

# Chapter 4

## Preandean Atacama Desert Endolithic Microbiology



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### 4.1 Introduction

Desert microbial communities are adapted to extreme environmental conditions and are particularly sensitive to climate change (IPCC 2012). In both hot and cold deserts, these communities are subjected to high ultraviolet (UV) and solar radiation, scarcity of water, intense desiccation, strong temperature fluctuations, and oligotrophic conditions (Wierzchos et al. 2012; Billi et al. 2017). As such, they are highly sensitive to perturbation and therefore of great interest for predicting the impacts of today's changing climate. Microorganisms from desert communities are known as extremophiles. They have been used as model systems to investigate the limits of life (Dassarma 2006; Pikuta et al. 2007), and a number of studies have addressed their metabolic diversity and survival strategies (Dassarma 2006; Pointing and Belnap 2012; Wierzchos et al. 2018). Additionally, because the most arid deserts around the world (Atacama, Antarctica, Mojave, The Qaidam Basin) are analogues for Mars' environment, the study of desert extremophiles might help guide our search for life elsewhere (Fairén et al. 2010; Foing et al. 2011; Smith et al. 2014; Xiao et al. 2017; Bull et al. 2018). More recently, extremophiles have gained interest in applied research as potential sources for high-value bioactive compounds due to their ability to resist extreme environmental conditions (Finore et al. 2016; Stan-Lotter and Fendrihan 2017; Neifar et al. 2015).

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In the world's arid and hyperarid deserts, microorganisms find refuge inside rock substrates as a survival strategy, colonizing what is known as the endolithic habitat (Golubic et al. 1981; Wierzchos et al. 2012). There are many examples of these endolithic microbial communities (EMCs), which are photosynthetic-based with primary producers supporting a diversity of heterotrophic microorganisms (Friedmann 1980; Friedmann et al. 1988; De Los Ríos et al. 2005, 2014; Dong et al. 2007; Schmidt et al. 2011; Wei et al. 2015) and more specifically in the Atacama Desert (Wierzchos et al. 2006, 2011, 2013, 2015; DiRuggiero et al. 2013; Robinson et al. 2015; Crits-Christoph et al. 2016a, b; Meslier et al. 2018).

Several ecological properties of EMCs, initially proposed by (Friedmann and Ocampo-Friedmann 1984) and summarized by (Walker and Pace 2007) include:

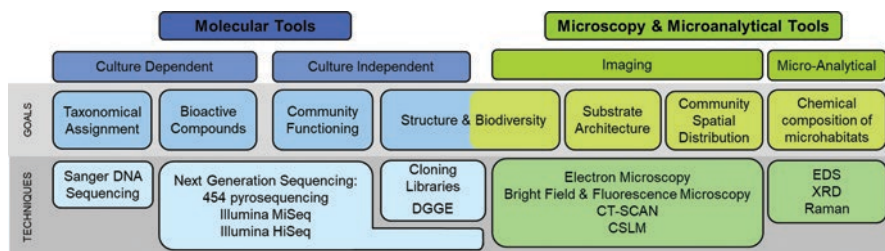
- (a) EMCs are among the simplest microbial ecosystems.
- (b) EMCs are characterized by a core group of microorganisms that co-occur within a defined habitat.
- (c) The extreme endolithic environment is seeded from a relatively small reservoir of microorganisms highly adapted to this unique environment.
- (d) The composition of EMCs is influenced by biogeography and environmental factors such as the physical and chemical properties of substrates and climate.

Most studies of EMCs from the Preandean Depression of the Atacama Desert have focused on the determination of (1) the diversity, structure, and composition of the communities (who is there?) (Crits-Christoph et al. 2016b; Meslier et al. 2018; DiRuggiero et al. 2013), (2) the physicochemical structure of the substrate, also called the architecture, and the spatial organization of the community within that substrate (where are they?) (Wierzchos et al. 2018; Meslier et al. 2018; Cámara et al. 2015), and (3) adaptation strategies at the community and/or cellular levels (how are they able to survive?) (Wierzchos et al. 2015; Vitek et al. 2016, 2017).

In this chapter we will focus on the diversity, structure, and composition of EMCs from the Preandean zone of the hyperarid Atacama Desert, emphasizing the need to comprehensively address the diversity of these communities while considering the principles underlying their assembly, such as low-complexity, highly adapted microbiota, and influences of the biogeography, climate, and rock properties.

## 4.2 A Multidisciplinary Approach for Describing EMCs Structure, Composition, and Spatial Arrangement

The first reports on EMCs from hyperarid deserts involved the use of direct microscopy methods to visualize the microbe-rock interface and the endolithic settings (Wierzchos and Ascaso 2001 and references therein). At the time, EMCs were mostly characterized by their phototrophic members (prokaryotic- or eukaryotic-based communities), because of the difficulty in identifying heterotrophic members solely based on their morphology (Friedmann et al. 1988; De Los Ríos et al. 2014).



**Fig. 4.1** Research tools used to study EMCs classified by techniques and specific goals

Early identifications of the heterotrophic component of EMCs were performed using culture-based methods (Hirsch et al. 1988; Siebert and Hirsch 1988), but because of the limitations of these methods, their diversity remained largely unexplored at the time. The emergence of high-throughput sequencing tools has deeply changed our view of microbial diversity across ecosystems, including that of the endolithic habitat (Walker and Pace 2007). Nowadays, characterization of EMCs, including those found in the Preandean area of the Atacama Desert, is routinely done with a multidisciplinary approach that involves sophisticated microscopy and molecular tools (Fig. 4.1).

The main contributions of microscopy and microanalytical tools to the study of EMCs have been the visualization and characterization of the microhabitat, including the spatial distribution of the microorganisms within. Scanning electron microscopy in backscattered electron mode (SEM-BSE) was essential in defining the different endolithic microhabitats and type of colonization, enabling one to distinguish (1) the cryptoendolithic habitat (Golubic et al. 1981), where microorganisms colonized the pore spaces of the lithic substrate, (2) the chasmoendolithic habitat (Golubic et al. 1981) characterized by colonized cracks and fissures, and (3) the hypoendolithic habitat (Wierzchos et al. 2011), where the colonization is located underneath the lithic substrate. This method has also provided invaluable information on the distribution of the microorganisms within each of these microhabitats (Wierzchos et al. 2011, 2013, 2018; Cámara et al. 2015; Crits-Christoph et al. 2016b; DiRuggiero et al. 2013; Meslier et al. 2018) and, together with computed tomography scanning (CT-Scan), allowed the description of the substrate's architecture (Wierzchos et al. 2018). The concept of the substrate's architecture has been defined as the space available for colonization and includes the pores, fissures, and cracks of the substrate and how they are connected to the surface (Wierzchos et al. 2015). The use of SEM at low temperatures (LTSEM) brought additional information, such as cytological identification of cells in situ and the characterization of their ultrastructural features (Wierzchos and Ascaso 2001). Other microscopy methods such as bright field microscopy provided the identification of the major phototrophic members (Wierzchos and Ascaso 2001; Wierzchos et al. 2013, 2015), while fluorescent microscopy and confocal laser scanning microscopy (CSLM) gave us essential information about the metabolic status of the microorganisms inhabiting EMCs. In particular, these methods revealed assemblages of live and intact dead

cells (Wierzchos et al. 2011) and the spatial organization of cyanobacterial aggregates surrounded by extracellular polymeric substances (EPSs) (Crits-Christoph et al. 2016a, b; Robinson et al. 2015) and embedded in a matrix of heterotrophic microorganisms (Wierzchos et al. 2011). Microanalytical tools such as SEM-BSE and energy dispersive X-ray spectroscopy (EDS) have revealed the spatial arrangements of microbial cells around sepiolite nodules in gypsum rocks (Wierzchos et al. 2015; Meslier et al. 2018). This is of great significance because sepiolite is a mineral with high efficiency for water retention. X-ray powder diffraction (XRD) has also provided the mineral composition of many different lithic substrates, such as calcite, ignimbrite, and gypsum (Wierzchos et al. 2015; Meslier et al. 2018), and Raman spectroscopy has been used to characterize the distribution of pigments in the endolithic microhabitat of gypsum, ignimbrite, and halite (Vítek et al. 2010, 2013, 2014a, b, 2016, 2017).

Microscopy tools combined with culture-independent methods such as denaturing gradient gel electrophoresis (DGGE) (Wierzchos et al. 2013; Cámara et al. 2015) and, more recently, next generation sequencing (NGS) (DiRuggiero et al. 2013; Meslier et al. 2018; Crits-Christoph et al. 2016b; Wierzchos et al. 2015) have been used to characterize the phylogenetic diversity of EMCs. Pioneer studies revealed the discrepancies of biomass estimates between microscopy and molecular methods. For example, Dong et al. (2007) reported that cyanobacteria in gypsum endolithic communities represented 95% of the community when using microscopy, whereas the number fell to 40% when molecular methods were used. They suggested that those differences were potentially the result of contamination, the difficulty in isolating DNA from cyanobacteria, and the bias introduced by amplification of the DNA by PCR (Dong et al. 2007). Today, molecular tools such as amplicon sequencing of marker genes (i.e., 16S rRNA gene) and whole genome shotgun sequencing (WGS), combined with microscopy methods, have led to a more complete description of the endolithic microbiome. Habitats for these microbiomes include (1) the chasmoendolithic habitat of calcite (DiRuggiero et al. 2013; Meslier et al. 2018; Crits-Christoph et al. 2016b) and granite (Meslier et al. 2018) and (2) the cryptoendolithic habitat found in gypsum (Wierzchos et al. 2015; Dong et al. 2007; Meslier et al. 2018) and ignimbrite (Wierzchos et al. 2012; Cámara et al. 2015; Crits-Christoph et al. 2016b; Meslier et al. 2018) (Table 4.1).

Some of the most diverse EMCs found in the Preandean Atacama Desert are that of gypsum from Cordón de Lila and Tilocalar (Table 4.1). Phototrophs in these communities included *Cyanobacteria* (36–83%) and algae belonging to the *Chlorophyta* class. The algae were only detected at very low abundance, first by microscopy (Wierzchos et al. 2015), and their occurrence was later confirmed by cloning of the 18S rRNA gene and by metagenome sequencing (Meslier, pers. com.). Major heterotrophic bacteria of the gypsum EMCs included *Actinobacteria* (10–25%) and *Proteobacteria* (13–30%) and at lower relative abundance *Chloroflexi* (0–11%) and *Gemmatimonadetes* (0–6%) (Table 4.1).

Another high diversity EMC of the Preandean area of the Atacama Desert is the chasmoendolithic community of calcite from the nearby Valle de la Luna area. In this substrate, primary producers were exclusively *Cyanobacteria* with a relative

**Table 4.1** Endolithic microbial communities found in lithic substrates from the Preandean area of the Atacama Desert: main members and relative abundances in the community

| Substrate  | Shannon Index | Main phyla relative abundance (%) |                       |                       |                    |                         | Other phyla detected | References      |
|------------|---------------|-----------------------------------|-----------------------|-----------------------|--------------------|-------------------------|----------------------|-----------------|
|            |               | <i>Cyanobacteria</i>              | <i>Actinobacteria</i> | <i>Proteobacteria</i> | <i>Chloroflexi</i> | <i>Gemmatimonadetes</i> |                      |                 |
| Gypsum     | 2.2–6.1       | 36–83                             | 10–25                 | 13–30                 | nd–11              | <5–6                    | ns                   | [1] [4] [5] [7] |
| Calcite    | 3.7–6.1       | 50–60                             | 10–20                 | 3–5                   | nd–10.9            | <5–15                   | nd                   | [1] [2] [5]     |
| Ignimbrite | 4.3–4.9       | ns - 80                           | 5–14                  | < 5                   | <5–11              | <1                      | nd                   | [1] [2] [3] [6] |
| Granite    | 3.8           | 77                                | 17                    | 0.3                   | 4                  | <1                      | nd                   | [1]             |

Abbreviations: *ns* not specified, *nd* not detected. [1] Meslier et al. (2018), [2] Critis-Christoph et al. (2016b), [3] Cámara et al. (2015) [4] Wierzechos et al. (2015), [5], DiRuggiero et al. (2013), [6] Wierzechos et al. (2012), [7] Dong et al. (2007)

abundance of 50 to 60%, while the heterotrophs included *Actinobacteria* (10–20%), *Proteobacteria* (3–5%), *Chloroflexi* (0–11%), and *Gemmatimonadetes* (0–15%) (Table 4.1). Using WGS Crits-Christoph et al. (2016b) identified additional heterotrophic bacteria with significant occurrence, such as *Deinococcus–Thermus* and *Bacteroidetes*.

EMCs from ignimbrite and granite were found to harbor significantly less diverse communities than other EMCs of the Preandean Atacama. In these substrates, *Cyanobacteria* were the only primary producers, reaching relative abundances of 80% and 77% in ignimbrite and granite, respectively, while *Proteobacteria* relative abundances dropped below 5% in the ignimbrite community and below 1% in the granite community (DiRuggiero et al. 2013; Crits-Christoph et al. 2016b; Meslier et al. 2018). The low relative abundance of heterotrophic bacteria in these EMCs might be the result of phototrophs' low metabolic activity in the harshest environments, leading to a reduced amount of fixed inorganic carbon and limiting, in turn, the abundance and diversity of the heterotrophic component of the community (Wierzechos et al. 2018; Meslier et al. 2018).

Abiotic factors promoting the diversity and composition of EMCs in the Preandean Atacama have been investigated by a number of multidisciplinary approaches (DiRuggiero et al. 2013; Wierzechos et al. 2015; Crits-Christoph et al. 2016b; Meslier et al. 2018). These studies have shown that the rock architecture, i.e., the space available for colonization, embodied by the size of the cracks, fissures, and pores and their connection to the surface, which is tightly linked to substrate water retention capacities, were the main drivers of community structure and diversity. In addition, specific properties of the substrates were also found to confer beneficial advantages to the EMCs; these include sepiolite nodules in gypsum, which considerably increase the water retention capability of the substrate, or the high thermal conductivity of calcite, promoting dewfall formation (DiRuggiero et al. 2013; Wierzechos et al. 2015; Crits-Christoph et al. 2016b; Meslier et al. 2018).

By colonizing rock substrates, EMCs find protection from the extremely intense solar irradiance found in hyperarid deserts (Rondanelli et al. 2015). Additional adaptation strategies, in particular against the deleterious effects of UV, include protective cell-layering, an array of screening pigments, and lipid production by phototrophs (see below; Vítek et al. 2013, 2016, 2017; Wierzechos et al. 2015, 2018). While UV can be significantly attenuated by the substrate, the decline in visible light transmission occurs at a much lower rate, providing sufficient light for photosynthesis (Hughes and Lawley 2003; Amaral et al. 2006). Meslier et al. (2018) measured the light transmittance in several substrates from the Preandean Atacama and found a direct relationship between the spectral properties of the substrate and the depth of the colonization zone; higher light transmitting substrates (calcite, gypsum, and granite) showed EMCs located deeper in the substrate, while EMCs from ignimbrite were located closer to the surface (Meslier et al. 2018).

The recent use of metagenomics has brought insights into the adaptation of EMCs to their unique environment. The functional analysis of calcite and ignimbrite EMCs revealed a broad diversity of stress response pathways, especially linked to survival under harsh conditions (Crits-Christoph et al. 2016b). These pathways

were involved in (1) carbon starvation and low-nutrient stress, (2) cold shock genes, (3) oxidative stress genes related to osmotic stress/desiccation tolerance, and (4) secondary metabolites production (Crits-Christoph et al. 2016b). Using comparative metagenome analysis, the authors found that the ignimbrite community was significantly enriched in non-ribosomal peptide synthase (NRPS) and polyketide synthase (PKS) genes, suggesting a highly competitive environment for resources and space. The large number of gene clusters related to iron acquisition in the ignimbrite community also suggested iron starvation, while the presence of mycosporine-like gene clusters in the calcite community, but not in the ignimbrite community, indicated possible differences in UV radiation exposure of the EMCs (Crits-Christoph et al. 2016b). The differential abundances of secondary metabolites demonstrate the key role played by the substrate in the molecular adaptations of community members. Surprisingly, pathways for nitrogen fixation were not found in the metagenome of any of the Atacama EMCs investigated so far (Crits-Christoph et al. 2016a, b; Finstad et al. 2017). It is likely that the long-term accumulation of nitrate in the Atacama Desert, via atmospheric deposition, provides a major source of nitrogen to microbial communities in the form of nitrate and ammonium (Michalski et al. 2004; Crits-Christoph et al. 2016b; Finstad et al. 2017).

As demonstrated by the discussion above, only a comprehensive approach to the study of EMCs, using a combination of methods and tools, will allow for the elucidation of the mechanisms that generate and maintain their diversity.

### 4.3 Supporting the Microbial Community: Photoautotrophs as Primary Producers

Phototrophs are essential for the survival of EMCs because they are the only primary producers in a system where the import of exogenous organic carbon is negligible. As such, *Cyanobacteria* and microalgae carry essential functions in EMCs.

Phototrophic microorganisms perform oxygenic photosynthesis via two photosystems, PSI and PSII, connected by an electron transfer chain, similar to plants (Falkowski and Raven 2013). In oxygenic photosynthesis, photons collected by antenna complexes coupled to photosystems are transferred to chlorophyll molecules located in the photosystem core. This photon energy is used to break water molecules producing reduced nicotinamide adenine dinucleotide phosphate (NADPH) with oxygen as a by-product. In a subsequent step, NADPH is used to synthesize organic carbon from carbon dioxide via the Calvin cycle. The two main elements required for oxygenic photosynthesis, liquid water and light, are often limiting factors for the chlorophototrophs inhabiting endolithic substrates in hyper-arid deserts. Endolithic phototrophs can only perform photosynthesis during periods of time when liquid water is available and, because of high solar and UV radiations, they also need to use strategies to prevent photo-inhibition and photo-oxidative damage to their photosystems (Vítek et al. 2013, 2016, 2017; Wierzechos



et al. 2015, 2018). While substrate colonization at greater depths inside the rock might give access to more retained water and increase protection against damaging UV irradiation, it might also decrease essential requirements for photosynthesis such as photosynthetic active radiation and CO<sub>2</sub> exchange (Boison et al. 2004; Rothschild et al. 1994). An example of such a strategy is the spatial arrangement of *Cyanobacteria* within Preandean EMCs habitats (Meslier et al. 2018) and will be discussed below.

### 4.3.1 *Cyanobacteria*

*Cyanobacteria* are found in most types of illuminated environment and were responsible for the “Great Oxidation Event” 2.4–2.1 billion years ago (Lyons et al. 2014). Their success as primary producers is due to several essential features (Whitton and Potts 2000).

- (a) Their temperature optimum is higher by several degrees than that of most eukaryotic algae (Castenholz and Waterbury 1989), allowing them to colonize warmer environments.
- (b) Desiccation and water stress tolerance made them some of the most successful organisms in hypersaline environments (Hu et al. 2012; Oren 2012).
- (c) They display high tolerance to high levels of UV light radiation (Castenholz and Garcia-Pichel 2012).
- (d) They can perform efficient photosynthetic CO<sub>2</sub> reduction with low concentrations of inorganic carbon (Pierce and Omata 1988; Raven 2012).

Most of the *Cyanobacteria* in EMCs from the Atacama Desert are members of *Chroococcidiopsis* (Wierzbos et al. 2011, 2015, 2018; Vitek et al. 2013, 2016, 2017; DiRuggiero et al. 2013; Cámara et al. 2015; Crits-Christoph et al. 2016b; Meslier et al. 2018). This cyanobacterial genus from the *Chroococcidiopsiales* order (Komarek et al. 2014) is the most abundant cyanobacteria in hyperarid environments where its adaptability to extreme conditions has been widely demonstrated (Smith et al. 2014). *Chroococcidiopsis* are often accompanied by other cyanobacterial taxa including members of other unicellular orders such as *Chroococcales* and *Synechococcales*, and even members from filamentous orders such as *Oscillatoriales* and *Nostocales* (Table 4.2). Despite the detection of other cyanobacterial genus, *Chroococcidiopsis* is the only genus that has been consistently detected in all EMCs using microscopy approaches (Table 4.2). This discrepancy between molecular and microscopy methods with regard to cyanobacterial diversity is the result of a number of factors.

First, there is a technical factor associated with the evolution of research tools over the past decade, from DGGE to clone libraries and more recently to high-throughput sequencing platforms (454 pyrosequencing, Illumina-MiSeq, Illumina HiSeq). Additionally, all these methods have intrinsic limitations with DNA isolation, the selection of marker genes and their primers, library preparation, read



**Table 4.2** Cyanobacterial taxa in endolithic microbial communities from the Preandean area of the Atacama Desert and the approaches used for their detection

| Order                | Genus                    | Tools used for cyanobacterial detection |            | Substrate        | References                     |
|----------------------|--------------------------|---|------------|------------------|--------------------------------|
|                      |                          | Molecular                               | Microscopy |                  |                                |
| Chroococcidiopsiales | <i>Chroococcidiopsis</i> | X                                       | X          | Gyp Ca<br>Ign Gr | [1] [2] [3] [4]<br>[5] [6] [7] |
| Chroococcales        | <i>Gloeocapsa</i>        | X                                       |            | Ca               | [2]                            |
|                      | <i>Halothece</i>         | X                                       |            | Gyp Ca           | [1]                            |
| Synechococcales      | <i>Acaryochloris</i>     | X                                       |            | Ca               | [2]                            |
|                      | <i>Synechococcus</i>     | X                                       |            | Gyp Ca           | [1]                            |
| Oscillatoriales      | <i>Aerosakkonema</i>     | X                                       |            | Gyp Ca<br>Ign Gr | [1]                            |
|                      | <i>Phormidium</i>        | X                                       |            | Ca               | [5]                            |
| Nostocales           | <i>Anabaena</i>          | X                                       |            | Gyp Ca           | [5]                            |

Abbreviations: *Gyp* gypsum, *Ca* calcite, *Ign* ignimbrite, *Gr* granite. [1] Meslier et al. (2018), [2] Crits-Christoph et al. (2016b), [3] Cámara et al. (2015), [4] Wierzchos et al. (2015), [5] DiRuggiero et al. (2013), [6] Wierzchos et al. (2012) [7] Dong et al. (2007)

length, and sequencing depth. Each of these steps can introduce significant biases that make it very difficult to compare studies (Rastogi and Sani 2011). The analysis of the sequencing data may also introduce significant biases with, in particular, the choice of parameters in defining unique taxa and the type of database (and its version) used for taxonomic annotation. While culture-independent methods have provided a large amount of sequencing information, especially during the past few years with NGS platforms, the increasing number of sequences in databases that belong to “uncultured cyanobacterium clone” seriously hinders accurate taxonomical assignments of this phylum. On the other hand, taxonomical assignment using microscopic methods is limited to morphologically different *Cyanobacteria*, their relative abundances in the sample, and requires a great deal of experience.

Another issue is the fact that the taxonomy and phylogeny of *Cyanobacteria* is an ongoing discussion, especially because of their antiquity, existing fossil representatives with very similar morphology to present-day species (William Schopf 1974; Knoll 2008), and a complex evolutionary history. Several features, in addition to genetic sequences, should be taken into account when defining cyanobacterial taxa, including morphological characteristics, ultrastructural details such as thylakoid structure, and type of cell division (Komarek et al. 2014). This is essential for accurate *Cyanobacteria* taxonomy assignment but is not always practical, in particular, in studies with large numbers of samples.

Several adaptation strategies to water stress have been described for *Chroococcidiopsis*. For one, *Chroococcidiopsis* belongs to the group of anhydrobiotic cyanobacteria. These cyanobacteria cope with the lack of water by entering an ametabolic state involving structural, physiological, and molecular changes (Feofilova 2003). Another adaptation to the scarcity of water is the production of

EPSs providing a depository for water and stabilizing desiccation-related enzymes and molecules (Wright et al. 2006).

To protect themselves from the damaging effects of UV radiation, *Chroococcidiopsis* from EMCs of the Preandean Depression synthesize UV-absorbing and/or screening compounds. One such compound, the sunscreen pigment scytonemin, has been detected in the EPS sheath of EMCs from gypsum from the Preandean Depression and other hyperarid regions of the Atacama Desert (Wierzychos et al. 2015; Vítek et al. 2014a, 2016). It has also been hypothesized that the simultaneous exposure to both desiccation and UV radiation may further induce scytonemin biosynthesis (Fleming and Castenholz 2007). Recently, a novel light-adaptation strategy was discovered in *Cyanobacteria* inhabiting ignimbrite rocks (Vítek et al. 2017). The authors attributed the shift in carotenoid composition (red-shift of  $\nu_1$  (C=C) band) in the cyanobacteria to a light-dependent change in carotenoid conjugation that would mediate a non-photochemical quenching mechanism (Kirilovsky and Kerfeld 2016). Since *Cyanobacteria* are major components of EMCs, and are most often located in the upper part of the endolithic microhabitat, the strategies developed by this phylum to deal with extreme environmental conditions constitute a benefit for the entire community.

### 4.3.2 *Eukaryotic Phototrophs*

Eukaryotic microalgae constitute a basic component of the world's ecosystems as they contribute to about 40% of global productivity (Andersen 1992). Apart from their important role in marine ecosystems, they are found as important primary producers in desert soils (Lewis and Lewis 2005) and in lithic microhabitats as free-living organisms (Meyer et al. 1988; Robinson et al. 2015; Wierzychos et al. 2015; Vítek et al. 2016) or as photobionts of lichens (Palmer Jr and Friedmann 1990; Wierzychos et al. 2011).

While most endolithic communities in the Preandean Depression do not harbor microalgae, their occurrence has been reported in gypsum from the Cordón de Lila depression (Wierzychos et al. 2015). The authors suggested that while these algae have morphological similarity with three genera of *Chlorophyta* (*Spongiochloris*, *Deasonia*, and *Neochloris*), they also have novel features, in situ and in culture, and therefore should be classified as a new genus of the *Chlorophyceae* class. Similar to *Cyanobacteria*, EMCs' algae show special strategies to deal with environmental stresses such as the accumulation of photoprotective carotenoids and storage lipids (Wierzychos et al. 2015; Vítek et al. 2016). In gypsum, both carotenoid and storage lipids increased in algal cells with their closeness to the surface of the substrate where solar radiation is the highest (Wierzychos et al. 2015; Vítek et al. 2016). Carotenogenesis has also been attributed to photoprotection against high solar radiation (Oren et al. 1995) and also as a strategy to mitigate high salinity and nutrition stresses in other aerial microalgae (Aburai et al. 2015; Oren et al. 1995; Hanagata and Dubinsky 1999). In gypsum of Cordón de Lila, the algae were located in the

upper part of the substrate (with first red and then green cells) followed by *Cyanobacteria*. This very special arrangement suggests that they may act as a protective barrier for the community against the harmful effects of high levels of solar radiation because of their high carotenoids content (Vítek et al. 2017).

#### 4.4 Diversity of Heterotrophs in Communities of the Preandean Depression of the Atacama Desert

Before the use of molecular tools to characterize EMCs, heterotrophic members of these communities received little attention compared to their phototrophic counterparts. This was most likely because of the difficulty in characterizing heterotrophic bacteria morphologically and also because of the idea that the main contributors to the activity and resilience of EMCs were primary producers. Indeed, heterotrophic microorganisms benefit from photosynthetic conversion of CO<sub>2</sub> into organic carbon, provided either by *Cyanobacteria* or microalgae. Nonetheless, investigations of the diversity and community structure of EMCs have since revealed far more diverse heterotrophic assemblages than previously thought (Walker and Pace 2007; Dong et al. 2007; Lacap et al. 2011; DiRuggiero et al. 2013; Crits-Christoph et al. 2016b; Meslier et al. 2018), emphasizing the idea that primary producers can nurture and support the development of a high diversity of heterotrophic microorganisms.

In EMCs of the Preandean Atacama Desert, the most abundant heterotrophic phyla have been assigned to *Actinobacteria*, *Chloroflexi*, and *Proteobacteria*, although additional phyla such as *Bacteroidetes*, *Gemmatimonadetes*, *Deinococcus-Thermus*, *Firmicutes*, *Planctomycetes*, and *Verrucomicrobia* have also been consistently reported in several lithic substrates (Table 4.3) (Dong et al. 2007; DiRuggiero et al. 2013; Rasuk et al. 2014; Wierzchos et al. 2015; Crits-Christoph et al. 2016b; Meslier et al. 2018). In contrast, arid and hyperarid soils are typically dominated by sparse heterotrophic microorganisms with mostly members of the *Actinobacteria* phylum (Costello et al. 2009; Bull 2011; Lynch et al. 2012, 2014; Neilson et al. 2012; Crits-Christoph et al. 2013; Schulze-Makuch et al. 2018). While the recent sequencing of the genome of *Pseudonocardia* sp. from a volcanic soil showed that chemoautotrophic microbes may provide organic carbon to a community, it was a rather specific case where trace gases from volcanic activity provided the energy sources for carbon fixation (Lynch et al. 2014).

In the *Actinobacteria* phylum, the main identified taxa included *Blastococcus*, *Geodermatophilus*, *Modestobacter*, *Jatrophihabitans*, *Marmoricola*, *Microlunatus*, *Pseudonocardia*, *Euzebya*, *Solirubrobacter*, *Conexibacter*, and *Rubrobacter* genera, for which the relative abundances could vary greatly between substrates (Table 4.3). For the most part, these genera were also consistently recovered in lithic substrates and soils of hyperarid deserts around the world (Connon et al. 2007; Lacap et al. 2011; DiRuggiero et al. 2013; Crits-Christoph et al. 2013, 2016b; Wierzchos et al. 2015; Meslier et al. 2018; Bull et al. 2018) and recognized for their

**Table 4.3** Major heterotrophic taxa detected in calcite (Ca), gypsum (Gy), ignimbrite (Ig), and granite (Gr) substrates from Preandean Depression of the Atacama Desert

| Phylum             | Class              | Order                  | Family                     | Ca                            | Gy                         | Ig            | Gr             | References  |             |
|--------------------|--------------------|------------------------|----------------------------|-------------------------------|----------------------------|---------------|----------------|-------------|-------------|
| Actinobacteria     | Acidimicrobia      | Acidimicrobiales       | Other/uncultured           | d(+)                          | d(+)                       | d(-)          | d(-)           | [1]         |             |
|                    |                    | Frankiales             | Frankiaceae                | d(+)                          | d(-)                       | d(-)          | d(+)           | [1] [2]     |             |
|                    | Actinobacteria     |                        |                            | Geodermatophilaceae           | d(+)                       | d(+)          | d(+)           | d(+)        | [1]         |
|                    |                    |                        |                            | Other/uncultured              | d(+)                       | d(+)          | d(+)           | d(+)        | [1]         |
|                    |                    |                        |                            | Intrasporangiaceae            | nd                         | d(-)          | d(-)           | d(+)        | [1]         |
|                    |                    |                        |                            | Nocardioidaceae               | d(+)                       | d(+)          | d(+)           | d(+)        | [1]         |
|                    |                    |                        |                            | Propionibacteriaceae          | d(+)                       | d(+)          | d(-)           | d(+)        | [1] [2]     |
|                    |                    |                        |                            | Pseudonocardiales             | d(+)                       | d(+)          | d(-)           | d(-)        | [1]         |
|                    |                    |                        |                            | Euzeyales                     | d(+)                       | d(+)          | d(+)           | d(-)        | [1]         |
|                    |                    |                        |                            | Rubrobacterales               | d(+)                       | d(+)          | d(+)           | d(+)        | [1] [2] [4] |
|                    |                    |                        |                            | uncultured bacterium          | d(+)                       | d(+)          | d(-)           | d(-)        | [1]         |
|                    |                    |                        |                            | Gaellales                     | d(-)                       | d(+)          | d(-)           | nd          | [1]         |
|                    |                    |                        |                            | Solirubrobacterales           | d(-)                       | d(+)          | d(-)           | nd          | [1]         |
|                    |                    |                        |                            | uncultured bacterium          | d(+)                       | d(+)          | d(+)           | d(+)        | [1]         |
|                    |                    |                        |                            | Conexibacteraceae             | d                          | nd            | d              | nd          | [1]         |
|                    |                    |                        |                            | Other(0319-6M6, S1-80, 480-2) | d(+)                       | d(+)          | d(+)           | d(+)        | [1]         |
|                    |                    |                        |                            | Chloroflexi                   | Chloroflexi Incertae Sedis | Unknown Order | Unknown family | d(+)        | d(+)        |
| Chloroflexia       | Chloroflexia       | Kallotenuales          | AKI781/Other               | d(+)                          | d(+)                       | d(+)          | d(+)           | [1]         |             |
| Thermomicrobia     | Thermomicrobia     | AKYG1722, JG30-KF-CM45 | Other/uncultured bacterium | d(+)                          | d(+)                       | d(+)          | d(+)           | [1] [2] [4] |             |
| Other <sup>†</sup> | Other <sup>†</sup> |                        |                            | d(+)                          | d(+)                       | d(-)          | d(-)           | [1]         |             |

|                |                          |                  |                                   |             |             |             |             |                  |  |
|----------------|--------------------------|------------------|-----------------------------------|-------------|-------------|-------------|-------------|------------------|--|
| Proteobacteria | $\alpha$ -Proteobacteria | Caulobacterales  | Caulobacteraceae                  | <b>d(+)</b> | <b>d(+)</b> | d(-)        | nd          | [1] [4]          |  |
|                |                          | Rhizobiales      | Methylobacteriaceae               | <b>d(+)</b> | <b>d(+)</b> | d(-)        | d(-)        | [1] [4]          |  |
|                |                          |                  | Rhizobiaceae                      | d(-)        | <b>d(+)</b> | d(-)        | nd          | [1] [3]          |  |
|                | $\beta$ -Proteobacteria  | Sphingomonadales | Other (D05-2, JG34-KF-361, P-102) | <b>d(+)</b> | <b>d(+)</b> | d(-)        | d(-)        | [1] [4] [5]      |  |
|                |                          |                  | Sphingomonadaceae                 | <b>d(+)</b> | <b>d(+)</b> | d(-)        | d(-)        | [1], [3] [4] [5] |  |
|                |                          |                  | Other (Ellin6055, JG34-KF-161)    | <b>d(+)</b> | <b>d(+)</b> | <b>d(+)</b> | <b>d(+)</b> | [1]              |  |
|                |                          |                  | Burkholderiales                   | d           | <b>d(+)</b> | d           | nd          | [1] [4]          |  |
|                |                          |                  | Methylococcales/Other             | d           | d           | d           | nd          | [4] [5]          |  |
|                | $\gamma$ -Proteobacteria |                  |                                   |             |             |             |             |                  |  |

Abbreviations: *d* detected taxa, *nd* not detected; (+) relative abundance average > 1.10E-3; (-), relative abundance average < 1.10E-3. <sup>a</sup>Other Chloroflexi comprising taxa belonging to TK10, Gitt-GS-136, JG30-KF-CM66 and KD4-96. Data covering the Preandean Depression of the Atacama Desert are from Meslier et al. (2018) [1], completed by Crits-Christoph et al. (2016b) [2], Wierzechos et al. (2015) [3], DiRuggiero et al. (2013) [4] and Dong et al. (2007) [5]

ability to resist extreme desiccation (*Geodermatophilus*, *Blastococcus*, *Rubrobacter*), high UV and ionizing radiation (*Geodermatophilus*, *Rubrobacter*, *Modestobacter*), oligotrophic conditions (*Modestobacter*, *Rubrobacter*), temperature fluctuations (*Modestobacter*, *Rubrobacter*), high salinity (*Marmoricola*, *Pseudonocardia*), and high concentrations of metals (*Rubrobacter*) (Bull 2011; Mohammadipanah and Wink 2016; Idris et al. 2017; Schulze-Makuch et al. 2018; Bull et al. 2018). The identification and characterization of *Actinobacteria* from the extreme biosphere have been of particular interest over the past decade because of their incredible potential as sources of novel bioactive compounds for agricultural, pharmaceutical, and industrial applications (Bull 2011; Mohammadipanah and Wink 2016; Idris et al. 2017; Rateb et al. 2018). Indeed, some researchers argue that most of the novel chemical diversity will likely be discovered in the rare actinobacterial biosphere (Mohammadipanah and Wink 2016). Although culture-dependent methods are challenging, and only reveal a fraction of the microbial diversity in any given environment, they are necessary for the discovery and production of bioactive compounds.

Members of the *Chloroflexi* phyla, such as *Thermobaculum* and *Thermomicrobia*, and various genera of *Proteobacteria*, mainly from the *alpha*-, *beta*-, and *gamma*-*proteobacteria* (*Methylobacterium*, *Ensifer*, *Sphingomonas*, and *Burkholderia*) are known to be anoxygenic photosynthesizers (Table 4.3). However, no anoxygenic photosynthesizers have been found so far in EMCs from the Preandean area of the Atacama Desert (Crits-Christoph et al. 2016b; Frigaard 2016; Meslier et al. 2018). *Chloroflexi* relative abundances in various desert soils and lithic habitats are highly variable (Lacap et al. 2011; Neilson et al. 2012) and, although unique adaptive traits have been reported, such as atypical peptidoglycan contents, their functional role remains to be elucidated (Neilson et al. 2012).

Variations in the detection and relative abundances of members of the *Proteobacteria* have also been reported in desert soils and lithic communities, yet, some genera display several putative functional advantages for survival in hyperarid deserts (Drees et al. 2006; Dong et al. 2007; Connon et al. 2007; Neilson et al. 2012; Crits-Christoph et al. 2013; Rasuk et al. 2014; Makhallanyane et al. 2015; Van Goethem et al. 2017). Some examples include (1) members of the *Methylobacterium* genus known to use methanol as both carbon and energy source (Makhallanyane et al. 2015), (2) members of the *Burkholderia* genus, a common soil inhabitant that promotes plant growth via nitrogen fixation (Coenye and Vandamme 2003; Suárez-Moreno et al. 2012; Stopnisek et al. 2016), and (3) members of the *Ensifer* genus that harbor mineral weathering activity, such as potassium feldspar-solubilization, and potential nitrogen fixation (Rogel et al. 2001; Wang et al. 2016; Peng et al. 2017). Recently, the combined use of metagenomics and metatranscriptomics in hypoliths from the Namib Desert demonstrated the close relationship between active members of *Cyanobacteria* and *alpha-Proteobacteria* and their key role in maintaining and facilitating nutrient cycling in the community (Van Goethem et al. 2017). While the functional contribution of *Proteobacteria* in EMCs of hyperarid deserts needs to be further investigated, it is likely that their characterization and isolation will be of great interest, notably for their potential production of secondary metabolites (Suárez-Moreno et al. 2012).

## 4.5 Future Directions of Research

Endolithic microbial communities are excellent models for microbial ecology studies because of their low complexity and containment. However, they are challenging to study because of the difficulties in collecting samples and because of their low biomass. Nevertheless, the combination of state-of-the-art microscopy and molecular methods has revealed novel and diverse communities with unique adaptations to their extreme environments. Despite this progress, many knowledge gaps still remain.

In particular, very little is known about the interactions between the biotic and abiotic components of these unique ecosystems. Greater efforts, using sophisticated microscopy, are needed to characterize substrate architecture, define the different microhabitats within each substrate, and how these are colonized by different members of the community. Interactions between functional groups in the community and the role of viruses in shaping these communities should also be investigated to obtain a holistic picture of EMCs.

Cultivation efforts and single cell genomics will provide the opportunity to study the genetic diversity of EMCs members, refine taxonomic annotations, and investigate the potential role of biogeography in shaping these communities. Additionally, having isolates at hand will allow for the production of secondary metabolites for agricultural, pharmaceutical, and industrial applications.

Finally, the use of omics strategies and longitudinal studies will give us insights into the functioning of these communities at the ecosystem level, their response to environmental stresses, and help us predict how resistant and resilient these microbial communities might be to climate change. Because arid and hyperarid deserts, at the dry limit for life, are fragile ecosystems, their inhabitants will be on the front line of the major changes in climate ahead of us.

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