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Bioweathering of lava flows: the case of Xitle volcano in Mexico City

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Abstract

This contribution describes biological weathering features produced by microbial communities growing on rock surfaces denominated biological rock crusts. We provide arguments related to the importance of recognizing rocks as an ecological niche and a review of main recognized bio-weathering processes in basaltic bedrock. We particularly address the features found in the lava flow of the monogenetic volcano Xitle, which is located in the volcanic field of the Sierra del Chichinautzin in the south of Mexico City. We found that the diversity and distribution of organisms within the rock crusts varies depending on the superficial texture and porosity of the lavas. Mosses have a preference for vesicles and crevices, while lichens can establish in smoother and more exposed areas. The predominant biological weathering features we have found associated with these crusts are incrustation, penetration, vesicle infilling, endolithic colonization, fractures, and particle entrapment. It is worth noting that bioweathering features are related to specific biological groups: lichens exert all of the features found, while mosses are mostly associated with particle entrapment and vesicle infilling, and biofilms are related to penetration and endolithic colonization. Therefore, this article discusses the importance of geoheritage conservation in relation to the biodiversity these lavas harbor.

Key words: Biological rock crusts, bioreceptivity, andesitic basalt, biofilms, monogenetic volcanoes.

Resumen

En esta contribución se describen los rasgos de intemperismo biológico producidos por comunidades microbianas que crecen sobre superficies rocosas denominadas costras saxícolas. Se presentan argumentos relacionados con la importancia de reconocer a las rocas volcánicas como un nicho ecológico, se hace una revisión de los principales procesos de intemperismo biológico reconocidos en lechos rocosos basálticos, abordando en particular los rasgos encontrados en el flujo de lava del volcán monogénico Xitle, ubicado en el campo volcánico de la Sierra del Chichinautzin al sur de la Ciudad de México. Se encontró que la diversidad y distribución de organismos dentro de las costras varía dependiendo de la textura superficial y la porosidad de las lavas. Los musgos tienen preferencia por vesículas y grietas, mientras que los líquenes pueden establecerse en áreas más lisas y expuestas. Las características de biointemperismo predominantes que hemos encontrado asociadas con estas costras son incrustación, penetración, relleno de vesículas, colonización endolítica, fracturas y atrapamiento de partículas. Las características de biointemperismo están relacionadas con grupos biológicos específicos: los líquenes están asociados con todos los rasgos encontrados; los musgos están más asociados con el atrapamiento de partículas y el relleno de vesículas, mientras que los biofilms se relacionan con la penetración y la colonización endolítica. Se analiza la importancia de la conservación del patrimonio geológico en relación con la biodiversidad que albergan estas lavas.

Palabras clave: Costras saxícolas, biorreceptividad, basalto andesítico, biofilms, volcanes monogenéticos.

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1. Introduction

Volcanic eruptions are destructive forces that cover everything in their path; however, they construct new surfaces at the same time, which are subject to the establishment and development of life. Monogenetic volcanoes—which erupt only for a period—are geological edifices with a heterogeneous rocky relief and diverse microenvironments that make the establishment of a wide variety of life forms possible. The material expelled from them cools and crystallizes, giving rise to large extensions of volcanic rock. The properties of the lavas (density, viscosity, pressure and temperature) determine the physical and chemical properties of the rocks once cooled. Since rock surfaces are exposed to the atmosphere after volcanic eruptions, they are rapidly colonized by microbial communities (Martínez-Martínez *et al.*, 2024). Rocks constitute an ecological niche for multiple life forms, although microorganisms are the dominant inhabitants, as they tend to better tolerate the extreme environmental conditions that these territories offer and are the pioneers in primary ecological succession (Miller *et al.*, 2023). Rocks are a microscopic landscape subject to habitation: their diverse surface and interior structure with vesicles, cracks, voids, and mineral grains are spaces for the establishment of life. By intercepting wind-blown compounds, they are coherent agents between the atmosphere and the lithosphere, and they play a key role in geobiogeological cycles of elements. For example, one of the most ambitious goals in geobiology is to show how the atmosphere-rock interface can be an indicator of the climatic and geochemical changes we are currently experiencing (Antony *et al.*, 2012). Today's microscopic rock dwellers, like cyanobacteria and fungi, have evolved from their primitive ancestors and are widely distributed, forming cosmopolitan communities that are established in all biomes and human constructions such as ruins and historical monuments (Gorbushina, 2007; Liu *et al.*, 2020). The fossil record suggests that similar covers —predominantly of cyanobacteria— formed the earliest terrestrial ecosystems in Earth's history 2.6-2.7 billion years ago, long before the appearance of vascular plants (Elbert *et al.*, 2012; Gutierrez-Patricio, 2024).

The establishment of these communities in lava flows produces changes in the physical and chemical structures of the rock substrate. Understanding bioweathering gives insight into the first stages of soil development, colonization of lavas after an eruption, and primary ecological succession (Hadland *et al.*, 2024). It can also assist in a better conservation of historical monuments, archaeological ruins and places of cultural importance (Macedo, 2009). The morphological and physiological adaptations of pioneer organisms in colonization are also of interest in astrobiology, since some volcanic environments, such as lava tubes, are studied as analogous to Mars, and the metabolisms of the microorganisms that inhabit them can give great insight into life outside Earth (Miller *et al.*, 2020).

Despite the ecological importance of biological crusts and their role in bioweathering, there is little information regarding this on lava outcrops. Mexico—as one of the regions in the world with a long geological history of volcanoes— offers many opportunities to research the process of life establishment that can be studied at different geological times. In the case of Xitle, a volcano that erupted approximately 1670 years ago (Siebe, 2009), its lavas host one of the most diverse biological ecosystems described (Lot and Cano-Santana, 2009). Its lava flow is an exquisite opportunity to document—over a sufficient amount of time—how the rock has been the habitat of undocumented microscopic life. In this light, the objective of this study is to approach the biodiversity held within these communities and the bioweathering features associated with them. This allows us to better understand the close relationship between geodiversity and biodiversity, while also providing an enhanced view of geoheritage. In the present study, we address the bioreceptivity of volcanic rocks; then, we continue with the different crust communities that inhabit the lava substrate, and the ways in which they can do so. Then, we proceed to review the main features associated with biological weathering presented in the case study carried out in the basaltic rocks of the Xitle lavas.

1.1 Bioreceptivity

Bioreceptivity is the suitability of rocks to be colonized by life (Guillitte, 1995). This depends on the rock's intrinsic properties as well as the tolerance ranges and adaptations of the species colonizing the substrate. Bioreceptivity of rocks also depends of the organism's tolerance to environmental factors that the rock surface is exposed to, such as: daily fluctuations in direct solar radiation, temperature oscillations, periods of extreme desiccation and rehydration, and scarcity of nutrients and available organic matter (Büdel, 2002; Hernández-Mariné and Roldán, 2012; Favero-Longo and Viles, 2020). Although there are other habitats with more extreme temperature conditions —namely salinity or pH—, they are rarely subject to fluctuations as rapid as bare rock surfaces do; therefore, life in rocks can be considered an extreme environment for the organisms living in them. These organisms and those living in extreme environments share similar adaptation mechanisms, such as: wide tolerance ranges, dormancy periods, physiological adaptations like pigment production (e.g. carotenoids) to protect themselves from direct UV light, or the formation of biofilms for efficient use and sharing of resources (Belnap y Lange, 2003; Gorbushina, 2007; Sanmartin *et al.*, 2021). In addition, rock composition as an habitat harbors life differentially: the colonization of rocks that dissolve quickly—such as limestone—develops scarce biological growth compared to harder rocks—such as basalt or granite—, which are receptive to harbor communities for longer periods of time, hereby accumulating microscopic layers of biological, mineral and organic material (Souza-Egipsy *et al.*, 2002).

Bioreceptivity of volcanic rocks involves different factors coming together (Figure 1). These can be grouped in three categories: environmental factors, biotic factors, and the intrinsic properties of the rock itself. The environmental factors are related to the geographical location of the lava flow (altitude, latitude), the orientation and/or inclination of the outcrop—which also have to do with the exposure to climatic conditions such as temperature and humidity and atmospheric conditions, which refer to the concentration of gasses like CO_2 or pollutants. Lichens, for example, are very sensitive to atmospheric conditions and can be used as bioindicators of the air quality (Will-Wolf *et al.*, 2017). The surrounding ecosystem and its proximity to a lava flow is relevant because organisms established in the lavas arrive from surrounding vegetation. Another biotic factor is the specific tolerance ranges of species to environmental factors. There are lichens which can live on exposed rock surfaces due to their tolerance to direct sunlight and temperature resistance, while some are more sensitive to drastic temperature changes or have a preference for shaded areas (Froehlich, 2006). Finally, the bioreceptivity is related to the intrinsic rock properties such as its chemical composition, superficial texture (smooth, rough), porosity, and the size and distribution of crystals (Guillite, 1995; Martinez-Martinez, 2024).

1.2. Biological rock crusts

The organisms that are established on rock surfaces are denominated saxicolous. Communities of cryptogamic organisms that are strongly attached to the rock surface without vegetation or soil coverage are biological rock crusts (BRC) or saxicolous crusts. They are a consortium made up of microscopic organisms such as bacteria, fungi, algae and archaea, and macroscopic organisms such as bryophytes and lichens (Büdel *et al.*, 2004). Some animals—like small arthropods—are associated since they use the crusts as shelter, nest, or food sources (De la Cruz, 2017). These crusts can also share species of soil-living archaea and bacteria accumulating on crevices of lava flows (Biderre-Petit *et al.*, 2020). BRC can also be established on subsurface volcanic rocks like lava tubes and are composed by a high diversity of thermophiles and actinobacteria too (Bergsten *et al.*, 2021; Miller *et al.*, 2023). A BRC can be considered from individual populations—such as a single crustose lichen—or complex communities—like microbial mats—within a multi-specific mosaic of organisms from different kingdoms and biological domains. Microbial mats are self-organized and stratified communities with maximum energy and resource efficiency. These mats can go from a few millimeters to several centimeters thick, often

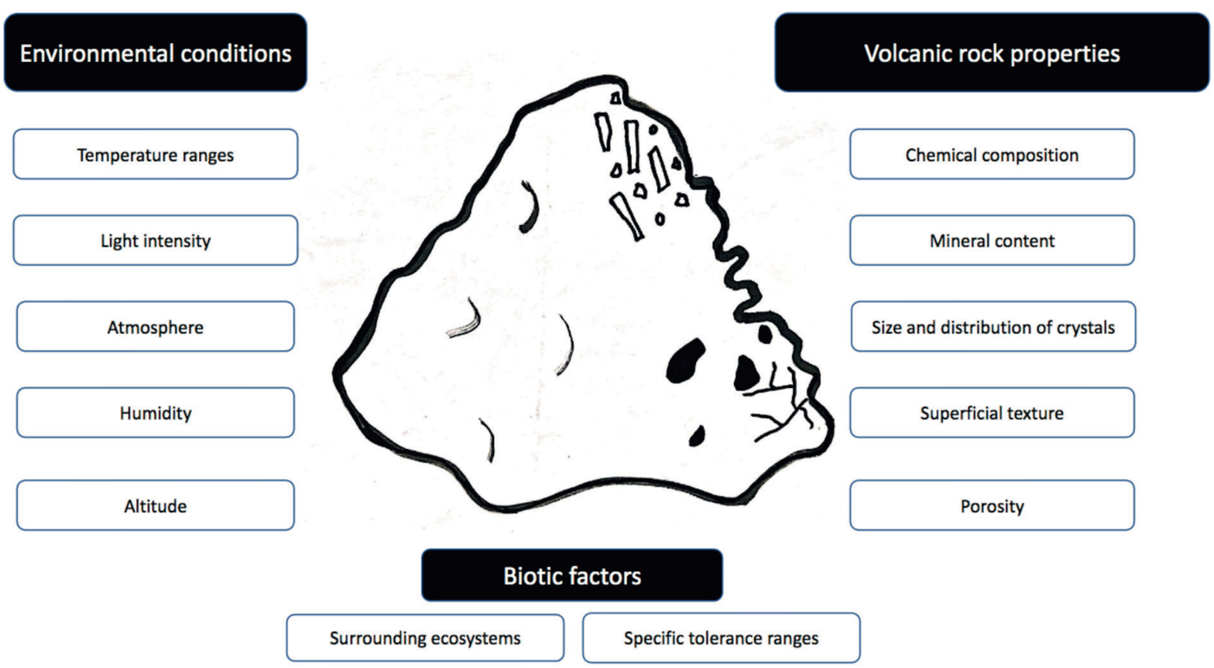

Figure 1. Factors driving volcanic rocks as an ecological niche. Different factors come together in giving volcanic rocks, their specific bioreceptivity can be grouped into: environmental conditions, biotic factors, and the intrinsic properties of rocks.

stratified because of their particular metabolisms in layers like sheets, photoautotrophic organisms (cyanobacteria and algae), as well as heterotrophic (fungi, actinomycetes). They develop chemical gradients compacted by viscous secretions produced by themselves, called extracellular polymeric substances (EPS). The appearance of the crusts (color and texture) can be determined by the species' present and their structural arrangement, together with the settling substrate. Biological rock crusts can be classified according to dominance of biological groups (cyanobacterial crust, algae crust or lichen crust) (Büdel, 2002); according to their morphology (smooth, rough, rolled and pinnacle crust) (Eldridge, 2001), or according to their main metabolism (photosynthetic crusts, chemolithotrophic crusts) (Ramírez *et al.*, 2010) (Figure 2).

Biological rock crusts are ideal models in the study of ecological interactions, since they are composed of diverse metabolisms interacting with the mineral surface while also being the interface between the atmosphere and the lithosphere (Büdel *et al.*, 2004; Sánchez and Torres-Alvarado, 2005). Moreover, they fulfill other ecological functions, such as the facilitation of seed germination of vascular plants, carbon sequestration and capture of atmospheric pollutants, nitrogen fixation and regulation of hydrological processes (runoff and infiltration) (Belnap and Lange, 2003). Studying biological rock crusts is also relevant because of their contribution to soil development and role as bioindicators of climate change due to their slow growth and sensitivity to atmospheric compounds (Northup *et al.*, 2011).

1.3 Bioweathering

In the history of the Earth, there are constructive processes that give rise to new surfaces, and destructive processes that weather away the exposed surface material in short or long periods of time, such as erosion and weathering. Weathering is defined as the set of processes that alter and disintegrate rocks, and it is fundamental for soil pedogenesis (Wilson, 2004). Multiple factors are involved and determine the speed at which it takes place: the type of parental material, climatic regime, time, and biological activity (Duque-Escobar, 2017). Bioweathering refers to the physical and chemical alterations exerted by organisms on rocks and minerals, increasing the available area for the successive establishment of more organisms and favoring the colonization of cracks and deeper layers (Ekendahl *et al.*, 1994). The physical and chemical changes they exert on rocks occur due to the segregation of organic acids and extracellular polymers that adhere to the mineral phase. This action releases elements contained in the minerals that are then taken in by organisms, a process known as biomineralization. Figure 3 lists the main bioweathering features that different organisms from biological rock crusts exert on basaltic rocks.

The colonization of rocks directly contributes to their physical alteration through different penetration or incrustation patterns that —depending on their mineralogy and microstructure— can extend from a few micrometers to several millimeters (Favero-Longo *et al.*, 2015). The incorporation of rock and mineral fragments into their thalli or embedment in their hyphae is another mechanism carried out by lichens (Ascaso and Wierzchos, 1994). Some crustose lichens incorporate quartz, feldspar, and mica when colonizing granite (Prieto Lamas *et al.*, 1995; Vingiani *et al.*, 2013); others produce patterns of penetration and branching in calcareous rocks and—in rocks rich in mica— the penetration of the hyphae further separates their laminae by this exploration (Barker *et al.*, 1997). It has been shown that volcanic glass altered by Archaea produces conspicuous micron-scale

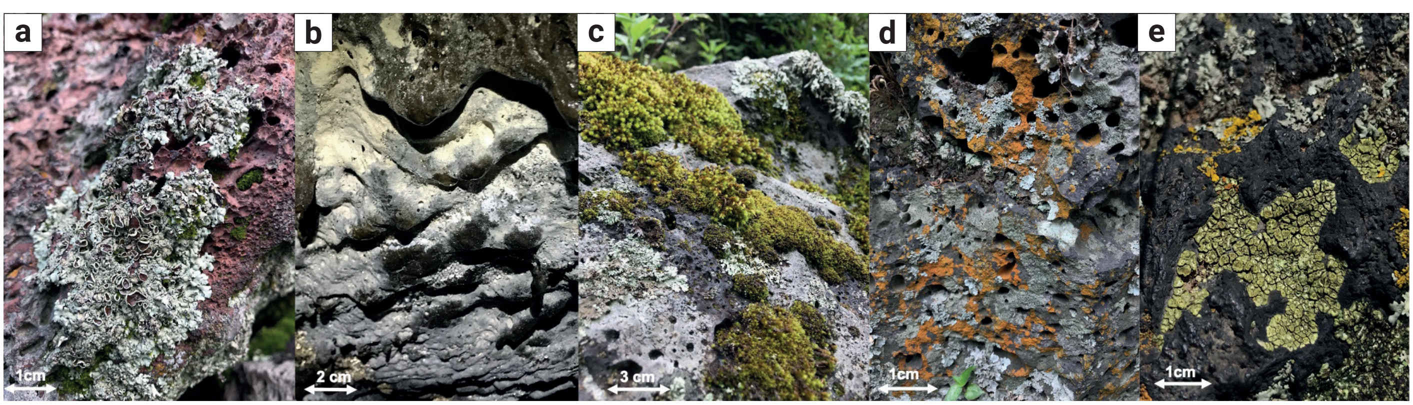

Figure 2. Diversity of saxicolous crusts along the Xitle volcano landscape at Sierra Chichinautzin, Mexico. a) Biological rock crust composed of foliose lichen and moss on a fragment of scoria in the crater. b) White bacterial biofilm developing inside a lava tube. c) Biological rock crust composed of bryophytes, algal mats, crustose and foliose lichens on a tumulus. d) Biological rock crust of crustose and foliose lichens and algal mats established in a vertical section of a crack within the lava flow. e) Rock crust of various crustose lichens on ropey lavas. Photographs by: Martínez-Baez, 2023.

granular and tubular textures on the surfaces they are attached to. This granular glass alteration happens because the colonizing microbes selectively dissolve the glass in the contact area, forming a sponge-like interconnected network of micron-sized cavities along glass surfaces. Other microorganisms like cyanobacteria produce tubular alteration, while fungal hyphae can produce tunneling in feldspars (Staudigel *et al.*, 2008). The mechanical breakdown of rocks can also occur due to the expansion and contraction of substances present in the matrix of biofilms and crusts. These biofilms have a high water-retention capacity that causes fractures in the substrate when frozen (Chen *et al.*, 2000; Liu *et al.*, 2020). The crystallization of salts such as oxalates formed by the activity of lichens separates minerals or rock fragments at their interface and/or in the thallus (Sand, 1997; Puy-Alquiza *et al.*, 2015) (Figure 4).

Bioweathering also generates chemical alterations, such as the dissolution of mineral grains that results in the mobilization of essential nutrients and metals (P, S, Na, K, Mg, Ca and Fe) for the development of life (Estroff, 2008). The EPS matrix of biofilms contains enzymes and proteins capable of hydrolyzing and solubilizing the surface of rocks and mineral surfaces, which are nucleation sites for the formation of secondary minerals (Büdel, 2002; Belnap and Lange, 2003; Liu *et al.*, 2020). Although not all minerals respond to pH changes such as olivines

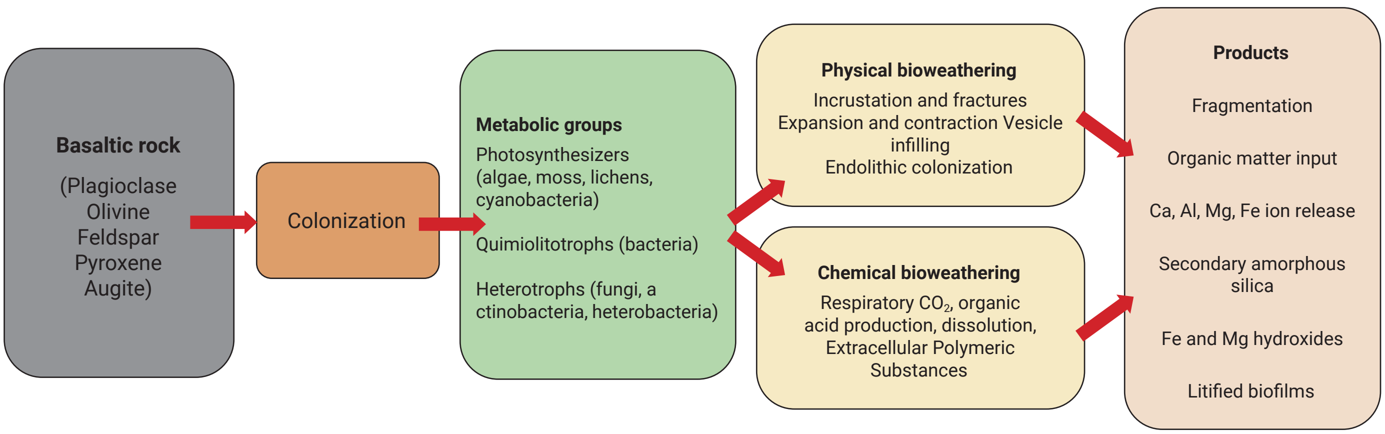

Figure 3. Bioweathering scheme of a basaltic rock carried out by organisms that are part of biological rock crusts.

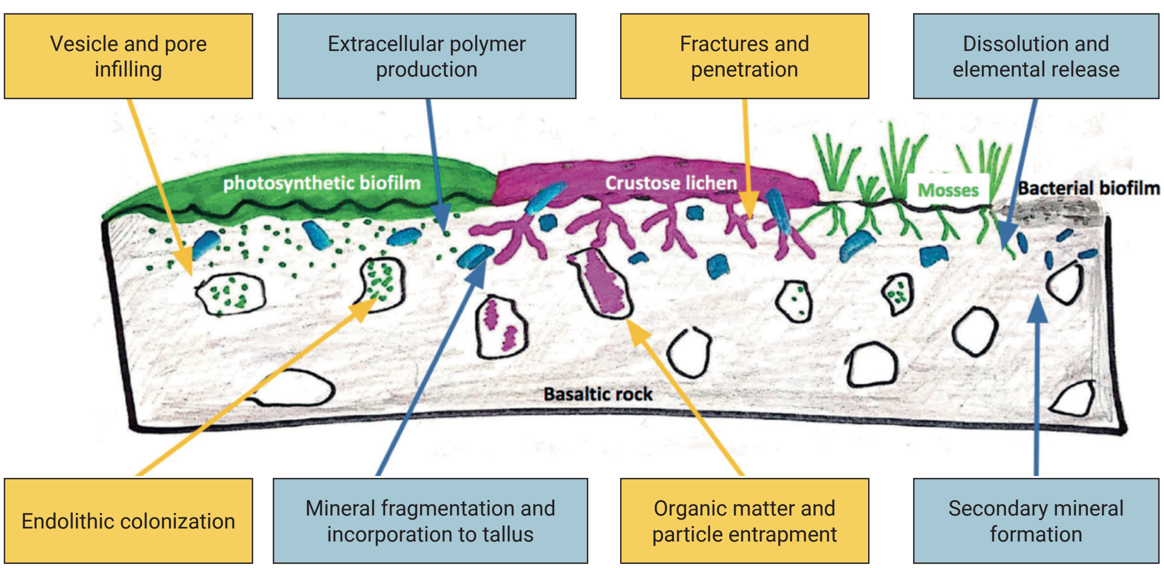

Figure 4. Representation of the main biological weathering mechanisms of the different groups forming the biological rock crusts that exert on the colonized rocks. The mechanisms of physical bioweathering are indicated in yellow and those of chemical bioweathering in blue (from: Berthelin *et al.*, 2000; Wilson, 2004; Liu *et al.*, 2020).

and pyroxenes contained in basaltic rocks, the reduction of pH through microbial respiration accelerates the release of elements from the rock. This happens because when CO_2 combines with the water surface, carbonic acid is formed and mediates solubilization (Chen *et al.*, 2000; Büdel *et al.*, 2004; Ibarrondo *et al.*, 2012). Cyanobacterial crusts also increase the pH—under alkaline (basic) conditions— and increase the dissolution of silicate compounds such as feldspars, biotite, and interstitial glass, using them for their growth and photosynthetic activity. Basic rocks are more susceptible to fungal attack than acidic rocks (Olsson-Francis *et al.*, 2012; Purvis, 2014).

One of the most studied mechanisms in bioweathering is corrosion by organic acids (oxalic acid, citric acid, nitric acid, sulfuric acid, sulfurous acid), which releases water-soluble salts such as sulfates and nitrates (Burford *et al.*, 2003), thus transforming siliceous minerals, precipitating iron oxides and hydroxides, and forming aluminosilicates. Basalt minerals—under the presence of organic acids from lichens and other microorganisms— release iron and magnesium from pyroxene and olivine, followed by calcium and aluminum from feldspar (Simpson, 2013). Other compounds that increase dissolution rates are low molecular weight organic ligands (acetate, oxalate, formate, lactate, pyruvate, succinate and propionate) that synergize the alteration made by organic acids and attack mineral surfaces by complexing with ions, weakening oxygen-metal bonds, and catalyzing dissolution reactions (Ferris *et al.*, 1994). Quartz, whose dissolution by acids is not so easy, is susceptible to the conjugate action of organic ligands (Abdulla, 2009). When organic acids (oxalic and gluconic) react with limestone, a neutralization reaction occurs, resulting in oxalates that form intracellularly within the wall of lichen hyphae and— as they increase in length—protrude from the wall cell towards its external surface (Addadi *et al.*, 2003). In rocks where calcium is present in low quantities—such as in serpentinite, formed almost entirely of magnesium silicate—, other oxalates—such as crystalline magnesium ones—can originate in the thallus of the lichen (Burford *et al.*, 2003). On the one hand, rocks with feldspars, which constitute the most abundant aluminosilicate minerals on the Earth's surface, react strongly with compounds produced by microorganisms. Alkaline feldspars release potassium cations after primary dissolution followed by secondary precipitation of a mineral phase (Abdulla *et al.*, 2008). Other examples have been documented in dark iron-rich sandstones whose solubilization occurs by endolithic lichens forming ferric oxide, and its dark deposition is observed in the lichen cortex and millimeters below (Estroff, 2008). Lichens also biodegrade micas or phyllosilicates in rocks transforming biotite to vermiculite, and to smectite and illite under the thallus of volcanic andesites (Barker *et al.*, 1997).

1.4 Bioweathering of volcanic rocks

Weathering of volcanic rocks plays an important role in the long-term carbonate-silicate cycle, which may contribute to regulating planetary temperatures over geological time. Among these, the weathering of basalt reduces the overall CO_2 production of the rocks by 30% (Dessert *et al.*, 2003). Identifying the biological components present in volcanic rocks and their potential to accelerate mineralization is important for a deeper understanding of Earth system processes. Weathering of volcanic rocks also plays an important role in the flow of nutrients to the biosphere (Dessert *et al.*, 2003). The composition of volcanic rocks influences rates of chemical weathering. The effects of organisms in the weathering process on the minerals that form volcanic rocks are noted in the morphology and composition of the rock, which includes modifications in the mineral surface, fragmentation of grains, dissolution of ultrafine crystals, and the precipitation of amorphous gels on mineral surfaces. The microbial communities that inhabit volcanic rocks facilitate and accelerate the extraction of elements in the rocks by modifying the pH of the solution in contact. For example, *Anabaena cylindrica*, a cyanobacteria growing on basalt in laboratory conditions, accelerated the rock dissolution and the rate release of Ca, Mg, Si and K five times quicker than abiotic controls (Olsson-Francis *et al.*, 2012). Oxalic acid-producing species of fungi, e.g. *Aspergillus niger* has been shown to degrade olivine and feldspar, and *Penicillium simplicissimum* has been shown to release Al from aluminosilicates. Although fungi contribute to the weathering of Fe and Mn-bearing minerals, the amount of degradation of these substrates that can be directly attributed solely to fungal activity in natural ecosystems is still unknown (Burford, 2003). Microorganisms facilitate the dissolution of minerals, but the influence of rock composition on biomineralization rates is still not well known (Chen *et al.*, 2000). It has been experimentally shown that the main rock-forming minerals of basalt (olivine, feldspar and pyroxene) are subject to attack by organic acids. Therefore, the biological weathering process is characterized by the mobilization of iron and magnesium and the release of calcium and aluminum from primary minerals, mainly ferromagnesian and calcium-rich plagioclase in basalt surfaces colonized by lichens and other microorganisms (Simpson, 2013).

1.5 Bioweathering processes due to biological rock crusts in the Xitle lava flow.

Xitle is a monogenetic volcano located south of Mexico City, and it belongs to the Chichinautzin Volcanic Field. It is a volcano with a scoria crater whose lavas are olivine basalts with tubular crystals of plagioclase and augite (De la Vega, 1994). The surface lavas are of pahoehoe type with irregular shapes such as tumuli, cracks, planes, and have smooth, braided, or corded textures. Variations in the substrate and relief favor the development of tephritic Regosol-type soils in the cone from unconsolidated volcanic ash and hyper-skeletal Leptosol in the cracks in the lower zone of the lava flow (Guilbaud *et al.*, 2021). It has a maximum altitude of 3100 meters above sea level and an altitudinal gradient with two climatic zones: Cf in the highest areas, and Cw in the lowest—in which diverse vegetation types are established ranging from coniferous forests at maxim altitude to a xeric shrubland in the lowest distal area (Carrillo-Trueba, 1995).

2. Methods

In order to get a representative sample that covers most of the geo and bio diversities, we took samples along climate and vegetation gradients, and in different lava geoforms along the Xitle lava flow (Figure 5). At each of the sampling sites, the biological groups forming the saxicolous crusts and their coverage were documented in quadrants (Martínez-Báez, 2020).

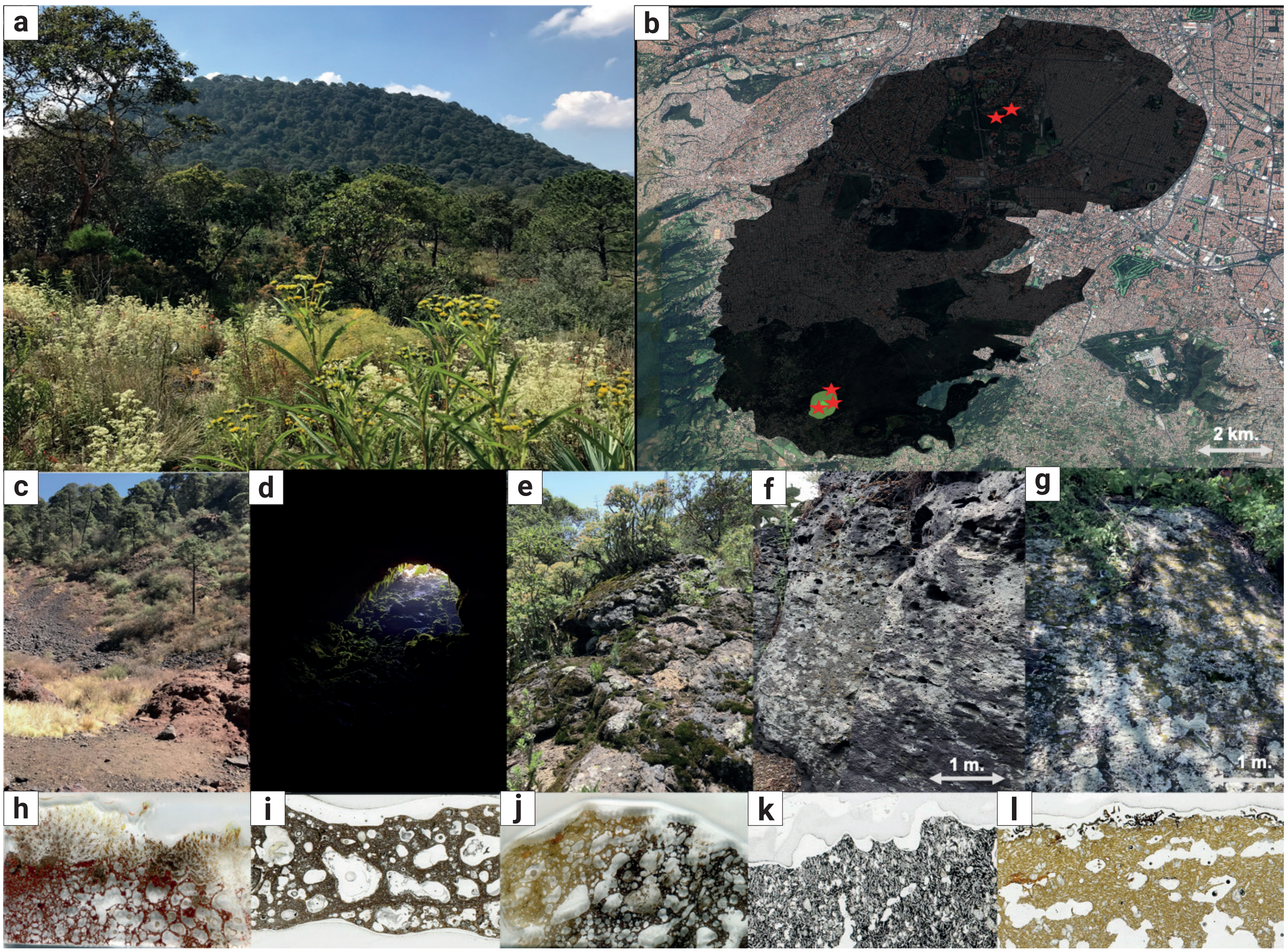

Figure 5. Sampling sites along the Xitle volcano landscape to document the structure of saxicolous crusts and their contribution to basalt bioweathering in the Sierra Chichinautzin, Mexico. a) Panoramic view of the Xitle cone showing two distinct vegetation types as the altitude decreases. b) Xitle volcano (green) and its lava flow (gray). The red stars indicate the sampling sites. Near the cone: crater, lava tube, tumulus on the slopes; on the distal part of the cone inside Reserva Ecológica del Pedregal de San Ángel: vertical cut on tumulus and ropey lavas on a flat lobe. c) Panoramic view of the crater. d) View of the entrance to the lava tube. e) Panoramic view of the tumulus on the slopes. f) Panoramic view of the wall of a crack in the lower area of the lava flow. g) Panoramic view of the flat site with cordate lavas in the lower zone of the lava flow. Basaltic rock matrix and porosity in thin sheet sections of the crust–rock interface in the crater (h), lava tube (i), tumulus (j), in the wall of a crack (k) and corded lavas (l).

The collection was carried out with a geological hammer selecting lava fragments on which biological crustal coverage measurements were taken. The fragments were observed in a stereoscopic microscopy to identify the biological groups at each site. Thin sections of each sample were made to document the rock-crust interface and bioweathering features (Pointing and Belnap, 2012; Potysz and Bartz, 2022). This also allowed for a more detailed observation of microscopic biological groups like bacterial and algal biofilms. The thin sections were observed in light microscopy, and—by using scanning electron microscopy (SEM) and the interaction at the crust—rock interface was also documented (Figure 6).

3. Results and discussion

We found 14 different morphological groups belonging to three main biological groups (lichens, bryophytes and biofilms) in the rock crusts of all the sites. The biodiversity richness and abundance of the biological rock crusts differed in each site (Martínez-Báez *et al.*, 2023). We found that certain biological groups have a preference for a specific volcanic consolidation of the rocks. For example, ropey lavas from flat lobes are mostly covered by different species of crustose lichens and mosses on the crevices; crusts developing on the vertical cut with a smooth surface are composed of photosynthetic biofilms (algae and cyanobacteria), dusty lichens and liverworts. Likewise, the rock from the tumulus with a rougher surface and the loose scoria from the crater have crusts made up of foliose and crustose lichens; mosses growth particularly on vesicles and algal biofilms, while the crusts in the stalactites from the lava tube are composed of different bacterial biofilms. All this evidence shows that the rock—depending on its cooling position in the relief—has a differential receptivity to be colonized by different types of organisms.

Although the basaltic rock has the same chemical composition along the Xitle lava flow, some properties of the rock (such as porosity and superficial texture) were different in the five sampling sites. The variations in physical properties of lava during crystallization—due to factors like density and gas content—are influenced not only by these characteristics but also by environmental factors such as altitude, which affects climate and surrounding vegetation. Together, these elements regulate the bioreceptivity of the lavas, as illustrated by the diversity of biological rock crusts (Figure 1).

The main bioweathering features found at the five study sites were: the incorporation of organic matter and aeolian particles (Figure 6A, C, H, K, Q), the features of biological encrustation such as penetration of root-like structures in mosses called ricines and hyphae (Figure 6B, D, E, F, O), fractures immediately beneath the lichen thallus (Figure 6M, N), detachment and incorporation of minerals into the crust (Figure 6B, L, Q), the filling of vesicles endolithic colonization (Figure 6G, H, I, J,R, S), and lithification of biofilms (P, T).

Bioweathering features are related to specific biological groups. Lichens exert all of the features found—although they are particularly associated with fractures immediately beneath their thallus and penetration of the hyphae—, while mosses are mostly associated with particle entrapment and vesicle infilling. Endolithic colonization and penetration are features associated with both photosynthetic and chemolithtrophic biofilms. (Viley, 1995)

The bioweathering features associated with the different biological groups is a result of the morphological adaptations of the organisms as well as their metabolisms. Lichens are strongly attached to the rock surface because of the fungal hyphae that are their anchoring structure. These structures are so thin that they are able to explore and penetrate the micro structure of the rock (Figure 6O). They also segregate organic acids into the mineral surface, thus causing further fracturing and mineral detachment and allowing them to colonize the interior of the rock. The morphology of mosses facilitates the entrapment of particles and organic matter beneath them, thickening the crust-rock interface, retaining moisture, and further contributing to the weathering of the rock. The main bioweathering feature associated to bacterial biofilms is the penetration they exert on the rock (Chen *et al.*, 2021). They were found not only on the surface of the stalactites but also within their interior structure. This can happen because the bacteria integrating these crusts are not dependent on light and—once they settle on the surface of the lavas—they can further colonize thanks to their chemolithotroph metabolism (King, 2007).

The biodiversity that we found in these biological rock crusts follows the geodiversity of the lavas. The distribution patterns are alike to those reported in the literature. The dominant group in biological rock crusts of the Xitle lava flow are lichens, which are present in the four superficial sampling sites. Lichens have a preference for smoother textures and surfaces with high exposure to sunlight, like vertical cuts of a tumulus, scoria on the crater, and the higher areas of ropey pahoehoe lavas. Mosses and photosynthetic biofilms (made up of terrestrial algae and cyanobacteria) were also common in all superficial lavas; although they dominate on rougher textures, crevices show a preference for vesicles and rocks with more porosity. The stalactites inside lava tubes are only inhabited by bacterial biofilms. The documentation of these biofilms is a contribution to the life forms that can develop in volcanic environments, specifically novel in Xitle volcano. It is crucial to continue exploring this line of research because understanding bioweathering has multiple

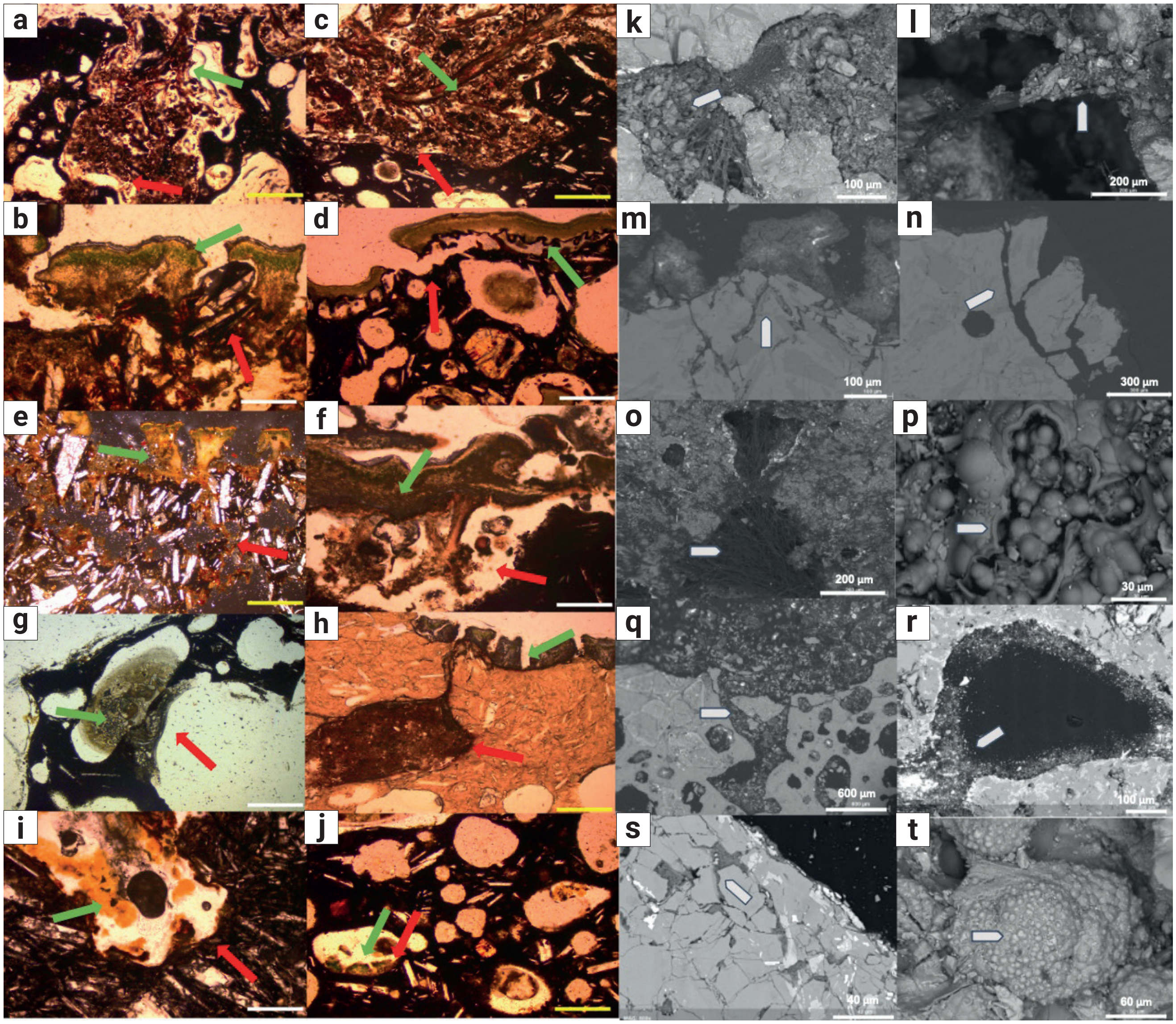

Figure 6. Bioweathering processes associated with saxicolous crusts (biological rock crusts) in different microenvironments along the Xitle volcano lava flow in Mexico City. On the left side: light microscopy of thin sections, white bars= 50 µm, yellow bars = 200 µm; on the right side: SEM images from rock fragments and thin sections. Left: a) Accumulation of organic matter and particles (red arrow) entrapped by the ricin (green arrow) of a moss in a sample of a loose scoria fragment collected from inside the crater. b) Crustose lichen (green arrow) penetrating the rock substrate in a sample from the tumulus in the slopes of the volcano. Red arrow shows a fragment of glass partially wrapped in the lichen thallus. c) Ricin of moss with organic matter and mineral fragments attached to it. d) Foliose lichen encrusted on basalt surface. The red arrow shows fragments of the mineral surface attached to the lichen thallus. e) Crustose lichen on a rock from a sample from a vertical section of a tumulus. The green arrow indicates the lichen on the surface and the red shows the hyphae penetrating the pores and fractures of the rock. f) Hyphae from crustose lichen with tiny mineral fragments in the crust-rock interface. g) Endo- lithic colonization by a grayish bacterial biofilm developing inside a vesicle (green arrow) and the advance towards a neighboring vesicle (red arrow) in a rock from the crater. h) Crustose lichens in a sample of the tumulus. The green arrow indicates the lichen thallus and red the filling of organic matter and particles. i) Bacterial biofilm (green arrow) developing inside a vesicle of a stalactite sample taken from the lava tube. j) Endolithic colonization (red arrow) of crustose lichens (green arrow) in the vesicles of a lose scoria from the crater. Right: k) Lichen hyphae exploration of the rock structure with particle entrapment around the cells (white arrow) l) Ricin from the moss *Campylopus pilifer* and aggregation of particles and organic matter (white arrow). m) Lichens embedded in a sample from a vertical rock surface. Fractures and detachments are observed on the surface of the basalt that are incorporated into the lichen thallus (white arrow). n) Rock fragmentation immediately beneath the thallus of lichen crust. o) Exploration of hyphae (white arrow) from crustose lichen within the basalt structure. The cells are not only growing inside vesicles but the cracks and crevices of the rock. p) Lithified globular shape growth bacterial biofilm and the organo-mineral layers in a sample from the lava tube (white arrow). q) Crust–rock interface that shows mineral fragmentation and detachment (white arrow) as well as the accumulation of particles and organic matter. r) Endolithic colonization of vesicles (white arrow) of a sample taken from a tumulus in the slopes of the volcano. s) Endolithic colonization (white arrow) of the vesicles and cracks of a lava tube stalactite sample. t) Lithified biofilm (white arrow) in the vesicles of a loose scoria sample from inside the crater.

applications (Cozzolino *et al.*, 2022). These include: conserving cultural heritage, describing undiscovered biological diversity, and recognizing the role of these organisms in biogeochemical cycles and ecological processes such as primary succession, colonization after eruptions, and soil formation.

Furthermore, the morphological and physiological adaptations of biological rock crusts are also important to explore for astrobiology and bioremediation studies. More studies which focus on specific groups on specific lavas are needed.

4. Conclusions

Monogenetic volcanoes have rocky substrates that are subject to the colonization and establishment of life. The morphology and metabolic activities of the communities that are established in the rocks cause alterations called bioweathering. Many factors influence the presence of specific species assemblages, and these assemblages also have various effects on the bedrock. A central theme in geobiology is understanding the interactions between organisms and their abiotic environment. In the past, the focus was on abiotic weathering processes, and today, attention is increasingly focusing on the biological processes by which organisms break down minerals and use or release elements into the environment.

Although bioreceptivity and bioweathering of lavas is a subject that has recently been more studied, the bioweathering features associated with biological rock crusts settled in different microenvironments of the Xitle lava flow had not been described before. The pioneer communities and interaction of each group—and even more so, of each species— are multiple and we found they respond to rock properties of porosity and superficial texture, as well as the environmental conditions of each site. However, this is only a first insight into the biodiversity held within these communities and the bioweathering features they exert on the substrate.

This research contributes to the description of the natural biological and geological heritage in the Xitle lava flow.

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