Chapter 9
Lithobionts: Cryptic and Refuge Niches

Thulani P. Makhalanyane, Stephen B. Pointing and Don A. Cowan

Abstract Lithic-associated microhabitats, referred to as lithobiontic ecological niches and their communities are termed lithobionts. Lithic niches are widely dispersed in Antarctica and allow microbial communities to circumvent environmental stressors such as temperature fluctuations, low moisture levels, and high ultraviolet radiation. Here, we assess the status of research on the three recognized classes of lithobiont communities (epiliths, hypoliths and endoliths). We describe the microbial diversity of lithobionts, the factors that influence colonization, and the roles played by these communities in the Antarctic soil ecosystem. In order to understand community dynamics, such as beta-diversity patterns and factors that drive them, we advocate the application of "omics-based approaches" that can reveal both the functional capacities and adaptive potentials of complex microbial communities.

9.1 Introduction

The ice-free polar desert landscapes of Antarctica present an extremely challenging environment for life. Severe thermal, moisture and UV stress is exacerbated by an ultraoligotrophic terrestrial landscape that is comprised largely of mineral soils and rocks (Cary et al. 2010). Higher plants and animals are absent

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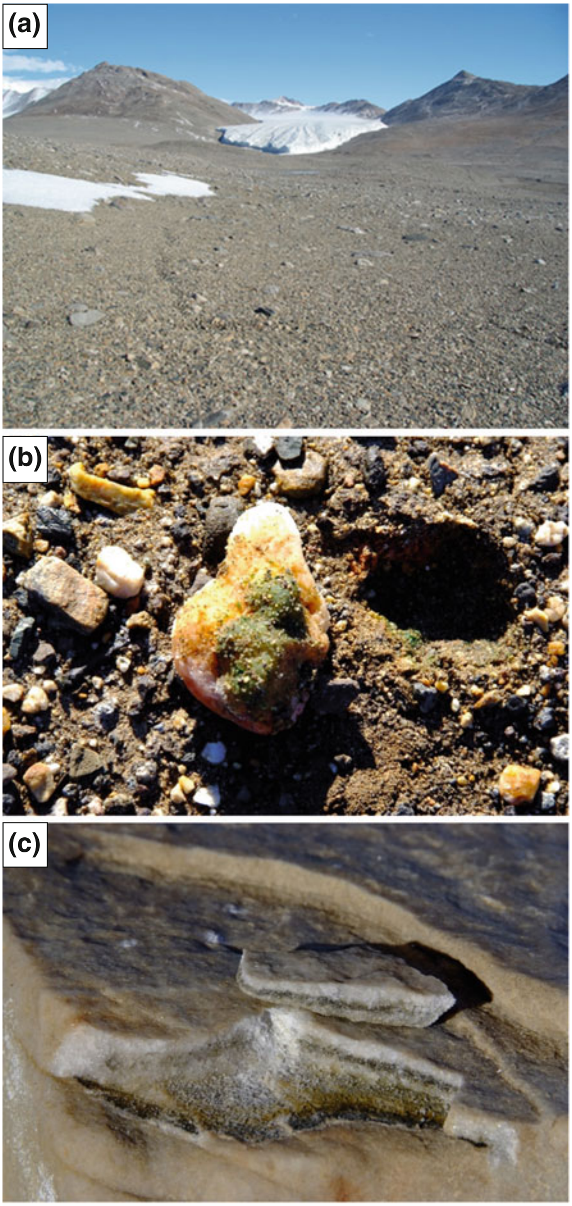

Fig. 9.1 Microbial colonization in hyperarid deserts. **a** Landscape of Miers Valleys, Antarctica illustrating a desert pavement covered with rocks supporting the development of **b** hypolith and **c** endolith communities (Photograph credits: Don A. Cowan)

from this environment, and instead, the biotic component of this ecosystem is almost exclusively microbial (Cowan and Tow 2004). The largest and best understood of the ice-free regions is the McMurdo Dry Valleys (Fig. 9.1), and this hyperarid desert supports vast expanses of exposed rocky substrate. Microbial colonization of various rock substrates occurs, although this is cryptic and not

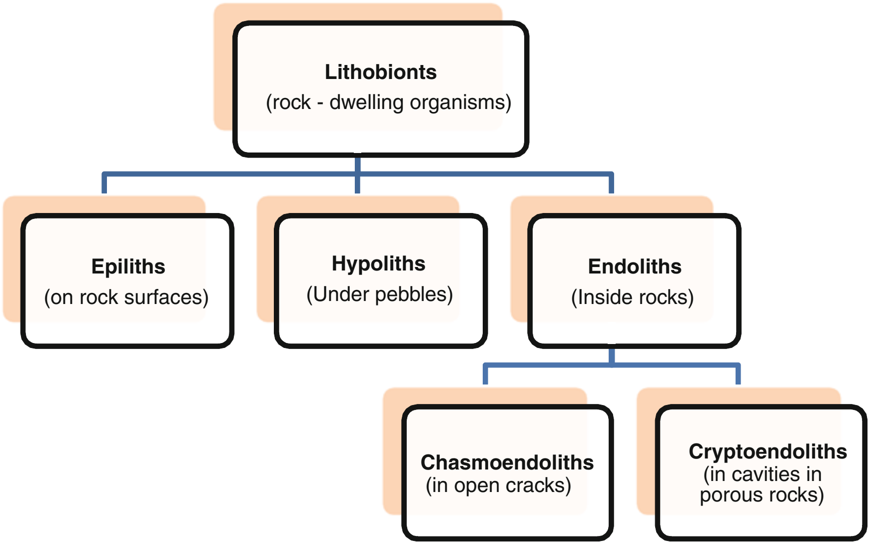

Fig. 9.2 Classification of lithobiont niches inhabited by desert microorganisms

readily observed on many surfaces. These lithic-associated microhabitats are referred to as lithobiontic ecological niches, and their communities are termed lithobionts (Golubic et al. 1981). Numerous studies have shown that lithobionts [also referred to as soil rock surface communities (SRSCs)] are widespread in both hot and cold deserts and are often the only visible life in such extreme terrestrial environments (Pointing and Belnap 2012). These communities are thought to contribute significantly to the ecology and function of both hot and cold deserts.

In this chapter, we review the status of research on the three recognized classes of lithobiont communities (Fig. 9.2): epiliths adhere to the surface of the rock, endoliths are found within the rock matrix, and hypoliths attach to ventral rock surfaces. We describe the microbial diversity of lithobionts, factors that influence colonization and the role played by these communities in the Antarctic ecosystem.

9.2 Lithobiontic Ecological Niche

The three lithobiontic niches are delineated largely as a function of the mineral substrate. Epiliths are perhaps the least fastidious and occur on various igneous rock surfaces. Endolithic colonization is restricted to porous sandstones and weathered granitic rocks, while hypoliths generally develop beneath translucent quartz and marble rocks (Pointing and Belnap 2012). Examples of epilithic, endolithic and hypolithic colonization are shown in Fig. 9.1.

9.2.1 Epiliths

Epilithic organisms populate the surfaces of stable rock substrata with access to sufficient quantities of moisture (Wynn-Williams 2002; Smith 1982). The establishment of epiliths is often associated with moss and lichen communities on the rock surfaces (Pointing and Belnap 2012; Nash et al. 1977), although heterotrophic fungi and cyanobacteria also appear to be key constituents (Staley et al. 1982; Gorbushina 2007).

Epilithic colonization is perhaps the most vulnerable of the three lithic types, as they are exposed to strong winds, ultraviolet radiation (UVR), desiccation and other perturbations (Cockell et al. 2008; Wynn-Williams and Edwards 2000). As a consequence, epiliths are often restricted to the milder lower latitude Antarctic regions such as Princess Elizabeth Land and Mac Robertson Land (Broady 1981a, 1996; Wynn-Williams and Edwards 2000).

9.2.2 Endoliths

Endolithic microbial communities colonize the interior of rocks by adapting to the different ecological sub-niches within the lithic substrate (Golubic et al. 1981). Depending on the micromorphological and structural properties of the rock, endoliths can be found as interstitial habitats of cracks and fissures (chasmoendoliths or chasmoliths) and also in pore spaces between mineral grains (cryptoendolithic) (Golubic et al. 1981; Nienow and Friedmann 1993; Budel et al. 2009). Chasmoliths are commonly found in siliceous rocks, but also have been reported in granite, marble, silicified sandstone, gypsum crusts and anorthosite (Friedmann 1982; Broady 1981b; de los Rios et al. 2005b). In contrast, cryptoendoliths are principally associated with porous sandstone rocks (Bell 1993; Friedmann and Ocampo-Friedmann 1984; Nienow et al. 2003; Omelon 2008; Sun et al. 2010), but may also be recovered in other suitable mineral types including granite, gneiss, limestone, marble, gypsum, halite and evaporites (Cockell et al. 2002; Nienow and Friedmann 1993; Boison et al. 2004; Wierzchos et al. 2006).

It has been demonstrated that cryptoendolithic microbial communities in Beacon sandstones, in the Antarctic Dry Valleys, promote biogenic weathering of rock substrates, and colonized sandstones show distinct exfoliation patterns on the rock surface (Friedmann and Weed 1987; Nienow and Friedmann 1993). Colonized sandstones display different coloured patches (white, yellow, orange or brown), the result of both the constructive aeolian weathering process and the destructive biogenic weathering process (Sun and Friedmann 1999; Sun et al. 2010). Long-term microbial colonization and the biogenic accumulation of oxalic acid dissolve the cementing substances between the mineral grains, resulting in exfoliation of the surface crust and loss of biomass (Sun and Friedmann 1999). This exfoliative weathering process is cyclic, and each phase is estimated to last for 1×10^4 years

(Friedmann et al. 1993; Sun et al. 2010). The process contributes to both the formation of mineral soils and the organic carbon fraction in the soil phase (Nienow and Friedmann 1993).

Chasmoliths are found in both the vertical fissures and horizontal cracks in rocks; the former are common in quartz glacial debris, whereas the latter are common in charnockite (a rare type of granite containing pyroxene) substrates (Vincent 2004). They are also frequently described in the fine fracture zones of marble which is common to the Antarctica landscape (Vincent 2004; Cowan and Ah Tow 2004). Chasmoliths are not exclusive to Antarctica, and they have been reported from other deserts in central Asia, central Australia, south-western USA and Mexico (Broady 1981b; Friedmann et al. 1967; Friedmann and Ocampo-Friedmann 1984).

9.2.3 Hypoliths

Hypolithic microbial communities (hypolithons) inhabit the ventral surfaces of rock substrates at the rock–soil interface (Friedmann et al. 1967; Golubic et al. 1981). Hypolithons typically colonize translucent rocks such as quartz, gypsum and granite (Broady 1981a, b) but may also be found under opaque rocks (e.g. dolomite and gneisses) (Cockell and Stokes 2004, 2006). As with endoliths, hypolithic communities are dominated by photoautotrophs such as cyanobacteria, which require a minimum level of photosynthetically active radiation (PAR) for photosynthesis (discussed below) (Friedmann et al. 1993).

In an observational study, three types of hypolithic communities were reported in the Miers Valley: the cyanobacterial dominated (Type I), the fungal dominated (Type II) and the bryophyte dominated (Type III) (Cowan et al. 2011a, b). The morphological characteristics of growth in these communities differ, and the hypolithons may be either loosely attached to the rock or unattached depending on the main community components. Type I hypoliths adhere directly to the rock forming a biofilm composed primarily of filamentous oscillatorian cyanobacterial morphotypes (Pointing et al. 2009). Type II communities comprise a filamentous network structure cemented to the rock surface, while the macroscopic moss structures of Type III communities are embedded in the soil under the translucent rock (Cowan et al. 2010a). These hypolithic types are both morphologically complex and diverse in composition. The community structures of hypolithic communities has recently been determined using amplified RNA intervening sequence analysis (ARISA), terminal restriction fragment length polymorphism (T-RFLP), clone library construction and pyrosequencing analysis of the 16S rRNA gene phylogenetic market gene (Wood et al. 2008; Pointing et al. 2009; Cowan et al. 2011a, b; Makhalanyane et al. 2013a).

9.3 Establishment of Lithobiontic Communities

Lithic communities have been described associated with a variety of substrates, including fine-grained Beacon sandstone, limestone, gypsum and flint (Nienow and Friedmann 1993; Cowan et al. 2010c; Cary et al. 2010; Cockell and Stokes 2004). Colonization of the rock is thought to depend on a combination of abiotic factors including macro- and microclimate (discussed below), ultrastructure, mineral composition and pH, which together contribute to the ability of the rock to host microorganisms (Friedmann and Ocampo-Friedmann 1984). Biotic factors are also involved during the colonization process. For instance, cyanobacteria are known to dominate habitats with high pH values and high levels of calcium and magnesium carbonates (Johnston and Vestal 1989). Fungal-dominated habitats have been reported from high altitude locations with high metal oxide concentrations (Connell et al. 2006; Pointing et al. 2009).

9.3.1 *Temperature*

The temperature of the lithobionts has been found to be closely linked to the ambient air temperature and the level of solar radiation (Nienow and Friedmann 1993). However, thermal buffering, due to the black body absorption effect of opaque rocks or the “greenhouse effect” of translucent quartz rocks, has been detected (Friedmann 1980; McKay et al. 2003; Schlesinger et al. 2003; Wynn-Williams 2002; Cowan et al. 2011a, 2010c). Daytime peak rock-air temperature differences in the Antarctic Ross Desert and in the Sonoran Desert in North America were 15 and 10 °C, respectively, indicating similar trends for both hot and cold deserts (Friedmann 1980; McKay and Friedmann 1985). However, three recent studies (Azua-Bustos et al. 2011; Makhalanyane et al. 2013b; Tracy et al. 2010) measuring microclimatic variables in hypolithons from hot deserts reported lower temperatures at the rock surface interface in daytime and night-time, and warmer night-time temperatures when compared to open soil in conflict with earlier studies (Schlesinger et al. 2003).

Depending on a number of factors including aspect, elevation and other geographical features, the annual temperatures in the McMurdo Dry Valleys ranges from -14.8 to 30 °C, with differences between the maximum and minimum of approximately 50 °C (Doran et al. 2002). These extreme temperature ranges impose severe freeze–thaw stresses on microorganisms (Nienow et al. 1988). Therefore, it has been hypothesized that the thermal buffering provided by rocks is perhaps most significant in polar deserts as lithobionts are protected from rapid freeze–thaw stress (Wynn-Williams 2002; Cowan et al. 2010c, 2011a). The effect of katabatic wind episodes, which have a direct effect on both temperature fluctuations and the physical stability of soil crusts, is also minimized by the lithobiontic lifestyle. Reports suggest that surface rock temperature can be up to 20 °C higher than ambient air temperatures during sunny periods (Kappen et al. 1983). The warmer rock mass may also prolong the period of lithophytic microbial growth in polar deserts during polar summers (Wynn-Williams 2002).

9.3.2 Water Availability

The rock microhabitat has been shown to offer improved water availability compared to the surrounding soil (Tracy et al. 2010; Cowan et al. 2010c; Chan et al. 2012; Warren-Rhodes et al. 2006). In rainfall zones (such as the Antarctic Peninsula), the overlying rock provides protection from raindrop impact during precipitation, but provides a narrow annuli of unsealed soil near the sheltered margins of stones, that serve as sites for water entry and air escape for lithic niches (Thomas 1997). The rock also serves as a collector of water during precipitation, fog and dew events (Warren-Rhodes et al. 2006).

Liquid water is an essential requirement for the development of epilithic colonists. Increases in precipitation have been reported to lead to surges in cover and biomass (Broady 1996, 1989). As a result, epilithic colonization is highest at moist coastal areas and locations with frequent irrigation by snowmelt or high atmospheric humidity, and around bases of nunataks where exposed rocks meet surrounding ice fields (Broady 1981b, 1989, 1996). The diversity of Antarctic epiliths has been reported to drop significantly along moisture gradients. For example, the total lichen species diversity was found to decrease from 18 genera in Dronning Maud Land (approximately 200 km inland) to only 5 genera a further 1,000 km from the coast in the Pensacola Mountains (Cameron 1972; Engelskjøn 1986; Wynn-Williams 2002).

Hypolithons access water from rainwater runoff collected and from condensation on the rock surface during fog and dew events (Bullard 1997; Warren-Rhodes et al. 2006). The overlying rock also serves as a physical impediment to evaporation (Wynn-Williams 2002). The water content of Dry Valleys soils below hypolithon-colonized rocks has been shown to range from 6 to 14 % w/w, with open soils containing significantly less moisture (0.5–2 % w/w) (Smith et al. 2000). Other factors, such as porosity of the rock, have also been shown to help retain moisture (see below) (Friedmann 1980; Kappen et al. 1983).

Water availability in soil has been shown to regulate the upper boundary for growth, while the lower boundary is determined by the light regime, controlled by the translucence of the overlying rock substrate. In Antarctic hypoliths, quartz rocks have been reported to effectively filter UVA and UVB radiation, both potentially detrimental to colonization (Cowan et al. 2010c). Moisture also improves light transmittance through the rock, because light scattering is reduced when all air spaces between mineral particles are filled with water (Vincent 2004).

Extracellular polymeric substances (EPS) have been described for several lithobiontic communities (de los Ríos et al. 2003, 2005a; Pointing and Belnap 2012). The role of EPS is thought to be essential in terms of water relations in lithobionts. Both composition and hygroscopic properties provide a matrix for water absorption and retention and for absorbing organic compounds and ions. de los Rios et al. (2004) have speculated that EPS may be essential both for preserving the microbial populations in lithobionts and for facilitating photosynthesis in endolithic cyanobacteria. Microbial EPS can also promote soil fertility, as the components of the matrix create a mosaic of polyfunctional binding sites that retain excess heavy metals while concentrating growth-promoting nutrients on the sheath (Gadd 1990). The collection and absorption of dew by hypolithons have been quantitatively correlated with EPS abundance (Gorbushina 2007).

9.3.3 Light Availability

The translucence of the rock substrate is critical for refuge lithobiont colonization and growth. Although light transmission through the quartz pebbles of 13–80-mm thickness was filtered to 0.9–2.7 % of the incident sunlight (Broady 1981b), the presence of cyanobacterial-dominated microbial communities is tangible evidence that such low light levels are sufficient to support photoautotrophic processes. Porosity and translucence of the rock substrate are the most important properties which enable colonization in endoliths (Cowan and Ah Tow 2004). The interior surfaces of the rock are characterized by a steep light gradient along depth due to light attenuation by rock substrates (Friedmann 1980). The porosity of rocks ranges from 0 to 50 % and is influenced by many factors such as rock type, the mineral content and grain particle size (Šperl and Trčková 2008).

In the polar regions, it has been reported that the hypolithic colonization of opaque rocks was promoted by local periglacial activities (the freezing and thawing of ground water) which sort rocks and stones into polygonal spatial arrangements, creating openings around the margins of quartz rocks and facilitating the penetration of light to the undersides (Cockell et al. 2002; Cockell and Stokes 2004). The attenuation of light by rocks also assists microbial colonization by effectively reducing UVR stress in refuge lithic niches (Broady 1981b; Cowan et al. 2010c; Wong et al. 2010a).

The extent of light penetration through different rock substrates has been found to determine the abundance of hypolithic colonizations under translucent and opaque rocks (Berner and Evenari 1978). For instance, colonizations under translucent rocks were mostly observed <25 mm thick and up to 40 mm thick, while lower abundances were observed under opaque rocks, generally of <15 mm and up to 30 mm thick (Berner and Evenari 1978). Other authors, e.g. Nienow and Friedmann (1993), found that hypolithic colonizations below quartz rocks ranged from several mm to 60 mm in depth. Microbial colonization beneath thicker rocks is confined to the periphery, as insufficient light to support photosynthesis is transmitted to the community at the base of the rock (Broady 1981b; Schlesinger et al. 2003).

9.4 Microbiology of Lithobionts

Lithobiontic diversity analysis was initially based on microscopic observations of morphological and ultrastructural features of cultured isolates (Friedmann 1980; Friedmann et al. 1988). More recently, culture-independent approaches have allowed a more comprehensive and representative knowledge of the composition of lithobiontic microbial communities (Khan et al. 2011; Smith et al. 2006; Pointing et al. 2009; Chan et al. 2013; Babalola et al. 2009; Makhalanyane et al. 2013a).

9.4.1 Epilith Diversity

Very little is currently known about epilithic microbiology, compared to the endolithic and hypolithic niches. By using culture-dependent approaches we know that *Chroococcidiopsis*, *Myxosarcina*, *Gloeothece*, *Plectonema*, *Lyngbya* and *Calothrix* species are commonly found in epilithic communities in Princess Elizabeth Land and Mawson Rock (Broady 1981a, b). In the same geographical area, 13 epilithic cyanobacterial species were identified (Broady 1989). Epiliths appear to be dominated by cyanobacterial taxa, perhaps as a consequence of their abilities to withstand UV irradiation (Campbell et al. 1998; Castenholz and Garcia-Pichel 2002). Further work, employing modern metagenomic approaches, is required to understand the "true" diversity of epilithic communities.

9.4.2 Endolith Diversity

Free cyanobacteria, together with lichenized structure, have been found to dominate endolithic communities (Friedmann et al. 1988). The cyanobacterium *Choroglea* sp. was detected in translucent gypsum crusts formed on sandstone surfaces on Alexander Island (Hughes and Lawley 2003). In the Taylor Valley, different genera of cyanobacteria, mainly *Chrocooccidiopsis* sp. with some *Cyanothece* cf. a*eruginosa* and *Nostoc* sp. (Büdel et al. 2008), have been identified. Cyanobacteria of the genera *Gloeocapsa* were first described in Victoria Land (Friedmann et al. 1988). Later, Friedmann et al. (1988) distinguished and characterized the diversity of the two types of cryptoendolithic communities inhabiting the Ross Desert: lichen-dominated and cyanobacterial communities. A total of 17 cyanobacteria from the McMurdo Dry Valleys were described. Depending on the dominant cyanobacterium, three communities were observed: *Gloeocapsa*, *Hormathonema–Gloeocapsa* and *Chroococcidiopsis*.

Using molecular techniques, lichenized endolithic communities were shown to be dominated by a single green algal species *Trebouxia jamesii* (de la Torre et al.

2003). *T. jamesii* is a known constituent of lichen associations, such as the lichenized fungal genus *Letharia* (Friedl and Rokitta 1997).

The analysis of the prokaryotic members of the community showed a diverse range of phylotypes related to Actinobacteria, α- and γ-Proteobacteria and Planctomycete species, and an abundance of uncultured bacteria (de la Torre et al. 2003). Clone libraries from endolithic communities showed a high actinobacterial diversity. Endoliths were dominated by cyanobacteria of the *Chroococcidiopsis* lineage (Friedmann 1982) and cyanobacteria morphologically similar to *Gloeocapsa, Plectonema* and *Hormathonema* species (Pointing et al. 2009; Wong et al. 2010b; de la Torre et al. 2003; de los Rios et al. 2004, 2005b).

9.4.3 Hypolith Diversity

The community structure and prokaryote species diversity of hypoliths are the best understood of all the lithobionts (Bahl et al. 2011; Chan et al. 2012, 2013; Cowan et al. 2010b; Khan et al. 2011; Makhalanyane et al. 2013b; Pointing et al. 2009). The prokaryotic composition of Antarctic hypolithons has been assessed using a range of approaches.

A combination of microscopy and culture-independent approaches has identified cyanobacteria as the predominant phylum in hypolithic colonization globally (Bahl et al. 2011; Lacap et al. 2010; Pointing et al. 2007; Stomeo et al. 2013; Warren-Rhodes et al. 2007), including Antarctica's McMurdo Dry Valleys and other ice-free areas (Broady 1981b, 2005; Smith et al. 2000; Pointing et al. 2009). Morphological studies suggest that cyanobacteria found in Antarctica and other cold deserts are dominated by filamentous oscillatorian morphotypes, with a lower species richness than other deserts (Smith et al. 2000; Chan et al. 2012). Communities in the Vestfold Hills showed the presence of oscillatorian cyanobacteria with morphologies typical of the *Lyngbya/Phormidium/Plectonema* group and coccoid cells morphologically similar to *Chroococcidiopsis* (Smith et al. 2000). Hypolithic communities have also been shown to harbour other bacterial phyla such as Actinobacteria, α- and β-Proteobacteria, Planctomycetes, Firmicutes, Acidobacteria and Verrumicrobia (Makhalanyane et al. 2013a; Bahl et al. 2011; Caruso et al. 2011). Archaeal phylotypes recovered were phylogenetically affiliated with a large group of uncultured *Crenarcheota* (Khan et al. 2011).

Although the majority of studies have focused on the bacterial composition in these communities (Bahl et al. 2011; Caruso et al. 2011; Makhalanyane et al. 2013a; Wood et al. 2008), there is evidence that the eukaryotic composition is more complex than initially anticipated (Khan et al. 2011; Gokul et al. 2013; Pointing et al. 2009). Eukaryotic phylotypic analysis showed that free-living ascomycetous fungi, chlorophytes and mosses were present in hypolithons (Khan et al. 2011). A detailed study focusing on the microeukaryotes in all three Antarctic hypolith types reported populations of novel uncharacterized Bryophyta, fungi and protists (Gokul et al. 2013). The presence of these taxa suggests that hypoliths may harbour quite complex food webs and therefore may be important in the cycling of nutrients in the cold desert oligotrophic environment.

Interestingly, it has been suggested that the different Antarctic hypolithic community morphotypes represent sequential stages of succession (Makhalanyane et al. 2013b; Cowan et al. 2010b). The bacterial community compositions of the three hypolith types in the east Antarctic Miers Valley show separate and statistically significant clustering. Using a probabilistic dissimilarity matrix analysis (Makhalanyane et al. 2013b), the species composition (beta-diversity) was shown to vary between different sites and was found to be higher in Type I hypolithons than in Types II and III. These differences suggest that deterministic processes in the bacterial component of hypolithons might increase in the order Type I => Type II => Type III. As it is currently assumed that the effects of stochastic variation may become less important as communities develop over time (Fierer et al. 2010), these findings suggest that the Type I (cyanobacteria-dominated) hypolithic community might be the founder community in the succession process. These patterns have important implications as communities of higher beta-diversity are likely to be vulnerable to climate change (McKnight et al. 2007).

9.5 The Role of Lithobionts in Depauperate Environs

Lithobionts are widely dispersed in depauperate environments (Broady 1981b, 2005; Pointing and Belnap 2012; Chan et al. 2012), and in Antarctic terrestrial ice-free environments lithobiontic are often the only primary producers. Hypoliths, which are by far the most widely distributed Antarctic lithobionts, were shown to cover up to 66 $cm^2 m^{-2}$ in some regions and contributed up to 0.85 mg chlorophyll m^{-2} of total biomass (Broady 1981b). Moreover, in the Arctic, the productivity of hypolithons was estimated to be approximately 0.8 ± 0.3 g m^{-2}. Given the fact that the total average productivity from plants, lichens and bryophytes in the same area was only 1.0 ± 0.4 g m^{-2} (Bliss et al. 1984), hypolithic productivity was estimated to almost double the productivity estimates (Cockell and Stokes 2004). All together these results suggest hypolithic communities potentially represent a major fraction of the total photosynthetic capacity in Antarctic terrestrial ecosystems.

Hypoliths have also been shown to possess the both the genetic and functional capacity for nitrogen fixation (Cowan et al. 2011b). Nitrogenase activity, determined using the acetylene reduction assay, estimated that total contribution of hypolithic communities to the Miers Valley region at approximately 14,200 mmol N $year^{-1}$ (0.38 kg N $year^{-1}$), indicating that these communities are important contributors to fixed nitrogen budgets in Antarctic Desert soils. In consequence, the direct contribution of lithic communities to the total carbon and nitrogen turnover in cold desert ecosystems may be highly significant (Cowan et al. 2011b; Hopkins et al. 2009; Chan et al. 2012).

A recent investigation to establish metabolic capabilities in lithobionts (chasmoendoliths, cryptoendoliths and hypoliths) and open soil from the

McKelvey Valley, using a metagenomic approach with GeoChip-based functional gene arrays, was able to reveal certain functional traits that drive community assembly and microbial survival (Chan et al. 2013). This study identified, for the first time, the primary metabolic pathways in lithobionts and showed a high level of genetic plasticity in autotrophs, heterotrophs and diazotrophs. Important differences were found between the open soil, hypolithic and endolithic communities, with new pathways reported for stress-, thermal-, osmotic-responses and nutrient limitation in lithobionts (Chan et al. 2013). The results of this study add substantially to our knowledge of the critical roles played by lithobionts in the Antarctic Desert ecosystem.

9.6 Concluding Remarks

The apparent simplicity of lithobiontic communities makes them good model systems for studies assessing community origins and evolution, trophic functioning and interspecies relationships, and for addressing wider ecological questions. For example, understanding the assembly patterns in hypoliths could shed light on how microbial guilds in other environments might respond to different stressors. Lithobionts may also be good markers for aridity and climate change and may also serve as “ecosystem engineers” (Chan et al. 2012).

Since the initial explorations of the Antarctic lithobiontic ecological niche, we understand considerably more about the microbial diversity within these communities. We are, however, only beginning to learn about their community function and community dynamics, i.e. beta-diversity patterns and the factors that drive them. Modern “omics-based” approaches are potentially very valuable in revealing both the functional capacities and adaptive potentials of microbial communities. For instance, the coordinated use of proteomic and transcriptomic methods could give insight into key metabolic functions and their responses to macro- and microenvironmental changes. There are, however, severe methodological limitations, not the least that both biomass levels and intrinsic process rates are typically low in in situ Antarctic Desert communities. Such limitations notwithstanding, an understanding of the functional guilds in Antarctic lithobiont communities has a particular significance, as these communities are likely to be the basis for the survival of the entire ecosystem.

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