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Altitude and fungal diversity influence the structure of Antarctic cryptoendolithic Bacteria communities

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Summary

Endolithic growth within rocks is a critical adaptation of microbes living in harsh environments where exposure to extreme temperature, radiation, and desiccation limits the predominant life-forms, such as in the ice-free regions of Continental Antarctica. The microbial diversity of the endolithic communities in these areas has been sparsely examined. In this work, diversity and composition of bacterial assemblages in the cryptoendolithic lichen-dominated communities of Victoria Land (Continental Antarctica) were explored using a high-throughput metabarcoding approach, targeting the V4 region of 16S rDNA. Rocks were collected in 12 different localities (from 14 different sites), along a gradient ranging from 1,000 to 3,300 m a.s.l. and at a sea distance ranging from 29 to 96 km. The results indicate Actinobacteria and Proteobacteria are the dominant taxa in all samples and defined a 'core' group of bacterial taxa across all sites. The structure of bacteria communities is correlated with the fungal counterpart and among the environmental parameters considered, altitude was found to influence bacterial biodiversity, while distance from sea had no evident influence.

Keywords: Environmental factors, Adaptation, Antarctica, Cryptoendolithic lichen-dominated communities, Stress-tolerance, 16S Metabarcoding

Introduction

Assessment of microbial diversity in extreme environments can provide perspective on the ecological function and strategies for adaptation to resource limited and harsh ecosystems. Most prior investigations on microbial diversity in terrestrial Antarctic soils have focused on Bacteria and Archaea. Studies of soils in sites in East Antarctica including Bratina Island and Windmill Islands (Smith *et al.,* 2006; Chong *et al.,* 2009), West Antarctica South Shetland Archipelago (Ganzert *et al*., 2011), and Luther Vale, located near the north border of Victoria Land (Niederberger *et al*., 2008), revealed a high estimate of bacterial diversity. Victoria Land spans southward from the west side of the Ross Sea from 70°30'S to 78°00'S and westward from the coastline to the edge of the polar plateau (USGS, 2014). It is divided into two regions: Northern Victoria Land, encompassing Terra Nova Bay, Edmonson Point and Cape Hallett, and Southern Victoria Land, including the widest ice-free area of the continent, the McMurdo Dry Valleys, and nearby coastal regions. Dry Valleys soils are highly oligotrophic and support relatively low biomass (Smith et al., 2006; Pointing *et al*., 2009; Rao *et al*., 2011; Lee *et* al., 2012). In this area, soil communities are dominated by Actinobacteria and other cosmopolitan taxa (Aislabie *et al.,* 2006; Smith *et al*., 2006; Niederberger *et al.,* 2008; 2012; Stomeo *et al*., 2012), while cyanobacteria-dominated biofilms are predominant in hypolithic communities (de los Rìos *et al.,* 2014a; Chan *et al*., 2012; Wei *et al*., 2016).

Rocks in the ice-free areas of the McMurdo Dry Valleys from mountain peaks that rise above the Polar Plateau, along the entire Victoria Land, are the primary substratum for life, supporting the highest permanent biomass in these regions of Continental Antarctica (Cowan and Tow, 2004; Cary *et al*., 2010; Cowan *et al*., 2014). The extreme stress conditions experienced by organisms living in these environments include low temperatures, wide thermal fluctuations, high radiation exposure, low relative humidity, and scarce liquid water availability, that have restricted life forms to almost exclusively specialized microbes (Nienow and Friedmann, 1993; Vincent, 2000; Zucconi *et al*.,

2016). The narrow window of permissive temperature, light and humidity regimes that can support life promotes the settlement of highly adapted, extremotolerant and extremophilic microorganisms, mostly dwelling inside rocks (endoliths) where the environmental condition are buffered from the extreme ranges of the exposed surfaces (Friedmann, 1982; McKay and Friedmann, 1985; Nienow and Friedmann, 1993; Cary *et al*., 2010; Cowan *et al*., 2014). Among endoliths (Golubic *et al.*, 1981; Nienow and Friedmann, 1993; de los Ríos *et al*., 2014b), cryptoendolithic communities are among the most widespread in the McMurdo Dry Valleys. They are complex assemblages of microorganisms, including bacteria, cyanobacteria, Chlorophyta and both free-living and lichen-forming fungi (Friedmann, 1982; de la Torre *et al*., 2003).

Despite the increasing interest in investigating the extremotolerant and extremophilic microbes adapted to endolithic lifestyles in the Antarctic desert, investigation of microbial diversity of these peculiar ecosystems has been limited owing to the difficulty of collecting samples. Available data are patchy and based on a small number of rock samples from different locations or on few samples from a single site (de La Torre *et al*., 2003; Pointing *et al*., 2009; Yung *et al*., 2014; Archer *et al*., 2017) and the relative importance of environmental gradients in shaping these communities remains unexplored. With appreciation of the rapidity of global climate change, it is urgent to develop a baseline knowledge of Antarctic terrestrial ecosystems in order to allow future comparisons and to identify possible changes on these ecosystem (Hogg and Wall, 2011; NAS 2011). In this study we investigated diversity and community composition of bacterial assemblages associated to cryptoendolithic lichen-dominated communities in 42 samples collected over a wide area along Victoria Land (Continental Antarctica), exposed to different degrees of environmental pressures due to variation in altitude and sea distance. The fungal community makeup of these same samples was recently described by Coleine *et al*. (2018a).

The present work supplies a high-resolution inventory of microbial diversity and test if environmental constraints shape and structure diversity in these communities. These observations

are important for development of tools to evaluate how communities respond to changes in global temperature especial in polar regions where the change is expected to be most pronounced (Selbmann *et al*., 2017). A metabarcoding approach was used to measure and describe microbial diversity in a relatively unbiased manner (Ji *et al*., 2013). The V4 region of 16S rDNA was amplified from DNA extracted from rocks collected in 14 sites during the XXVI Italian Antarctic Expedition (2010-2011), along 14 sites along a latitudinal transect ranging from 73°29'26"S (Stewart Heights, Northern Victoria Land) to 76°54'36''S (Battleship Promontory, McMurdo Dry Valleys, Southern Victoria Land) from 1,000 (Battleship Promontory) to 3,300 m a.s.l. (Shafer Peak site 2) and from 29 km (Thern Promontory) to 96 km (Ricker Hills) distance from sea.

The primary aims of this study were to i) assess bacterial diversity, and community composition in the cryptoendolithic niches in Victoria Land; ii) identify 'core' group of bacterial members among samples analyzed; iii) to determine if and how differences in bacterial community structure are correlated with the fungal community or with altitude and distance from the sea. A detailed methodological information is reported in Appendix 1.

Results and discussion

In this study, 16S rDNA gene amplicon sequencing was used to profile bacterial composition and to test the effects on bacterial assemblages of environmental parameters (altitude and sea distance) and fungal diversity, already investigated in Coleine et al. (2018a), on bacterial assemblage.16S rDNA gene metabarcoding produced a total of 864,425 quality-filtered reads, ranging from 32,481 up to 75,174 reads per sample (Table 1). Sequences were grouped into 712 Operational Taxonomic Units (OTUs) and singletons and rare taxa (<5 reads) were removed (152 out of 712 OTUs; Appendix S1 in Supporting Material), generating 560 quality filtered OTUs. The species accumulation curve did not reach saturation; however, all rarefaction curves captured the dominant bacterial OTUs for each sample (see Supplementary Figs. 1S, 2S).

Across the dataset 14 bacterial phyla were detected with abundance varying considerably among sampling sites. Actinobacteria (20-50% of total reads) and Proteobacteria (10-30%) predominated, followed by Acidobacteria (3-13%), Firmicutes (2-15%), Armatimonadetes (1-13%) Cyanobacteria (3-10%), Bacteroidetes (4-7%) and Planctomycetes (0.1-9%). Taxa belonging to *Deinococcus-Thermus*, Fusobacteria and Verrucomicrobia were detected as only a small fraction (1-7%, 1-3% and 1-4%, respectively) and only from a few sites. Unclassified OTUs were present in all sites (5-30%) and these OTUs had no detectable similar sequence using BLASTN preventing taxonomy assignment at even the Phylum level (Fig. 1).

At the order rank, the communities were dominated by Actinomycetales (18-38%) (Actinobacteria), Rhodospirillales (3-18%) (Proteobacteria), Armatimonadales (3-12%) (Armatimonadetes) and Rubrobacterales (1-12%) (Actinobacteria); other orders, such as Bacillales (Firmicutes) were the rarest members, present only in some sites (Supporting information Fig. 3S).

A bacterial 'core' community (i.e. OTUs present in at least 75% of the samples) composed of 48 (out of 560) OTUs, less than 10% of total reads, was identified (Table 2), highlighting a very strong variability among sites analyzed. Most 'core' members belonged to the Phyla Actinobacteria (17) and Proteobacteria (12). Few taxa were assigned to Armatimonadetes, Acidobacteria, Bacteroidetes or Planctomycetes. Only a single phylotype of Cyanobacteria (unidentified) was recovered among the sample sites. Comparison of the genera present in the sample revealed *Acidisoma* (Proteobacteria), *Granulicella* (Acidobacteria) and *Mucilaginibacter* (Bacteroidetes) as 'core' community members (Table 2).

A graphical representation of the distribution of 'core' specimens was performed to identify association among the shared phylotypes and sampled locations. The 48 most informative taxa were present in almost all sites. The visited localities were further hierarchically clustered by 'core' OTUs abundance to identify patterns of similarities in community composition, but they did not exhibit a remarkable clustering of locations by geography (Fig. 2).

Previous works have recovered Actinobacteria and Proteobacteria from other Antarctic ecosystems including soil biotopes (Saul *et al*., 2005; Aislabie *et al*., 2006), cryoconite holes (Christner *et al*., 2003) and cryptoendolithic communities (e.g. Hirsch *et al*., 1988, 2004; de la Torre *et al*., 2003). Actinobacteria and Proteobacteria were reported as the predominant Phyla in these studies, suggesting that these heterotrophic bacteria may have important roles in these communities. These same Phyla were also dominant in other cold climate rock-inhabiting microbial communities from the Arctic (Choe *et al*., 2018), supporting the idea that highly stress-tolerant microbial communities may harbor similar microorganisms, even if found on different continents (Büdel, 1999; Fajardo-Cavazos and Nicholson, 2006). Their success in these environments may be due to a capacity to withstand multiple stress conditions as part of a global meta-community and unique adaptations to the lithic habitat (Walker and Pace, 2007).

Among the 'core' members, taxa belonging to *Acidisoma* sp. (Rhodospirillales, Proteobacteria) was never observed in ice-free areas of Victoria Land, but have been frequently detected in cold regions such as Alps (Nakai *et al*., 2013). *Granulicella* species (Acidobacteria) were also uniquely found in these ice-free areas which encompasses several cold-adapted species described from Arctic tundra soils (Männistö *et al*., 2012).

The sub-order Frankineae (Actinobacteria, G+) was previously reported from Antarctic soil communities (Learn-Han *et al*., 2012). This group together with Rhizobiales (Proteobacteria, G-) include nitrogen-fixing bacteria typically associated with plants. The family Rhizobiaceae (Rhizobiales) includes nitrogen-fixing bacteria, while the sub-order Frankineae encompasses 4 families, including the nitrogen-fixing genus *Frankia*. Since the used approach in this study, the identification of Rhizobiales OTUs can be resolved confidently only at order or sub-order level, and, even if it is well known that N-fixing bacteria are frequent in lichen microbiomes, we cannot conclude with certainty that nitrogen fixing bacteria belonging to these groups are actually present in the assemblages analyzed.

We found Cyanobacteria at low abundance in this survey, even though they are dominant members in other Antarctic endolithic ecosystems such as endolithic cyanobacteria-dominated communities (Friedmann and Ocampo-Friedmann, 1988; de los Ríos et al., 2004; 2007; Büdel et al., 2008). Cyanobacterial taxa were rarely isolated in cryptoendolithic lichen-dominated communities in McMurdo Dry Valleys (Friedmann and Ocampo, 1976; Friedmann *et al*., 1988);

Deinococcus-like organisms, well known for their ability to withstand the high solar irradiation of the South Pole, especially large amounts of UV, and also to survive to ionizing radiation, limiting damage to their DNA (Mattimore and Battista, 1996; Battista *et al.,* 1999), have been detected in endolithic communities (de la Torre *et al*., 2003; Hirsch *et al*., 1988; Siebert and Hirsch, 1988) and a lichen thallus of *Umbilicaria decussata* from Kay Island, Antarctica (Selbmann *et al*., 2010), but represented a very small fraction of recovered OTUs in our study.

Biodiversity analysis of species richness (from 50 to 287) and Shannon's index (ranging from 1.1 to 4.24) (Table 1) confirmed that Antarctic microbial endolithic communities harbor relatively low bacterial diversity (see also Archer *et al*., 2017; Selbmann *et al*., 2017; Coleine *et al.,* 2018), compared with temperate microbial biotopes, which typically have values of Shannon's index between 6 and 7 (Dunbar *et al*., 2000). The β diversity across the 14 sampled sites was measured with a Jaccard index and the contribution of altitude and sea distance in shaping the bacterial communities was estimated using an MRM analysis. A distance matrix was computed to investigate the contribution of altitude and sea distance in shaping the bacterial assemblages. There were not strong relationships between community composition and environmental variables. Sampled sites at similar altitude and distance from sea did not show a high degree of homogeneity in community composition in the two sites at Trio Nunatak, showing only 18%; for example, the two visited sites at Trio Nunatak showed only 18% of similarity; similar trend was obtained for Shafer Peak site 1 and 2 (25.4% of similarity) (data not shown).

The Pareto Lorenz curves inferred from community composition indicated a high degree of specialization of these communities. The average F0 value was 89% (Fig. 3), indicating the dominance of a very few but highly specialized species while other members occur at very low frequency (Marzorati et al., 2008). This is also supported by inferred Simpson's dominance indices (1-D), which ranged from 0.61 (Shafer Peak site 1) to Stewart Heights (0.98), with a mean value of 0.83 (Table 1), indicating a high degree of specialization of these ecosystems and suggesting a potential scant resiliency and recovery capacity after disturbance.

Additionally, bivariate analysis on the distance matrices and Spearman's correlation analysis indicated that the differences in community structure among the samples were not correlated with the differences in the environmental parameters (Figs. 4, S4) as estimated richness from Shannon's and Simpson's indices were similar among the samples ($p>0.05$), even though differences in altitude and sea distances were significant ($p<0.05$; data not shown).

Nevertheless, PERMANOVA analysis showed a clear influence ($p<0.05$) of altitude on bacterial community composition (incidence and reads abundance data), explaining more than 41% of observed variance, while the parameter sea distance did not show any influence ($p>0.05$).

It has been reported that lichen species and individual thallus traits may influence associated bacterial diversity (Bates *et al*., 2012; Cardinale *et al*., 2012); therefore, we also tested the effects of fungal community composition (reported in Coleine *et al*., 2018a) in our samples, where lichen species represent 91% of fungal community, on bacterial counterpart. The results clearly indicate a significant correlation between fungal and bacterial biodiversity (Fig. 5a); this relationship was highlighted by regression of pairwise comparisons of Bray-Curtis distances in community composition and Mantel test ($p<0.01$) (Fig. 5b). Actinobacteria and Proteobacteria resulted the predominant phyla in communities herein analyzed; the same findings were obtained in previous study based on culture-dependent approaches (Selbmann *et al.*, 2010).

These results indicated that the establishment and development of bacteria in the cryptoendolithic lichen-dominated microbial communities of Victoria Land are not influenced by sea distance, but altitude-induced environmental conditions were found to be important factors. This suggests these the combination of UV or temperature have more of an impact than proximity to sea for these cryptoendolithic communities in Victoria Land. Additionally, the positive correlation found between fungi and bacteria community diversity suggests that, as fungal assemblage changes, the bacterial community structure changes as well.

While this study improved our understanding of bacterial endolithic communities and their interactions with environmental factors, we hypothesize that additional microclimate environmental parameters (e.g. water availability, average rock temperature and sun exposure) may be more important determinants of community diversity and structure. Indeed, sun exposure, which likely influences temperature and water availability as well as generating visible difference in texture and weathering properties (McKay and Friedmann, 1985), has been implicated in shaping composition and distribution of functional groups of fungi in Antarctic endolithic communities (Coleine *et al*., 2018b). Further analysis of functional roles and capabilities of endolithic bacteria can clarify relationships between physical-chemical parameters and the possible functional redundancy in bacterial assemblages associated to these communities. In contrast to previous studies which were based on only 2-4 samples, this work sampled endolithic communities along 14 sites in Victoria Land (42 rock samples) and provides the first detailed picture of the bacterial biodiversity of Antarctic cryptoendolithic lichen-dominated communities.

Sequencing, bioinformatics, and molecular ecological analysis of this study was performed in same manner as previous study (Coleine et al., 2018a) and description of the materials and methods is available in Supporting Information Appendix S1. The amplicon sequence data and metadata have been deposited in the NCBI Sequence Read Archive database under BioProject accession number PRJNA379160.

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Table 1. List of sampling sites following an altitudinal gradient, with altitudes (m a.s.l.) and sea distances (km) reported. Diversity metrics for 16S rRNA gene sequencing for each site. Data are reported as follows: number of reads, species richness index (S), Shannon's index (H') and Simpson's Index of Dominance (1-D).

Sites	Altitude	Sea distance	16S-reads	S	H'	1-D
Battleship Promontory	1000	33.5	66,567	287	3.12	0.89
Trio Nunatak site 1	1000	82	64,152	57	2.59	0.88
Ricker Hills	1115	96	64,744	69	2.89	0.91
Mt Billing	1300	44	59,433	156	2.15	0.70
Trio Nunatak site 2	1400	84.5	32,481	101	2.24	0.82
Thern Promontory	1500	29	54,279	57	1.36	0.65
Bobby Rocks	1680	91	61,406	73	2.64	0.88
Mt Bowen	1874	39.5	58,002	157	2.64	0.86
Richard Nunatak	2000	71.6	70,826	86	2.55	0.87
Stewart Heights	2670	74	75,174	218	4.24	0.98
Timber Peak	2800	49.5	64,023	201	1.89	0.70
Mt New Zealand	2888	47	61,739	144	2.79	0.89
Shafer Peak site 1	3100	59	66,326	50	1.1	0.61
Shafer Peak site 2	3300	48	65,273	156	3.46	0.91

Table 2. Taxonomic identity of 48 core Operational Taxonomic Units (OTU) identified**.**

	Taxonomic assignment	
OTU id	**Phylum (confidence >1)**	**Identification (confidence >0.97)**
OTU1	Cyanobacteria	-
OTU4	Actinobacteria	Suborder Corynebacterineae
OTU7	Bacteroidetes	Family Sphingobacteriaceae
OTU8	Proteobacteria	Genus *Acidisoma*
OTU10	Proteobacteria	Order Rhizobiales
OTU11	Armatimonadetes	-
OTU12	Proteobacteria	Family Acetobacteraceae
OTU16	Proteobacteria	Family Acetobacteraceae
OTU17	Acidobacteria	Genus *Granulicella*
OTU18	Actinobacteria	Sub-order Frankineae
OTU20	Acidobacteria	Genus *Granulicella*
OTU21	Proteobacteria	Family Acetobacteraceae
OTU23	Actinobacteria	Order Actinomycetales
OTU24	Proteobacteria	Family Acetobacteraceae
OTU25	Proteobacteria	Family Acetobacteraceae
OTU27	Unclassified	-
OTU31	Proteobacteria	Family Acetobacteraceae
OTU32	Unclassified	-
OTU36	Actinobacteria	Suborder Corynebacterineae
OTU37	Armatimonadetes	-
OTU39	Actinobacteria	Family Conexibacteraceae
OTU40	Actinobacteria	Suborder Micrococcineae
OTU43	Acidobacteria	Subgroup Acidobacteria Gp1
OTU49	Bacteroidetes	Genus *Mucilaginibacter*
OTU58	Planctomycetes	Family Planctomycetaceae
OTU70	Bacteroidetes	-
OTU80	Proteobacteria	Family Acetobacteraceae
OTU81	Actinobacteria	Phylum Actinobacteria
OTU87	Armatimonades	-
OTU98	Actinobacteria	Order Actinomycetales
OTU115	Actinobacteria	Suborder Pseudonocardineae
OTU129	Unclassified	-
OTU150	Actinobacteria	Family Micromonosporaceae
OTU164	Actinobacteria	Family Conexibacteraceae
OTU 170	Planctomycetes	Family Planctomycetaceae

OTU191	Proteobacteria	Order Rhizobiales
OTU195	Actinobacteria	Suborder Micrococcineae
OTU217	Actinobacteria	-
OTU233	Actinobacteria	Family Conexibacteraceae
OTU245	Unclassified	-
OTU249	Proteobacteria	Family Acetobacteraceae
OTU281	Unclassified	-
OTU322	Actinobacteria	Order Actinomycetales
OTU334	Unclassified	-
OTU412	Actinobacteria	Sub-order Frankineae
OTU587	Actinobacteria	Order Actinomycetales
OTU614	Acidobacteria	Subgroup Acidobacteria Gp1
OTU621	Proteobacteria	Family Comamonadaceae

Figure Legends

Figure 1. Relative abundances of the dominant bacterial OTUs in the cryptoendolithic communities in Victoria Land, Antarctica. Abundances based upon sequence taxonomy classified at the rank of Phylum.

Figure 2. Heat map of the 'core' taxa relative abundance and UPGMA hierarchical clustering of sites. Values are scaled (log-transformed) by OTUs relative abundances across all sites. Abundances are indicated by the color intensity: dark and light red indicate higher relative abundances; orange and pale-orange indicate lower relative abundances. Yellow indicates a frequency < -1. Both the 'core' OTUs and sites were clustered using a Bray-Curtis index.

Figure 3. Pareto-Lorenz distribution curves based on the number of OTUs and their frequencies. The dashed vertical line at the 0.2 x-axis level is plotted to evaluate the range of the Pareto values. Each line represents a sampling site.

Figure 4. Spearman's correlation ranks of biodiversity indices (Richness, Shannon's diversity and Simpson's dominance indices) correlated to the altitudinal gradient.

Figure 5. Linear regression correlation between bacterial and fungal biodiversity (Fig. 5a) and fungal and bacterial composition distances (Bray-Curtis distances, usign Hellinger transformed OTUs tables). Correlation was also tested with Mantel test (<0.01).