Chapter 4
Endolithic Microorganisms and Their Habitats

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Abstract Endolithic microorganisms are widespread in desert biomes, where hostile environmental conditions limit the majority of life to rock habitats. In these habitats, microorganisms receive light for photosynthesis, moderated and warmer temperatures, protection from UV radiation, and prolonged exposure to liquid water. In general, these microbial communities are composed of phototrophic microorganisms as well as fungi and heterotrophic bacteria. Microbial composition is distinct from soil communities, suggesting these habitats select for microorganisms best suited to this environment. The habitat is not nutrient limited, which explains why these microbial communities colonize a wide range of lithic substrates with different mineralogies; however, greater environmental pressures select for those able to tolerate increasingly harsh conditions. Growth rates vary primarily as a function of moisture availability, resulting in long-lived communities in the driest deserts. While most microorganisms require liquid water for growth, some lichens with an algal phycobiont can photosynthesize with water vapor alone, a significant advantage in these water-limited biomes. Additional strategies against stress include synthesis of pigments, EPS, and osmoprotectants, which significantly offsets the growth of biomass. Microbial activity leads to physical and geochemical weathering, but can also result in stabilization of the lithic habitat. Identification of endolithic biosignatures and microbial fossils has resulted in their study from an astrobiological perspective in the search for life on other planets.

4.1 Introduction

The abundance and diversity of microorganisms in the biosphere reflect their capacity to harvest energy from diverse organic and inorganic substrates and ability to grow under a wide range of natural conditions. Often, however, the complexity of

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a microbial community depends upon the suitability of a given habitat for colonization and the availability of energy and carbon. In many cases, habitats exhibiting extremes in climatic or environmental conditions effectively limit the number of species that can exist within a given ecological niche. An example of this natural selection is found in *endolithic* ("endo-" = within; "-lithic" = rock) habitats (Goublic et al. 1981), where microbial colonization is restricted to those organisms able to acquire the necessary resources for growth within the physical confines beneath rock surfaces. The two most common forms of endolithic microbial communities are found as interstitial colonizers of cracks and fissures (chasmoendolithic) or in pore spaces between mineral grains (cryptoendolithic). Other lithobiontic habitats include the ventral surfaces of translucent or opaque rocks (hypolithic), within the underside of translucent rocks (hypoendolithic), or within porosity in rocks created through active boring by microorganisms into the substrate (euendolithic).

This endolithic habitat is most commonly colonized by microorganisms in hot and cold deserts throughout the world, where extremes in temperature, moisture, and radiation prevail at the Earth's surface. Colonization and development of diverse microbial assemblages results from preferential microenvironmental conditions within these endolithic habitats where extremes are moderated (Friedmann 1980; Warren-Rhodes et al. 2006). However, this life must also utilize specific strategies to ameliorate stresses such as desiccation and rapid temperature fluctuations. The metabolic activity of endolithic microorganisms can subsequently alter the local geochemical environment through microbe-mineral interactions, which can be constructive or destructive depending upon the nature of a particular mechanism or substrate. While destructive mechanisms such as leaching and mineral solubilization can lead to accelerated weathering of the endolithic habitat, constructive development of crusts can provide further protection from stresses. In addition, the formation and preservation of microbial fossils or biosignatures is of current interest in the context of studies in astrobiology and the search for evidence of life on other planets.

4.2 Global Distribution of Endolithic Microorganisms

Endolithic microorganisms have been reported from temperate regions where climatic extremes limit epilithic ("epi-" = upon) colonization (Bell et al. 1986; Casamatta et al. 2002; Ferris and Lowson 1997; Gerrath et al. 2000; Tang et al. 2012); however, endolithic and other lithobiontic microorganisms are more common in the vast arid desert climates of the world that make up the largest terrestrial biome on the planet (Pointing and Belnap 2012). These regions are identified by their low ratios of precipitation to potential evaporation (normally < 1), highlighting the fact that they are moisture limited. Lithobiontic microorganisms have been studied in hot deserts including the Mojave and Sonora (USA), Atacama (Chile), Gobi (China, Mongolia), Negev (Israel), Namib

(Namibia, Angola), the Al-Jafr Basin (Jordan), and Turpan Depression (China) and as well as polar deserts in the Arctic and Antarctic Dry Valleys (Bell 1993; Bungartz et al. 2004; Cockell and Stokes 2004; Cockell et al. 2003; Cowan et al. 2010; Dong et al. 2007; Friedmann 1980; Friedmann et al. 1987; Hughes and Lawley 2003; Lacap et al. 2011; McKay et al. 2003; Omelon et al. 2006a; Schlesinger et al. 2003; Smith et al. 2000; Stomeo et al. 2013; Warren-Rhodes et al. 2007a). They are also documented from high altitudes in mountainous regions of the world, including Europe and Asia (Hoppert et al. 2004; Sigler et al. 2003; Walker and Pace 2007b; Wong et al. 2010b). Given the scarcity of plant or animal life as well as low levels of soil nutrients, it is thought that these microbial communities are the dominant form of biomass in desert environments (Cary et al. 2010; Cockell and Stokes 2004; de la Torre et al. 2003; Pointing et al. 2009; Walker and Pace 2007a; Warren-Rhodes et al. 2006). Due to the abundance of desert pavements in arid climates that are colonized by hypolithic microorganisms, these have been intensively studied to determine what controls the limits to life on Earth as well as microbial diversity in these extreme habitats (Makhalanyane et al. 2013a, b). While outside the scope of this work, it will be interesting to observe how these studies are translated to future evaluations of the diversity of microorganisms within endolithic habitats and if these same findings hold true.

4.3 Microbial Diversity of Endolithic Habitats

In contrast to microorganisms inhabiting the deep subsurface where activity is driven by chemolithotrophic metabolisms such as sulfate reduction, iron reduction, or methanogenesis (Lovely and Chapelle 1995), endolithic communities at the Earth's surface consist of photoautotrophic primary producers such as algae, cyanobacteria, and lichens, as well as consumers and decomposers including fungi and heterotrophic bacteria (Cockell and Stokes 2004; Cowan et al. 2010; de la Torre et al. 2003; Friedmann et al. 1980, 1981; Friedmann 1982; Friedmann and Ocampo-Friedmann 1984a; Hirsch et al. 1988, 2004b; Omelon et al. 2007; Selbmann et al. 2005). Archaea have also been documented in endolithic habitats around the world (de los Ríos et al. 2010; Horath and Bachofen 2009; Khan et al. 2011; Walker and Pace 2007b; Wong et al. 2010b).

Being one of the first discoveries of widespread life in an extreme polar desert, microorganisms from cryptoendolithic habitats in the Dry Valleys of Antarctica have received much attention. Two primary assemblages are defined: (1) eukaryotic communities that include lichenized fungi and algae and (2) prokaryotic communities dominated by cyanobacteria, both containing heterotrophic bacteria and fungi (de los Ríos et al. 2014). The cyanobacterium *Chroococcidiopsis*, found in the Dry Valleys, has been widely reported from lithic habitats in desert biomes around the world (Schlesinger et al. 2003; Smith et al. 2000; Warren-Rhodes et al. 2006). The likely reason for their apparent cosmopolitan presence in these habitats is due to their ability to withstand long periods of desiccation (Potts 1999) and radiation (Billi et al. 2000) as well as their ability to produce unique survival cells under nitrogen-limited conditions (Fewer et al. 2002). In addition, they are capable of quickly reactivating photosynthesis after these long periods of desiccation when liquid water is available (Hawes et al. 1992).

Early work to characterize the microbial diversity of lithobiontic habitats focused on culturing techniques, whereby microorganisms including phototrophic cyanobacteria and algae as well as fungi and heterotrophic bacteria were identified by morphology. More recent culture-independent molecular techniques have led to a more complete understanding of the diversity of microorganisms in these habitats, which often include in addition to the *Cyanobacteria* a wide range of other microorganisms such as the *Acidobacteria*, *Bacteroidetes*, *Chloroflexi*, *Proteobacteria*, *Actinobacteria*, *Verrucomicrobia*, *Firmicutes*, and others. Numerous studies have shown that typically they are distinct from soil communities, despite the most notable fact that hypolithic microbial assemblages are in direct in contact with soils (Pointing et al. 2007, 2009; Schlesinger et al. 2003; Warren-Rhodes et al. 2006; Wong et al. 2010a). The argument has been made that these habitats worldwide select for microorganisms best suited for this environment (Sigler et al. 2003); however, a growing understanding of what "extreme" means from a microbial ecology standpoint appears to pinpoint the hyperarid core of the Atacama Desert as having conditions beyond which life cannot survive (Warren-Rhodes et al. 2006).

4.4 Geology of Endolithic Habitats

While endolithic microbial communities are generally restricted to terrestrial surface habitats, they colonize a diverse range of geologic substrates. In most cases, the lithobiontic environment provides a protective environment while still permitting enough light penetration to support primary productivity by photosynthesis (Warren-Rhodes et al. 2007b). Physical and chemical properties of the rock substrate such as mineralogy, porosity and permeability, capacity for moisture uptake and retention, pH, and access to nutrients and protection from climatic extremes are all important, especially in endolithic habitats (Cockell et al. 2009a, b; Herrera et al. 2009; Kelly et al. 2011; Omelon et al. 2007). In contrast to hypolithic habitats, endolithic microorganisms are provided addition protection from physical weathering such as wind abrasion due to the rigid framework of the rock matrix, which contrasts to ecosystems living at the soil-rock interface.

The most common occurrences are found in porous sedimentary rocks such as quartz-rich sandstone; however, weathered limestone and dolomites are also colonized (Ferris and Lowson 1997; Friedmann 1980; Norris and Castenholz 2006; Omelon et al. 2006a; Saiz-Jimenez et al. 1990; Sigler et al. 2003; Tang et al. 2012; Wong et al. 2010b). In the case of hypolithic habitats, both translucent and opaque rocks can host microbial life (Cockell and Stokes 2004). It has recently been shown that contemporary calcite precipitating from groundwater spring discharge is colonized by endolithic microorganisms as the lithic habitat become drier and more cemented (Starke et al. 2013).

Lithic microorganisms are found in other rock types including evaporites such as halite and gypsum (Boison et al. 2004; Cockell et al. 2010; Dong et al. 2007; Hughes and Lawley 2003; Stromberg et al. 2014; Wierzchos et al. 2006; Ziolkowski et al. 2013), weathered granite (Ascaso and Wierzchos 2003; de los Ríos et al. 2002, 2005, 2007; Wierzchos et al. 2003), and marble (Büdel et al. 2009; Sterflinger et al. 1997). Porosity in volcanic rocks including rhyolitic ignimbrites has been shown to support endolithic microbial communities (Wierzchos et al. 2013) as have deposits altered by meteorite impacts on Earth (Parnell et al. 2004; Pontefract et al. 2014) and silica associated with hot spring sinter (Phoenix et al. 2006; Walker et al. 2005). Although normally found in intertidal zones, euendolithic microorganisms have also been observed in terrestrial micrite (Hoppert et al. 2004).

4.5 Light Regime Within Endolithic Habitats

Phototrophic microorganisms dominate as primary producers and are the largest community in these near-surface environments. Given that they require sunlight for growth, they are limited to the maximum depth of light penetration into the lithic habitat, be it through a translucent pebble as in hypolithic habitats or into a rock matrix such as sandstones. Light diminishes rapidly with depth on the order of 70–90 % for each millimeter beneath the surface; however, measurements of the light regime show that these photosynthetic microorganisms can grow under very low light levels, down to 0.08 % and 0.005 % of the incident light flux in hypolithic and cryptoendolithic habitats, respectively (Nienow et al. 1988b; Schlesinger et al. 2003).

Degree of light penetration varies as a function of grain size, the presence of opaque minerals, as well as microbial biofilms. Temporal changes on various scales including the development of a surface crust or varnish (long term) and the presence or absence of water can significantly change light conditions within the endolithic habitat. Accumulation of allochthonous dust composed of iron oxides and clays on the rock surface will dramatically reduce light penetration; in one study, reduction by up to 90 % at a depth less than 0.5 mm beneath the rock surface was noted, further diminished to only 0.005 % of the incident light flux at the deepest point of colonization (Nienow et al. 1988b). In contrast, rocks having little to no surface crust are colonized to greater depths as light penetrates much deeper into the rock (Omelon et al. 2007). These differences, however, may be constrained to certain rock types or environments as limestone rocks inhabited by endolithic microorganisms showed no correlation between degree of light penetration and colonization depth (Matthes et al. 2001). In contrast, water in pore spaces enhances light penetration due to its high refractive index compared to air and combined with the reflective properties of certain substrates such as quartz grains can greatly increase the amount of light in the cryptoendolithic habitat (Nienow et al. 1988b).

The attenuating properties of the overlying rock mean that these habitats receive less incident UV and photosynthetically active radiation. While potentially beneficial for life by providing some protection from photoinhibition, analysis of the full spectrum of solar radiation penetrating into the endolithic habitat of colonized rock from the Antarctic Dry Valleys shows that the presence of water diminishes protection against UV radiation under saturated conditions (McKay 2012), leading to short-term higher doses of radiation until this water has evaporated. Despite the rarity of liquid water in these habitats, intense UV exposure to these slow-growing microorganisms for even short periods of time may limit microbial diversity to those that can tolerate higher UV levels.

4.6 Nutrients

Endolithic habitats are composed of rocks that vary in solubility but are generally not considered a source of nutrients for microorganisms. Studies of nutrient conditions within endolithic habitats from the Dry Valleys show colonized regions having adequate supplies of inorganic nitrogen as nitrates and ammonium (Friedmann and Kibler 1980; Greenfield 1988). In addition, microbial growth is not stimulated when these or other nutrients including phosphate or manganese are added to the system (Johnston and Vestal 1986, 1991; Vestal 1988a), suggesting that they are not lacking. Although in some cases it is possible that nutrients required for microbial growth are obtained directly by in situ weathering of the host rock (Siebert et al. 1996), there does not appear to be a general selection by endolithic microorganisms for a specific type of mineralogy (e.g., quartz, calcite, granite). This suggests that nutrients required for energy and growth are more likely derived from allochthonous sediments such as dust (Johnston and Vestal 1989; Omelon et al. 2007; Pontefract et al. 2014; Tang et al. 2012; Walker and Pace 2007a). Another reason that these microbial communities may not suffer from a lack of nutrients is due to the fact that they are active for only very short periods of time, either due to freezing temperatures (Friedmann and Kibler 1980) or desiccation (Wierzchos et al. 2013).

4.7 Microclimatic Conditions Within Endolithic Habitats

As primary productivity in lithobiontic habitats is based upon photosynthetic life, microorganisms inhabiting these environments are in close proximity to surface desert conditions, which range from cold to hot and semiarid to hyperarid. While their temperature and moisture regimes are dictated generally by the local climate, speculation that microenvironmental conditions in lithobiontic habitats differed from those outside the lithic environment was first raised in the 1960s in studies of algae in the Negev Desert (Friedmann et al. 1967). Since then, many studies have shown how these habitats provide necessary advantages that permit microbial life to flourish in an otherwise hostile environment. Characterization of the microclimate—most notably temperature and water availability—has provided important information regarding the activity of these microbial communities. Comparison of these microenvironmental conditions to the local climate provides insight not only into how these habitats provide refuge for lithobiontic microorganisms but also sources of water that are required to support life in severely harsh conditions.

Although not strictly endolithic, studies of phototrophic microorganisms in hot desert hypolithic habitats have shown that they can remain active over a wide range of temperatures (~0–50 °C) (Tracy et al. 2010), with tolerance up to >90 °C (Schlesinger et al. 2003). In contrast, seasonal darkness in polar environments results in long periods of subzero temperatures that effectively arrest microbial activity. Warming of cryptoendolithic habitats occurs through solar radiation reaching the rock surface; due to the heat capacity and transparency of rock, elevated temperatures are generated in the subsurface compared to the overlying air (Friedmann et al. 1987, 1993; Omelon et al. 2006a). Temperature differences between air and the endolithic habitat can be significant, with measured differences up to 20 °C (Cockell et al. 2003; Friedmann 1977; Kappen et al. 1981; McKay and Friedmann 1985; Omelon et al. 2006a). This enhanced heating of the endolithic habitat increases the time during which microorganisms can be metabolically active (Friedmann et al. 1987, 1993; Omelon et al. 2006a), which is especially important in polar deserts such as the Dry Valleys where temperatures are >0 °C for only 50–500 h year^{-1} (Friedmann et al. 1987, 1993; Kappen et al. 1981). The heat capacity of rocks can also moderate high-frequency rapid temperature fluctuations, which when oscillating around 0 °C generate freeze-thaw cycles that can lead to uncontrolled intracellular ice formation within microorganisms. While such conditions are thought to be at least partially responsible for controlling epilithic colonization of rock surfaces, it has been suggested that temperature fluctuations are moderated within endolithic habitats (McKay and Friedmann 1985; Nienow et al. 1988a).

Precipitation in the Antarctic Dry Valleys is rare and only in the form of snow, much of which sublimates back into the atmosphere and is therefore mostly unavailable for life (Friedmann et al. 1987). Water that does occasionally melt on rock surfaces by solar heating enters the endolithic habitat via percolation into pore spaces (Friedmann 1978; Friedmann and McKay 1985). Vital for sustaining life in these endolithic habitats is the fact that this infiltrated moisture persists in the subsurface long after precipitation events have passed (Friedmann et al. 1987, 1988; Kappen et al. 1981; Omelon et al. 2006a). This water is effectively trapped within the endolithic habitat and permits reactivation of desiccated biomass, with subsequent loss back into the atmosphere varying as a function of porosity, permeability, and the degree of surface crust formation that can severely retard evaporation rates (Friedmann and Ocampo-Friedmann 1984a).

This combination of cold temperatures and scarce water results in short periods of time for microbial activity, during which growth rates are slow; measurements of carbon turnover times of these microbial communities suggest that they are 10^3–10^4 years old (Johnston and Vestal 1991; Sun and Friedmann 1999). The remarkable age of this community points also to extreme stability of the endolithic habitat, as would be necessary to support and protect endolithic microorganisms over long time periods, and is shown by the rock surface having an estimated atmospheric exposure period of several thousand years (Friedmann and Weed 1987). In contrast, similar habitats at the same latitude in the Arctic experience warmer temperatures and much longer active growth periods of ~2400 h $year^{-1}$ (Omelon et al. 2006a). Combined with higher numbers of precipitation events including summer rainfall, carbon turnover times of 10^1 years show that these endolithic microorganisms are much younger (Ziolkowski et al. 2013). It is possible that this relative abundance of liquid water combined with longer periods of microbial activity in the Arctic leads to higher rates of erosion due to enhanced chemical weathering of the endolithic habitat.

Studies in search of life in the most extreme deserts on Earth have revealed that water is the most important determinant for survival in all lithobiontic habitats. In hot deserts, water can occur as sporadic rainfall but more commonly as fog or dew that condenses at night on rock surfaces, only to evaporate shortly after sunrise (Kappen et al. 1980; Kidron 2000; Warren-Rhodes et al. 2006). In some instances both rain and fog can contribute moisture, with fog in one case being more important to support life in these habitats (Warren-Rhodes et al. 2013). Semiarid desert conditions in Australia can support hypolithic photosynthetic activity for ~942 h $year^{-1}$ (Tracy et al. 2010), similar to time periods in other deserts such as China (200–922 h $year^{-1}$) (Warren-Rhodes et al. 2007a, b) and the Negev Desert (1400 h $year^{-1}$). These estimates are far greater than those calculated for the hyperarid core of the Atacama Desert, where photosynthesis is restricted to <75 h $year^{-1}$ (Warren-Rhodes et al. 2006). Such limited water availability and therefore short growth periods under extremely arid conditions result in long-lived communities, comparable in age to those found in cryptoendolithic habitats in the Antarctic Dry Valleys (Warren-Rhodes et al. 2006).

In addition to hypolithic habitats, endolithic microorganisms inhabit soil gypsum and anhydrite crusts that form by water migration and evaporation in semiarid and arid regions including the Atacama, Mojave, and Al-Jafr Deserts (Dong et al. 2007; Wierzchos et al. 2006). Halite in the hyperarid core of the Atacama also hosts endolithic microorganisms (de los Ríos et al. 2010; Gramain et al. 2011; Parro et al. 2011), which is thought to select for those microorganisms that can tolerate or manage osmotic stresses associated with hypersalinity. The Atacama has received much attention in recent years due to the extreme aridity of this hyperarid region, which is considered to be the driest place on Earth. Studies of hypolithic microbial communities in this area were thought to reveal the absolute limits to photosynthetic life (Navarro-González et al. 2003; Warren-Rhodes et al. 2006); however, that has since been challenged by confirmation of cryptoendolithic microorganisms colonizing volcanic rhyolitic ignimbrites (Wierzchos et al. 2013). As in all cases, these endolithic communities include photosynthetic microorganisms and heterotrophic bacteria and are afforded the same protective characteristics as in other endolithic habitats. Water in this part of the hyperarid core is observed as rainfall that occurs only sporadically, with estimates of photosynthetic activity at <100 h year^{-1} (Wierzchos et al. 2013) being comparable to that in hypolithic habitats reported previously from the Atacama (Warren-Rhodes et al. 2006).

Studies of calcium sulfate crusts in the Atacama showed that endolithic microorganisms were present in areas that experienced a cumulative relative humidity of $\mathrm{RH} > 60$ % but were absent in areas that were below this threshold (Wierzchos et al. 2011), suggesting a possible moisture limit to life in these types of endolithic habitats. Endolithic microorganisms inhabiting halite crusts benefit from condensation of water vapor in pore spaces at an $\mathrm{RH} > 75$ % that corresponds to halite deliquescence (Davila et al. 2008). Moisture measurements showed that this occurred within the endolithic habitat far more frequently than in the overlying air to create conditions amenable to photosynthesis for ~215 h year^{-1}, in contrast to 6 h year^{-1} in the latter. Perhaps even more remarkable was the discovery of endolithic microorganisms surviving in nanoporous halite crusts where water forms by capillary condensation at humidities lower than halite deliquescence, with the capacity to retain moisture far exceeding that in other endolithic habitats (Wierzchos et al. 2012).

4.8 Microbial Activity in the Absence of Liquid Water

While studies have attempted to define the minimum limits of moisture required for supporting growth of cyanobacteria such as *Chroococcidiopsis* in lithic habitats, much of that work has focused on lichens due to their poikilohydric nature, meaning that these microorganisms can tolerate low cell water content caused by long periods of dryness that allows them to live in such extreme arid climates without suffering damage. As has been observed in microclimatic studies of endolithic habitats in hot deserts, activity is often dictated by the presence of water at night that permits hydration and dark respiration followed by CO_2 fixation associated with net photosynthesis in the early part of the day. This activity subsequently ceases as temperatures rise and humidity levels drop, leading to desiccation due to water loss through evaporation (Lange et al. 1990, 2006).

Under more extreme arid conditions, it has been shown that lichens are metabolically active in the absence of liquid water, down to 70 % relative humidity (Lange 1969; Lange et al. 1970, 1994; Nash et al. 1990; Palmer and Friedmann 1990; Lange and Redon 1983; Redon and Lange 1983). Interestingly, lichens with algal phycobionts appear to function at these lower relative humidities, whereas those with cyanobacterial phycobionts do not, having a higher threshold cutoff near 90 % (Hess 1962; Palmer and Friedmann 1990). While all can revert back to active metabolism through contact with liquid water (Potts and Friedmann 1981), it has been shown that uptake of water vapor alone can reactivate photosynthesis in lichens with an algal phycobiont (Butin 1954; Lange and Bertsch 1965; Lange and Kilian 1985; Nash et al. 1990; Schroeter 1994). In contrast, lichens with cyanobacteria as phycobionts do not exhibit the same universal capacity and appear to require liquid water to activate photosynthesis (Lange and Kilian 1985; Lange et al. 1986, 1990, 1993, 2001; Lange and Ziegler 1986; Schroeter 1994). Microscopic examination of both types of lichens showed this to be due to the inability of cyanobacteria to attain turgidity when hydrated with water vapor alone (Büdel and Lange 1991). However, a cyanobacterial phycobiont isolated in the laboratory has been shown to achieve turgor and photosynthesize under conditions of high humidity (Lange et al. 1994). Such work brings validity to earlier studies showing that cyanobacteria can photosynthesize under arid conditions, including endolithic habitats (Brock 1975; Palmer and Friedmann 1990; Potts and Friedmann 1981).

While photosynthetic activity in the absence of liquid water has been documented in arid climates of temperate regions where local humidity can be high (Lange and Redon 1983; Redon and Lange 1983), metabolic activity of these microorganisms can also occur at subzero temperatures where water exists in a solid phase as snow or ice, often under snow cover (Kappen et al. 1986, 1990; Kappen 1989, 1993a; Kappen and Breuer 1991; Pannewitz et al. 2003; Schroeter and Scheidegger 1995). Melting of snow and ice can lead to moistening (Lange 2003), but water vapor by itself can support metabolic activity under cold temperatures (Kappen et al. 1995). This is believed to occur whereby a vapor gradient forms between ice and the dry lichen thallus (Kappen and Schroeter 1997).

The ability to attain net photosynthesis using water vapor alone as well as survive long periods of desiccation is an important survival strategy for microorganisms in desert habitats. Lichens with algal phycobionts appear to attain positive net photosynthesis under lower relative humidity conditions than those with a cyanobacterial phycobiont and experience much higher rates of photosynthesis when exposed to higher humidity levels. This suggests that they are the best opportunists to survive under the most arid conditions on the planet and only benefit from living in endolithic habitats that can provide advantageous moisture conditions.

4.9 Adaptation to Stress

Climatic stresses in desert environments are greatest on exposed surfaces, which is why endolithic habitats are normally the last refuges for life as they provide protection to some degree. However, the pressures of desiccation and excessive radiation are only partially offset by periodic moisture availability and radiative shielding. Various photoprotective-screening and photoprotective-quenching pigments are synthesized by cyanobacteria, algae, and fungi in cryptoendolithic habitats, which often results in a clear vertical zonation of these different microorganisms in response to light and UV levels. Examples include scytonemin, mycosporine-like amino acids, carotenoids, and melanin (Jorge Villar et al. 2005a, b; Selbmann et al. 2005; Wynn-Williams et al. 1999).

In addition to pigments, cyanobacteria and fungi in endolithic habitats produce abundant volumes of extracellular polysaccharides (EPS) (de los Ríos et al. 2004; Omelon et al. 2006b; Pointing and Belnap 2012; Selbmann et al. 2005), which help to regulate intracellular water loss (Adhikary 1998; Potts 1999; Tamaru et al. 2005; Wingender et al. 1999) and mediate cell wall damage resulting from shrinking and swelling associated with wide variations in temperatures and moisture (Grilli Caiola et al. 1993; Selbmann et al. 2002). In addition to reducing physiological stress imposed by desiccation, EPS likely helps control rates of cooling that, when occurring rapidly around freeze-thaw temperatures, would help regulate osmotic stress and control intracellular ice formation (Vincent 2007). Alternatively, cyanobacteria have been shown to resist desiccation by accumulating water-stress proteins or producing osmoprotectants such as trehalose and sucrose (Hershkovitz et al. 1991; Scherer and Potts 1989) with abundant free amino acids detected within the endolithic habitat (Greenfield 1988; Siebert et al. 1991). The abundance of these leached materials suggests that only a fraction (0.025 %) of gross productivity supports biomass growth (Friedmann et al. 1993).

4.10 Colonization Extent

Endolithic biomass is highly variable; however, measurements in colonized limestone ranged from 3 to 17 % dry weight that corresponded to rock porosity (Ferris and Lowson 1997). Given the nature of microorganisms inhabiting small spaces within rock and that rock porosity and grain size will vary, it seems reasonable to assume that biomass estimates will vary as well (Büdel et al. 2008; Kappen and Friedmann 1983; Kuhlman et al. 2008; Tuovila and LaRock 1987; Vestal 1988b). Examinations of endolithic microorganisms focus their efforts on studying and highlighting the presence of pigments (Fig. 4.1) associated with either photosynthesis or protection from excessive radiation. While it is true that heterotrophic microorganisms are only a small component of the biomass in these photic zones (Greenfield 1988; Hoppert et al. 2004), nonpigmented fungal hyphae and heterotrophic bacteria are often found penetrating deeper into the lithic habitat (Friedmann 1982; Hoppert et al. 2004; Ruisi et al. 2007). These more deeply penetrating populations are not always accounted for in studies of endolithic communities, and their presence should be determined when estimating biomass.

An example of this oversight stems from studies of microbial activity and carbon dynamics. Measurements of CO_2 concentrations in air in equilibrium with the endolithic habitat have shown that while cryptoendolithic CO_2 concentrations remain similar to atmospheric levels when dry, a net CO_2 flux from the subsurface into the atmosphere occurs upon wetting (Omelon et al. 2013). Analysis of 16S rRNA present both within the photic zone and deeper inside the rock showed a progression from cyanobacteria dominating 0.5 cm beneath the surface to a

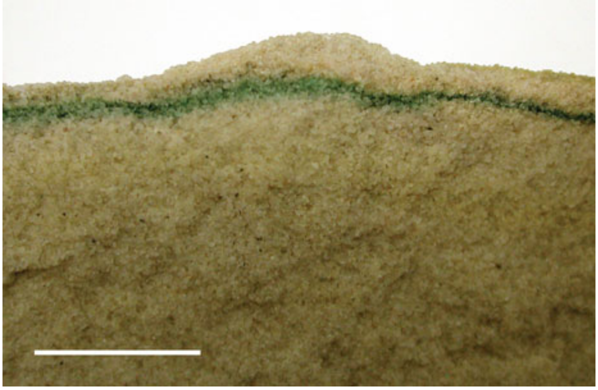

Fig. 4.1 Cryptoendolithic phototrophic microorganisms in sandstone rock from Ellesmere Island, Nunavut, Canada. Scale bar = 1 cm

community composed of *Actinobacteria*, *Alphaproteobacteria*, and *Acidobacteria* at a depth of 3.5 cm, which was beyond the point of light penetration. While phototrophic microorganisms are the primary producers, it would appear that they support a much larger community dominated by heterotrophic microorganisms at depth. These bacteria are an important part of endolithic microbial communities as decomposers (Ferris and Lowson 1997; Hirsch et al. 1988, 2004a, b; Siebert and Hirsch 1988; Siebert et al. 1996), which accelerate nutrient cycling of bioessential elements such as phosphorus (Banerjee et al. 2000). Microbial communities in hypolithic settings are also observed extending beyond the rock-soil interface, with the production of EPS binding soil particles to create a stabilized subsurface microenvironment (Chan et al. 2012) that could enhance biological sequestration of elements as well as provide moisture to support a larger microbial community.

4.11 Controls on Endolithic Microbial Community Structure

Endolithic microbial communities are thought to be some of the simplest ecosystems on Earth (Walker and Pace 2007a, b), but more recent work has shown that microbial diversity is higher in lithic habitats than in surrounding soils in more extreme environments such as the Antarctic Dry Valleys and the hyperarid Namib Desert (Pointing et al. 2009; Stomeo et al. 2013). Early delineation of lichen-dominated and cyanobacteria-dominated endolithic microbial communities in the Dry Valleys (de la Torre et al. 2003; Friedmann 1982) raised the question as to what controls diversity in these habitats and has become a major area of investigational focus given the growing number of studies assessing diversity in a wide range of desert environments. It was proposed earlier that variations in microbial community composition in endolithic habitats of the Antarctic Dry Valleys result either from differences in substrate pH as a function of moisture abundance (Friedmann et al. 1988; Johnston and Vestal 1989) or that moisture itself directly affects species biodiversity by selecting for microorganisms better adapted to aridity (Cockell et al. 2003). While not endolithic per se, a transect study of hypolithic microbial communities in China showed shifts in community structure as a function of liquid water availability that is influenced by the ability of individual microorganisms to tolerate dry conditions (Pointing et al. 2007). In contrast, another study showed the extent of UV transmittance through limestone to be the main driver between lichen-dominated endolithic communities and cyanobacteria-dominated communities, with the former able to survive under higher UV conditions (Wong et al. 2010b). It would seem that in more clement locations, endolithic habitats select for microorganisms that can tolerate these environments to create specific niches, with increasing pressures selecting for specific microorganisms that can tolerate increasingly harsh conditions.

4.12 Microbial Activity, Geochemistry, and Microbe-Mineral Interactions in Endolithic Habitats

Endolithic microorganisms are involved in physical weathering resulting from mechanical forces imposed on the host rock, such as the penetration of fungal hyphae into cracks, the expansion of colonized spaces through biofilm swelling and shrinking associated with hydration-dehydration cycles, or the filling of pore spaces by growth of the biofilm. In contrast, mineral weathering is a geochemical process that is tightly coupled with microbial activity through many different mechanisms. Examples of indirect processes include the production of organic and inorganic acids, EPS, and metal-complexing ligands, as well as respiration and photosynthesis that can alter the pH of the microenvironment, which not only lead to dissolution of minerals but also allow for microbial sequestration of nutrients and trace elements. Bacteria and fungi can also react directly with metals as a result of their reactive cell surfaces or by changing the redox state of elements such as iron or sulfur for use as energy sources to facilitate transport of those elements into the cell for metabolic requirements (Ehrlich 1998; Sterflinger 2000).

While only the basic geology of a rock containing endolithic microorganisms is commonly reported (e.g., sandstone, limestone), metals and minerals are often a component of the rock matrix. Beacon Formation sandstones hosting cryptoendolithic microorganisms in the Dry Valleys include feldspars, clays, and iron oxides within the rock matrix (Blackhurst et al. 2004, 2005; Edwards et al. 2004; Friedmann and Weed 1987; Weed and Ackert 1986), which is probably a common occurrence in sedimentary rocks. These habitats are also geochemically diverse, containing a wide spectrum of macronutrients and metals (Blackhurst et al. 2005; Ferris and Lowson 1997; Friedmann 1982; Johnston and Vestal 1989; Omelon et al. 2007). Analysis of concentrations of metals in Dry Valley uncolonized sandstones showed little change with increasing depth (Blackhurst et al. 2005), but the region colonized by microorganisms was depleted relative to the overlying surface crust and beneath, where metals accumulated (Johnston and Vestal 1989). Variability in metal concentrations between colonized and uncolonized regions of cryptoendolithic habitats has been observed in other endolithic habitats (Ferris and Lowson 1997; Omelon et al. 2007), suggesting this to be a widespread phenomenon. The most commonly reported form of chemical weathering of rocks colonized by endolithic microorganisms is the production of acidity by fungi, such as oxalic acid (Johnston and Vestal 1993; Sterflinger 2000). However, cyanobacteria are known to create high-pH environments that can effectively weather silicates and lead to erosion of these habitats (Büdel et al. 2004). Presence of bioessential metals or nutrients necessary for enzymatic function as a resource within the rock can be of key importance for endolithic microorganisms (Blum et al. 2002; Ferris and Lowson 1997), but this is not always a requirement as shown by cases where the endolithic habitat provides only a structural framework for microorganisms, with requirements for growth coming from external inputs such as allochthonous dust (Cockell et al. 2010; Omelon et al. 2006b; Pontefract et al. 2014).

Many studies have shown evidence for rock weathering by the activity of endolithic microorganisms and their by-products (Ascaso et al. 1998; Burford et al. 2003; Caneva et al. 2014; Danin et al. 1983; Garvie et al. 2008; Gaylarde and Gaylarde 2004; Hirsch et al. 1995; Lian et al. 2010; Omelon et al. 2008; Ortega-Calvo et al. 1995; Palmer and Hirsch 1991; Sand and Bock 1991; Sterflinger et al. 1997; Tang et al. 2012; Weed and Ackert 1986; Wessels and Schoeman 1988). While destructive in nature, rock weathering can contribute to soil development (Tang et al. 2012), and the resulting exposure of the underlying community may result in the dispersal of endolithic microorganisms into soils or at least provide a source of organic matter for other carbon-limited environments (Burkins et al. 2000; Friedmann et al. 1993; Hopkins et al. 2008). Concern for preservation of monuments and buildings against endolithic microorganisms has led to steps to ameliorate colonization through the assessment of different treatments; in one case, 70 % ethanol applied to the surface was the most effective in reducing activity and preventing growth (Rabe et al. 2013).

Weathering, however, does not always lead to erosion. A study of micritic carbonates in glacier forelands characterized rocks sequentially colonized by fungi, algae, and finally lichens (Hoppert et al. 2004). Fungi penetrated the subsurface by chemical dissolution to create cavities in the rock, but this did not lead to destabilization of the endolithic habitat. The mature lichen community reaches steady-state conditions whereby fungal hyphae cease to penetrate deeper into the substrate, creating a network of pores colonized by filaments that strengthens the rock matrix (Hoppert et al. 2004). The authors argue that this situation differs from porous rocks such as sandstones that are susceptible to mechanical and chemical weathering along fissures (Friedmann and Ocampo 1976; Friedmann 1980; Weed and Norton 1991; Wessels and Büdel 1995); however, microbial filaments and EPS production can contribute to surface crust formation that in turn can increase resistance to weathering in the endolithic region (Kurtz and Netoff 2001).

The activity of the lichen *Verrucaria rubrocincta* has been shown to be involved in both destructive and constructive processes in endolithic habitats in caliche (Garvie et al. 2008). As in most reported cases, fungal hyphae weather the rock by deeper penetration into the subsurface that increases porosity and potential for water storage during extended dry periods. However, algal photosynthesis leads to the precipitation of micritic carbonate at the rock-air interface (Garvie et al. 2008). This carbonate not only serves as a barrier to moisture evaporation from the subsurface but also provides a highly reflective coating that shields endolithic microorganisms from intense solar radiation.

Surface crusts are an important constructive component of endolithic microbial systems as they mediate moisture loss, attenuate radiation, and provide protection from wind abrasion. In the Antarctic Dry Valleys, surface crusts of Beacon Formation sandstones are composed of allochthonous dust that builds up on the surface to form a coating rich in clays, feldspars, and iron oxides (Blackhurst et al. 2004; Friedmann and Weed 1987; Weed and Ackert 1986; Weed and Norton 1991). Despite this protection, a combination of biomass accumulation, microbial production of oxalic acids and EPS, and freeze-thaw activity triggers the dissolution of silica cements between quartz grains and subsequent exfoliation of the overlying surface crust and loss of biomass (Johnston and Vestal 1993; Kappen 1993b; Sun et al. 2010; Sun and Friedmann 1999).

This process leads to the formation of distinct exfoliation patterns on rock surfaces (Friedmann 1982; Friedmann and Weed 1987; Nienow and Friedmann 1993; Sun and Friedmann 1999). Similar weathering patterns are observed in other deserts where endolithic microorganisms colonize sandstone outcrops such as the Arctic and South Africa; however, cyanobacteria dominating within these cryptoendolithic habitats drive silica dissolution by generating high-pH conditions during periods of photosynthesis (Büdel et al. 2004; Omelon et al. 2008). Exfoliation of the surface crust exposes the underlying microbial community, of which much is lost to the surrounding landscape due to wind erosion; the remaining biota must then reestablish itself within the cryptoendolithic habitat as a surface crust begins forming on the new rock surface (Fig. 4.2) (Sun and Friedmann 1999).

4.13 Endolithic Biosignatures

The exfoliation of surface crusts is an example of an indirect biosignature or biomarker as it leaves traces of past biological activity (Friedmann and Weed 1987; Kappen 1993b). In contrast to these indirect signatures, detailed examination of the colonized pore spaces of cryptoendolithic habitats in the Dry Valleys identified metals on the surfaces of both living and dead microorganisms (Ascaso and Wierzchos 2003; de los Ríos et al. 2003; Wierzchos et al. 2003). There are also reported occurrences of mineral biomobilization and biotransformation of inorganic deposits, including iron oxyhydroxide nanocrystals and biogenic clays to produce diagenetic biomarkers (Friedmann and Weed 1987; Wierzchos et al. 2003).

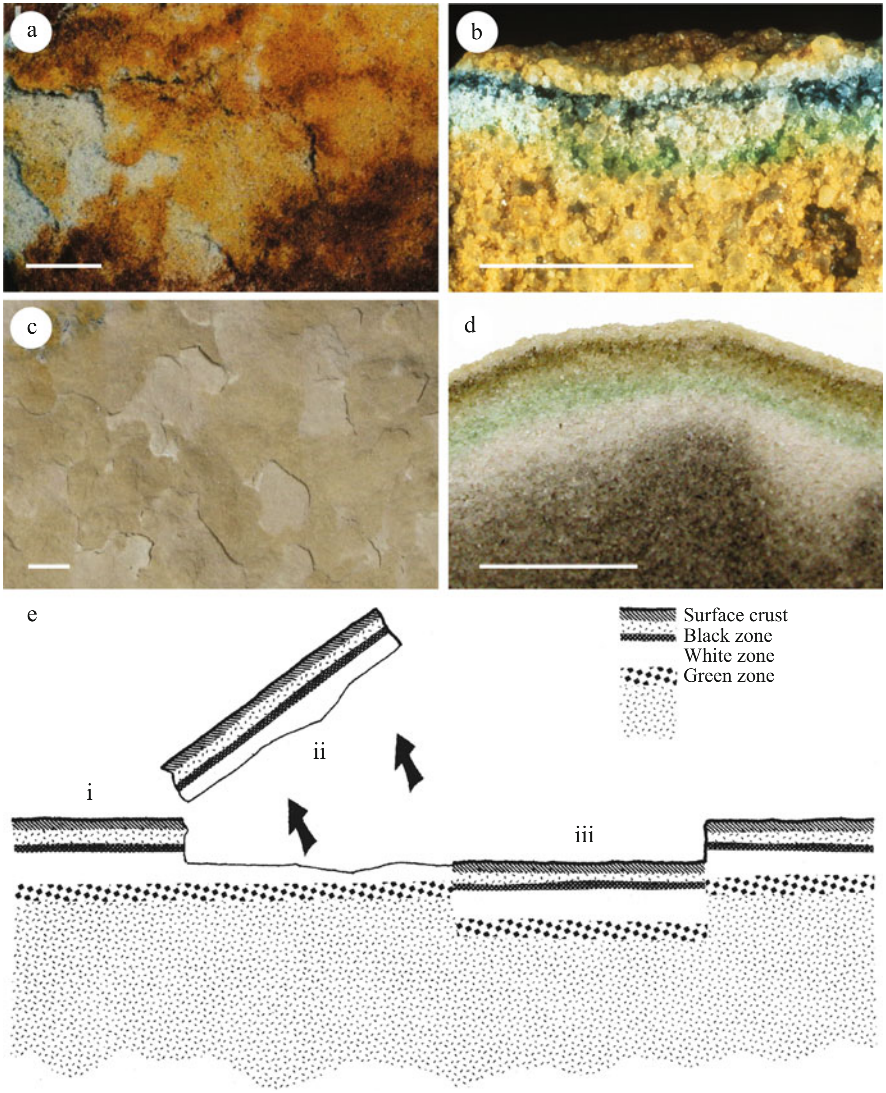

Fig. 4.2 Distinctive mottled surface patterns on sandstone rocks resulting from exfoliative rock weathering by cryptoendolithic microbial communities in the Antarctic Dry Valleys (**a**, **b**) and the Canadian high Arctic (**c**, **d**). Scale bars = 1 cm. Stages for weathering as described by Friedmann (1982), with zones in (**e**) corresponding to colors in (**b**). Stages include (i) initial establishment of endolithic lichen, (ii) exfoliation of crust by biological activity, (iii) reestablishment of lichen in area previously exfoliated. (**a**) From Friedmann and Weed (1987). (**b**, **e**) From Friedmann (1982)

Further progression of mineral encrustation leads to bacterial infilling to produce biosignatures and microfossils, containing either ultrastructural cellular elements or evidence for the transition from living microorganisms to deposits with no diagnostic cellular characteristics (Wierzchos et al. 2005). It is thought that these biosignatures are created through complex interactions between microorganisms and inorganic salts and minerals that preserve microfossils and therefore a record of their presence (Chap. 2 by Tomescu and coauthors). In contrast, similar studies of cryptoendolithic habitats in the Arctic show only the accumulation of clays embedded within EPS generated by microorganisms, with no evidence for in situ biomineralization as metal accumulations on cell surfaces or mineral precipitates, nor the presence of microfossils (Omelon et al. 2006b).

While bacteria can effectively bind metals to their surfaces leading to mineral precipitation, metal accumulation and mineral precipitation associated with microbial activity in natural environments require a source of metals brought near to or directly in contact with capsular material or cell walls. This is most commonly observed in aqueous environments, with water providing the medium to generate supersaturated conditions that drive most mineral precipitation reactions. Although this does not preclude the important activity of microorganisms in metal cycling and microbe-mineral interactions in soils where water is present (Gadd and Sayer 2000; Souza-Egipsy et al. 2002), the scarcity of water in deserts can provide only limited activity as both the solvent and transport agent for the introduction of metals and salts required for biomineralization processes.

The presence of microbial fossils in the Dry Valleys of Antarctica but not in the Arctic, despite both being cold deserts at similar latitudes, suggests that the relative abundance of water plays a crucial role in the formation and preservation of these biosignatures The Arctic receives substantially more precipitation in the form of liquid water than do the Dry Valleys (Omelon et al. 2006a), which enhances transport of dissolved metals and allochthonous debris such as clays into the Arctic cryptoendolithic habitat (Omelon et al. 2006b). This would suggest an increased likelihood for metal accumulation and mineral precipitation around Arctic microbial communities; however, these wetter conditions along with warmer summer temperatures also promote faster rates of biomass growth and turnover (Ziolkowski et al. 2013). In addition, higher Arctic growth rates and associated metabolic activity lead to higher rates of silica dissolution, evidenced by identification of oriented triangular etch pitting on quartz surfaces (Omelon et al. submitted) that can result from the presence of chelating acids or alkaline conditions that increase both quartz and feldspar solubility and dissolution kinetics (Bennett and Siegel 1987; Bennett 1991; Brady and Walther 1989; Brantley et al. 1986; Gratz et al. 1991; Gratz and Bird 1993; Hiebert and Bennett 1992). Evaluation of the upper pH limit at which cyanobacteria isolated from this habitat can fix dissolved inorganic carbon during photosynthesis shows that they can generate high-pH conditions (Omelon et al. 2008). In the presence of water, these high-pH conditions in the endolithic habitat could rapidly dissolve silica cements and quartz surfaces leading to exfoliation of the host rock, exposing the microbial community to harsh aerial conditions and their removal by winds (Omelon et al. 2006a).

In contrast, the colder and drier conditions of the Dry Valleys retard microbial growth rates and may also minimize detrimental stresses such as freeze fracturing associated with ice formation, thereby preserving older viable cryptoendolithic microbial populations (Bonani et al. 1988; Johnston and Vestal 1991). The longer residence time of these communities increases their exposure to aerial deposition of Fe oxides, quartz, and clays that form surface crusts (Friedmann and Weed 1987; Sun and Friedmann 1999; Weed and Ackert 1986; Weed and Norton 1991), which are believed to be the source for biomineralization and fossilization of these microorganisms (Wierzchos et al. 2005).

Previous work showed the varying degrees of viability of microbial communities resulting from the harsh environmental conditions of this region, which can lead to cell damage and mummification (de los Ríos et al. 2004; Friedmann and Koriem 1989; Wierzchos et al. 2004). Biotransformation of minerals was documented as physicochemical weathering of biotite, iron-rich minerals, biogenic clays, and silica as well as calcium oxalate around cells collected from granite rocks along the Ross Sea coastline at Granite Harbour (Ascaso and Wierzchos 2003; Wierzchos et al. 2003). The processes forming these deposits were explained by the inherent capacities of cell surfaces to immobilize cations and produce fine-grained minerals (Fortin et al. 1997, 1998; Fortin and Ferris 1998; Warren and Ferris 1998). While endolithic in nature, the formation of these minerals may be a function of the higher humidity levels experienced along the coast that increase water availability, the production of microbial EPS, and biotransformation rates of elements depositing around microorganisms.

In contrast, studies examining cryptoendolithic pores from the Mount Fleming region of the Dry Valleys observed rocks filled with living microorganisms and no mineral deposits or precipitates, as well as decaying microorganisms filled with clay-like minerals (Wierzchos et al. 2005) derived from airborne dust. Based on these observations, it was determined that inorganic processes occurring after the death of endolithic microorganisms were necessary for microbial fossil formation. These included the infilling of empty microbial molds by clay minerals, as well as mineralization of cell walls and interiors due to varying nucleation rates of silica and coexisting cations within an organic template. It is thought that differences in the elemental composition of cellular components result from multiple episodes of mineralization with intervening organic degradation rather than the primary replacement of organic material at the time of infiltration and that the mineralization variously occurs while cells are biologically active and after their decay to produce biosignatures (Wierzchos and Ascaso 2002). This is made possible through a concentration gradient by which metals or minerals diffuse into decayed microorganisms, resulting in fossilization substitution of organic substances with inorganic material (Wierzchos et al. 2005). The presence of biosignatures so close to the harsh polar desert environment only highlights the remarkable stability of these endolithic habitats, permitting fossilization to occur over timescales yet to be determined.

4.14 Astrobiological Significance

Interest in understanding the limits to life on Earth and potentially on other planets has led to the development of terrestrial analogue studies, which aim to evaluate whether or not life may exist elsewhere in the solar system. These analogues are targeted due to specific physical, chemical, or mineralogical characteristics that are comparable to those identified at extraterrestrial locations on planets including Venus, Mars, Europa, Enceladus, and Titan (Preston and Dartnell 2014). In addition to understanding habitability and the limits to life, analogue studies are also concerned with the identification, characterization, and preservation potential of biosignatures.

Endolithic habitats have been long considered potential locations to look for life on other planets, with those found in the Antarctic Dry Valleys receiving the most attention as terrestrial analogues for Mars ever since the early reporting of these microbial communities (Friedmann and Ocampo-Friedmann 1984b; Friedmann 1986; Friedmann et al. 1986; Friedmann and Koriem 1989; Wharton et al. 1989). Endolithic habitats in evaporite minerals precipitating from groundwater discharge have been considered potentially representative of life-supporting habitats on other planets (Grasby et al. 2003; Grasby and Londry 2007; Rothschild 1990), as are shocked rocks where porosity by impact craters creates new endolithic habitats that could subsequently be colonized (Pontefract et al. 2014).

It has been shown that the common endolithic cyanobacterium *Chroococcidiopsis* can survive damage induced by extreme conditions such as desiccation and radiation, which would be experienced in both space and on the surface of Mars (Billi et al. 2000, 2011). Given such understanding, studies have looked for Earth analogues for conditions found on Mars such as in the Atacama Desert, where discoveries of colonized endolithic habitats in hyperarid, salt-rich environments have provided new analogues for last refuges for life on that planet (Davila et al. 2008; Wierzchos et al. 2011, 2012, 2013).

More recent work has focused on characterizing the preservation of photosynthetic (i.e., fluorescent) pigments such as chlorophyll within these habitats, either by microscopy (Roldán et al. 2014) or spectroscopy (Stromberg et al. 2014). While the various states of preservation could be discerned in contemporary settings by confocal laser scanning microscopy (Roldán et al. 2014), placing endolithic microbial communities under simulated Mars conditions led to varying degrees of success as a function of the type of host mineral (Stromberg et al. 2014). Understanding how molecules degrade or are preserved in various minerals relevant to Mars will help in understanding the likelihood of finding biosignatures on other planets.

4.15 Conclusions

Endolithic microorganisms are afforded necessary respite from climatic stresses in desert habitats due to unique characteristics of the lithic substrate, which provide protection from temperature and radiation extremes as well as prolonged exposure to the rare occurrences of water that is transient at best outside the endolithic habitat. The successful survival of endolithic microorganisms, however, is not solely a function of the surrounding rock architecture, as shown by specific adaptive traits such as pigmentation to protect again UV, synthesis of EPS to fight desiccation, desiccation tolerance when necessary, and in some cases of lichens the ability to photosynthesize using only water vapor.

This activity leads to interactions with the surrounding habitat such as nutrient and element cycling, which can extend below the zone colonized by phototrophic microorganisms. Microbe-mineral interactions often lead to mineral precipitation or dissolution, but most requirements for metabolism and enzymatic function are sourced from outside the endolithic habitat. Some unique and protective aspects of these habitats result from abiotic processes (such as the formation of surface coatings), but microbial activity and microbe-mineral interactions are an important determinant of the success of these communities. In many cases microbial activity leads to weathering and destruction of the very habitat they require for survival, but this does not lead to the extinction of the microbial community. In others, the preservation of endolithic microorganisms or associated biosignatures provides not only a unique opportunity to understand how this terrestrial microbiota survives over long time periods but a fruitful prospect to investigate how biomineralization and fossilization proceed under extreme desert conditions.

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