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# Young volcanic terrains are windows into early microbial colonization

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Volcanic eruptions generate initially sterile materials where biological processes are absent, allowing for the fresh colonization by new organisms. This review summarizes the characteristics of volcanic habitats that are available for pioneer microbial colonization, including hot springs, fumaroles, lava tubes, and recently cooled rock surfaces and interiors. Eruptions provide unique insight into microbial community development in extreme environments. The trajectories that these ecosystems follow are largely dictated by the initial environmental conditions and identities of the colonizers, rather than the age of the system. The review also discusses how studies of microbial communities in young lava flow fields can provide insights into the possibility of life on Mars, which was volcanically and hydrologically active in the past. Understanding biosignature preservation as well as the metabolisms and survival mechanisms of microorganisms in volcanic systems has implications for how an ecosystem might have developed on early Earth and possibly Mars.

Pioneer species are organisms that first colonize a bare substrate created by a disturbance[1], such as soil exposure after glacial retreat (primary succession), freshly emplaced lava flow fields (primary succession)[2–4], or habitat destruction due to a wildfire (secondary succession)[5]. Investigating pioneer microorganisms following an eruption is essential because the initial microbial community composition and metabolisms will dictate the development of more complex ecosystems and biogeochemical processes. Most of the Earth's surface (including the seafloor) is of volcanic origin[6], which makes constraining succession in these systems fundamentally important for informing ecological processes.

Deepening the understanding of the taxonomic and metabolic identity, origin, and distribution of pioneer species is relevant in astrobiology because volcanic terrains were likely the first habitats to support life on Earth and could also have hosted, or could be hosting, life elsewhere. It is particularly timely because the search for life on Mars and other volcanically active planets is a top science priority in the Planetary Science and Astrobiology Decadal Survey 2023–2032[7]. Previous reviews recognized lava rocks can provide habitable environments for life[8–10], but there is a need for a holistic perspective regarding the abiotic and biotic factors that influence succession in the range of habitats within volcanic environments (Fig. 1).

We highlight the process of ecological succession within young terrestrial volcanic environments from the viewpoint of microbial communities and discuss key processes related to the habitability of basaltic rocks from an astrobiology perspective. We use the phrase "young volcanic terrains" to describe environments that have been affected by a geologically recent eruption (<2000 years), the phrase "volcanic rocks" to describe igneous rocks solidified on or near the surface[6], and the term "terrestrial" to describe processes occurring on land, as opposed to oceanic systems.

## The importance of volcanic terrains in understanding primary microbial succession

Volcanic rock is sterile upon emplacement due to its high initial temperature (e.g., basaltic lavas are typically erupted at ~1150 °C)[11]. This generates new surfaces where biological processes are initially absent. Colonizers of volcanic terrains must overcome low nutrient availability (e.g., <0.1 wt% carbon at some sites)[12,13], highly variable temperatures, oxidative stress, and high ultraviolet radiation (UV) at young, unvegetated sites[9]. These freshly emplaced materials are consequently low biomass (often ~$10^6$ cells/g)[14,15] and methodological limitations make it difficult to analyze biomarkers and to adequately document the early stages of succession. For example, the binding of cells to the hard mineral matrix in basalt and the enhanced potential for introducing exogenous contaminants further complicates the extraction of biomarkers[16]. These factors have limited the use of modern omics techniques, leaving little still known about the identity and metabolisms of initial colonizers.

Eukaryotic photoautotrophs such as algae (including lichen), mosses, and plants were previously thought to be the first colonizers of lava flows[17–21]. Yet, recent studies have shown that prokaryotes (bacteria and archaea; Supplementary Table 1) are able to establish limited communities within the lava as soon as three months after an eruption[14], some with

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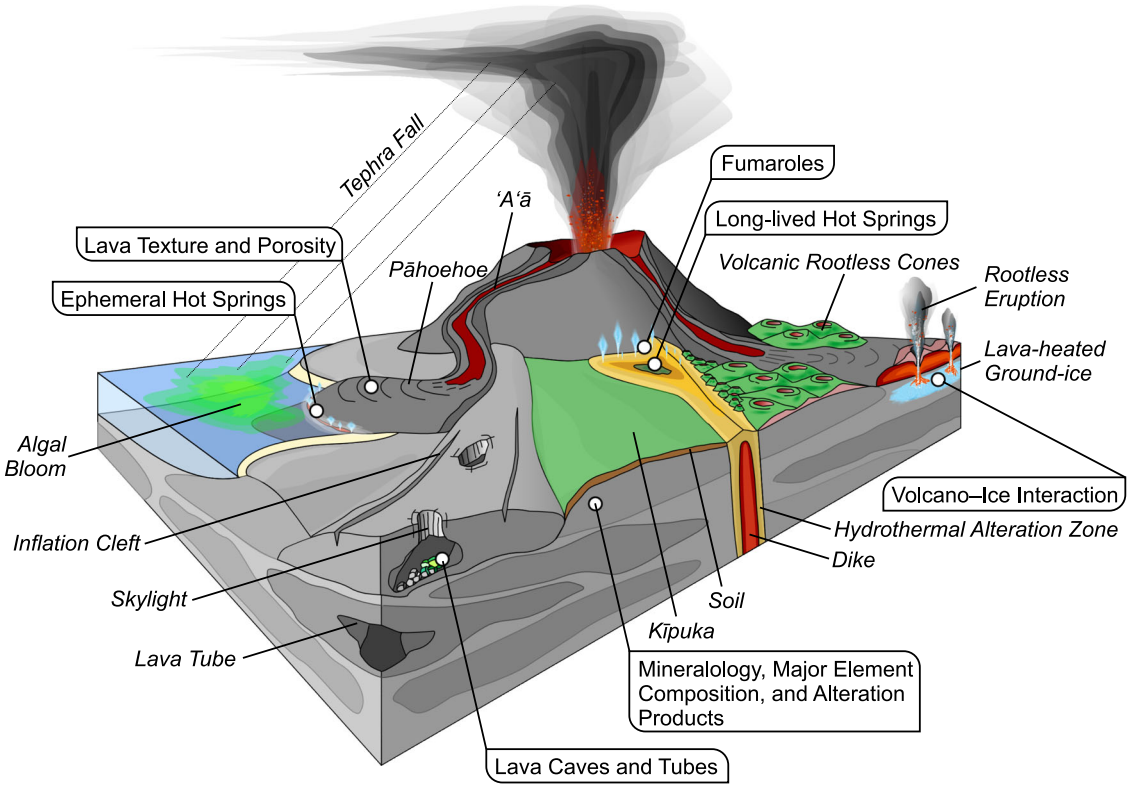



**Fig. 1 | Overview of possible microbial habitats associated with volcanic terrains.** Habitats for microorganisms associated with volcanic terrains including long-lived and ephemeral hot springs, fumaroles, lava tubes, and lava rocks, as well as melted ice and associated products from lava–ice interactions. Major abiotic factors discussed in this paper are indicated by circled text.

chemoautotrophic metabolisms (Supplementary Table 1) such as the oxidation of volcanically derived carbon monoxide (CO)[22]. Other studies have shown the initial microbial community is dominated by heterotrophs, suggesting organic carbon (C) must come from an external source such as the atmosphere, water percolation, or necromass[23–25]. However, uncertainties remain about the specific metabolisms because many of these studies relied on 16S rRNA gene sequencing data (Supplementary Table 1) for functional inferences.

Two types of processes—deterministic and stochastic—govern microbial community assembly during succession[26]. Deterministic processes involve abiotic and biotic factors that influence the type and relative abundance of certain species. For example, abiotic factors such as water availability, weathering, mineralogy, porosity, rock texture, and local weather control the conditions resulting in habitat formation, which directly affect the microbial community composition that can inhabit the cooled lava[27,28]. Stochastic processes are governed by random dispersal and changes in species abundance that are not due to environmental fitness[29]. An open question in the study of succession in volcanic environments is the relative importance of deterministic and stochastic processes over multiple timescales in generating variation in species composition across biogeographic regions[30].

Volcanism is inextricably tied to the history of life on Earth since the crust and atmosphere result from volcanic processes. One of the major theories regarding the origin of life is that the last universal common ancestor (LUCA) lived at deep-sea hydrothermal vents[31,32], which are driven by the rapid cooling of magma at oceanic plate boundaries[33]. Other ideas include the hypotheses that volcanic terrains were the first habitats to harbor life on land[34,35], or that LUCA first formed in terrestrial hot spring pools and later moved to the ocean to develop complex life[36]. Floating islands of pumice (glassy, frothy, pyroclastic volcanic rock) have also been proposed as the setting for the emergence of life on Earth[37]. Volcanism provides a source of life-sustaining nutrients and contributes to the cycling of the volatiles (Supplementary Table 1) that play a role in stabilizing planetary climate[38].

Understanding how microorganisms utilize and are preserved within habitats in volcanic systems has implications for our ability to detect possible life on other volcanically active planets. Mars has abundant evidence of both hydrological[39] and volcanic activity in the past[40–44], perhaps as recently as the past few million years[45,46]. For instance, Noachian-aged (Supplementary Table 1) craters on Mars, like Gusev[47] and Jezero[48], commonly exhibit evidence of paleolakes and lava that has undergone aqueous alteration[49–51]. The combination of liquid water and volcanic activity on ancient Mars has raised the question of whether it was habitable and once hosted life. Therefore, volcanic terrains on Earth have been used as analogs for similar Martian environments[25,52,53]. On icy moons, cryovolcanism is thought to be a plausible mechanism for potentially carrying biological material onto the surface ice[54].

In volcanic systems, factors such as pH, elemental composition[55,56], mineralogy[57], temperature[58], water content[59], and pressure[60,61] contribute to changes in microbial diversity and metabolic potential[62], and these variations can be observed at fine spatial resolutions, specifically scales smaller than one meter. Substantial work remains to understand how physicochemical and geologic conditions impact different types of habitats (Fig. 1), leading to microbial colonization on Earth, and possibly Mars or other planets.

## Hydrothermal systems

### Long-lived hot springs

Long-lived hot springs (>decades old) are known to harbor diverse and abundant microbial communities due to the presence of various temperature regimes, reduced chemical species, and profuse mineral depositional processes[63,64]. These systems form when a persistent magmatic heat source interacts with groundwater (Fig. 2a, b). The resulting fluids have a diverse range of chemical compositions, but can be grouped into three end-member

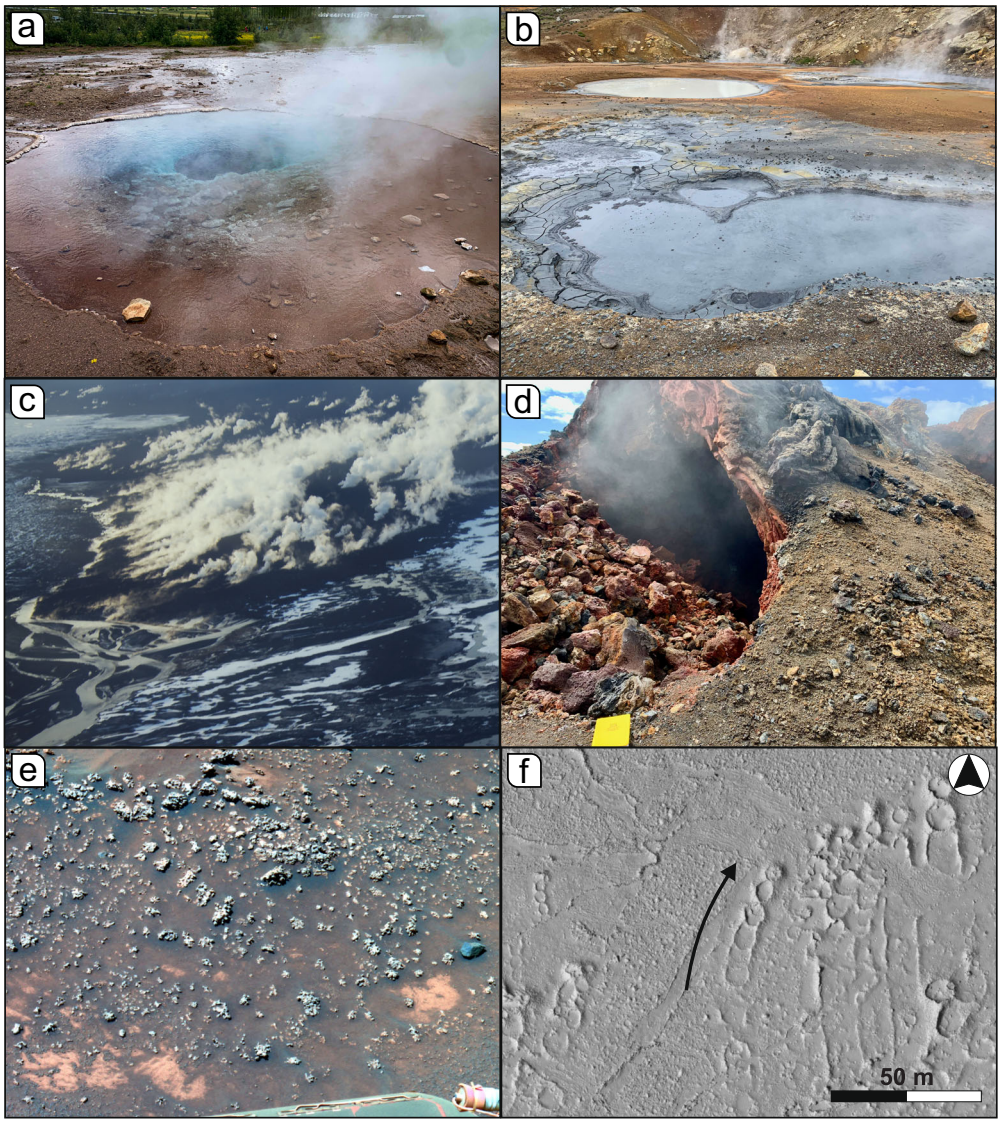



**Fig. 2 | Hydrothermal systems and lava–water interactions. a** Long-lived bicarbonate rich springs in the Geysir geothermal area, Iceland (photo credit: N. Hadland)[236]. **b** Long-lived acid-sulfate springs in the Krýsuvík geothermal area, Iceland (Photo credit: N. Hadland)[176]. **c** Ephemeral hot springs that formed following the 2014–2015 Holuhraun eruption in Iceland after the lava was emplaced into the Jökulsá á Fjöllum river (Photo credit: C. W. Hamilton). **d** Meteoric water percolating through permeable basalt to a hot center in a lava flow resulted in ephemeral fumaroles that lasted for several years after the 2018 Kīlauea eruption in Hawai'i (Photo credit: N. Hadland). **e** Evidence of past hydrothermal activity on Mars in the form of white nodular opaline silica deposits (amorphous $SiO_2 \cdot nH_2O$) (Mars Exploration Rover Spirit Pancam false-color image P2388; Photo credit: NASA/JPL-Caltech)[93]. **f** Chains of ring-mound landforms in Athabasca Valles on Mars, which are interpreted to be volcanic rootless cones formed by explosive lava–water interaction. The overlapping cones indicate the features in the upflow direction (black arrow) are younger[237] (High Resolution Imaging Science Experiment (HiRISE) image PSP_002938_1890; Photo credit: NASA/JPL-Caltech/UArizona).

categories: (1) bicarbonate-rich springs that can create travertine ($CaCO_3$; Fig. 2a); (2) alkali-chloride springs of nearly neutral pH that can form siliceous sinter deposits; and (3) acid-sulfate springs that develop when ascending hydrogen sulfide ($H_2S$) is oxidized to sulfuric acid ($H_2SO_4$) and reacts with surrounding rocks to create clays and oxides (Fig. 2b)[65]. In neutral to alkaline water, Cyanobacteriota (i.e., photoautotrophs) dominate, whereas chemoautotrophs and heterotrophs are more abundant in acidic and higher temperature regimes[64].

Microbial mats are ubiquitous geobiological features, and gradients in physicochemical parameters throughout the mat can result in layering that leaves morphological biosignatures[66,67]. Useful insights into successional processes in hot springs can be drawn from studies of newly formed sinter deposits[67–69] or by incubating submerged sterile microscope slides in mature systems to observe mat formation[63,70,71], though caution should be taken when extrapolating these conclusions to newly formed hot springs. Colonization onto new surfaces by chemoautotrophs (e.g., arsenite oxidation by *Hydrogenbaculum* spp., Fe(II) oxidation by *Metallosphaera yellowstonensis*, etc.) or photoautotrophs occurs rapidly (~hours to days)[70]. Later, the development of mature mat structures can result from extracellular polymeric substances and filamentous cellular morphologies capturing free-floating cells or precipitates[68], progressively building up layers. Oxygenic photosynthesis by Cyanobacteriota in the mat can locally increase the pH, leading to carbonate saturation and precipitation[72], further building up layers. Extracellular polymeric substances—mainly composed of polysaccharides, lipids and proteins—also facilitate carbonate precipitation and crystal nucleation[73]. These biomineralization byproducts allow for the later colonization of heterotrophs or organisms with anaerobic metabolisms due to the lack of oxygen ($O_2$) at the bottom of the mat, which is relevant to understanding early Earth ecosystems since they were also anaerobic[69,70].

Temperature and pH also play roles in the development of a microbial mat on a newly exposed surface. For example, beyond the upper limits for phototrophy (~72 °C)[74], species richness drops dramatically and morphologies in the biofilm become less diverse. Sinter deposition is even limited above 77 °C[68,71]. Consequently, temperature gradients can result in different biomineralization products and biosignatures on sub-meter scales.

### Ephemeral hydrothermal systems

Lava–water interactions generate ephemeral hot springs and fumaroles (Fig. 2c, d). Lava from effusive eruptions tend to occupy topographic lows and commonly encounter near-surface water[75]. Water can flow beside, under, over, and through lava to generate hot springs[76]. These systems differ from long-lived hydrothermal systems because once the eruption stops, the supply of heat will diminish, returning the water to ambient temperature[53]. Ephemeral hydrothermal systems also form via meteorite impacts, such as within the Haughton Crater in Canada[77] or the Chicxulub Crater in Mexico[78]. These systems are similar to lava flows in terms of primary succession since the impact effectively resets biological processes in the region[79].

On Earth, the best recent example of a lava-induced hydrothermal system occurred during the 2014–2015 eruption of Holuhraun in the central highlands of Iceland, where the lava was emplaced into part of the Dyngjujökull glacial floodplain and tributaries to the Jökulsá á Fjöllum river. Water ponded against the lava and flowed through the porous basalt to the distal end of the lava flow, where heated water emerged to generate a hydrothermal system (Fig. 2c). The warmest recorded temperatures in the pools and outflow springs were measured at 48.4 °C six months after the eruption ended, and the water declined to ambient temperature two years later[75,76]. However, hotter temperatures are implied by the development of fumarolic steam plumes in the interior portions of the lava flow (Fig. 2c). The hot springs were quickly colonized by microorganisms, which showed little similarity to the taxonomic diversity of the glacial river. Culture-based analysis revealed the presence of endospore-forming thermophiles (Supplementary Table 1) such as *Geobacillus stearothermophilus*. Interestingly, incubating glacial water at the warm lava-heated sites resulted in increased cell growth and taxonomic diversity. Sequences that dominated glacial water such as the sulfur (S)-oxidizing *Sulfuricurvum* sp., reduced in the warm treatment while photosynthesizers (e.g., Cyanobacteriota and microalgae) increased in number[53].

Another example of an ephemeral hydrothermal habitat is Surtsey, a volcanic island off the southern coast of Iceland created by a series of submarine, explosive, and effusive eruptions of basaltic lava in 1963–1967[80]. The associated Surtseyan eruption style is characterized by ejecta rapidly expanding upward through a shallow water column and resulting in glass-rich cocktail sprays of ash, rock, and lava (collectively called tephra) and the formation of new land. Other Surtseyan explosions were observed in association with Capelinhos (Azores) in 1957–1958[81] and the Hunga Tonga–Hunga Ha'apai (HTHH) eruption in the South Pacific in 2014–2015[82]. Human visitation to Surtsey has been relatively limited, creating an excellent natural laboratory for studying succession[83]. Microbial communities within Surtsey have been investigated using a borehole drilled in 1970 to access the subsurface hydrothermal environment that formed following the eruption. Temperature increased with depth up to biologically prohibitive temperatures but started to decrease ~100 m below the surface. A diverse unculturable microbial community was discovered at 145–172 m including methanogens (e.g., *Methanobacterium*), sulfate reducers (e.g., *Desulfosporosinus*, *Desulfatiglans*, and *Desulfotomaculia*), and sulfur oxidizers (e.g., *Thiomicrospira* and *Sulfurospirillum*), suggesting an active S cycle. Taxa typically found in seawater such as *Halomonas* and *Pseudoalteromonas* were also found, demonstrating that seawater infiltration into the porous lapilli layer is an important vector for colonization. However, many groups had little similarity in the 16S rRNA gene to any known lineages. Combined with a high-temperature ceiling at ~100 m (124 °C in 2017), this indicates this community is likely indigenous to the subsurface and suggests the eruption generated a massive underground biome for the thermophiles to occupy. Remnant heat has allowed the unique community to persist for decades after the eruption[84–86].

Eruptions in 1967 and 1969 on Deception Island, Antarctica, produced isolated basaltic cinder cone islands[87,88]. Similar to Surtsey, seawater interacted with magmatic heat, and ephemeral hot spring crater ponds formed, resulting in a semi-isolated saltwater system with algae and high levels of phylogenetic diversity compared to surrounding Antarctic waters[89,90]. Remarkably, some of the most abundant phyla found are rarely seen in other Antarctic ecosystems and are typically identified in marine hydrothermal vents (e.g., the thermophilic Calditrichota). Samples also contained ammonia oxidizers, contributing to primary productivity and the nitrogen (N) cycle and thus playing an important role during the dark polar winter months when photoautotrophy is severely limited[91].

From an astrobiology perspective, lava-induced hydrothermal systems are intriguing because lava flows on Mars may have interacted with near-surface water or ice-bearing permafrost[40,41]. These events may have created environmental conditions suitable for thermophiles[53,92]. Future missions could search for biosignatures in sites with evidence of lava–water interactions, such as in Gusev Crater (Fig. 2e)[93], Athabasca Valles (Fig. 2f)[41], or Jezero Crater[51].

### Volcano–ice interactions

Volcano–ice interactions can generate a range of habitats for microbial colonization[94]. This process has been reviewed in the context of astrobiology[95]. Subglacial eruptions can produce glacier caves[96] or melt the overlying ice layer to form glacial springs, meltwater lakes, or ice-melt-fed surficial hot springs[55]. Magma intrusions into a glacier could produce massive subsurface hydrothermal environments[97]. These environments represent transient volcanogenic habitats hypothesized during Snowball Earth scenarios (Supplementary Table 1)[98] or on Mars in the past[97]. On Mars, there could have been sufficient geothermal heat to cause hydrothermal circulation after melting the permafrost ice layer, potentially with enough exploitable redox gradients to support chemoautotrophic life[99], including S, hydrogen gas ($H_2$), and iron (Fe) driven metabolisms[55].

Microorganisms can also occupy the basal layer of glaciers and subglacial lava edifices, but these environments are difficult to access and study. Basalt from subglacial eruptions in Iceland have been exposed following glacial retreat and glass products have been shown to harbor Actinomycetota, Pseudomonadota, and Bacteroidota[23,24]. Microbial communities are also found on the surface of ice near active volcanoes, such as on Deception Island, Antarctica, or Kamchatka Peninsula, Russia. Reduced forms of Fe and manganese (Mn) present in basaltic ash embedded within the ice could serve as an energy source for chemoautotrophs, such as the Fe-oxidizing *Ferrimicrobium acidiphilum* (Actinomycetota) or the Fe-reducing *Rhodoferax ferrireducens* (Pseudomonadota). Volcanic gas containing S could also explain why S-metabolizing bacteria, such as *Thiomonas thermosulfata* (Pseudomonadota) have been found within ice[91,100].

### Fumaroles

Fumaroles form when meteoric or subsurface (i.e., phreatic) water is heated to form steam and escapes through lava flow surface cracks (Fig. 2c, d). Fumaroles generate stark physicochemical gradients that contrast sharply with the surrounding environment. Acidic pH, variable temperatures of steam discharge (~45–180 °C), and heavy metals require a great degree of specialization for microbial life and thus result in generally low biomass[101,102]. For example, on the Big Island of Hawai'i, fumaroles are abundant and most lava flows are less than 1500 years old (Fig. 2d)[103], allowing for the study of relatively young systems. Active fumaroles exhibit lower phylogenetic diversity compared to relict sites and unaltered basalt and microbial biomass is heterogeneous in distribution[25,52], likely due to prohibitively high temperatures for many organisms[104].

Fumaroles in more extreme environments, such as Mount Erebus in Antarctica or Socompa in the hyperarid Atacama Desert have a generally different trend compared to Hawai'i because the areas around the fumarole vents are the only abode of warmth or moisture, potentially creating islands of habitability. In these systems, there may be a higher spatial variability in phylogenetic diversity as a function of distance from the fumarole vent due

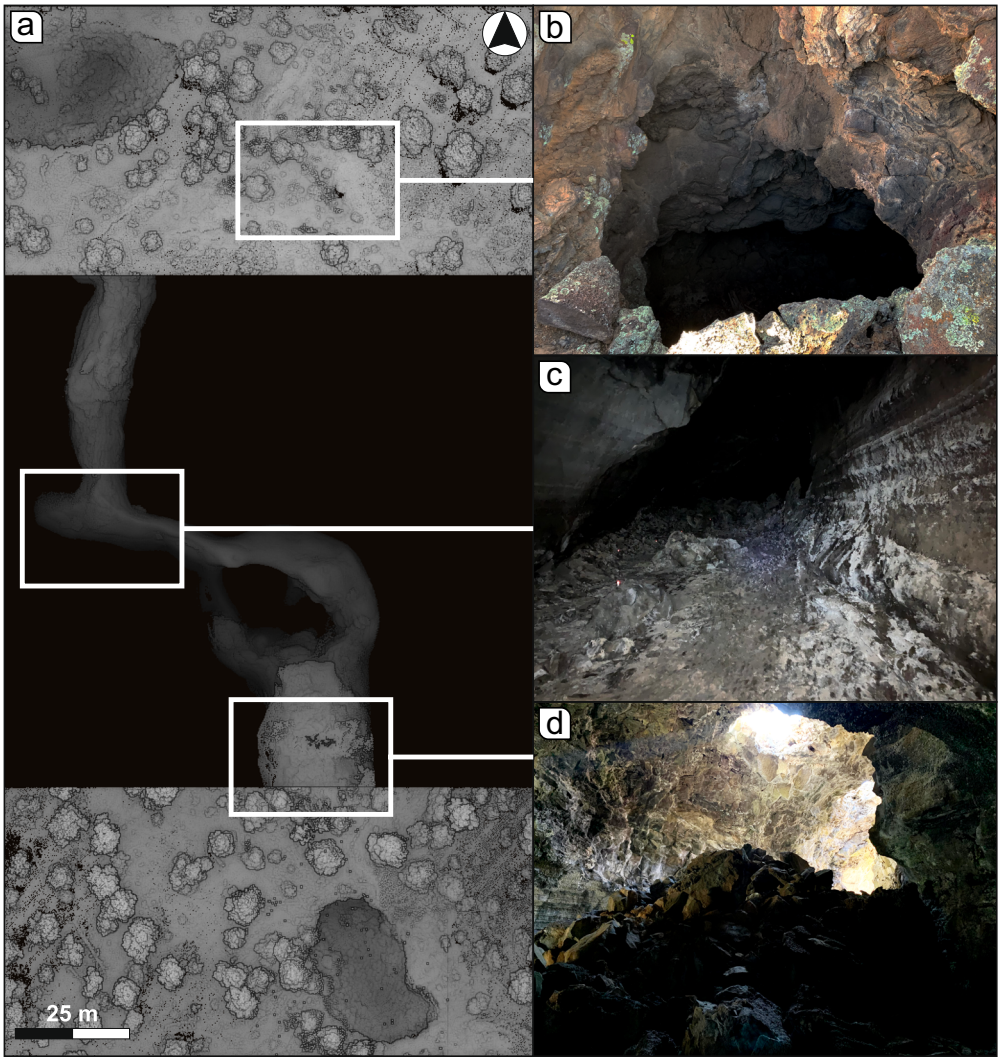



**Fig. 3 | Lava tube in El Malpais National Monument, New Mexico. a** Top-down view of point cloud LiDAR data of Four Windows Cave in El Malpais National Monument, New Mexico. Elevation values were converted to gray scale with dark colors corresponding to lower elevations. Shape edges were shaded with an eye-dome lighting model. The surface is removed in the center part of the figure to expose the subsurface lava tube (data from Bardabelias et al.[238]). The white boxes correspond to photographs **b**–**c**. **b** Top view of a skylight into Four Windows Cave (Photo credit: N. Hadland). **c** Dark interior of Four Windows Cave. Mineral precipitates and textured surfaces on the walls are visible (Photo credit: N. Hadland). **d** The edge of the twilight zone in Four Windows Cave where light progressively drops out. Directly beneath the skylight, moss and Cyanobacteriota films visibly dominate (Photo credit: N. Hadland).

to very large variations in temperature and moisture content[58,59]. In cold environments, steep thermal gradients can cause soil environments to transition quickly from thermophile to psychrophile-dominated communities[58]. Communities can also quickly transition in metabolic function—from photoautotrophs (e.g., Cyanobacteriota and algae) in the steam-heated soils near the fumarole to xerotolerant (Supplementary Table 1) endospore-forming heterotrophs on the outskirts (e.g., Actinomycetota)[59]. Communities with the highest phylogenetic diversity on Socompa were located in intermediary locations a few meters away from the fumarole and could still benefit from the moisture and nutrients from the steam vent without the extreme temperatures[59].

On Mount Erebus, soil pH acidifies further away from the fumarole as a result of S-oxidizing bacteria creating $H_2SO_4$ combined with the buffering effects of high temperature and carbon dioxide ($CO_2$) near the fumarole[58]. There may also be variations in the amount of organic C and other nutrients as a function of distance from the fumarole, which could influence the community[105]. At Marum Crater, Vanuatu, cell counts decreased with depth into the sediment surrounding a fumarole, but metabolic activity increased, suggesting that subsurface niches provide a more stable environment[106]. Together, these studies demonstrate that varying physicochemical factors likely result in gradients of microbial function and diversity as a function of distance away from the fumarole and depth into the sediment, because the environmental contrast between the near-fumarole ecosystem and the ambient surroundings is very large.

Discoveries of archaea and bacteria contained within condensed steam vent waters have opened insight into the primary succession of fumaroles and the dynamic coupling between subsurface and surface-based ecosystems[107,108]. Steam from Surtsey fumaroles harbored a distinct microbial community compared to subsurface hydrothermal fluids and seawater near the island. Cyanobacteriota, Deinococcota, and Acidobacteriota phyla were discovered in high proportions with some overlap with subsurface basaltic tuff deposits, suggesting that subsurface organisms could be transported to the surface by fumaroles[84]. In this way, fumaroles may be an important functional element in microbial community development by facilitating microbial transport from the subsurface to the surface.

## Lava tubes and caves

Lava tubes are common features in volcanic terrains (Fig. 3). They commonly form when the outer surface of a channelized lava flow[109] or a pāhoehoe (Supplementary Table 1) lobe network[110] solidifies, thereby

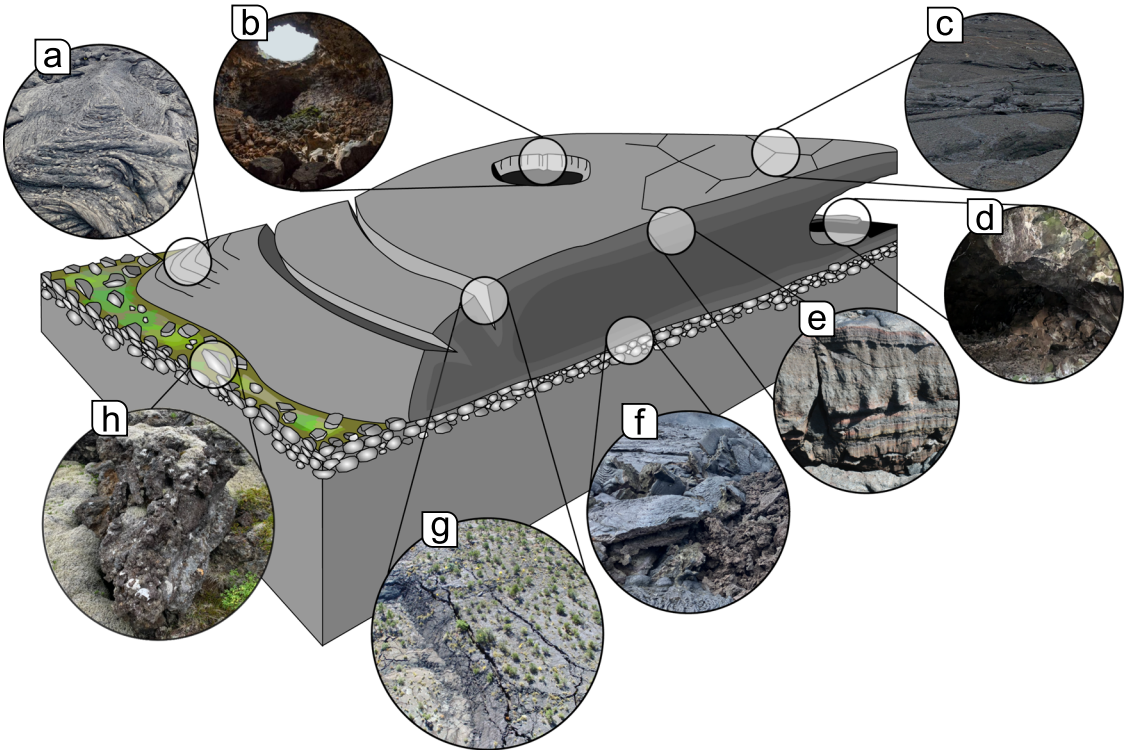



**Fig. 4 | Habitats due to texture variations within a lava flow.** Example of a pāhoehoe lava flow and associated habitats. **a** Pāhoehoe ropes (formed by a cooling surface that deforms above a flowing interior) can create variations in surface texture to create sheltered habitats for epiliths (organisms that can colonize rock surfaces). Image from the 2018 Kīlauea lava flow, Hawai'i (Photo credit: N. Hadland). **b** Skylights formed by collapses often create rubble piles within a lava tube or cave, which are colonized by photosynthesizers. Image from Four Windows Cave in El Malpais National Monument, New Mexico (Photo credit: N. Hadland). **c** Vent proximal lava is commonly extremely vesicular due to high gas content and has a somewhat glassy surface that provide habitats for cryptoendoliths (organisms that occupy vesicles and primary pores). Image from the 2018 Kīlauea lava flow (Photo credit: N. Hadland). **d** Twilight zone in Four Windows Cave at the edge of where photosynthetic groups can occupy (green film at the top of the image). Variations in textures on lava tube walls are caused by lava drips, extrusions, or fluctuating levels of lava during tube formation (Photo credit: N. Hadland). **e** Crystalline core of a pāhoehoe flow with few vesicles (Photo credit: Quinn Dombrowski; https://commons.wikimedia.org/wiki/File:Pahoehoe_Lava_Flow_at_Kilauea_in_Hawaii_20071209_B.jpg). **f** Transition between pāhoehoe and 'a'ā, which have dramatically different surface textures and vesicularity. Image from 2021 Fagradasfjall eruption, Iceland (Photo credit: N. Hadland). **g** Inflation processes can create large cracks and void spaces for chasmoendolith colonization (organisms that populate fractures and cracks). Perspective rendering from McCartys lava flow field in El Malpais National Monument (Photo credit: C. W. Hamilton)[113]. **h** Older lava is more weathered due to alteration processes as well as euendolith (actively penetrating/burrowing into a rocky surface) and autoendolith (metabolically induced mineral precipitation in pore spaces)[239] activity. Image from Reykjanes Peninsula, Iceland (Photo credit: N. Hadland).

thermally insulating the core of the flow and enabling preferred pathways to develop within the interior of a lava unit. When the eruption stops or the lava is diverted, part of the lava within the preferred pathway can drain, leaving a partially evacuated tube[111]. Inflationary processes can also result in lava-rise pits and caves[112,113]. Lava tubes and caves have less variation in environmental parameters than the surface. After the tube drains, gravitational and/or erosional effects can create skylights[111] that allow light to enter the otherwise thermally stable subsurface environment (Fig. 3b, d).

Lava tube environments have distinct selection pressures compared to the overlying lava flow. Subsurface communities often include diverse microbial biofilms and mats[114–116]. For example, little overlap was found between surface soil/lava and cave microbial communities in Lava Beds National Monument in California. There was a much higher abundance of Actinomycetota in cave samples than in the overlying soil, some members of which were capable of nitrate-dependent Fe-oxidation[117]. Other work has shown that species within lava tube habitats may have special adaptations compared to overlying soil—such as resistance to metals[118]—or even lose certain functional genes, such as UV radiation repair mechanisms[119].

The higher biomass environments in lava tubes generally occur in the twilight zone, or the areas around where light is reduced and photosynthetic organisms progressively drop out, but organisms can still benefit from the thermal stability (Fig. 3d)[115,120]. Deeper than this point in caves, entire communities can be supported by chemoautotrophic metabolisms (Fig. 3c)[116,121]. *Pseudomonas* sp. HerB isolated from lava tubes in the Oregon Cascades grew using olivine as an energy source via oxidation of structural Fe(II) during incubation experiments[122]. Heterotrophic microorganisms also can be supported by organic matter detritus that enters the cave through water percolation[123]. However, despite organic matter inputs, biofilms within caves at Lava Beds National Monument were supported primarily by active C fixation. Chemoautotrophs could have been the initial colonizing group in the newly formed lava tube and established a unique niche by providing fixed C to heterotrophs[124]. As overlying vegetation became established and nutrient input via water percolation increased and supported additional heterotrophs[125], the original chemoautotroph colonizers may have maintained their independent niche[124]. Metagenomic analysis in lava caves in Craters of the Moon National Monument, Idaho, found similar C fixation pathways and anaerobic sulfate reduction, nitrate reduction, and methanogenesis[126].

Phylogenetic diversity is lower in new geothermal caves compared to older lava tubes[102]. Similar to fumaroles, this suggests increased metabolic interactions among taxa are required to survive. Extreme environmental conditions in young geothermal caves with less organic C filter for certain species. In these environments, synergistic metabolic interactions may be important in the development of a microbial community. Primary producers in young geothermal cave environments have been described as hub organisms in phylogenetic network analyses—species linked with many

## Box 1 | Igneous rock classifications and microbial ecological succession

Igneous rocks can be split into several categories based on alkali and silica content (Box Table 1). Ultramafic and mafic lavas are lower in silica and contain Mg- and Fe-rich minerals such as pyroxene and olivine. Mafic (e.g., basalt) lavas are less viscous, have a higher liquidus temperature at the Earth's surface, and have less gas content. Felsic (e.g., rhyolite) lavas have higher concentrations of silica. These lavas are viscous, have a lower liquidus temperature, contain more volatiles, and contain a higher content of quartz and K-feldspar[6,240]. The effective eruptive temperature is highly variable, even within these compositional endmembers, but is generally below the liquidus (Box Table 1). Upon emplacement, the lava stiffens to the point where it is effectively brittle, a point called the rheological solidus which is higher than the chemically defined dry solidus temperature. The crust of the lava may be cooler than the bulk temperature, so it is at this point that the process of microbial ecological succession effectively begins.

Although most geomicrobiological studies focus on basaltic systems because they are the most widespread igneous compositions on terrestrial bodies, felsic lavas have also been shown to host complex microbial communities capable of accessing the nutrients within the rock[241]. Different compositional endmembers also generate different volcanic eruptions styles, which are broadly divided into effusive (i.e., lava forming) and explosive eruptions that produce varying outcomes for microbial colonization. For example, explosive eruptions generate tephra, which includes ash (<2 mm), lapilli (2–64 mm), and bombs/blocks (>64 mm)[6]. These pyroclasts can provide new substrates for microbial colonization, with finer-grained deposits being recolonized more quickly because of the thinner layer[219,242,243]. Higher volatile content (e.g., felsic magma) creates a high overpressure, sometimes resulting in destructive pyroclastic density currents. Conversely, these explosions can be mild due to low volatile content (e.g., mafic magma) and can result in constructive processes such as building cinder cones. In even lower-viscosity, high-temperature basaltic eruptions, low-intensity fountaining can construct spatter cones via the welding of fragmented magma to the cone's surface[244,245]. Cinder cones are made from unconsolidated tephra and therefore have increased soil aeration and water retention compared to spatter cones, which are denser due to the welding process, therefore resulting in different types of microhabitats available for microbial colonization.

**Box Table 1 | Overview of igneous rock classifications** Classification of volcanic rocks based on silica content. The solidus and liquidus temperatures are reported values for the Earth's surface at 1 bar

| Classification | Common Solidified Extrusive Rock | Solidified Plutonic (Intrusive) Rock | Volcanic Features | Chemical Composition | Dry Solidus T (°C) | Dry Liquidus T (°C) |
|---|---|---|---|---|---|---|
| Ultramafic | Komatiite | Peridotite | Large, but thin lava flows and shield volcanoes (Archean age) | <45% $SiO_2$, high in Mg, Fe, Ca | 1150[246] | 1500–1650[247,248] |
| Mafic | Basalt | Gabbro | Flood basalt, shield volcanoes | 45%–55% $SiO_2$, high in Mg, Fe, Ca | 1070[110] | 1250[110,249] |
| Intermediate | Andesite | Diorite | Strato/composite volcanoes | 55%–65% $SiO_2$, intermediate in Mg, Fe, Ca | 970[250] | 1200[249] |
| Felsic | Rhyolite | Granite | Dome, ash flow, ash fall | >65% $SiO_2$, low in Mg, Fe, Ca | 700[251] | 1050[249] |

other species—potentially depicting a symbiotic relationship with heterotrophs or a generally ecologically important role[102,127,128].

Lava tubes are of interest to astrobiology because of their stable environmental conditions (e.g., temperature, humidity), lack of harmful UV, entrapment of water, and secondary mineral precipitation, leading to diverse microbial communities and biosignature preservation[114,129]. Several lava tubes have been identified in lunar maria and on Mars[111,130,131]. Tubes on Earth are generally restricted to lava flows that are younger than a few million years[132] due to collapse via weathering processes or sediment/lava infilling. Tubes on Mars might be stable for much longer periods due to the lower weathering rates and lack of planet-wide tectonics activity. This stability may lead to a higher biosignature preservation potential for past life and possibly environmental conditions suitable for extant life[126,133].

## Lava texture and porosity

Lava can provide different types of habitats for endoliths (organisms that occupy the inner part of a rock) through variations in texture and porosity (Fig. 4). The correlation between porosity and microbial diversity is well known in soil at ~cm scales and drives the heterogeneous distribution of microbial biomass[134]. Surface area measurements and porosity are used in calculations of bulk microbial biomass in oceanic crustal basalts[135] because these parameters correlate with the space available for microbial colonization, the rate of fluid flow, macronutrient deposition, and chemical leaching[136]. Vesicular basalts in oceanic environments host euendoliths (Fig. 4h) that can bore into the rock and leave morphological biosignatures, including filamentous fossils and microtubules[137–141]. Similarly, in terrestrial volcanic rocks, the initial texture and porosity potentially play important roles in habitat development since pore spaces and variability in the surface texture can provide protected locations from exterior stressors. Nonetheless, these trends remain understudied for terrestrial systems. From an astrobiology perspective, this is a critical task since these trends could influence sample site selection on Mars by identifying which lava type has the highest potential for containing remnant microbial biosignatures.

Fissure-fed lava systems exhibit a diverse range of lava types leading to variability in texture that result from magma composition, temperature and eruption conditions, and mode of emplacement. Pāhoehoe generally form from high-temperature lava with lower viscosity, which is commonly emplaced at lower local effusion rates and lower strain rates than ʻaʻā (Supplementary Table 1). If temperature decreases, underlying topographic slope increases, or effusions rates increase, then pāhoehoe can transition to ʻaʻā due to increasing crystallinity and viscosity as well as increased shear strain rates[6,142]. Subsequent episodic disruption events and passive cooling at different stages results in these various transitional lava types (Fig. 4f)[143]. The resultant surficial texture may play an important role in the initial colonization of organisms. For example, rough ʻaʻā flows will dampen surface windspeeds, thereby leading to increase boundary-level humidity, while individual spinose clinker clasts will have small surfaces cavities that favor the accumulation of aeolian sediments, which contain nutrients and help to hold water. Narrow, sharp, and protruding points of a rock face capture biomass at much higher rates than smoother surfaces, which are comparatively barren[144]. Moreover, the temperature and water retention rate are strongly dependent on the aspect of the surface exposure (e.g., north/south facing), with daily temperature fluctuations on rock surfaces often twice that of air temperature[145]. These temperature fluctuations could provide niches for mesophiles (Supplementary Table 1) or thermophiles in cold environments[146]. On Deception Island, Antarctica, coarser particle fractions and higher slopes in the topography correlate with richer communities on the volcanoes, likely due to increased water percolation[90].

Vesicles in igneous rocks form as a result of the exsolution of supersaturated volatiles during magma ascent and cooling[147]. Vertical variations in vesicularity within a lava unit may affect the microbial biomass distributions. These spaces contribute to increased microhabitats and

consequently higher levels of biomass relative to other lava types[52,148,149]. For example, the solid crystalline core shown Fig. 4e has few spaces for microbial colonization compared to the vesicular glassy surfaces (Fig. 4c). Vesicular rock can also shape microbial diversity by increasing the relative surface area available for colonization, improve macronutrient retention, and potentially provide electron donors and acceptors from the crystalline rock itself[106,136,150]. Basalt has a high compressive strength, which allow vesicles to remain open in buried lava flows at greater depths and could encourage the preservation of past biosignatures[151]. Exhumed vesicular igneous rocks should be considered as potential targets in the search for past life on Mars.

The amount of water retained in volcanic rocks affects the growth of microorganisms living inside them. Basaltic rocks lose near-surface water rapidly (~tens of hours after a wetting event), but retain water in deeper pores (~10 cm depth) for extended periods[152]. The frequency of precipitation and humidity in the environment also plays a role in the diffusion of water to deeper pores. Since water retention in basaltic environments is low due to low organic C[153] and water distribution can be heterogeneous, endolithic organisms may be adapted to survive dry and wet cycles similar to hypolithic Cyanobacteriota in the hyperarid core of the Atacama Desert, which can be rapidly reactivated following salt-driven deliquescence[154] or rare precipitation events[155].

Diffusion of $O_2$ to deeper pore spaces is much slower when the rock is saturated with water, creating transitory anoxic environments[152]. The heterogeneous distribution of nutrients deposited by the diffusion of water through the pores may also create pockets of higher biomass[24]. These regions of higher heterotrophic activity may exacerbate the development of localized anoxic environments in the pores through aerobic metabolic pathways[152]. These factors may restrict the initial endolith colonization of the interior of lava to facultatively or obligately anaerobic taxa, which have been frequently found within young basaltic rocks[14,24].

Surprisingly, photosynthetic groups including Cyanobacteriota have been observed in deep pore spaces within volcanic rocks, including generally opaque obsidian[156]. The largest reasonable depth for photosynthetically active radiation to penetrate in solid volcanic glass is ~50 μm, but cracks and vesicular networks may increase this depth (Fig. 4c, g)[148,156]. This depth provides advantages since harmful UV radiation cannot penetrate the basalt[157]. Unconsolidated basaltic regolith (Supplementary Table 1) increases the depth for photosynthetically active radiation further, while still providing protection from UV, which some studies have hypothesized could allow for near-surface photosynthetic life on Mars[158].

## Mineralogy, major element composition, and alteration products

### Initial composition and emplacement environment

The composition of magma feeding a volcano is one of the major controlling parameters in the evolution of an eruption, largely influencing its eruption style, eruption products, and the mineralogy of the resultant igneous rocks. From a geomicrobiology perspective, mineralogy may control nutrient sequestration, inorganic nutrient availability for chemoautotrophs, and the ability for euendoliths to burrow into the rock[8]. Some microbes can off-load electrons onto Fe or Mn within the mineral matrix[159,160] while others can access electrons from reduced structural Fe(II) in basalt[161]. Composition also influences the texture and porosity of the lava and the mineralogy, which can strongly affect microbial colonization[57,162]. Differences in community structure have been observed between different lava compositional end-members (Box 1). For example, a rhyolitic lava flow in Iceland was shown to have a higher Shannon diversity index compared to a basaltic flow, though the difference could be due to porosity and water retention[163]. Additionally, cinder cone sites have a higher phylogenetic diversity than spatter cones, likely due to these compositional and morphological differences (Box 1)[164].

Another major factor that has been shown to influence primary succession is the relative glassiness/crystallinity of the material due to the weatherability and homogeneity of basaltic glass compared to crystalline rocks[9]. Basaltic glass forms when lava is rapidly quenched upon contact with ice or water. The amorphous homogeneity of glasses results in greater nutrient availability while in crystalline materials bioessential nutrients may be less evenly distributed and concentrated in specific minerals (e.g., plagioclase or olivine) and therefore less accessible[8,9,23,149,156]. Microbial colonization of glasses also results in alteration textures such as tubular and granular microborings and secondary biogenic minerals useful for biosignatures in astrobiology[8]. However, substantial tunneling does not occur for at least 1000 years[139].

In oceanic environments, colonization of freshly formed basaltic glass occurs rapidly ( ~ days) by species involved in C, N, S, and Fe cycles[165]. Some microorganisms, such as metal-oxidizing bacteria (e.g., *Pseudomonas stutzeri* or *Mariprofundus ferrooxydans*) are able to scavenge elements from glass within the oceanic crust[161,166,167]. There is a strong influence of nutrient availability on biofilm formation on oceanic basaltic glass[161]. Nutrient-deprived environments resulted in greater attachment because basalt may be the only source of phosphorus (P), Fe, or other biologically essential nutrients. However, these trends are likely to be different in terrestrial systems than in oceanic environments because the glass is exposed to variable precipitation/desiccation and nutrient deposition.

Floating rhyolitic pumice in a freshwater lake from a 2011 eruption in Chile was a major source of P for the initial microbial community before becoming a nutrient sink as the community grew[168]. Conversely, incubation experiments have found that although structural phosphorus pentoxide ($P_2O_5$) within the basalt—a bioavailable form of P[169]—can be leached into solution, it is not sufficient to sustain microbial growth[13,161]. Additional work is still needed to understand the effect of various $P_2O_5$ concentrations in basalt on microbial growth, particularly in terrestrial systems. Lava at Craters of the Moon, Idaho, has elevated concentrations of $P_2O_5$ and is comparable to Mars (up to 10× higher than Earth)[170]. $P_2O_5$ is also more abundant in basalt (up to 1 wt%) compared to rhyolite (as little as 0.02 wt%)[171]. Basalts are N-poor, generally less than 0.01%[172]. The addition of N to seafloor basalts in incubation experiments stimulated the growth of Fe-oxidizing taxa, which suggests that these groups are generally N-limited[173,174]. Additionally, multiple studies have shown that basalt can enhance the growth of organisms in Fe-limited media by providing structural Fe(II) for Fe-oxidation pathways[13,161,167]. These trends might be more important in lava tubes where chemoautotrophy is a major form of primary productivity and specific minerals drive microbial distribution and niche partitioning. For example, certain chemoautotrophic strains preferentially colonized basalt under simulated subsurface oligotrophic conditions[175]. Although basalt can be beneficial to microbial growth, the presence of transition metals bound in the glass matrix could be inhibitory to certain taxa. Some isolates in Icelandic basaltic glass have been found to have some degree of heavy metal resistance[23].

### Alteration products and weathering

Hydrothermal activity impacts the mineralogy and bulk chemistry of a substrate and therefore results in a range of microbial activity. In many cases, alteration mineral assemblages are controlled by acid supply, temperature, and meteoric water input, with local rock lithology playing a minor role[56,176]. Local geochemistry dictates the pH and bioavailability of electron acceptors and donors, such as various forms of S and Fe. When $SO_2$ in shallow magma is emitted, it can interact with groundwater to create high-temperature $H_2S$-enriched fluids. Pyrite, native S deposits, and other secondary phases subsequently form, resulting in a higher fraction of organisms with S-redox metabolisms[56,177]. Fumarolic and syn-emplacement alteration (interaction with volatiles during emplacement) create unique suites of minerals such as sulfate-bearing phases like natroalunite and thenardite[178]. In Hawai'i, the differences in phylogenetic diversity between unaltered and altered sites within lava flows (excluding trends with active fumaroles) were variable and lacked a consistent trend. Conversely, at Craters of the Moon in Idaho, the arid climate may require specialized adaptations and resulted in a concentration of microbial biomass in specific niches, specifically altered rock[25,52].

Post-emplacement alteration (e.g., non-geothermal) also has been hypothesized to increase the relative habitability of terrestrial basalts. For example, basaltic glasses can weather via dissolution processes to palagonite under high water/rock ratios, which forms rinds on the interior surfaces of

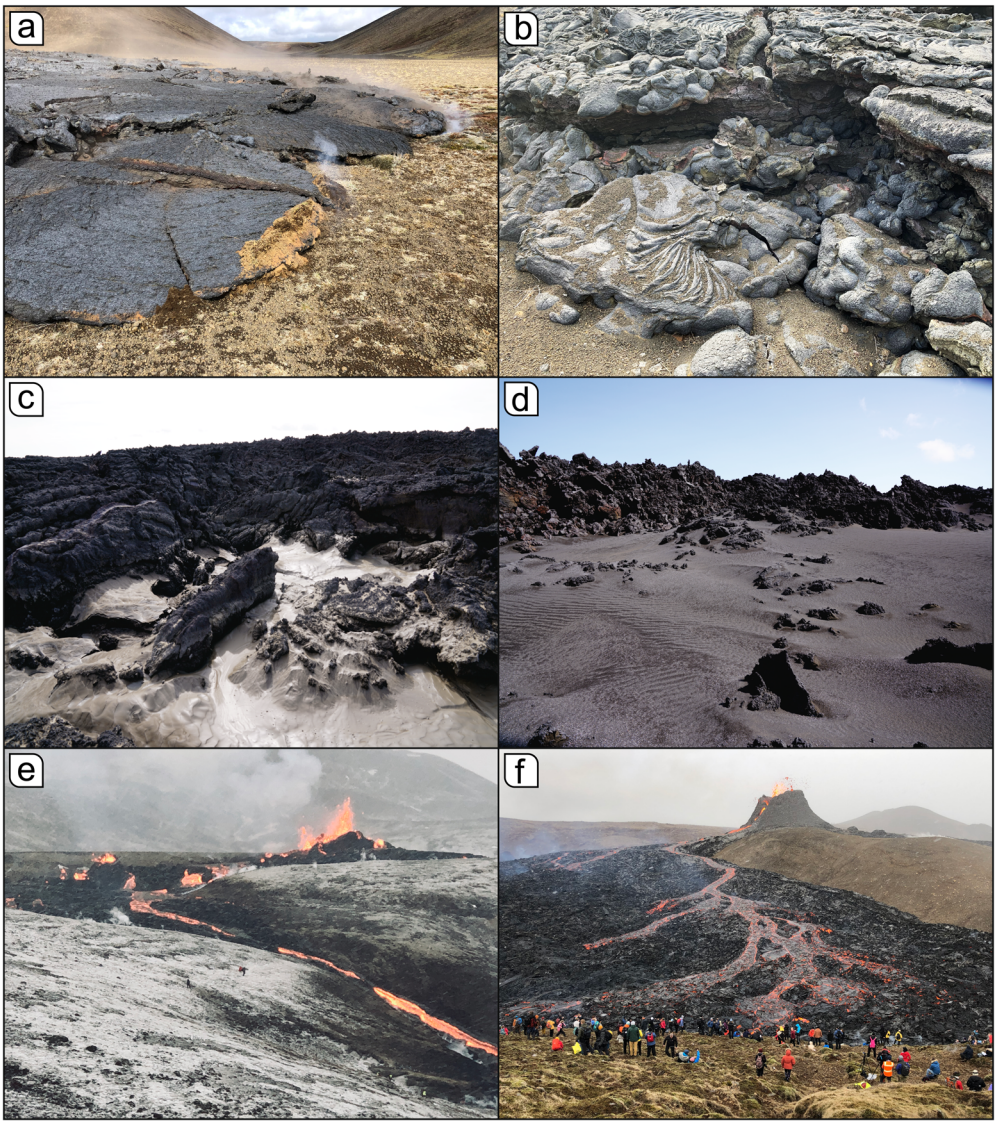



**Fig. 5 | Mechanisms for microbial deposition in volcanic terrains. a** Syn-emplacement mechanism for soil deposition on the surface of lava. In the foreground, lava scraped or bulldozed underlying soil followed by an inflationary process that lofted particles onto the surface of the flow. Saturated soils also flashed to steam as lava flowed over the substrate, carrying soil particles as the steam escaped through cracks. Dusty steam plumes are visible at the back of the image. Image from the 2021 Fagradasfjall eruption, Iceland (Photo credit: C. W. Hamilton). **b** Finer-grained soil particles have been blown onto the surface of lava at Fagradasfjall post lava emplacement (Photo credit: N. Hadland). **c** Wet sediment deposited onto the surface and interior of the lava from fluvial systems. Image of the 2014–2015 Holuhraun lava flow field, Iceland (Photo credit: C. W. Hamilton). **d** At Holuhraun, coarser-grained sand has been blown up against the side of the lava flow, progressively building up sand ramps to deposit material on the surface of the flow and even cover portions (Photo credit: N. Hadland). **e** Snow and rain fell on Fagradasfjall lava during emplacement, potentially carrying microorganisms (Photo credit: C. W. Hamilton). **f** Human and animal visitors to lava flows, such as shown here at Fagradasfjall, can also bring microbial colonizers (Photo credit: C. W. Hamilton).

vesicles. These rinds have been shown to host higher concentrations of cells[156] and potentially increase nutrient accessibility[23]. Basaltic glass in oceanic environments have an enrichment of amorphous Fe and titanium (Ti) on the rim of the palagonite, potentially encouraging the use of the palagonite sheet on fracture walls as an anchoring site for Fe-oxidizing organisms[139,179]. Additionally, P is often the limiting nutrient in basaltic glass environments and $P_2O_5$ and organic C have been suggested to be enriched in palagonite sheets[139,179]. Consequently, the need for P and organics may accelerate microbial alteration processes and increase the rate of microbial colonization of palagonite sheets in the pore spaces.

Basaltic rocks are major reservoirs of C as $CO_2$ reacts with calcium (Ca) and magnesium (Mg) to form carbonates, often through biogenic processes in hot spring environments[180]. It has been estimated that microbially induced weathering (e.g., alteration textures, local dissolution, carbonate formation, etc.) is the dominant process of glass alteration in the upper 250 m of the oceanic crust[139,181–183]. Under high water/rock ratios, vesicles and fractures can be filled with authigenic mineral precipitates over time, potentially resulting in the entombment of the microbial biofilm and the preservation of biosignatures[139]. However, some of these weathering processes occur on longer timescales ( ~ centuries or longer) and therefore is unlikely to have an impact on the primary succession of volcanic materials in its early stages[184,185], particularly in terrestrial systems.

Water plays an important role in cooling terrestrial lava flows and in the formation of unique secondary substrates that could serve as additional habitats for microorganisms. For example, explosions can occur when lava advances over a water-bearing substrate. Tephra from these interactions forms radially symmetric deposits that build into cratered cones (i.e., volcanic rootless cones) through successive explosion cycles (Fig. 2f)[186,187]. These features are important for identifying sites of past lava-induced hydrothermal activity[40,41] and potentially fossil habitable environments on

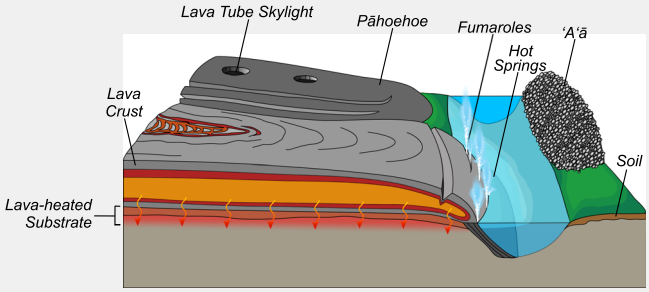
## Box 2 | Feedbacks in microbial ecological succession in volcanic terrains

Volcanic environments generate numerous habitats for microbial colonization. However, volcanic activity alone does not provide a suitable habitat for microbial life—liquid water, a specific range of environmental conditions, energy, and essential elements in bioavailable forms are also required[56]. The degree to which the concatenation of these environmental conditions drives habitability at multiple temporal scales throughout the process of ecological succession remains unclear. Individual habitats illustrated in Box Fig. 1 have specific pressures that can impact microbial community assembly. For example, in lava, the combination of glassiness, vesicularity, texture, depth into the rock, secondary mineralogy, nutrient fluxes, and local gas emissions all influence the microbial community. In hydrothermal systems, pH, temperature gradients, and geochemistry result in dramatically different types of biofilms and community functions. Biotic controls can also impact succession because cooperative and competitive interactions can dictate the success of a species in a particular niche. Throughout different stages of community assembly, biotic and abiotic forces exert varying degrees of influence and can impact each other (Box Fig. 2). For example, biomineralization products change the physicochemical conditions in the microhabitat, entomb cells, and change the surface area available for colonization[239], thus feeding into the abiotic controls.

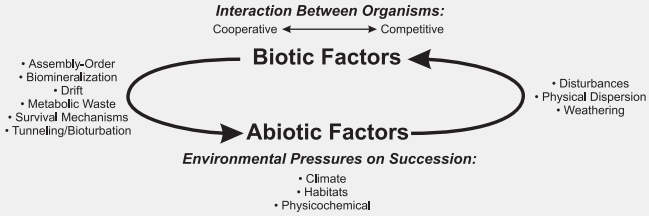
On the other side of the feedback loop, disturbances (e.g., the heated substrate in Box Fig. 1) can change microbial community function[252], resulting in different metabolic products in the local environment. The order of microbial community assembly may also play a role in both microbial succession and even ecosystem-level processes because certain taxa may have an inhibitory or facilitative effect on later-arriving organisms[220]. Some studies have modeled these feedbacks and found that even in extreme soils, environmental filtering is secondary to stochastic assembly (e.g., dispersal) in influencing microbial succession[253]. Other models suggest the opposite for different types of systems, such as geothermal caves[102]. Still, a synthesis of previous results studying community assembly in volcanic systems suggests that variation in community assembly over time can be divided into three stages:

(1) Early dispersal of different populations well-suited to the abiotic factors[14,211,253]
(2) Intermediate stage driven by competitive exclusion, habitat filtering, and complex metabolic networks[102]
(3) Late stage with a mature community, potentially subdued abiotic selection pressures, and comparable environmental conditions to surrounding environments (e.g., local soil ecosystems)[225,254]

Substantial work remains to evaluate these models for volcanic environments, specifically at different successional stages, and may largely be dependent on the type of system, the spatial scales involved, and the source of colonization.




**Box Fig. 1 |** Habitats and environmental pressures in a general volcanic system. Abiotic controls on succession include various habitats in volcanic terrains and the associated environmental controls.




**Box Fig. 2 |** Feedbacks between biotic and abiotic factors. Schematic of the overall processes impacting succession. Products from abiotic (Box Fig. 1) and biotic processes (e.g., interspecies interactions and community composition and function) can feed into each other to change the dynamics of the microbial community.

Earth and Mars[53,188]. Explosive lava–water interactions resulting in volcanic rootless cones are important targets for astrobiology because the transport of altered substrate material onto the surface could have carried remnant microbial biomass from subsurface hydrothermal environments[187]. Future Mars missions could investigate these deposits in search of biosignatures and microfossils.

## Mechanisms of microbial deposition

The mechanisms of microbial deposition to young lava flows or hydrothermal systems are poorly understood. Rigorous statistical approaches such as Bayesian source tracking, which uses a probabilistic model to infer the origin of microbial communities to an environment[189], have yet to be used to estimate the proportion of microorganisms in volcanic terrains coming from different sources. These could include soils, hydrothermal systems, bioaerosols, precipitation (e.g., rain and snow), or fluvial systems (Fig. 5). Still, broad ecological trends can provide insights into mechanisms of microbial deposition and colonization in volcanic terrains. For example, microorganisms can be transported globally as bioaerosols (Supplementary Table 1)[190,191], or locally from nearby soil particles (Fig. 5a, b, d)[192,193]. Survival in the atmosphere requires tolerance to various selection pressures, which

are also generally faced by microorganisms in volcanic terrains. Adaptations such as cell pigmentation, aggregation, endospore formation, and modifications to the cell membrane have been shown to be important protection mechanisms against desiccation and solar radiation in the atmosphere[194,195] and should enhance the ability of a particular species to survive in young volcanic systems.

After surviving airborne transport, microorganisms must also survive the depositional process. Bioaerosol particles can be removed from the air by wet (e.g., precipitation) or dry (e.g., collisions, gravitational settling) deposition[196]. For wet deposition, clouds may buffer the extreme conditions in the atmosphere, provide an oasis for life[197], and support metabolically active microorganisms[198]. Microorganisms also serve as cloud condensation nuclei[199]. Precipitation may be an important driver of microbial colonization in volcanic terrains as microorganisms are deposited from the falling raindrops or snow (Fig. 5e)[200]. For dry deposition, major aeolian dust events in the Sahara[201], Gobi[202], and potentially polar deserts[203] may allow certain organisms to spread via attachment to dust particles which mitigate stressors by reducing desiccation and shielding the organism from radiation. While it is unknown what the balance between local sources of soil and globally transported dust is during primary succession, dust-mediated transport increases bacterial viability compared to free-floating cells[204,205]. Therefore, both local and atmospheric dust are likely important inputs to volcanic systems.

Environmental filters, particularly in extreme climates, may impose additional selection pressures on colonizing organisms. Although certain taxa, such as endospore formers, are particularly adapted to global distribution in the troposphere[206], it has been hypothesized that hyperthermophilic microorganisms may exhibit a higher degree of dispersal limitations due to the lack of cellular mechanisms for survival over the large distances between geothermal sites[207]. Nonetheless, spore-forming thermophilic groups such as the genus *Geobacillus* have been cultivated from Saharan dust deposited in Europe[208] and from newly formed hydrothermal systems in Iceland[53]. Phylogenetic relationships were used to infer that the thermophiles colonizing fumaroles in Hawai'i likely came from other geothermal sites[101]. Thermophilic groups on Tramway Ridge, Antarctica, fumaroles were indistinguishable from groups found in geothermal sites in Yellowstone, likely because of long-range dispersa[209]. The subsurface communities, however, were largely endemic, suggesting these communities could outcompete exogenous sources of microorganisms before permanent establishment. The colonization of newly formed fumaroles and hydrothermal sites may in some cases be restricted to regional populations that are highly adapted to that particular combination of environmental filters[210], and endemic microorganisms will only be found locally near the emission point[196].

In addition to bioaerosols and dust, another mechanism for microbial deposition may be surface and subsurface water (Fig. 5c). For example, there were different fluvial inputs into the ephemeral hydrothermal system created by the 2014–2015 Holuhraun eruption in Iceland. Cold spring water, glacial meltwater, and water emerging from beneath the lava flow all could have contributed microorganisms to the hydrothermal system, though a wide range of temperature adaptations would be required. Several taxonomic groups showed the highest sequence similarity to basaltic aquifer ecosystems, suggesting that hydrological connections could potentially transport microorganisms from the subsurface to the hot springs[53]. For Surtseyan eruptions, seawater infiltration into subsurface habitats may be an important vector for colonization, with fumarolic activity helping to transport microorganisms to colonize the surface. Similarly, microorganisms colonizing the newly formed HTHH islands in the South Pacific were likely transported from the seafloor from nearby submarine hydrothermal systems during the eruption event or from nearby fumaroles on other volcanic islands as bioaerosols[211].

In some systems, animal life may introduce certain taxa to the volcanic environment. Cell counts within different soil types on the island of Surtsey, Iceland, dramatically increased in those contaminated with bird feces and contained unique taxa, such as *Enterobacteriacae*[86]. On HTHH, however, bacterial taxa associated with the bird microbiome was rare, though they did not sample near bird nesting sites[211]. In addition to animal life, human visitation likely plays a role (Fig. 5f). Studies on Deception Island, Antarctica, after the formation of new cinder cones in 1967 noted that human and animal contamination was immense in the area, with boat wreckages and animal feces contributing to the microbial colonization of the new island[89,100].

Finally, though it is difficult to imagine how organisms would survive such a blast, the dispersal of organisms via explosive volcanic eruptions has been observed in eukaryotes[212] and hypothesized for prokaryotes[209,213]. The exact mechanism is unknown, but an explosion with enough force to eject lithic material (Supplementary Table 1) prior to superheating could potentially launch microorganisms into the atmosphere, enabling long-distance dispersal. Organisms could presumably remain viable by staying encased in the lithic material isolated from magmatic heat during the explosion[212].

## Age dependence

### Trends in biomass and diversity

Overall trends in microbial biomass, phylogenetic diversity, and the complexity of metabolic interactions within a community may have some correlation to the age of the system. While it is impossible to select samples of different ages that have identical environmental parameters without conducting multi-year fixed-site samplings[214], several studies have attempted to isolate the effect of age on ecological succession in lava flows[15,28,102,215–219]. In deglaciated soils[3,220] and in seafloor lavas[221], phylogenetic diversity generally increases with age. However, similar trends in lava flows have conflicting results[15,102,216] and there may be variability in deterministic and stochastic processes at different successional stages, so age may change how the relative roles of different assembly processes impact the microbial community (Box 2)[30,222]. The rate and complexity of assembly is also likely highly affected by the geographical location and the general type of system. For example, a microbial mat within a mature hot spring system can form in a matter of days[70,71], while an established community within a lava flow in a colder climate could take months to years[14,15].

The earliest reported sampling of a freshly emplaced lava flow was conducted by Kelly et al.[14] three months after the Eyjafjallajökull volcano in Iceland erupted in 2010. Their samples surprisingly already had ~$10^6$ cells/g, whereas ~decades-old lava flows in Iceland have ~$10^7$–$10^8$ cells/g[15]. Centuries-old lava flows in Idaho and Hawai'i have comparable numbers[25,52,215], potentially suggesting an upper limit on cell abundance in basaltic rocks. However, widefield fluorescence microscopy and flow cytometry remain underused techniques for cell counts because of the low biomass and high background fluorescence[25], which can be solved with catalyzed reporter deposition fluorescence in situ hybridization and confocal microscopy. Additional work is required to understand the general trends in cell abundance as a function of age.

Trends in phylogenetic diversity are generally more complex. Lava flows of different ages ( ~ tens to hundreds of years old) on Fogo Island, Canada[28] and on Kīlauea, Hawai'i[216], were shown to have no correlation between phylogenetic diversity and age, suggesting a greater impact of environmental parameters. Studies along non-vegetated lava flows in Iceland also found that relatively small age differences ( ~ years to decades) do not impact microbial community structure[15]. Organic C likely correlates with increasing deposit age[215] so some studies have suggested that the organic depositional rate is more important than age[15,28,219]. Conversely, in lava tubes in Hawai'i, ~centuries-old sites were generally more phylogenetically diverse than ~decades-old sites[102]. Over longer timescales (thousands of years or more), phylogenetic diversity and biomass estimates of volcanic deposits increase over time, are similar to environmentally comparable soil environments, and are likely controlled by vascular plant distribution in the area[223–225]. The effect of age may therefore reflect geographical location as well as the rate of plant colonization and rock

weathering as the environment becomes increasingly spatially homogenous and nutrient rich (Box 2).

### Trends in metabolisms

Phototrophs are abundant in young deglaciated soils[4,226]. However, the prevailing theory that phototrophs dominate the earliest successional stages in volcanic environments has been challenged with the advent of culture-independent methods[14,211]. Kelly et al.[14] reported few taxa associated with phototrophs and instead found a high proportion of heterotrophs in the phyla Actinomycetota and Pseudomonadota in three-month-old samples in Iceland. They also found potentially N-fixing groups such as *Herbaspirillum*—which has been reported in volcanic deposits elsewhere[227]—and the S-oxidizing genus *Thiobacillus*. However, caution should be taken when making functional inferences using 16S rRNA gene sequencing and next-generation omics techniques are generally required to evaluate metabolic potential[228].

Shotgun metagenomic sequencing was used on samples from HTHH and genes associated with S-redox metabolisms, CO oxidation, and $H_2$ oxidation were found. Notably, there was an absence of photosynthetic Cyanobacteriota, but genes associated with anoxygenic photosynthesis in members of the families *Beijerinckiaceae* and *Acetobacteraceae* were present, presumably using S as an electron donor[211]. Trace gasses such as CO and $H_2$ have long been suggested to support chemoautotrophic bacteria in volcanic systems, many of which are capable of N fixation[121]. Trace gas measurements on Kīlauea, Hawai'i, found that CO and $H_2$ consumption by microorganisms supported a large proportion of metabolic activity in unvegetated sites[22,215,229]. In vegetated sites, leaf litter and contributions from the rhizosphere likely were the primary sources of organic matter. Similarly, culture-based studies on Surtsey found a community predominantly composed of aerobic heterotrophs in fumaroles and subsurface samples[85].

Together, these studies indicate that organic C inputs must initially come from meteoritic water, necromass, or from the chemoautotroph groups. Subsequently, biomass likely expands with endogenous organic matter production, photoautotroph colonization, and from additional external inputs. Trace gas oxidizers and chemoautotrophic groups may therefore play a similar functional role in early stages, as photoautotrophs do in deglaciated soils[3,220], by providing a source of fixed C. These trends are also likely different in lava tubes, where percolating organic matter often remains unused in older tubes due to the high proportion of chemoautotrophs[124].

Lava flows may also be severely N-limited, which could select for the colonization of N-fixers and ammonia oxidizers[230]. For example, nitrification potential was the highest in the youngest lava flows in the south of Chile[231]. Similarly, on Mauna Loa, Hawai'i, N-fixation rates were generally constant as a function of lava age, whereas the keystone N-fixer changed from lichen in decades-old lavas to rhizosphere-associated bacteria in centuries-old lavas[232].

A fixed-site study spanning six years after an eruption on Miyake-jima[217], Japan, reported a large population of acidophilic, Fe(II)-oxidizing species, (e.g., *Leptospirillum*, *Acidithiobacillus ferrivorans*, and *Acidithiobacillus ferrooxidans*, which are all capable of N fixation, with the latter also capable of $H_2$ oxidation). In these basaltic pyroclastic materials, the relative proportion of the class Betaproteobacteria (Pseudomonadota) increased as a function of age while the proportion of Fe-oxidizing taxa decreased. Similarly, as systems in Hawai'i increased in age and geothermal systems cooled to ambient, Pseudomonadota and Actinomycetota likely became more prevalent[102]. Studies of older lava flows in Hawai'i and in Craters of the Moon, Idaho, did not detect any known Fe-oxidizing taxa and instead were also dominated by Pseudomonadota, Acidobacteriota, and Actinomycetota[25], though analysis using metagenomic techniques found genes associated with Fe uptake and Mn oxidation in Craters of the Moon lava caves[126].

$SO_2$ exposure from volcanic emissions had a major impact on microbial community assembly on Miyake-jima. No sequences associated with Cyanobacteriota were found in samples younger than 10 years, likely due to acidic pH and $SO_2$ exposure. Despite being younger, sites less exposed to $SO_2$ were more similar to mature forest soils and had a smaller proportion of Fe-oxidizing taxa and N-fixation pathways than heavily exposed sites[12]. These results again suggest short-term variations in age may be less important than habitat filtering and competitive biological interactions (Box 2)[233]. Fe-oxidizing taxa are of particular interest to astrobiological studies of Mars due to abundant reduced Fe within the subsurface and their ability to produce biosignatures such as biomineralization products, distinctive Fe-isotope patterns, and morphological biosignatures in a rock[121,234]. Their presence in low-biomass volcanic terrains is promising in the search for life on Mars.

## Conclusions

Bacteria and archaea play crucial roles in the weathering of rocks and the development of soils that lead to the colonization of more complex life. Recent work has shown that the trajectories of assembly are largely influenced by habitat type, environmental filters, and competitive biological interactions (Supplementary Table 2). Still, the microbial ecological succession in young volcanic terrains remains a largely unexplored frontier due to the extreme conditions of these environments. Future research should aim to achieve a definitive mechanistic understanding of the abiotic and biotic factors contributing to primary succession (Box 2) and provide more information about the metabolic capabilities of these microbial communities. Next-generation sequencing is just beginning to be employed in volcanic terrains and analysis of the metatranscriptome has rarely been used. The study of succession in volcanic environments has applications beyond microbial ecology, including astrobiology[118,235]. Mars has a hydrological and volcanically active past[39,40]. By examining the microbial communities in analogous environments on Earth, we can gain insights into the possibility of life on Mars[53,92]. Given that the search for life on Mars has been identified as a high-priority science objective by the planetary science community, studying these systems remains timely and relevant[7].

## Data availability

Data sharing not applicable to this article as no datasets were generated or analyzed during the current study.

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## Author contributions

N.H. led the writing of the manuscript and generated figures; C.W.H. helped write, edit, and generated figures; and S.D. contributed to writing and editing the manuscript.

## Competing interests

The authors declare no competing interests.

## Additional information

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