the surface of human teeth, which are composed of hydroxyapatite minerals [13]. Altogether, these studies demonstrate that minerals, whatever their chemical nature and the environment considered, are colonized by specific taxa characterized by effective mineral weathering potentials.

3.2. Are mineral-associated bacterial communities physiologically active or dormant?

Using metabolic assays, Certini et al. [35] revealed that the metabolic potential of mineral-associated microorganisms was different from those of the surrounding soil, and that higher metabolic potentials were observed for the smaller rather than the larger mineral fractions. Epifluorescence microscopy, applied on mineral particles incubated several years in forest soil, also showed active bacterial cells using a vital stain [67]. Performing a BIOLOG analysis on effective mineral weathering bacterial strains isolated from these mineral particles, Lepleux et al. [49] highlighted that, in contrast to those of the surrounding bulk soil or the mycorrhizosphere, mineral-associated (mineralosphere) bacteria metabolized few substrates and with a very low intensity, suggesting an oligotrophic behaviour. Surprisingly, glucose appeared as the most intensively and unique substrate consumed by the mineralosphere bacteria. On the contrary, bacteria in the bulk soil preferentially metabolised amino and carboxylic acids with high intensity, with comparatively poor glucose metabolism. Finally, Frey *et al.* [63] showed that the most effective mineral weathering bacterial strains also produced high concentrations of oxalate. Similarly, tooth-associated bacteria are metabolically active and produce organic acids contributing to the formation of dental caries [13, 68]. These observations demonstrate that mineral-associated bacterial isolates are physiologically active, metabolise organic substrates and produce metabolites, suggesting that they may participate in mineral weathering and nutrient cycling.

3.3. Do minerals drive bacterial gene expression?

While minerals appear to be colonized by bacterial communities harbouring particular functional abilities, our knowledge regarding the feedback effect of these minerals on the physiology of the mineral-associated bacteria remains limited. Many attempts have been undertaken using chemoheterotrophic bacteria capable of respiring metals contained within minerals. Differential gene expression or protein production were observed when the cells were forming biofilms on minerals [69]. Comparatively, few analyses have been performed on heterotrophic bacteria. Olsson-Francis et al. [70] addressed the above question using a microarray approach to decipher the molecular mechanisms used by *Cupriavidus metallidurans* CH34 to weather basalt in a minimal medium lacking iron. Their microarray analyses revealed that siderophores were produced only in the absence of basalt, and that other functions (ca 4% of the genes) were up- or down-regulated. Notably, transport-related genes and multiple genes involved in motility were up-regulated only in the presence of basalt. On the contrary, genes encoding TonB-dependent outer membrane transporter and putative cytochromes were down-regulated in the presence of basalt. In another context (*Gaeumannomyces graminis*/*Pseudomonas* interaction), Almario et al. [71] while trying to decipher the impact of iron availability on the production of 2,4-diacetylphloroglucinol by *Pseudomonas* CHA0, revealed a significantly higher induction of the metabolite production in the presence of iron-rich vermiculite than in presence of illite. Altogether, these results suggest that due to their physicochemical properties, minerals influence gene expression.

4. Concluding remarks and future perspectives

Based on the *in situ* observations and *in labo* demonstrations presented above, we propose to define the mineralosphere as the specific interface and habitat encompassing the rocks (or mineral surfaces) and the surrounding soil, which are physically, chemically and biologically under the influence of minerals. Physically, the mineralosphere is characterized by several zones, including pores and cracks which modify water circulation and can be considered as microbial sanctuaries. Indeed, microorganisms can accumulate in these zones due to passive diffusion and develop with relative protection against external environmental pressures (e.g. pH, temperature, predation). Chemically, the mineralosphere can be considered as a nutrient reserve and a reactive interface. Surface charges and the exchange capacity of minerals have been shown to impact colonization of mineral surfaces. Indeed, positive charges (such as in the phyllosilicate interlayers) can attract negatively charged bacterial cells. Besides electrostatic processes, chemotactism can operate. The nutrients contained within minerals can attract or repel microorganisms due to their nutritive or toxic value. While some of the released nutrients can be directly available for microbes, other can form precipitates (oxides) requiring solubilisation by microbes to become available. These nutrients can be passively released from mineral surfaces due to abiotic processes, or actively due to biological activities. Biologically, the mineralosphere is enriched in specific microorganisms adapted to low carbon and mineral-rich environments, and potentially capable of contributing to mineral weathering. In this habitat, the mineral weathering ability of microorganisms may be regulated by their nutritional requirements, nutrient availability and/or the mineral type. Of course, this specific habitat is impacted by environmental conditions, which for soil include parameters such as pH and water availability, or the inputs of organic and inorganic nutrients.

Notably, the mineralosphere shares common properties with the well-known rhizosphere. As with the rhizosphere, minerals, due to their physico-chemical properties and the nutrients released during their dissolution, modify their environment chemically and physically. In this regard, we suggest that the mineralosphere may be considered as the inorganic twin of the rhizosphere (**Box 3**), where bacteria are not selected by organic nutrients coming from roots, but rather by the physico-chemical properties of minerals. This concept brings a new perspective to soil microbial ecology, as our current knowledge of the structure and diversity of microorganisms in soil environments is mainly based on composite geologically heterogeneous samples. The selective effect of minerals on the soil bacterial communities may account at least partly for their heterogeneous distribution in the soil. Of course, more studies combining environmental geomicrobiology, geochemistry, mineralogy, microscopy and genomics (**Box 4**) are required to fully comprehend the complex interaction of factors, both intrinsic and extrinsic, governing the bacterial colonisation of minerals as well as by fungi, and to determine their relative role in mineral weathering, nutrient cycling and ecosystem functioning.

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Glossary

Corundum : Al_2O_3

Critical-zone: interface of the lithosphere, atmosphere, and hydrosphere, which encompass the soil and terrestrial environments.

Quartz : SiO_2

Intrinsic factors : Factors related to the mineral characteristics (chemical composition, porosity,…).

Eukaryotes: fungi, plants, lichens

Extrinsic factors : Factors related to environmental parameters (pH, nutrient availability, …)

Geomicrobiology : The study of the interactions between minerals and microorganisms.

Mineral : Inorganic and solid compound characterized by a chemical formula, a crystal form and an atomic structure.

Mineralogy : The study of the chemistry and crystal structure of minerals.

Mineralosphere : Volume of soil under the influence of the nutritive and toxic elements contained into the minerals

Mycorrhizosphere : Volume of soil under influence of mycorrhizal-roots.

Nutritive content : The content of inorganic nutrients entrapped into the minerals.

Prokaryotes: archaea, bacteria

Rhizosphere : Volume of soil under root influence.

Rock : naturally occuring solid composed of one or more minerals.

Saprolite : Rock particles formed during weathering of bedrock and present in soil profiles.

Surface and subsurface minerals : Define the physical location of minerals submitted to atmospheric event (surface) or below ground (subsurface).

Weatherability : weathering capacity of a mineral in specific conditions

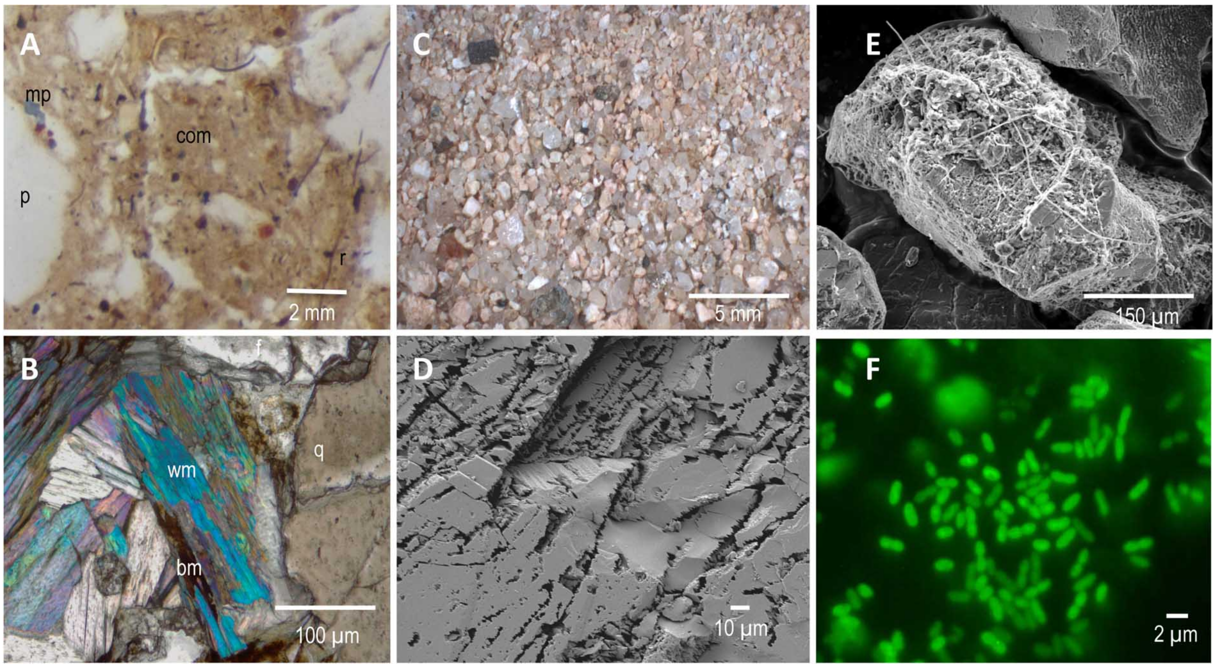
Box and Figure legend

Figure 1: Mosaic of environments and microbial colonization.
A. Thin layer section of soil surfaces imaged with a stereomicroscope. This panel presents the soil heterogeneity, with tree roots (r), pores (p), mineral particles (mp), clays and organic matter (com). **B**. Focus on a granite particle (q,quartz; wm, white mica; bm, black micas; f, feldspaths). The particle was imaged using a polarised microscope. **C**. Granitic saprolite showing the different mineral particles present (quartz, micas, feldspaths) and the variability of size and colour, imaged with a stereomicroscope. **D**. Focus on an apatite particle imaged with a scanning electron microscope. This figure presents the different cracks and fissures, which can be used, as habitat by microorganisms. **E**. Apatite particles imaged after several years of incubation in soil conditions (mesh bag approach). The apatite particles appeared covered by a complex organo-mineral biofilm containing fungal hyphae and bacteria. **F**. Bacterial cells on biotite surfaces imaged by epifluorescence microscopy. Bacteria colonize mineral surfaces where they can establish complex biofilms. Such biofilms have been observed *in situ* on the surface of various stone monuments and aquifer minerals [40], *in labo* using pure-culture based experiments [41], but rarely *in situ* on soil minerals. However, panel E of this figure clearly shows a complex organo-mineral structure on the surface of the apatite particles. Interestingly, Certini et al [35] reported the presence of complex mats on mineral surfaces considering sandstone rocks.

Box 1: a simple method to analyse mineral-associated microbial communities: the mesh bags. Although the technics based on microscopy have strongly evolved, the bottleneck still remains the rocks or minerals themselves. Indeed, if it is possible to analyse the functional and taxonomic diversity of microbial communities colonizing minerals collected in the field, these minerals are rarely pure, not of the same size and porosity, giving conclusion difficult to establish. To limit such problems, several studies have developed a pure mineral strategy. Pure and calibrated minerals can be introduced directly *in situ* or conditioned in mesh bags in terrestrial and aquatic environments. Mesh bags containing minerals are used since decades [73], and this method was initially used to determine mineral weathering in environmental conditions (Figure I). More recently, this approach was used to determine the impact of plants [74-75] on minerals, and which fungi [76] or bacteria [22,50] are able to colonize minerals. Interestingly, this approach can be modulated to test single type or mixed minerals, different size of minerals and permits or not the penetration of plant roots inside the mesh bags. Notably, Augusto et al. [74] developed a method permitting to measure mineral weathering based on mass loss. Similar systems have been developed in aquatic environment. Figure I: Mesh bags approach. **A**. Pure and calibrated apatite particles (3 grs; particle size 0.5-1 mm) have been conditioned in mesh bags (mesh size 50 μm; 4 × 10 cm). **B**. Installation of mesh bags in the organic horizon of forest soil. Red arrows indicate the location of the mesh bags. Minerals have been incubated several years in soil before mineralogical and microbial analyses. **C**. Apatite particle imaged before incubation in soil conditions. **D**. Apatite particle imaged after several years incubation in soil conditions. This image illustrates the complex biofilm formed on apatite surface.

Box 2: Relationship between mineral weatherability and distribution of the bacterial communities In order to get inside the potential relation between mineral weatherability and bacterial diversity, pure and calibrated minerals (apatite, plagioclase, phlogopite) were incubated in acidic forest soil conditions during four years using the mesh bag approach. Such approach has permitted to determine both mineral weathering level and bacterial diversity. Using a small-scale 16S rRNA clone library (70 sequences per condition), Uroz et al. [22] revealed that the mineral-associated bacterial communities were distinct from those of the surrounding soil. This analysis also highlighted that the most weathered minerals (apatite) were characterized by a decrease of diversity (shannon index) and an enrichment of specific taxa such as Beta-Proteobacteria in comparison to the less weathered minerals (phlogopite), suggesting that a correlation may exist between the bacterial diversity and the level of weathering of the minerals. Notably, this finding was confirmed using a more resolving approach (16S rRNA pyrosequencing; 30,000 sequences per condition) on apatite samples incubated in different soil conditions [50]. Interestingly, a significant correlation (Figure I) between the level of weathering and the abundance of 16S rRNA sequences was obtained for the Beta-Proteobacteria, the Burkholderiales as well as the Burkholderia, which have been described as effective mineral weathering taxa on this experimental site. These observations suggest that these effective mineral weathering taxa colonize minerals and may play an important role in mineral weathering and nutrient cycling. Figure I: Relation between mineral weathering of apatite and relative abundance of 16S rRNA gene sequences affiliated to Beta-Proteobacteria (based on 16S rRNA sequences). Minerals have been incubated in soil conditions (4 years) in the experimental site of Breuil-Chenue below different tree species (beech, douglas fir, spruce, Corsican pine, coppice with standards). Open circles correspond to analyses performed by cloning-sequencing and solid circles to analyses performed by 16S rRNA pyrosequencing.

Box 3: The mineralosphere: the inorganic twin of the rhizosphere ? The structuring effect of the microbial communities by the tree root system was reported in various environments and for various plants (77). Here, we are presenting the common ecological traits and the specificities of the rhizosphere and mineralosphere habitats.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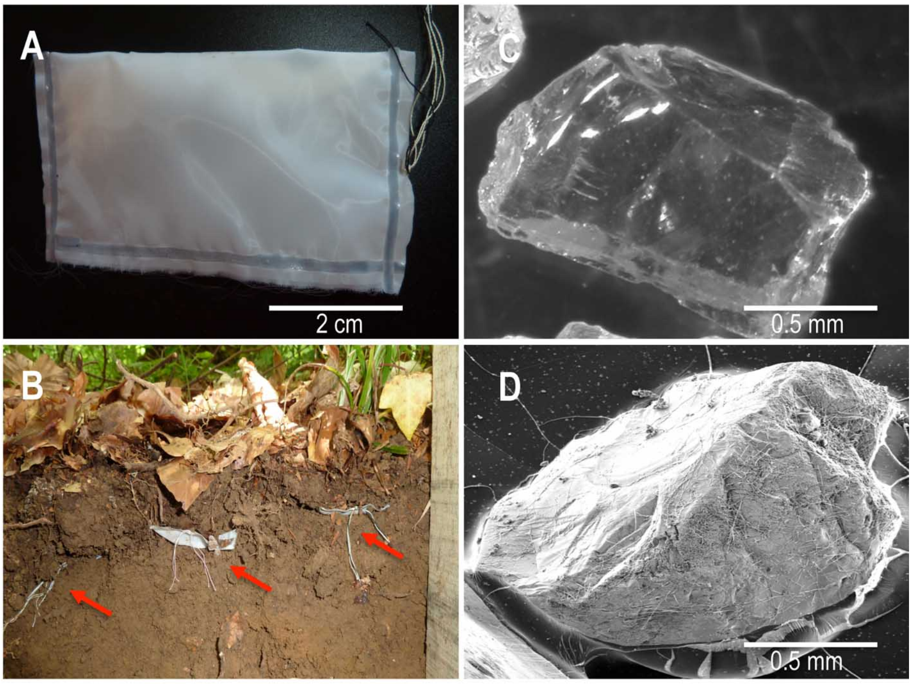
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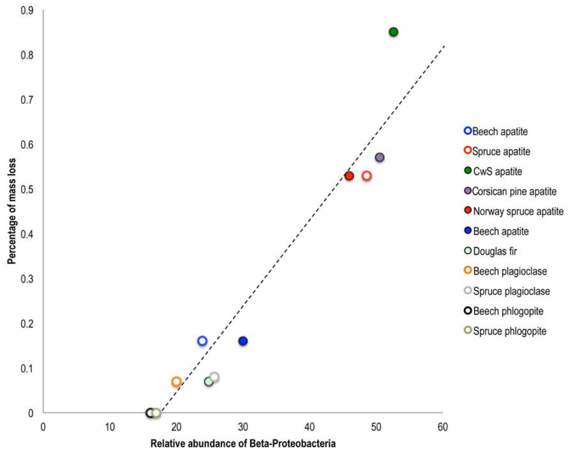
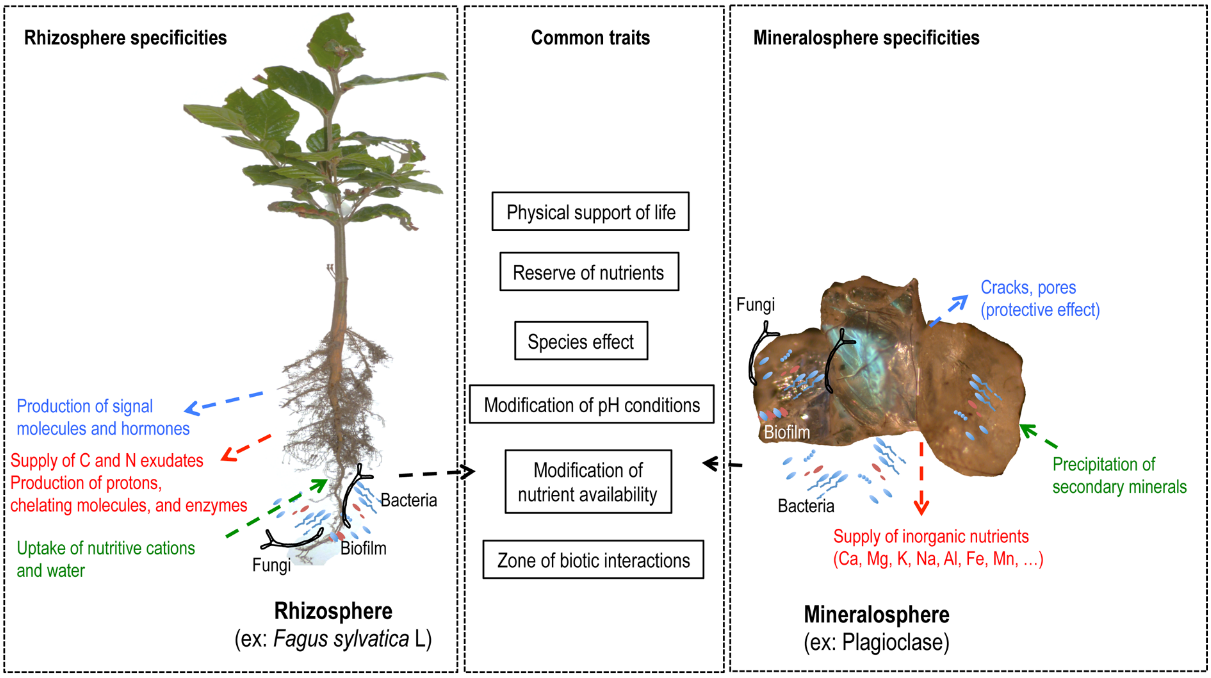


Percentage of mass loss
Relative abundance of Beta-Proteobacteria
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
0
10
20
30
40
50
60
Beech apatite
Spruce apatite
CwS apatite
Corsican pine apatite
Norway spruce apatite
Beech apatite
Douglas fir
Beech plagioclase
Spruce plagioclase
Beech phlogopite
Spruce phlogopite



Rhizosphere specificities
Common traits
Mineralosphere specificities
Production of signal molecules and hormones
Supply of C and N exudates
Production of protons, chelating molecules, and enzymes
Uptake of nutritive cations and water
Bacteria
Biofilm
Fungi
Rhizosphere
(ex: Fagus sylvatica L)
Physical support of life
Reserve of nutrients
Species effect
Modification of pH conditions
Modification of nutrient availability
Zone of biotic interactions
Fungi
Cracks, pores (protective effect)
Biofilm
Precipitation of secondary minerals
Bacteria
Supply of inorganic nutrients (Ca, Mg, K, Na, Al, Fe, Mn, …)
Mineralosphere
(ex: Plagioclase)

Box 4 : Outstanding questions

1) Given the environmental and mineral heterogeneity, can we develop tools applicable to any mineral/rock environments, especially in soil to test mineral chemistry effect on microbial communities (i.e. mesh bag systems, artificial labelled minerals)?
2) How can we best assess mineral surfaces, and especially image mineral-associated microorganisms, given both methodological challenges and the complexity of mineral/rock samples?
3) Can we demonstrate if mineral-associated microbes are selected by the physico-chemical properties of a mineral or by the higher nutrient availability occurring in its vicinity?
4) Do mineral-associated microorganisms characterized by functional and physiological specificities? Do mineral-associated microorganisms regulate their physiology according to the mineral types? Is there a functional complementation between the mineral-associated microbial communities?
5) More studies are needed to analyse in situ geochemistry of minerals, release of nutrients from their surface and transfer to plants ? How to determine in situ the relative contribution of soil microorganisms to this transfer of nutrients?