

REVIEW ARTICLE OPEN



The contribution of living organisms to rock weathering in the critical zone

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Rock weathering is a key process in global elemental cycling. Life participates in this process with tangible consequences observed from the mineral interface to the planetary scale. Multiple lines of evidence show that microorganisms may play a pivotal—yet overlooked—role in weathering. This topic is reviewed here with an emphasis on the following questions that remain unanswered: What is the quantitative contribution of bacteria and fungi to weathering? What are the associated mechanisms and do they leave characteristic imprints on mineral surfaces or in the geological record? Does biogenic weathering fulfill an ecological function, or does it occur as a side effect of unrelated metabolic functions and biological processes? An overview of efforts to integrate the contribution of living organisms into reactive transport models is provided. We also highlight prospective opportunities to harness microbial weathering in order to support sustainable agroforestry practices and mining activities, soil remediation, and carbon sequestration.

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INTRODUCTION

At the surface of the Earth, tectonic forces continuously expose rocks to weathering. This geological process leads to the progressive decay of rock substrates, turning bedrock into regolith and releasing elements that fuel global biogeochemical cycles¹. In particular, the chemical weathering of Mg- and Ca-silicates coupled to the deposition of Mg- and Ca-carbonates results in a net flux of CO₂ from the atmosphere to the lithosphere that controls atmospheric CO₂ concentrations, and hence, climate over geological timescales (>10⁵ years)². In addition, rock-forming minerals constitute an essential source of elements required to form secondary aluminosilicate minerals constitutive of the soil matrix and necessary to the development of ecosystems³.

The need for a fundamental understanding of the dynamics of the present (and past) atmospheric composition, pedogenesis and element cycles in general, has been accentuated in recent years with pressing climate and sustainability challenges requiring precise models for the evolution of greenhouse gases and the renewal of limited resources including soil and nutrients⁴. This has led to increasing efforts to understand and quantify the process of rock weathering.

Initially conceptualized in terms of abiotic dissolution reactions alone, the past two decades have seen growing evidence of the potential of living organisms, including bacteria⁵, fungi⁶, plants⁷, and animals⁸ to influence weathering, alone or synergistically⁹. Depending on the environmental or experimental conditions, organisms have been observed to increase weathering rates and also occasionally to inhibit the effect of abiotic weathering processes (i.e., bioprotection, BP), retarding mineral weathering^{10–12}. Several terms have been coined to describe the accelerating effect of living organisms on weathering processes, including biological weathering^{13,14}, bioweathering¹⁵, or biogenic weathering¹², equivalently referred to as BW in the following. The contribution of microorganisms (i.e. bacteria, fungi, and archaea) to BW—or microbially mediated weathering¹⁶—will be referred to

here as MW. BW, BP, and MW mostly take place in the Critical Zone (CZ), which corresponds to the portion of the Earth's crust—usually extending from the top of the tree canopy to the bottom of surface aquifers—where rocks meet life (including humans) and where the interplay of chemical, biological, physical, and geological processes support life at the Earth's surface^{13,17}. CZ processes affect factors ranging from the chemistry and texture of the soil to the topography of the Earth's surface via weathering, biogeochemical cycling and erosion, and are critical to the development of natural ecosystems and human societies.

The contribution of life to mineral weathering was reviewed several times in the past, either with a general perspective^{18–20} or by focusing on specific organisms (plants⁷, bacteria²¹, mycorrhizal symbiosis²², and fungi²³) or specific systems (forested ecosystems¹⁴, ecological niches such as the mineralosphere⁵, mineral substrates such as carbonate rocks²⁴ or silicate glasses²⁵). In addition, MW was also reviewed through the prism of specific research hypotheses¹³ or topics (e.g., spatial scales)¹⁴.

The present review specifically examines the BW role of plants and microorganisms, which together account for >99% of the Earth's biomass²⁶ (Fig. 1), with an emphasis on bacteria and fungi that may deserve a particular attention as demonstrated below. Because this topic was already extensively reviewed, we aim here at highlighting key points and at opening debates that we believe are essential to advance our understanding of BW.

In the first section, we outline the role of two key players, plants and microorganisms. We highlight the following points: (1) the study of the effect of plants on weathering processes, beyond fundamental implications, has also stimulated the study of underlying MW processes, and (2) microorganisms play an important role in BW processes. We show that they constitute most of the interface between the lithosphere and the biosphere, where they are adapted to interact with mineral substrates on the one hand, but also with some symbiotic partners on the other hand, thereby supporting the development of ecosystems. In a

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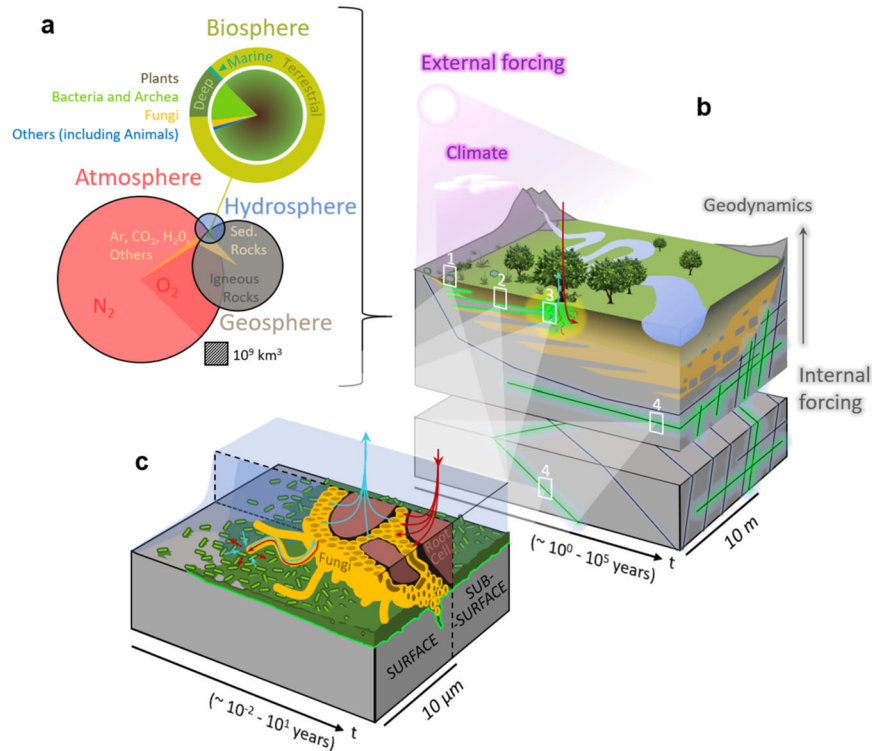


Fig. 1 Fluid–mineral–(micro)organism interactions across scales. **a** Earth system science representation of the biosphere at the intersection of the different components of the Earth system scaled to their respective volumes, providing an approximate global composition (in vol. %) of the compartments interacting at the surface of the Earth as well as the color code used in this review. **b** Co-evolution of a rock substratum and above-ground landscape driven by “external forcing” (i.e., solar radiation driving climate and photosynthesis) and “internal forcing” (mostly mantle processes resulting in geodynamics including uplift, volcanism, etc.). The (bio)chemical weathering of rocks is an important consequence of these forcings, along with other processes such as erosion. Regolith develops from the bedrock— with the formation of saprolite and soil horizons (pedogenesis)—as plants and microorganisms develop on mineral surfaces (ecosystem development). Rock substrates colonized by archaea and bacteria (green) as well as fungi (yellow), either on bare rocks (1), in the rhizosphere (2), in soil environment (3), or deeper in the subsurface (4), constitute potential bioweathering hotspots (see white boxes). **c** Similar representation at lower space and timescales for surface and subsurface environments, where mineral surfaces colonization by pioneering microorganisms is followed by biofilm development by bacteria, archaea, and fungi (green). Note, in both panels (b) and (c), the presence of microorganisms at the interface between mineral surfaces and their environment (either bulk fluid or the rest of the ecosystem) where they can mediate fluxes that are key to BW processes. These include water and inorganic nutrient transfer (blue arrows), as well as a reciprocal flux of carbon and nitrogen from the atmosphere (CO_2 , N_2) to the rhizosphere (organic molecules such as acids or carbohydrates—red) mostly mediated by plant photosynthesis and nitrogen fixation.

second section, we briefly describe the state of the art of bioweathering, with a particular emphasis on microorganisms. We review (1) the main BW mechanisms (How?), (2) current BW enhancement factors found in the literature (How much?), and (3) the possible ecological meaning behind BW (Why?).

In a third section, we highlight some of the current challenges and recent developments found in literature through three questions: (1) Is it possible to combine the relevance of field experiments with the precision of laboratory experiments? (2) Can we define a physical and genomic signature of weathering? (3) How can we model BW? Finally, we review several sustainable and technological opportunities that would benefit from a better understanding of BW.

LIVING ORGANISMS AND ROCK WEATHERING

The overall effect of vegetation on weathering

Interactions between biota and geological processes started early in the evolution of life on Earth. Hazen and Morrison²⁷ suggested that the formation of microbially mediated minerals could have occurred as early as 3.5 Ga. Today, about half of the mineral species we know result directly or indirectly from biological processes, and more than a third form exclusively as a consequence of biological activity²⁷. The terrestrial expansion of

early photosynthetic communities in the late Precambrian^{28,29} perhaps constitutes one of the best examples of the reciprocal interactions between life and the mineralogy of the Earth’s surface. Land surface colonization is believed to have increased terrestrial weathering by producing organic acids, inorganic acids and chelating agents that promote mineral dissolution, and by enhancing fluid–mineral interactions (with *larger contact area* generated through microfracturing of mineral grains by roots and hyphae, and a *longer contact time* due to the stabilization of the soil matrix by root systems)³⁰. This led to profound changes in pedogenesis, to secular shifts in sediment composition (i.e., increase in pedogenic clay minerals) and to an increased flux of lithophile elements to continental margins³¹. All of these processes contributed to an abrupt drop in atmospheric CO_2 ³² concomitant with a greater burial of organic C. This resulted in a stepwise rise of atmospheric O_2 ³³, partly driving the evolution of life toward the complex multicellular organisms that we know today³⁴. In this perspective, BW is arguably one of the key underlying processes that shaped the transition from the Precambrian to the “Phanerozoic world”³⁵.

These findings constituted an important step in our current understanding and conceptualization of BW processes³⁶, and the current paradigm considers that “vegetation” (including plant

roots and their microbial symbionts)³² accelerates rock weathering overall^{35,37}, even though this simplified picture is still debated¹².

Several approaches were used to investigate the role of vegetation on weathering at different scales. In pioneering studies, the extent to which vegetation accelerates “abiotic” weathering at the global scale was essentially estimated from sensitivity analyses against the evolution of atmospheric CO₂ concentrations over the past ~600 million years^{2,38} deduced from soil studies^{39,40}. Second, some of the effects of vegetation on weathering rates, including the influence of plants on hydrology (e.g., water uptake and evapotranspiration, which tend to limit the extent of chemical weathering) and on solution chemistry (through respiration processes, nutrient uptake, or organic acid release, which tend to enhance chemical weathering) were incorporated in contemporary weathering models^{41,42}. The latter modeling approach, instead of *deducing* BW from estimates of past climates, rather relies on state-of-the-art parameters and phenomenological laws from laboratory mineral dissolution experiments and decadal record of environmental parameters (used as a calibration) to *predict* the effect of vegetation on weathering. This produced valuable predictions of mineral weathering over seasonal to centennial timescales and over small (<1 km²) to large (>1.8 million km²) watersheds^{41,43,44}. A third kind of approach, which consists in estimating the contribution of vegetation *directly* in the field, has proven more challenging and therefore more equivocal for several reasons. First, the intrinsic pervasiveness of life deeply entangles biotic and abiotic processes occurring in the field⁴⁵. In addition, the “geogenic” flux of elements released by slow rock weathering processes is small compared to the flux of nutrients recycled from decayed organic matter (e.g., by one to two orders of magnitude in certain contexts)^{12,46}. The dependence of net primary production on rock weathering can be further complicated by element transfers, which do not involve mineral dissolution, such as atmospheric wet deposition or element exchanges with clay phases. Nevertheless, approaches combining model-dependent (e.g., closed system or steady-state hypothesis) proxies were developed to improve element mass balances involving vegetation and weathering rates at the soil profile or plot scale and discriminate the different elemental fluxes: the combination of stable and/or radiogenic isotope systems have helped to identify plant–mineral interactions and recycling by vegetation (Mg and Ca isotopes), uptake by vegetation (B), sources of mineral nutrients and ecosystem cycling of elements released by weathering (Sr), as well as weathering and erosion processes (U or Be)^{12,47–50}. Data generated by these methods, in combination with climate or vegetation gradients, was for instance used to try to disentangle the role of variables such as mean annual precipitation or net primary productivity in weathering rates¹².

Overall, current hypotheses consider that weathering and biology are strongly coupled. The exact nature of this coupling is however complex and likely depends on factors such as the erosion regime or the space and timescales considered¹³ (Fig. 1).

The effect of microorganisms on weathering: why does it matter?

While the contribution of vegetation to rock weathering has been historically scrutinized and tentatively modeled, the underlying contribution of microorganisms is still overlooked despite several factors indicating that MW deserves more attention on its own.

First, microorganisms are ubiquitous in the critical zone (Fig. 1). They have been colonizing mineral surfaces since the early Precambrian and have been able to do so in most of the extreme environments existing on Earth⁵¹ (e.g., dry, glacial, and deep). Microorganisms are also forming symbiotic associations with plants such as mycorrhiza—a symbiosis between plants and fungi—establishing nutritional relationships that have evolved independently in many lineages in the plant and fungal kingdoms

since the emergence of fungi in the Neoproterozoic^{28,52,53}. Such symbioses are widespread, with as much as 50,000 species of fungi being able to form mycorrhizal associations with ~250,000 species of plants (~80%)⁵⁴.

Microorganisms also occupy a strategic role in the trophic networks that structure ecosystems, by mediating part of the element transfer at the interface between the lithosphere and the biosphere (Fig. 1). Microorganisms can grow in mineral environments where plants are unable to develop, in particular through microbial chemosynthesis supported by mineral weathering^{55,56}. Thus, they can fulfill a pioneering role in the temporal succession of ecosystems. This has been evidenced, for instance, in the forefield of numerous receding alpine, subpolar, and polar glaciers, constituting temporal sequences of colonization⁵⁷. In these environments, microorganisms pave the way for subsequent plant colonization as nutrients are gradually accumulating into the ecosystem⁵⁸, partly due to rock MW⁵⁹ by pioneering fungi⁶⁰ or bacteria⁶¹. In ecosystems bearing plants (either in more favorable environments or at later ecosystem development or successional stages), soil fungi and bacteria also have a central role in sourcing nutrients. In mycorrhiza for instance, the fungal partner helps the host–plant to acquire the nutrients and the water needed to synthesize organic compounds and biomass, thereby improving the fitness of the plant⁶². In exchange, the fungal partner is rewarded by a portion of the photosynthate routed back to the rhizosphere. Of note, similar cooperation mechanisms in the mobilization of inorganic nutrients have also been demonstrated in lichens^{63,64}.

Several traits of mycorrhiza are well-adapted for nutrient uptake from organic and mineral substrates and for improving the hydraulic conductivity in soils, which are key features of “vegetation”, as highlighted in the previous section. Fungal mycelium is made of filaments (hyphae) that are more extensive and finer than root hairs (~30 μm vs. 2–3 μm for hyphal tips) which, in turn, substantially increases their contact surface area with mineral surfaces and soil organic particles. Globally, the top 10 cm of soils in boreal forest is estimated to host 4.5 10¹⁷ km of cumulated fungal hyphae⁶⁵, which translate into a hyphal surface area of 2.5 times the current continental land surface. Overall, hyphal networks are typically 2 to 3 orders of magnitude longer than roots⁶⁶, and renewed several times per year. The mineral–microorganism interface area therefore exceeds by far the plant–mineral interface area. Beyond the symbiotic fungal partner, mycorrhiza also interact with complex bacterial and fungal communities at physical, metabolic and functional levels⁶⁷, further expanding the reach of the plant root system within the soil. These communities include so-called “mycorrhiza helper bacteria”, which can be fungus-specific⁶⁸, and promote mycorrhizal functions, including mineral-weathering abilities⁶⁹. Because the mineral–microorganism interface far exceeds the mineral–roots interface⁶⁶, rhizosphere microorganisms are central to the mechanisms underlying plant weathering abilities.

With 10² to 10⁶ bacterial phylotypes per gram⁷⁰, soils host some of the most diverse microbiomes on Earth⁷¹. Such immense intrinsic richness, amplified by strategies such as dormancy, which generates “seed banks” within communities⁷², helps endowing microbial communities with an adaptability that makes them particularly suited to mediate element exchanges between plants and soils. Microbial consortia are therefore able to fine-tune their strategy both spatially and temporarily in response to their local environment, their mineral substrate, or the need of their symbiont. In addition to adapting to plants, as highlighted in the case of mycorrhiza, some studies show that microorganisms can also adapt to their “mineral” environment. Crystallographic properties of the mineral substrates (composition, structure) have indeed been shown to influence soil bacterial and fungal communities at taxonomic and functional levels^{73,74}, as well as their colonization patterns⁷⁵. The effect on the taxonomic

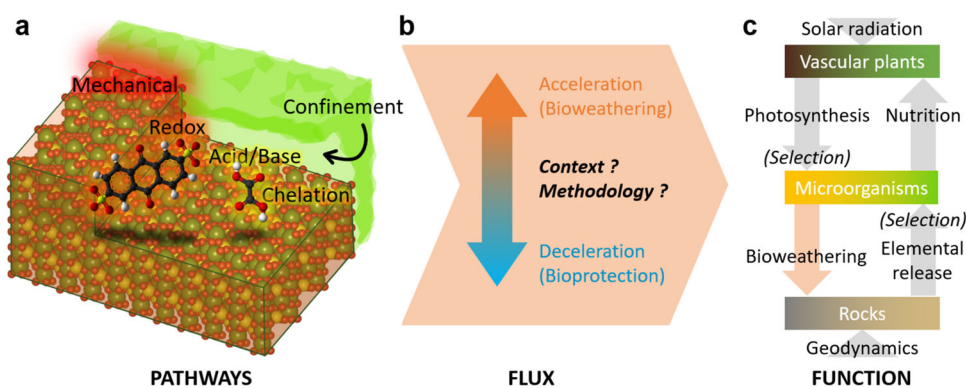


Fig. 2 The impact of living organisms on mineral weathering. **a** Main pathways by which living organisms impact mineral-weathering rates. These pathways involve either direct contact with the mineral (mechanical processes and redox through membrane-bound enzymes for instance), close proximity (confinement of the fluid–mineral interface achieved by the secretion at the direct vicinity of the mineral of a porous matrix of extracellular polymeric substances (EPS)), or mediated through the fluid by the secretion of chemical compounds (acids, bases, redox-active molecules, or chelators). Confined space, enclosed between the mineral surface and the microbial cell or EPS (represented indiscriminately by organic matter in light green, panel **a**), can enable the control of the chemical activities of solutes independently from the bulk fluid. **b** These pathways have been shown to accelerate mineral weathering, even though some of them may similarly lead to lower rates (by reaching close-to-equilibrium conditions in confined space, or through competition for reactive sites). No consensus has however been reached on this point due to significant methodological variations or the diversity of contexts considered (see the text). **c** Bioweathering is part of a larger set of element fluxes occurring on Earth ecosystems, and there is increasing evidence that BW, mostly driven by microorganisms, supports the development of continental ecosystems by stimulating the release of rock-derived nutrients.

structure has been reported for both complex mineral assemblages occurring naturally⁷⁴ or for laboratory-grade monominerals^{76–79}. Similar results were obtained in a wide variety of environments, including subglacial environments⁸⁰, mature forest soil profiles⁷³, or surface aquifers⁸¹. These field observations were also corroborated by laboratory experiments, which established formal relationships between the structure of bacterial communities—that is, the different kinds of organisms and their abundances—and the beneficial effect (e.g., nutrient content⁸²) or deleterious effect (e.g., release of toxic element⁸³) of the mineral. The nature of the mineral substrate was also shown to impact bacterial communities at the functional level, such as their ability to solubilize P, or mobilize Fe⁸⁴. A fraction of the microbial communities inhabiting the CZ would thus be under the direct influence of the mineral-released nutrients or toxic elements⁵, which, in a way, structure the microbial communities according to selection processes²¹. The term “stonesphere” was initially coined to designate this microhabitat, at the direct interface of primary minerals⁸⁵. Its definition was later formalized under the concept of “mineralosphere”, by analogy to other ecological niches, such as the rhizosphere^{5,21,73}. This emerging concept extends mineral–microorganism interactions beyond BW by proposing the existence of a feedback from the nature of the mineral on the bacterial and fungal communities.

Overall, microorganisms are ubiquitous in the critical zone, and hold pioneering roles in temporal ecosystem successions, in addition to a strategic positioning and wide development at the plant–mineral interface. Microorganisms can also adapt to their surrounding environment, including plant partners on the one hand, as well as to mineral substrates on the other. Because they also possess a broad spectrum of weathering capabilities ranging from local acidification to biomechanical forcing at the submicron scale^{86–88}, as outlined in the following sections, they are potentially efficient and versatile weathering agents, woven in the critical zone fabric.

STATE OF THE ART ON BIOWEATHERING

How can living organisms impact mineral weathering?

As highlighted in the previous section, vegetation can indirectly impact rock weathering by modifying soil hydrology, or by changing the fluid–mineral interface area or the fluid–mineral

contact time. In addition, plant roots and microorganisms directly accelerate mineral weathering by degrading rock-forming minerals mechanically or chemically (Fig. 2).

First, both plants and microorganisms utilize physical processes to alter rocks. Roots are commonly observed to break substrates apart (e.g. sidewalks, rocks, soils, etc.³⁵, generating fresh, weatherable mineral surface area. Similar processes have been reported for fungi, where turgor pressures can reach up to 8 MPa in fungal appressoria, a specific structure designed to penetrate host organisms⁸⁹. These forces, together with the pulsatile, apical growth of hyphae and the strong adhesion forces binding it to mineral surfaces⁹⁰ may contribute to the formation of “trenches” of ~100 nm in depth on the surface of biotite and chlorite basal planes⁸⁸. This peculiar growth modality tends to push away and to fragment the topmost material, creating fresh reactive surface on an otherwise fairly inert basal plane⁹¹. Physical strain of the mineral structure due to fungal colonization is not limited to the surface. In the case of biotite, fungal presence causes the oxidation of a large proportion of structural Fe(II) up to 2 μm below the hypha–biotite interface and induces the growth of Fe(III) hydroxides. Those subdomains produce a volumetric change and thus a strain of the biotite lattice structure large enough to distort the crystal lattice⁸⁶ and to form microcracks beneath the hypha⁹¹. Analogous mechanisms have been observed for lizardite alteration by the fungus *Talaromyces flavus*⁹². These observations illustrate the tight coupling that can exist between chemical and mechanical alteration processes at the submicron scale.

Acidolysis reactions are the most studied mechanisms of chemically induced mineral biodegradation. These processes can be promoted by plants⁹³ and microorganisms¹⁸ (and to a certain extent by some animals⁸) in particular by the secretion of organic acids, which can be produced by a wide range of organisms^{94,95}. Respiration processes can also shift the pH, enhancing mineral dissolution⁹⁶.

The secretion of chelating molecules by the above-mentioned organisms can promote the dissolution of primary minerals by forming inner-sphere complexes at the mineral surface⁹⁷ or by shifting chemical equilibria. This is particularly true for Fe chelators (i.e., siderophores) such as vibrioferrin or pyoverdine⁹⁸. These molecules are ubiquitously produced among bacteria or fungi and can exhibit exceptionally high Fe association constants

($\log(K) = 12\text{--}52$)⁹⁹. These constitute likely mechanisms that prevent the decrease of mineral dissolution rates and that keep iron available for microbial productivity¹⁰⁰.

More specific to microorganisms is their ability to bypass the average conditions prevailing in their surrounding environment by forming biofilms at the fluid–mineral interface¹⁰¹. In these microenvironments (see Fig. 2a), microorganisms control the local chemical potential of targeted species to generate favorable conditions (hygrometry, pH, etc.) and protect themselves against hazardous situations (drought, fluctuations in the composition of solutions, etc.). Their impact on mineral weathering by regulating locally some of the most important rate-controlling parameters such as the pH^{92,98,102} (see “acidolysis”, above), the production of complexing agents⁹⁸ (see “chelating molecules”, above), the redox potential^{103–105} (see below), or even fluid–mineral contact (cf. “hydraulic decoupling” phenomena¹⁰¹) has been evidenced.

Redox processes are one of the primary drivers of mineral bioweathering and are accomplished by microorganisms that have developed strategies to harvest energy from electron transfers with minerals or mineral-derived elements, harnessing membrane potential to do work (e.g., generate ATP molecules to store chemical energy)¹⁰⁶. When the redox sensitive elements considered are very insoluble (e.g. Fe(III)), direct contact between Fe(III)-reducing bacteria and Fe(III)-bearing minerals (such as Fe(III) oxides¹⁰⁷, biotite¹⁰⁸ and chlorite) may constitute an efficient strategy for dissimilatory Fe(III) reduction^{107,109}. In fact, Fe-phyllsilicates can serve both as electron donors for Fe(II)-oxidizing microbial communities hence producing oxy-biotite or Fe(III) oxides¹¹⁰ and as electron acceptors for microbial Fe-reducers under anaerobic conditions¹¹¹. Those interfacial electron transfers are often carried out by membrane-bound enzymes (cytochromes) for members of the *Geobacter* and *Shewanella* genus, through the contact of organic conductive pili called “nanowires” (produced by e.g., *Geobacter metallireducens*, *Geobacter sulfurreducens* or *Shewanella oneidensis* under electron acceptor limitation)¹¹², or through the production of soluble electron shuttles and/or Fe(III)-chelating compounds by species like *Geothrix fermentans*¹¹³. By oxidizing Fe, bacteria can also influence the weathering of Fe-containing silicates: microbially oxidized diorite is for instance more susceptible to proton-promoted dissolution than unoxidized diorite¹⁶. Fungi are, as well, able to oxidize elements like Mn and Fe using superoxide¹¹⁴, or laccase¹¹⁵. Moreover, it was hypothesized that the fungus *Trichoderma guizhouense* could promote hematite dissolution by triggering catalytic oxidation with extracellular superoxide (O_2^-) production¹¹⁶. On the other hand, the oxidation of structural Fe in biotite by both bacteria or fungi has resulted in its alteration via the release of K and Fe (due to a charge excess) or the formation of microcracks, respectively^{91,110}.

What is the quantitative contribution of living organisms to weathering?

While a majority of studies show the ability of living organisms—such as plants, bacteria, and fungi as outlined in the previous section—to impact mineral weathering, (1) the direction of this impact (i.e., acceleration or a retardation) and (2) its quantitative contribution to overall weathering rate (and therefore the significance of biota to overall weathering fluxes) remains an open question (Fig. 2b). As stated by Frings and Buss¹¹⁷ “the actual enhancement beyond an abiotic control is hard to quantify, simply because no control sites exist on Earth today”. In addition, laboratory experiments constitute an imperfect abiotic reference, since other factors beyond the effect of organisms contribute to the well-known field-laboratory discrepancy by several orders of magnitude. Some studies have compared weathering fluxes in environments only differing by their vegetation cover (lithology, topography, climate, etc. being otherwise kept as similar as

possible), with varying results. Forested basaltic substrate was shown to weather two to five times more rapidly than basalts only covered by mosses and lichens¹¹⁸ (even though the difference between these contexts was beyond strict removal of vegetation), whereas this could reach a factor of 10 in the case of Hawaiian basalts¹¹⁹. The variability in BW quantification is even more striking when considering the contribution of microorganisms with respect to a hypothetical, pure abiotic system. Field estimates of the weathering fluxes associated with the formation of tubular features of potential biogenic origin vary from 0.5 to 50% of the total flux¹²⁰. As for the extent of basalt weathering beneath lichen, it was essentially identical compared to barren basalt surfaces^{119,121}. Because of the diversity of settings and metrics used to derive those “enhancing” factors, the literature provides a wide range of BW acceleration factors (“microbially enhanced” rate/“abiotic” rate): close to 1 for olivine weathering by microbial communities from the A horizon of a forest soil^{122,123}, a factor of 1.5 for the dissolution of biotite in the presence of *Bacillus subtilis*¹²⁴, a factor of 3 for the alteration of glass by *Pseudomonas aeruginosa*¹²⁵, 5 for hornblende weathering (based on Fe release rate) by bacteria of the genus *Streptomyces*¹²⁶, or 8 for microbial communities from glacial sediments and meltwater. This factor reaches up to 2 orders of magnitude for the action of *Paxillus involutus* hyphae on biotite⁸⁷, for rock-inhabiting fungi on olivine¹²⁷, or for the weathering of silicates (Feldspar, biotite) in bacterial cultures from various soil contexts¹⁰² for instance. A virtually infinite acceleration of the weathering of magnetite during its reduction to green rust by *Shewanella putrefaciens* has been observed¹²⁸ as well as for most Fe oxides¹²⁹ and Mn oxides. On the other hand, organisms have also been observed to decelerate weathering (i.e. bioprotection), especially when abiotic weathering processes are more intense¹³⁰. Studies provide factors of 0.7 for the in situ weathering of limestone by the lichen *Bagliettoa baldensis*¹³¹, 0.4 for the in vitro dissolution of olivine by *Escherichia coli* (the factor decreased upon higher bacterial loads)¹³², and 0.1 for the dissolution of olivine by a bacterial and fungal consortium (using a model as an abiotic control)¹¹. Of note, obtaining precise elemental budgets on these systems is however challenging. It was for instance argued in batch experiments that the observed inhibited delivery of Mg from olivine to the fluid phase was likely due to the organisms serving as a sink for Mg¹¹. Determining timescales over which organisms sequester weathering products in ecosystems (residence time) requires precise determination of the biomass (volume), as well as input and output fluxes to and from this system. Those are possibly controlled by an array of processes, including mineral-weathering rates, turnover of living organisms, and recycling rate of decayed biomass. While this information is rarely available in the above-mentioned experiments, this has been quantified more routinely for natural systems, with the use of isotope proxies. The apparent scatter of BW acceleration factors currently available can be attributed partly to the variety of experimental settings, conditions (in vitro, in situ, pH, nutrients, stirring etc), and methods used to quantify BW rates. Such dispersion also reflects the broad diversity of organisms, environments and processes considered. It highlights the paramount importance of understanding the underlying mechanisms and feedbacks controlling BW. In which context do organisms favor weathering? How is this process triggered? How does it impact nutrient limitation or biomass buildup and how is mineral weathering impacted in return by ecosystem changes?

The ecological role of weathering: why would organisms contribute to weathering fluxes?

Beyond the problem of the quantification highlighted previously, a significant portion of current debates is related to the ecological significance of BW. The effect of microorganisms on weathering—

ranging from enhancement to inhibition (BP)—highlights the importance of the context of observations. What environmental factors or feedbacks do control BW in situ? Does it necessarily fulfill an ecological function (e.g., nutrient supply), or can it occur as a simple side effect of other unrelated metabolic processes?

Rock weathering is a spontaneous process, since most rock-forming minerals exhumed by tectonic processes are in thermodynamic disequilibrium with respect to the average conditions prevailing at the Earth's surface⁶³. However, because of their specific stoichiometry, living organisms do not always require elements at the same rate as delivered by abiotic weathering nor in the same proportions at which they occur in the Earth's crust. Thus, plant and microorganisms need to develop strategies to maintain physiological homeostasis and to be able to grow and reproduce. One likely mechanism to overcome this paradox consists in accumulating bio-essential elements by scavenging them as they are released by weathering processes, and by efficiently recycling organic matter to avoid these elements to cycle back to the hydrosphere or lithosphere. In addition, it has been hypothesized that organisms could actively use BW to bypass the kinetic bottleneck of abiotic weathering and ensure the bioavailability of nutrients of interest as part of the overall ecosystem functioning scheme (Fig. 2c)¹³. This hypothesis is supported, for instance, by active targeting of certain minerals of nutritive interest observed in the context of mineral-specific C allocation to ectomycorrhizal fungi¹³³. Yet, no consensus has been found on this question, partly because of the limited quantitative information available regarding biomass growth or decay, and inputs (weathering and atmospheric deposition) vs. outputs (imperfectly recycled biomass and export of matter). These different nutrient dynamics have also been shown to succeed one another as different successional stages, with the gradual replacement of a weathering-dominated regime—where rapid uptake of available organic and “fresh” mineral soil resources by biota—by a biocycling-dominated regime where e.g. tree growth slows down to a steady-state value and weathering and denudation rates become small and not significantly different¹³⁴. P constitutes a particularly interesting example among the organic elements (C, N, H, O, S, and P) in that it does not bear any significant volatile form and ultimately needs to be sourced from minerals¹³⁵. BW might therefore be central for the long-term maintenance of vegetation, even though most actual, natural ecosystems exert a tight control on the recycling of e.g., P contained in soil organic matter and thus only partly rely on weathering to meet their need in P¹³⁶. This recycling rate is however below 100% and, thus, the maintenance of vegetation has been hypothesized to require prolonged and continual de novo rock weathering¹³⁷. Overall, as P from soils is incorporated into the biota or exported out of the CZ over time, primary productivity of stable landscapes (where denudation rates are slow) will decline because of P limitation (or sometimes N and P co-limitation¹³⁸) and needs to be resupplied from weathering unless atmospheric deposition¹³⁹ is large enough to compensate losses, or unless a catastrophic disturbance occurs¹⁴⁰. As such, during ecological succession of stable landscapes, ecosystems will develop to reach a maximal-biomass phase during which their symbiotic or free-living microorganisms may—through their BW activities—effectively control mineral weathering¹⁴⁰. Eventually, as P pools accessible to weathering decline and supply gradually slows down, the ecosystem may tend to reduce its productivity and its plant biomass¹⁴⁰. The timing of this decline may depend partly on lithology (which conditions the size of the P pool and its susceptibility to be weathered) and on the intensity of physical processes such as denudation that expose fresh rock to weathering processes.

It is also clear that microbial processes resulting in BW are not limited to alleviate the kinetic “bottleneck” of weathering reactions. Indeed, the concentration of base cations (e.g., Ca²⁺,

Mg²⁺) supplied by weathering in most drainage waters often exceeds ecosystem's needs. Still, weathering of Ca-bearing minerals is greatly enhanced by microbes via the production of Ca-binding exudates like oxalic acid triggering the formation of Ca-oxalate precipitates¹⁴¹. In Schmalenberger, et al.¹⁴², oxalic acid secretion by *Paxillus involutus* was mineral-specific and positively correlated with the Ca content of mineral phases. In this case, it was suggested that mineral weathering result from a detoxifying process directed at lowering the dissolved Ca²⁺ concentration in the surrounding of mycorrhiza. Thus, in this case, BW can be considered either as a side effect from a detoxifying strategy aiming at limiting dissolved Ca concentrations¹⁴³ or as a mechanism aiming at purposely enhancing the dissolution of Ca counterions such as P in apatite minerals¹⁴⁴. Distinguishing between the two mechanisms (indirect “metabolic side effect” vs. direct “metabolically driven nutrient mobilization”) is made further difficult by the fact that the versatility of weathering mechanisms deployed by microorganisms goes well beyond the realm of mineral dissolution. In other words, the secretion of compounds such as organic acids and/or chelators mentioned above might not be exclusively directed at mineral dissolution. One common example is the fact that mineral dissolution reactions can be promoted indirectly by the production of CO₂ by heterotrophic organisms via respiration processes or the production of nitrous acid (HNO₂) by nitrifying bacteria, both lowering the pH of their surrounding environment²¹. Extracellular superoxide (O₂⁻) production, triggering catalytic hematite dissolution¹¹⁶, is a widespread function among fungi involved in lignin degradation, host defense, hyphal branching, as well as cell differentiation^{145–147}. Some siderophores such as pyoverdine or ferrichrome fulfill cell-to-cell signaling functions¹⁴⁸ or exhibit antibiotic properties¹⁴⁹, respectively. In addition, they may be used by some microorganisms to inhibit quorum sensing mechanisms¹⁵⁰. Low molecular weight organic acids fulfill a large spectrum of functions, not necessarily related to inorganic nutrients cycling. For instance, while oxalic acid helps mobilizing nutrients by promoting both mineral dissolution and degradation of organic matter¹⁵¹, it is also involved in processes such as calcium extraction from cell walls¹⁵². Finally, turgor pressure generation, allowing the expansion of the cell wall at the hyphal tip¹⁵³, can be used as a mechanical forcing by some fungal pathogens to perforate their host's cuticle or cell wall⁸⁹, or, similarly, to penetrate the rock surface as a possible BW mechanism⁸⁶. Those examples indicate that care should be taken when assigning a causal relationship between mineral weathering and mechanisms such as organic acid secretion as the latter may respond to other process than mineral weathering.

The driving force behind mycorrhizal fungi is photosynthetically derived organic C, which fuels biomass growth, production of protons, organic acids, chelators, and enzymes that increase mineral weathering, and allow the selective uptake of nutrients by mycorrhiza. Overall, about 2–15% of the plant C-photosynthate (up to 26% between arbuscular mycorrhiza *Glomus fasciculatum* and cucumber plant) is typically invested into supporting their fungal symbionts^{154–157}, adding up to a transfer of C from plants to mycorrhiza yielding globally ~12% of the terrestrial C cycle⁶⁵, mycorrhizal networks have transformative effects on soil physicochemical properties via their inputs of organic matter and selective uptake of elements and water. As such, BW can be seen as part of a solar-to-chemical energy conversion by plants into mycorrhiza, which partly links below-ground C allocation to mineral weathering and nutrient acquisition¹⁵⁸ and allows to sustain the extended and dynamic fungi–mineral interface area.

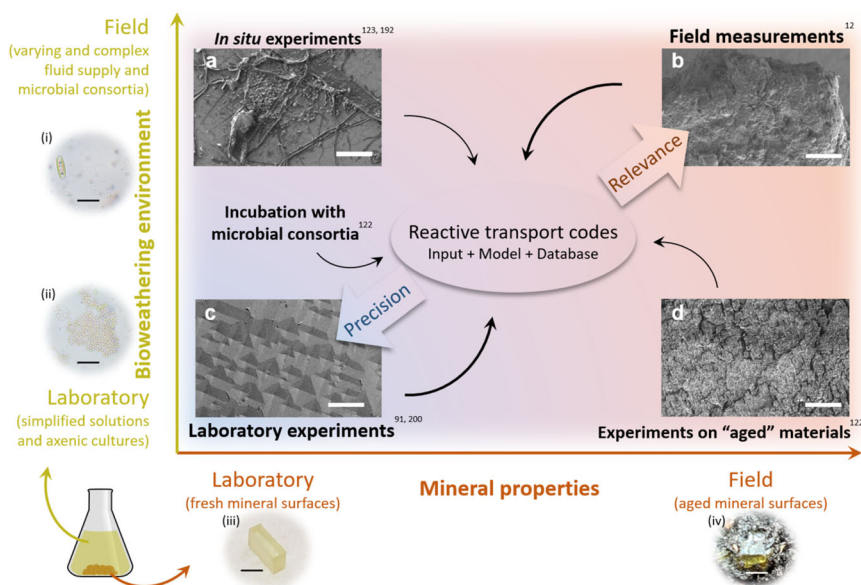


Fig. 3 Main approaches used to probe the microbial contribution to weathering fluxes between the laboratory and the field. These approaches feed the different components of reactive transport codes (including inputs, models and databases), which in turn enable a quantitative comparison of results obtained with different methodologies or contexts. Corresponding experiments take into account both the effects of the reactive environment (green, vertical axis), ranging from simplified abiotic solutions or axenic microbial cultures to complex environmental fluids carrying potentially complex microbial communities, and the effect of the mineral interface involved in the reaction (brown, horizontal axis), ranging from fresh mineral interfaces calibrated in the laboratory (sieved powders, oriented, and polished monocrystal surfaces, etc.) to complex interfaces encountered in the field. (i) Freshwater microbial community collected at lake Carnegie, NJ, USA (scale: 30 μm), (ii) cultured cyanobacteria *Chroococcidiopsis thermalis* (scale: 50 μm), (iii) olivine sample with polished (001) surface exposed on top (scale: 3 mm), (iv) olivine single crystal recovered in a litter layer developed on a 45 years old weathered lava flow (Sainte-Rose, Reunion Island; scale: 2 mm). The main panel depicts typical interfaces as encountered in the different contexts, including **c** precise in vitro experiments under controlled conditions in laboratory setups (example of etch pits developed on a (104) calcite surface during in vitro incubation at pH = 2; scale: 70 μm), **b** direct field measurements performed on complex materials found in natural settings which have been exposed to relevant but sometimes uncertain weathering condition and durations (example of a complex mineralogical assemblage composing the porous matrix of a chemically depleted schist sample recovered in a vadose zone context in central New Jersey, USA; scale: 100 μm), **a** in situ experiments which offer an intermediate accuracy vs. relevance trade-off by incubating "laboratory grade" samples directly in field conditions, thus enabling close-to-laboratory-grade accuracy under relevant field conditions (example of a the basal plane of a mica sample incubated in a soil environment for several months exhibiting abundant microbial colonization; scale: 30 μm), and **d** example of an artificially aged feldspar interface; scale: 100 μm .

CHALLENGES AND ONGOING DEVELOPMENTS

Field-lab discrepancy

Determining relevant quantitative estimates for the contribution of MW to overall weathering fluxes is challenging. Along reasons related to the intrinsic nature of microorganisms (small size, large diversity, high turnover rates, etc.) is the necessity of conceding some methodological trade-off. In short, simplified systems have generally enabled a tighter control of experimental parameters and therefore a better quantification of dissolution rates and a clearer understanding of the mechanisms involved, but often at the expense of a reduced relevance for natural systems (Fig. 3).

At one end of this trade-off, some estimates of the microbial weathering contribution were derived from direct field observations on complex systems resulting from the interaction of fluids endowed with naturally occurring microbial communities with aged mineral surfaces over an imperfectly known duration (Fig. 3b). These observations include tubular microchannels left by mycorrhizal or saprotrophic fungi in silicate minerals such as feldspar and hornblende^{159,160} or granular and tubular patterns created by bacteria or archaea in basaltic glass¹⁶¹. These morphological features in naturally weathered silicate materials have often been considered as possible fingerprints of bio-dissolution^{159,162–164}. However, these observations remain debated, as the biotic origin of microchannels are difficult to ascertain¹⁶⁵. The identification of biosignatures based on shape or size of features left at mineral interfaces has often proven equivocal as etch pits and

microchannels similar to those attributed to microbial activity^{162,166}, could be reproduced abiotically^{167–169}. In addition, factors such as the complexity of the 3D channeling network (bioweathered volume) or the lack of precise timing for the geologic history of the weathered material (BW time) has limited the precision of associated BW rate estimates (=bioweathered volume/BW time)¹²⁰. Overall, direct observations of field material (resulting from real field biogeochemical conditions, therefore achieving an ultimate degree of *relevance* and *accuracy*) seem to exhibit an intrinsic level of complexity mostly incompatible with *precise* estimates of BW rates.

At the other end of the 'precision vs. relevance tradeoff', microbial dissolution was indirectly quantified by incubating well-characterized fresh minerals with various simplified "biotic" fluids, only containing model metabolites involved in microbially-driven mineral dissolution—i.e., organic acids, siderophores or other chelating molecules (Fig. 3c)^{170–172}. An abundant literature (see e.g., ref. ⁹⁵ for a review) has shown the accelerating effect of these compounds on weathering, and has unraveled some of the molecular-scale mechanisms. However, the direct extrapolation of these quantitative results to natural systems has remained challenging, since the minimum concentration of metabolites required to measure a significant effect on dissolution (i.e., in the order of 10^{-1} to 10^{-4} M for organic acids and ligands^{94,173–175} and 10^{-5} M for siderophores¹⁷⁶), is typically 1 to 3 orders of magnitude higher than bulk concentrations in soil solutions^{177,178}. Most importantly, the acid and ligand concentrations in the local

microenvironments controlled by microorganisms (e.g., in the extracellular polymeric substances surrounding the cells or at the mineral-microorganisms interface) are still essentially unknown.

A higher degree of relevance was achieved by inoculating the reactive fluid with microbial isolates known for their weathering abilities such as the bacteria *Burkholderia* sp.¹⁷⁹, *Paenibacillus polymyxa*¹⁸⁰, and *Bacillus subtilis*⁷⁵, or the fungi *Paxillus involutus*¹⁸¹ and *Talaromyces flavus*^{92,182}. Even though this approach has shown the catalyzing role of microorganisms on mineral dissolution, it presents several limitations: (1) A discrepancy may exist between metabolism and phenotype expressed in *in vitro* experiments and in natural conditions, (2) the use of axenic cultures may oversimplify more complex microbial communities found in the field and (3) may not be fully representative of the effective distribution of these microorganisms in the field¹⁸³, and (4) the focus on solution-based biotic dissolution may mostly evaluate the weathering capabilities of microorganisms mediated through the fluid (i.e., their ability to influence fluid–mineral systems via e.g., pH changes in the bulk fluid, as opposed to weathering occurring at the direct mineral–microorganism interface). The latter contrasts with *in situ* conditions, especially along unsaturated rock fractures, or forest soil which are freely draining and seasonally dry for extended periods of time¹⁸⁴. Thus, there is a need to study BW in soil environments under those conditions. The above-mentioned limitations were partly overcome in recent studies where minerals were either exposed to more complex microbial communities^{122,185} or to air and mycorrhizal consortia^{86,87,90,91,186,187}. Nevertheless, reproducing close-to-natural conditions in the laboratory remains challenging for many environments, and this also concerns the properties of the mineral surfaces used. Indeed, in addition to using microorganisms of limited relevance, most BW studies so far have used freshly ground, cleaved or polished mineral substrates, known to exhibit a higher reactivity than the mineral surfaces typically found in the field¹⁸⁸. One important overlooked parameter in these experiments is the effect of previous weathering of the mineral surface (either abiotically¹²² or inherited from a previous colonization event, sometimes referred to as “mineral ageing”, which tends to influence mineral dissolution rates and to change the properties of the mineral interface, and therefore impacts fluid–mineral–microorganisms interactions).

In situ “incubation” experiments, in which well-characterized mineral samples are buried in the field to probe microbial colonization and dissolution, constitute another approach that combines part of the relevance of field conditions to some of the precision of laboratory experiments (Fig. 3a). *In situ* mineral incubations in an aquifer was used to demonstrate that microbial colonization of silicates is controlled by the chemical composition of the mineral substrate^{83,162} or by that of its mineral inclusions¹⁸⁹. These pioneering studies concluded that silicate weathering was promoted by the presence of surface-colonizing microbes using organic ligands to extract nutrients (e.g., P or Fe) from silicate matrices^{76,81}. A similar approach was applied to forest soils, where significant colonization of incubated minerals by fungal hyphae was observed, and dissolution rates (as determined by weight loss) were higher in environments with intense microbial activity (i.e., topsoil and rhizosphere)^{190,191}. This approach was further developed by Quirk et al.¹⁹² who assessed the *in situ* fungal dissolution of silicate minerals by measuring changes in the microtopography of cleaved-muscovite flakes by vertical scanning interferometry. Recently, this technique was further developed in order to distinguish the local contribution of microbial weathering from dissolution due to fluid–mineral interactions, by the addition of a height reference¹²³. *In situ* incubation has proven to be a powerful approach to probe mineral–microorganism interactions directly in the field^{77,193}. Their application, however, still needs to be expanded to improve their statistical relevance and to increase the number of natural settings and contexts probed.

New approaches: from actors and tools to functions and signatures

Efforts to further develop meaningful metrics for *in situ* mineral weathering (in the field) are ongoing. It is now admitted that MW mostly occurs at a submicron scale, thereby bypassing the bulk environment and associated measurement approaches (see previous sections). In parallel, the reach of “omic” techniques and biostatistical methods has also extended to large datasets and to an increasing diversity of environments¹⁹⁴. Classical approaches focusing exclusively on taxonomic information derived e.g., from 16S rRNA gene metabarcoding (weathering “actors”) or on the effect of specific dissolution-enhancing microbial metabolites (weathering “tools”) have however proven insufficient to upscale MW measured locally. Some form of generalization of MW processes is needed, to characterize (1) metabolic pathways underpinning microbial weathering in natural settings (“functions”); (2) their occurrence in the genome of—and their expression by—microbial communities *in situ*, and (3) their physical imprints at the surface of minerals (“signature”).

Since mechanisms of mineral weathering are relatively well known and ubiquitously distributed among bacterial and fungal communities, and since the relationship between dissolution rate enhancement and the nature of the different weathering agents has already been well explored, there is a need to focus upcoming studies on the screening of these functions and of their expression in field-relevant settings, using metagenomic and metabolomic tools (while taxonomic survey only provide at best indirect information on that matter). Such developments are currently ongoing, with the application of terabase-scale cultivation-independent metagenomics to BW systems, which is able to accurately reconstruct the metabolism and ecological roles of microbial consortia from natural samples^{195–197}. In parallel, a growing corpus of literature is actively seeking for the genes involved in microbial weathering—or the “weathering microbiome”¹⁹⁶—e.g. through the study of gene deletion mutants^{198,199} (see also ref. 200 in this issue). On the other hand, the application of nm-resolved techniques to the study of microbially weathered surfaces^{91,123,192,201} should help characterize imprints of microbial process left behind at mineral surfaces and in the geological record. A shift from “actors” to “functions” (to be compared to what would be referred to a shift from *species-based approaches* to *trait-based approaches* in community ecology), constitutes an important step in upscaling BW processes characterized in the laboratory to more complex natural environments with larger microbial diversity. Similarly, direct quantification of microbial weathering *in situ* will enable to bypass the limitation of “tools-rate” relationships (e.g., relationships between rate increase as a function of the concentration of organic acid, the value of which in natural environments is largely unknown and the direct relationship of which with taxonomic data is controversial). Such a “function-signature” framework should constitute a relevant alternative to the “actors-tools” approaches inherited from laboratory approaches and mostly effective on simplified systems. It should also facilitate the incorporation of the effect of microorganisms into weathering models.

Upscaling: integrating BW processes into reactive transport models

Reactive transport models (RTMs) constitute important tools to relate observations of weathering processes performed at different scales and establish reliable estimates of past and future weathering fluxes. BW effects, however, still need to be included more widely in these models. RTMs estimate weathering rates based on common components such as experiments and observations (Fig. 3)²⁰². These components include a set of *inputs* (the features of the studied site and/or physicochemical conditions prevailing *in situ*, as available), a *model* (soil hydrology as

well as rate laws) and a *database* (thermodynamic and kinetic parameters derived from laboratory experiments). Numerous models have been developed, including PROFILE²⁰³, KIRMAT²⁰⁴, WITCH⁴¹, and CrunchFlow²⁰⁵, which offer a varied range of specificities²⁰⁶. Dissolution rate laws underlying most reactive transport codes used to determine the weathering fluxes on large temporal and spatial scales have an empirical basis^{207,208}, although mechanistic elements underlie some of the terms of these rate laws (e.g., ref. ²⁰⁹).

Historically, one of the first attempts to capture the complex interplay between biology and weathering was achieved in a process-based model of silicate weathering that linked biological productivity, microbial respiration, soil water hydrology and chemistry into the so-called “biological proton cycle” and connecting it with mineral dissolution reactions⁴. Building on this framework, Taylor et al.²¹⁰ developed a model incorporating the role of plants and of their mycorrhizal fungi in the weathering of silicate minerals. In this model, BW was controlled by the biomass, mineral–microorganism contact surface area and the capacity of roots and their mycorrhizal partners to interact physically and chemically with minerals (e.g., through exudation of organic acids). Ultimately, all those weathering agents and their activities were governed by the rates of carbon allocation from photosynthetic organisms into the mycorrhizosphere (i.e., the portion of soil which is under the influence of living roots and their fungal partners). These models, however, do not account for the variability of temperature, land lithology, and the effect of continental configurations on climatic conditions, as well as their implications in terms of vegetation and associated mycorrhizal partners. To overcome these limitations, Roelandt et al.⁴² coupled a spatially explicit dynamic global vegetation model with a multilayer, mechanistic chemical weathering model. Later, Taylor et al.²¹¹ further improved their previous model by implementing it on a two dimensions grid (latitude and longitude) to capture the regional variability of vegetation, mycorrhizal fungi, and climate on continental weathering processes. This updated model combined (i) a coupled ocean–atmosphere general circulation model (HadCM3L – Beerling and Woodward²¹²) with (ii) the Sheffield dynamic global vegetation model (SDGVM)²¹³ and (iii) the “biological proton cycle” weathering model⁴ to calculate spatially resolved continental base cations fluxes. At present, another option used to incorporate BW into existing weathering models consists of fitting some fixed amount of field data and extrapolating those to an overall accelerating factor accounting for the effect of alteration by living organisms²¹⁴, without elucidating the details of the underlying mechanisms. BW can alternatively be incorporated by predicting the effect of microorganisms and plants on key chemical variables driving the kinetics and extent of dissolution reactions, such as pH. Such approach, for instance, is proposed in ref. ²¹⁵ through an empirical description of root respiration, including microbial respiration. The overall contribution of vegetation and associated factors, such as respiration processes, organic acid production, or element uptake and release, was also successfully incorporated in other contemporary weathering models^{41,42}.

Despite those important advances, several steps are still needed to fully model the impact of biosphere on regolith evolution²¹⁶. In particular, the integration of microbial processes with plant functions (e.g., accurate modeling of rhizosphere functioning) still needs to be achieved²¹⁶, while the representation of underlying mechanisms, including organic–mineral chelation or ligand-promoted dissolution, could be further improved⁴⁴. Other important aspects of BW, at the heart of fungal mineral alteration are still not represented in current large-scale weathering models. Those models rely exclusively on the capacity of mycorrhiza to alter porewater chemistry and pH, despite the fact that microbially controlled reactions are not necessarily mediated through the “bulk” fluid chemistry, as considered in current reactive transport

models, but can instead be driven by conditions imposed locally at the mineral/microorganism or mineral/biofilm interface⁶³. Current models incompletely account for the specific weathering processes occurring at the interface and in close vicinity of hyphae in contact with the mineral surface (see previous sections for a detailed review on those processes). In addition, it was shown that surface-bound mycorrhiza were able to alter minerals in a humid environment, yet with no free water present^{87,187}, which shifts the way mineral weathering may need to be conceptualized and studied, with free water not being the sole media controlling mineral-weathering reactions. Moving forward, evaluation of the spatial heterogeneity related to, for example, mineral surface coverage by microorganisms and its temporal evolution represent key steps in the formulation, parameterization, and validation of future “microbially informed” reactive transport models²¹⁷. These models could incorporate mycelium growth models developed for arbuscular fungi (see e.g., Schnepf et al.²¹⁸ combined with the spatial distribution of plant-mycorrhizal associations obtained at the regional scale²¹⁹ as well as at the global scale²²⁰ to generate estimates of BW fluxes).

HARNESSING THE EARTH'S WEATHERING ENGINE

Beyond fundamental questions related to biogeochemical cycles or ecosystem functioning, numerous critical processes, and emerging sustainable environmental and agronomic practices depend on our understanding of mineral weathering. These fields, reviewed by Mapelli et al.²²¹, include mining, enhanced weathering, amendment practices, some soil remediation processes, safe repository of spent nuclear fuels or the manufacturing of durable glass materials. All have the potential to benefit from a better understanding of BW (Fig. 4).

Mining is by far the area where the use of BW, and in particular MW, is the most widely exploited and readily available at scale (for reviews, see ref. ²²², ref. ²²³, and ref. ²²⁴). Biomining, which consists in the extraction of metals like Cu, Zn, Ni and Co from ores and waste materials, has been praised for its reduced environmental cost and low carbon footprint compared to energy-intensive metal recovery processing used in traditional mining operations such as smelting²²³. It can theoretically enable higher recovery rates as it allows the treatment of materials that would normally be considered as waste²²⁴ and is currently being evaluated for extraterrestrial applications²²⁵. Historically, mostly acidophilic chemolithotrophic prokaryotes have been used to recover metals of interest from ore. Biomining techniques can be classified in different subcategories depending on whether microbial solubilization targets a metallic element (bioleaching), or minerals occluding the target metal, causing its enrichment prior to its solubilization in a second step (bio-oxidation). Biomining also encompasses biomineralization techniques, aiming at the enrichment of the target metal from liquid wastewaters. Species of interest belong mostly to the bacterial genera *Acidithiobacillus*, *Sulfobacillus*, and *Leptospirillum*, and the archaeal genera *Ferroplasma*, *Acidianus*, and *Sulfolobus*²²³ and were often isolated from acid mine drainage²²⁶. Phytoextraction, i.e. the use of hyperaccumulator plants to extract metals and metalloids from mineral substrates, constitutes another promising type of biomining, however still under development. While plant symbionts, and more specifically arbuscular mycorrhiza have been shown to modulate bioaccumulation processes (see ref. ²²⁷ for reviews), the contribution of MW and more generally the geochemical processes in the rhizosphere interface of the roots of such plants is still a major unknown²²⁸. Note that the same principle applies as well to phytoremediation strategies to clean fields contaminated with heavy metals²²⁹.

Carbon dioxide removal (CDR) constitutes another area that would benefit from a better understanding of BW processes. Enhanced rock weathering (ERW) is an important CDR technology

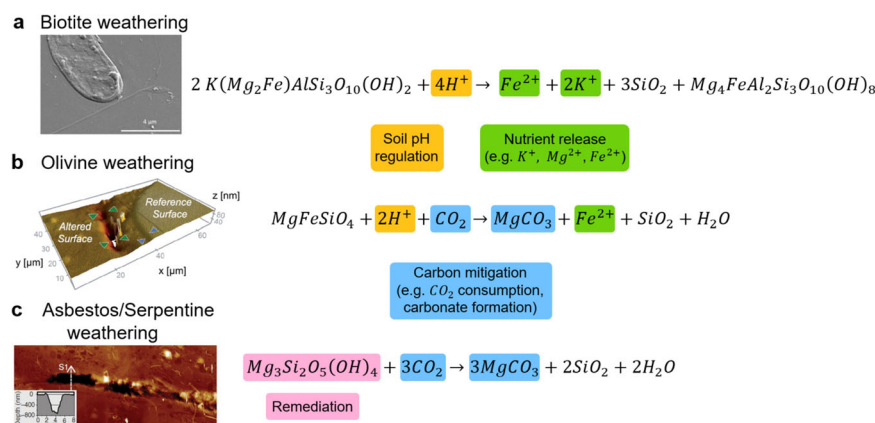


Fig. 4 Examples of silicate minerals for which the local contribution of microorganisms (fungal hyphae) to mineral dissolution was assessed experimentally in a quantitative manner, using microscopy techniques. Examples include biotite (a), olivine (b), and serpentine (c); simplified theoretical equations for their dissolution are provided. These minerals could—in theory—present interesting benefits for agricultural purposes (nutrient release, highlighted in green, and soil pH regulation, in yellow), carbon mitigation (consumption of atmospheric CO₂, blue), or remediation (e.g., asbestos dissolution, pink)²⁵⁹. Images of biotite, olivine and serpentine weathering from ref. ⁹¹, ref. ¹²³, and ref. ⁹², respectively.

currently being tested as part of the portfolio of negative emission technologies urgently needed to reach the global targets to constrain global warming to +2 °C (possibly +1.5 °C) as agreed at the Paris summit in 2015^{230,231}. ERW entails the spreading of powdered Ca- or Mg-rich silicates on croplands to expose them to weathering processes and ultimately capture atmospheric CO₂ under the form of solid or dissolved carbonate²³². Target rocks include easily weatherable minerals from the olivine group and rocks such as basaltic or even kimberlitic rocks (Fig. 4b). Besides these natural silicates, artificial silicate-containing compounds like steel slag or concrete from demolition may be used for ERW^{233,234}. The global CO₂ sequestration potential of ERW is estimated to reach 0.5–5 Gt CO₂ per year²³⁵, reduced recently to 0.5–2 Gt CO₂ per year in a recent nation-by-nation quantitative analysis²¹⁴. However, the actual gross CO₂ removal of ERW relies on the amount of material that can be dissolved within relevant timeframes and the fate of the dissolved Mg and Ca (e.g., incorporation in biomass, adsorption to oxides,...). The extent of such weathering rates depends on a range of properties related to the powdered materials themselves, such as the grain size (where a trade-off with energy consumption due to grinding still need to be optimized)^{236,237} or related to the in situ reactivity of the mineral phases and its sensitivity towards environmental factors (e.g., pH, temperature, humidity, microbiota, etc.). Based on in vitro studies, BW processes are expected to increase the ERW potential²³⁸, yet this is still to be tested more extensively. As crop cultures establish mycorrhizal symbiosis preferentially with arbuscular fungi, there is an urgent need to assess the potential of this association (as opposed to the more extensively studied ectomycorrhizal fungi mostly present in temperate forest) to effectively accelerate ERW in various field conditions as this effect is likely context-dependent. Arbuscular mycorrhiza colonization of crop culture is indeed primarily controlled by the plant nutrient status²³⁹. Usually, as nutrient limitation sets in, plants tend to invest more energy into mycorrhizal networks to mitigate nutrient shortage¹⁸⁷. Conversely when nutrient (especially P) supply is large as in soils subjected to fertilization, plants invest less into arbuscular mycorrhizal symbiosis¹⁸⁷. All those competing processes—in addition to agricultural practices such as soil tillage or glyphosate application—contribute to low abundance of arbuscular mycorrhiza observed in conventional crop cultures compared to natural settings^{240,241}. Nevertheless, there is an opportunity to favor arbuscular mycorrhiza and optimize ERW. In this context, a better understanding of the response of AM fungi

and measure ERW rate and its dependence on environmental parameters and agricultural practices is urgently needed.

The dissemination of materials for ERW has raised a number of concerns that should be carefully addressed before their application²⁴². In particular, care should be taken in selecting the material to be weathered to maximize carbon mitigation and agricultural benefits and prevent potential health and environmental hazards. Applying slags (especially nonferrous slags) for ERW operations has been criticized as it contains heavy metals as well as sulfides, the dissolution of which might enhance the weathering of carbonates²⁴³. The application of olivine also might be detrimental to soil microorganisms and plants as an increase in the Ni bioavailability and an inhibition of plant Ca uptake were observed²⁴⁴. On the other hand, application of silicate minerals produces alkalinity (under the form of HCO₃⁻) that could contribute to buffer soil pH (“liming-like effects”) against acidification caused by agricultural practices which are, otherwise, treated by costly application of lime on croplands²⁴⁵. Also, plant yield tends to increase upon application of basalt due to the supply of additional macronutrients (i.e., K, P, Si) and trace elements (Mn)^{245–248}. This effect, if confirmed, may reduce the need for NPK fertilizers in “conventional” agriculture, and thus their associated cost. Beyond economic benefits, other environmental, advantageous side-effects of ERW include the possible lowering of N₂O emission—an extremely potent greenhouse gas—released from intensively fertilized lands^{214,249}.

More generally, the use of efficient mineral-weathering bacteria to replace inorganic/chemical fertilization and sustainably improve crop production represents another potential application of MW-related biotechnologies²⁵⁰. These microbes have been recognized for their ability to promote plant growth by releasing mineral nutrients locked into mineral phases²⁵¹, hence reducing both the economical cost and environmental impact (e.g., eutrophication) associated with inorganic fertilizers.

Other emerging outputs for MW include the development of fungal-mediated weathering as a potential bioremediation strategy for asbestos-rich soils and asbestos-contaminated environments (Fig. 4c)^{252–255}. Studies showed that fungal or lichen species, as well as microbial exudates such as siderophores, can indeed alter chrysotile (the most widely used asbestos mineral) and lower its toxicity through the removal of structural Fe or Mg^{256–258}. Finally, a better understanding of the impact of MW on glass alteration under natural conditions is also foreseen as an important step towards the development of a next generation of

glass-including devices and structures (see ref. ²⁵ in this issue for a review).

OUTLOOK

Interactions between minerals and microorganisms, which date back to the earliest times of life on Earth, have largely contributed to shape the surface of our planet and its mineralogy, for instance by inducing the formation of about half of the minerals known today. In a leap of evolution, the emergence of terrestrial plants allowed for the allocation of photosynthetically derived carbon compounds to microbial symbionts thereby fueling bioweathering processes. This created a new component of the weathering engine at work in the CZ, and a new pathway for the contribution of solar radiant energy to rock weathering, in addition to the water cycle and climate. Since then, plants and their microbial symbionts (and syntrophic partners) have co-evolved in their capabilities to gain access to certain nutrients. Microbial weathering has also been observed beyond the rhizosphere, and its role is particularly salient in mineral environments where element recycling from e.g., decaying organic matter is low, such as in periglacial environments, at the bottom of soil profiles, or deeper in the lithosphere (ocean floor or deep biosphere microbial communities). In all these contexts, future research should continue to identify the “actors” (who?) and “tools” (how?) of BW. Conversely, extrapolating laboratory observations to more complex systems and upscaling local mineral–microorganism interactions to larger scales will likely require further developments regarding the identification of rock weathering functions at the microbial community level (BW potential) and the identification of possible BW signatures (BW assessment and quantification). Even though BW processes seem ubiquitous, their overall contributions to mineral-weathering budgets are still debated. When BW processes are quantified, common formalism describing BW or comparable experimental setups are absent, which lead to large variability and uncertainty in the determination of a “BW enhancement factor”, even at the small spatial scale. Combined with the complexity of upscaling small-scale processes to the catchment scale (and all the more so to the global scale), this has sometimes required to overly simplify BW processes in models. Yet, plants and their associated microorganism have a systemic effect on weathering and some of the largest biomes of Earth (e.g., temperate and boreal forest) rely on microorganisms to maintain an efficient uptake of nutrients through BW processes. Understanding BW and its responses to environmental variables, could help mitigate anthropic pressure on climate and ecosystems through the integration of BW process in the design of carbon mitigation strategies and sustainable land management practices. Harnessing the weathering potential of (micro)biota (of which mycorrhiza are key players) could for instance improve the capture of atmospheric CO₂ by enhanced weathering technologies while delivering other beneficial effects to soil systems (pH buffering, nutrient release, etc.), provided the optimization of the weathering rate using microbiota while considering the potential environmental risks. Understanding BW could also help optimize metal recovery from ore to alleviate the environmental burden of mining processes or help in soil decontamination.

DATA AVAILABILITY

All data used to compile this manuscript can be made upon reasonable request to the corresponding author.

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AUTHOR CONTRIBUTIONS

All authors contributed to the manuscript.

COMPETING INTERESTS

The authors declare no competing interests.

ADDITIONAL INFORMATION

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