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ORIGINAL PAPER

Diverse metabolic and stress-tolerance pathways in chasmoendolithic and soil communities of Miers Valley, McMurdo Dry Valleys, Antarctica

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Abstract The majority of biomass in the McMurdo Dry Valleys of Antarctica occurs within rocks and soils, but despite the wealth of biodiversity data very little is known about the potential functionality of communities within these substrates. The putative physiological capacity of microbial communities in granite boulders (chasmoendoliths) and soils of a maritime-influenced Antarctic Dry Valleys were interrogated using the GeoChip microarray. Diversity estimates revealed surprisingly high diversity and evenness in both communities, with Chlorobi and Deinococci in soils accounting for major differences between the substrates. Autotrophs were more diverse in chasmoendoliths, and diazotrophs more diverse in soils. Both substrates revealed a previously unappreciated abundance of Halobacteria (Archaea), Ascomycota (Fungi) and Basidiomycoyta (Fungi). The fungi accounted for much of the differences between substrates in metabolic pathways associated with carbon transformations, particularly for aromatic compounds. Nitrogen fixation genes were more common in soils, although nitrogen catabolism genes were abundant in chasmoendoliths. Stress response pathways were more diverse in chasmoendoliths, possibly reflecting greater environmental stress in this exposed substrate compared with subsurface soils. Overall diversity of stress-tolerance genes was markedly lower than that recorded for inland locations where environmental stress is exacerbated. We postulate that the chasmoendolithic community occupies a key role in biogeochemical transformations in Dry Valley systems where granite substrates are abundant among open soils. The findings indicate that a substantial upward revision to estimates of biologically active surfaces in this system is warranted.

Keywords Antarctica · Chasmoendolith · Dry Valleys · Geochip · Stress response

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Introduction

The McMurdo Dry Valleys are a largely ice-free polar desert protected by international treaty as an Antarctic special managed area (SCAR 2004). The terrestrial landscape is dominated by oligotrophic mineral soil with extensive rocky outcrops (Thomas 1997). The Dry Valleys possess an extreme climate (Doran et al. 2002), with severe environmental stress from low temperature, lack of liquid water, UV exposure and oligotrophic substrates. This limits life to refuge habitats in this ecosystem (Fraser et al. 2014). The major biotic component of the system is microbial, although invertebrates are also encountered (Wynn-Williams 1990). The microbial biodiversity of the Dry Valleys has been extensively studied using environmental rRNA gene diversity estimates (Cary et al. 2010). A high degree of niche-specialization in terms of rRNA gene-defined community assembly has been recorded between open soil, hypolith (colonized ventral surfaces of quartz), chasmoendolith (colonized cracks and fissures in sandstone and granite) and cryptoendolith (colonized pore spaces in weathered sandstone; Pointing et al. 2009; Bahl et al. 2011; Pointing et al. 2014), despite widespread airborne dispersal of microbial propagules (Bottos et al. 2013).

Soils in the Dry Valleys are dominated by bacterial phyla, mainly Acidobacteria, Actinobacteria and Alpha Proteobacteria (Pointing et al. 2009; Lee et al. 2012), Hypolithic communities are patchily distributed in soil and are dominated by cyanobacteria (Pointing et al. 2009; Cowan et al. 2011). They can also act as nucleation sites for development of mosses (Wong et al. 2010a; Chan et al. 2012). Algae and fungi are depauperate in these habitats but more abundant in rocky substrates (Pointing et al. 2009). Antarctic cryptoendoliths display a distinctive layered colonization of melanised fungi shielding a lower cyanobacteria-dominated layer, and possibly also lichen associations (Friedmann 1982; de la Torre et al. 2003; Pointing et al. 2009). This has been termed the 'microbial cabana' strategy (Pointing and Belnap 2012), and in Antarctic sandstone cryptoendoliths the pleurocapsalean cyanobacterial genus *Chroococcidiopsis* dominates the community (de la Torre et al. 2003; Pointing et al. 2009). Chasmoendoliths in sandstone are not distinct from cryptoendoliths, but recent work has highlighted that weathered granite is also a chasmoendolithic niche, and supports a strikingly different community (Wierzchos et al. 2013). Exposed granites in the McMurdo Dry Valleys display a severe weathered surface and laminar flaking of surface layers. These are sites for chasmoendolithic colonization, and studies have shown that this is cyanobacterial with possible lichen associations (de los Rios et al. 2005, 2007; Yung et al. 2014). The community is significantly different from surrounding soils and other lithic colonization (Yung et al. 2014).

Chasmoendolithic colonization of granite is widespread in low- and mid-altitude valleys, and so it has been postulated that the contribution of chasmoendoliths to geobiological processes may be significant to the Dry Valley ecosystem (Yung et al. 2014). These communities have also been implicated in bio-weathering of the substrate (Wierzchos et al. 2013). However, explicit studies of how they contribute to ecosystem processes in Dry Valleys are lacking, only a single study has addressed the issue of functional ecology for this system (Chan et al. 2013). This revealed that sandstone lithic communities possessed a functional capacity for carbon and nitrogen transformations on a par with soils and hypoliths at a high-altitude inland valley (Chan et al. 2013). Interestingly the lithic communities also possessed a greater diversity in stress response pathways than soil communities, and this was linked to the relatively more exposed rock substrate (Chan et al. 2013).

Here we report an interrogation of functional diversity in chasmoendolithic communities of granite, a major lithic substrate for microbial colonization in low-mid altitude valleys. We employed a metagenomic approach using the GeoChip functional microarray platform to obtain an estimate of putative metabolic capability in bacterial, archaeal and fungal phyla (He et al. 2007). The findings are compared to data obtained for surrounding soils in order to allow assessment of the likely relative contribution of rock and soil communities to geobiological transformations, and the range of stress tolerance pathways that are behind the adaptive basis for community assembly in these two niches. This is the first report of functional ecology in a granite chasmoendolithic system.

Materials and methods

Miers Valley is a granite-dominated valley occupying a maritime location within the McMurdo Dry Valleys Antarctic Special Managed Area. It is a long-term ecological study site for the New Zealand Terrestrial Antarctic Biodiversity Survey ($_{NZ}$TABS, http://nztabs.ictar.aq). The valley lies between the latitudes 78°060 S and 78°070 S and longitudes 163°440 E and 164°120 E and comprises a wide valley floor characterized by moraine deposition, and steep scree and boulder slopes. A landscape ecological survey of biodiversity conducted in 2009 (Yung et al. 2014) was used to identify the most diverse soil and chasmoendolith assemblages, and these were used for all GeoChip analysis in this study (north-facing slope, S78″05.110 E163″48.906). Triplicate independent replicates were obtained from three weathered white granite boulders 200 m apart, and triplicate soil samples were collected

10 m from each boulder to minimise the effects of recent chasmoendolith input to soils via rock weathering.

Recovery of environmental DNA was with a protocol optimized for edaphic desert microorganisms (Pointing et al. 2007). Microarray interrogation using GeoChip was conducted for triplicate samples from soil and granite ($n = 6$). The GeoChip contained probes for functional genes involved in major biogeochemical and other processes. We grouped these into five categories: carbon fixation; carbon catabolism; nitrogen fixation; nitrogen catabolism and stress response (He et al. 2007). Hybridization was carried out as previously described (Zhou et al. 2008). The normalized hybridization output data was then re-organized based upon functional category.

GeoChip 4 contains about 84,000 50-mer oligonucleotide probes covering 152,000 gene variants (i.e. individual sequences from a gene) from 401 distinct functional gene categories involved in major biogeochemical, ecological, and other processes (He et al. 2007). The array mainly targets known bacterial loci, but also includes archaeal and fungal loci for many of the pathways. A phylogenetic marker (*gyrB*) was specific to bacteria and archaea and was interrogated using 658 probes. Among the 34,473 probes returning positive signals, 5,888 were derived from genes involved in carbon, 2,820 nitrogen cycling, and 7,230 from stress responses. Output from the array data were grouped into functional categories related to major metabolic processes. The level of redundancy created by the large number of pathway-specific GeoChip oligonucleotides allowed a high degree of confidence in signal recovery inferring occurrence of any given pathway (He et al. 2007). Hybridization of DNA from chasmoendolith and soil samples was achieved with an average of 64.0 % of the probes, covering 93.2 % of the targeted genes of interest on GeoChip 4. The GeoChip dataset reported in this paper is publicly available at http://ieg.ou.edu/4download/.

Alpha diversity indices [Species Richness (S), Diversity indices; Margalef's Diversity (Da), Shannon's Diversity (H') and Simpsons Diversity Index (D)]; and equality of species abundance (Pielou's Evenness (J')] were calculated from *gyr*B diversity data. Visualization of different phylum-level and/or class-level contributions to each metabolic pathway was achieved using spider dendrograms, where each arm of the plot was specific to a given phylum and signal intensity was used as a proxy for relative abundance (Chan et al. 2013). Statistical testing using analysis of similarity (ANOSIM) and analysis of variance (ANOVA) were performed to indicate confidence in similarities/differences observed. All analyses were performed using PRIMER-E v6 (Clarke 1993).

Results

Biodiversity

For determining prokaryotic diversity GeoChip utilized highly specific probes targeting DNA gyrase subunit B (*gyrB*), which are functional genes with higher evolutional rates than 16S rRNA genes. We used multiple diversity metrics to demonstrate soils were significantly more diverse than chasmoendoliths (Table 1). Both communities displayed similarly high levels of evenness, indicating contribution to abundance was similar among all species (Table 1). The most abundant phyla in chasmoendoliths were Proteobacteria (the alpha, beta, gamma, delta, epsilon and zeta proteobacteria are shown separately in Figs. 1, 2, 3 and 4) and Halobacteria, with relatively high abundance of Acidobacteria, Cyanobacteria and Thermoplasmata (Fig. 1). Soils were dominated by Acidobacteria, Chlorobi and Halobacteria, also with high abundance of thermoplasmata (Fig. 1). The Deinococci and Archaeoglobi appeared specific to soil only, whilst Nitrospirae were markedly more abundant in chasmoendliths. The remainder of the 27 phyla detected occurred in both substrates with different relative abundance.

Functional diversity

In this study, we focused on microbial diversity that underpinned metabolic potential in carbon cycling, nitrogen cycling, and stress tolerance. Both chasmoendoliths and soil supported a functional diversity that included photoautotrophic, heterotrophic, diazotrophic, and stress response pathways. However, overall difference in metabolic pathways indicated for these two communities was significant (ANOSIM: global $R = 0.761$, $P = 0.0027$).

Table 1 Diversity metrics for chasmoendolith and soil communities using DNA gyrase subunit B (*gyr*B) as a phylogenetic marker

	Chamsoendolith		Soil	
	Mean	SD	Mean	SD
Species richness (S)	347	34.67	440	13.56
Shannon's diversity index (H')	5.834	0.049	6.071	0.106
Simpson diversity index (D)	0.984	0.003	0.987	0.002
Margalef's diversity (Da)	59.24	2.77	72.26	6.34
Pielou's evenness (J)	0.997	0.001	0.998	0.001

A significant difference was observed for species richness (ANOVA: $F = 10.33$, $P = 0.032$, $n = 6$), Shannon's diversity index (ANOVA: $F = 10.61$, $P = 0.025$, $n = 6$) and Margalef's diversity (ANOVA: $F = 12.72$, $P = 0.031$, $n = 6$) between the two communities. No significant difference in the Simpson index or Pielou's evenness was observed

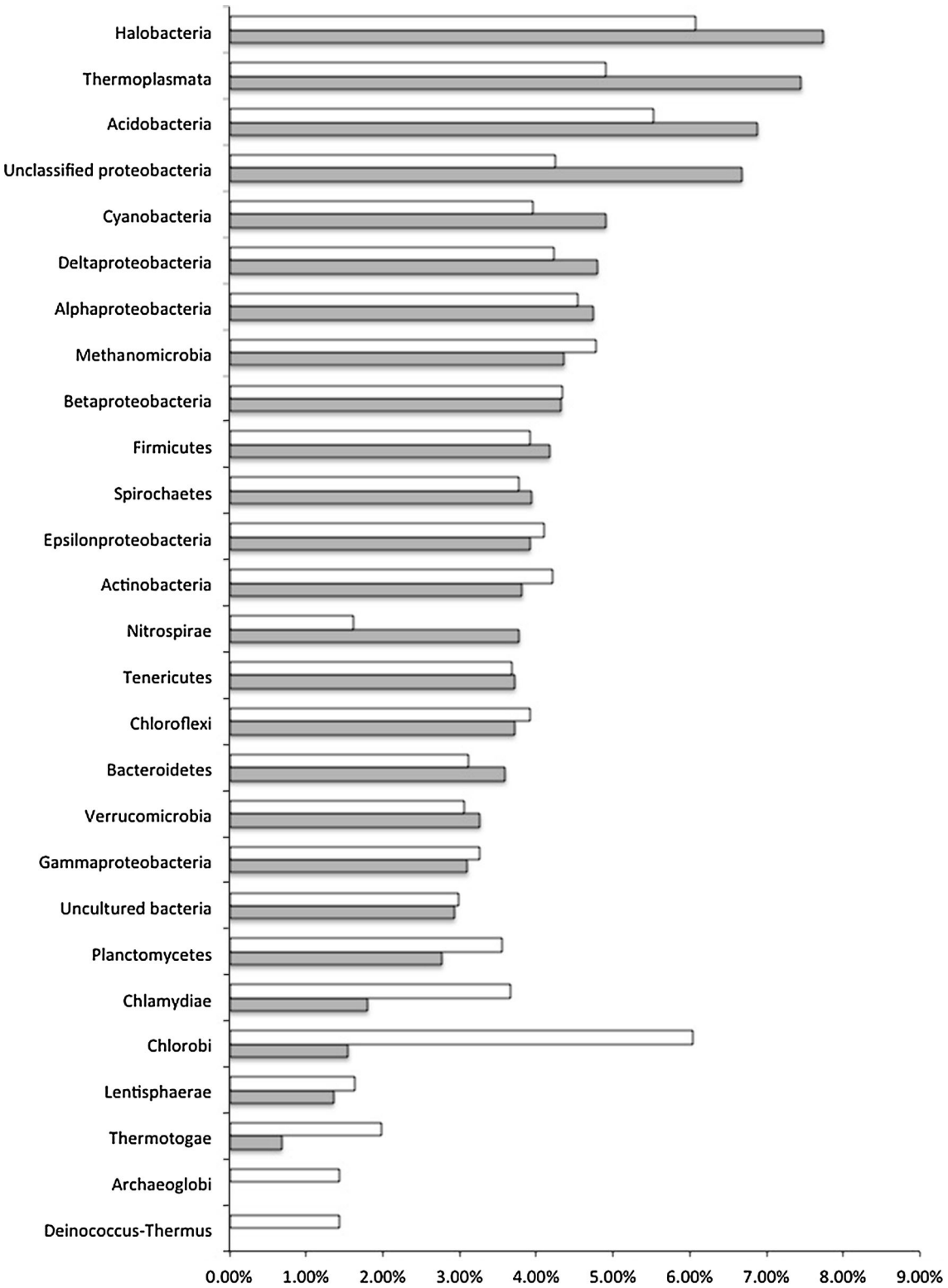


Fig. 1 Biodiversity estimates for chasmoendolith and soil communities using DNA gyrase subunit B (*gyr*B) as a phylogenetic marker. *Dark bars* denote chasmoendolith, *light bars* denote. Estimates were obtained by screening environmental DNA using the Geochip microarray (He et al. 2007). (Color figure online)

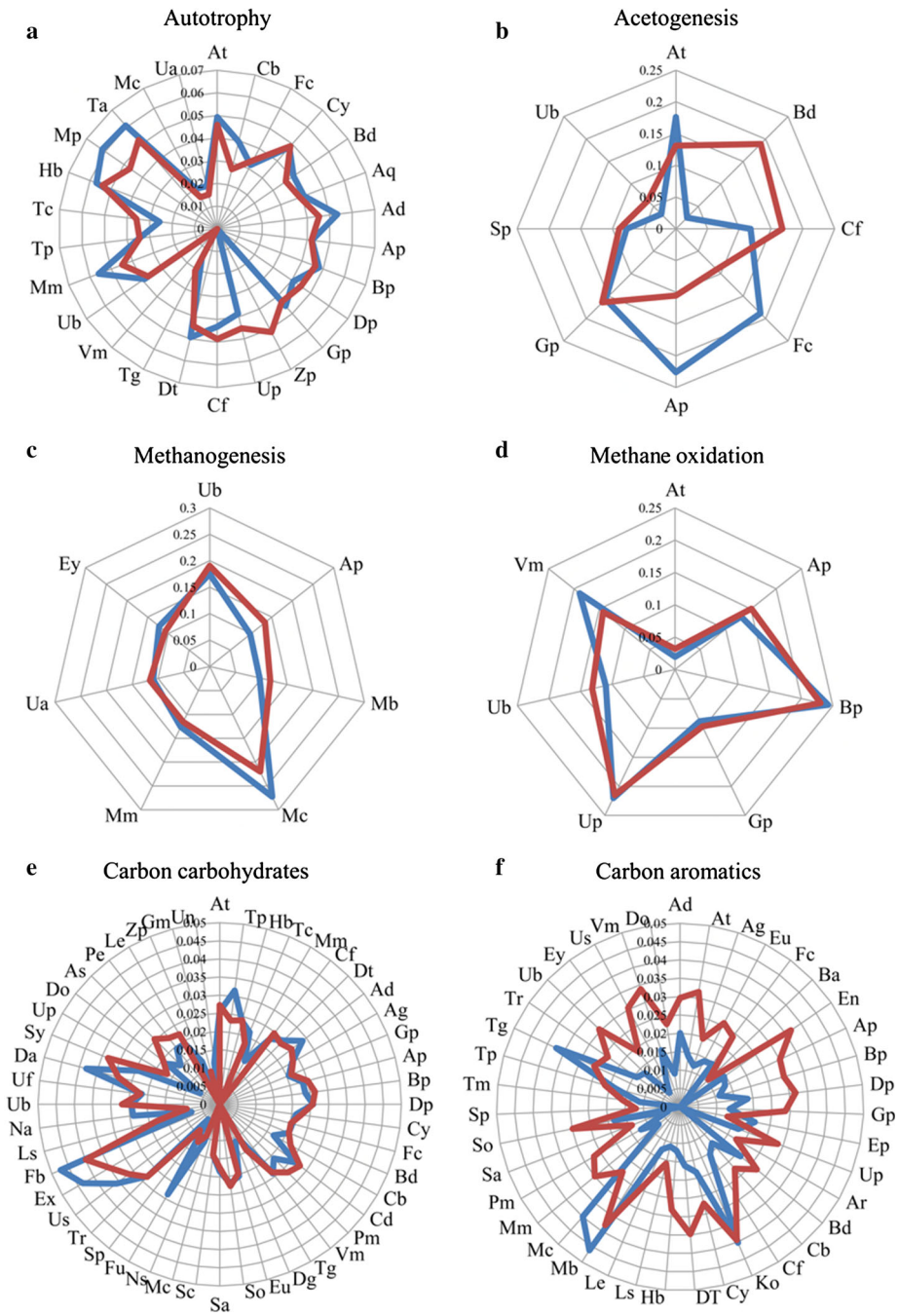
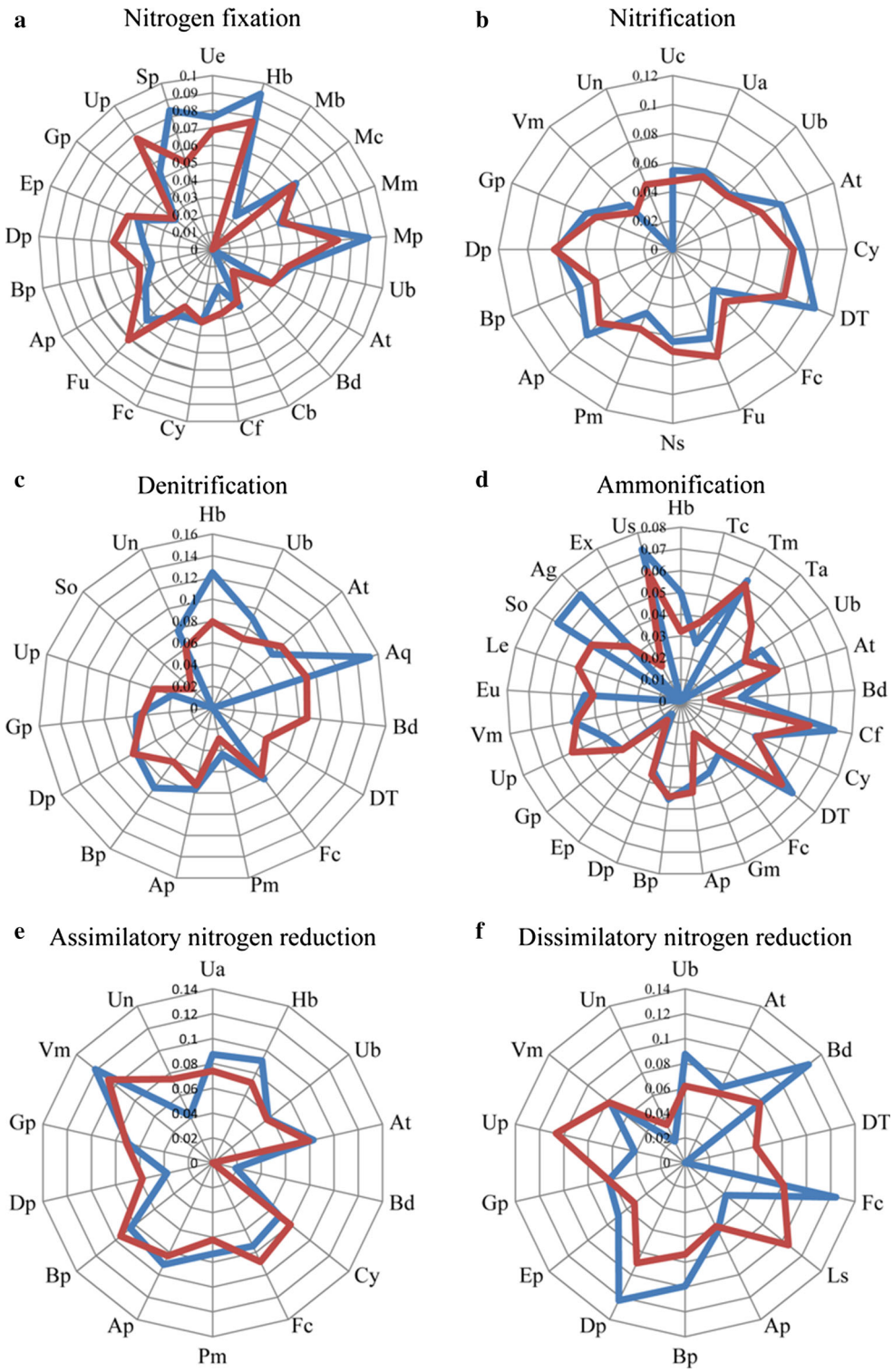


Fig. 2 Taxa-function relationships for carbon cycling genes. The relative signal intensity was normalized for the number of probes per taxon. Mean values of samples from respective niches (chasmoendoliths [*blue*] and soils [*red*]) were plotted for the carbon cycling genes involved in **a** autotrophy, **b** acetogenesis, **c** methanogenesis, **d** methane oxidation, **e** carbon carbohydrates, **f** carbon aromatics and others. Two-letter codes denote microbial phyla as follows: *Ad* Acidobacteria, *Ag* Agaricomycetes, *Ap* Alphaproteobacteria, *Aq* Aquificae, *Ar* Archaeoglobi, *As* Ascomycota, *At* Actinobacteria, *Ba* Basidiomycota, *Bd* Bacteriodetes, *Bp* Betaproteobacteria, *Cb* Chlorobi, *Cd* Chlamydiae, *Cf* Chloroflexi, *Ck* Candidatus korarchaeum, *Cr* Crenarchaeota, *Cy* Cyanobacteria, *Da* Dacrymycetes, *Df* Deferribacteres, *Dg* Dictyoglomi, *Do* Dothidiomycetes, *Dp* Deltaproteobacteria, *DT* Deinococcus-Thermus, *En* Entomophthoromycota, *Em* Elusimicrobia, *Ep* Epsilonproteobacteria, *Eu* Eurotiomycetes, *Ex* Exobasidiomycetes, *Ey* Euryarchaea, *Fb* Fibrobacteres, *Fc* Firmicutes, *Fu* Fusobacteria, *Gm* Gemmatimonadetes, *Hb* Halobacteria, *Ko* Korarchaeota, *Le* Leotiomycetes, *Ls* Lentisphaerae, *Mb* Methanobacteria, *Mc* Methanococci, *Mm* Methanomicrobia, *Mp* Methanopyri, *My* Mycetozoa, *Na* Neocallimastigomycota, *Ns* Nitrospirae, *Pe* Pezizomycetes, *Pm* Planctomycetes, *Sa* Saccharomycetes, *Sc* Schizosaccharomycetes, *So* Sordariomycetes, *Sp* Spirochaetes, *Sy* Synergistetes, *Ta* Thaumarchaeota, *Tb* Thermobaculum, *Tc* Thermococci, *Tg* Thermotogae, *Tm* Thermoplamsata, *Tn* Tenericutes, *Tp* Thermoprotei, *Tr* Tremellomycetes, *Ub* Unknown bacteria, *Uc* Unknown Crenarchaeota, *Ue* Unknown Euryarchaeota, *Uf* Unknown fungus, *Un* Unknown, *Up* Unknown proteobacteria, *Us* Ustilaginomycetes, *Vm* Verrucomicrobia, *Zp* Zetaproteobacteria, *Zy* Zygomycota. (Color figure online)


a
Nitrogen fixation
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◀**Fig. 3** Taxa-function relationships for nitrogen cycling genes. The relative signal intensity was normalized for the number of probes per taxon. Mean values of samples from respective niches (chasmoendoliths [*blue*] and soils [*red*]) were plotted for the nitrogen cycling genes involved in **a** dinitrogen fixation, **b** nitrification, **c** denitrification, **d** ammonification, **e** assimilatory nitrogen reduction, **f** assimilatory nitrogen reduction. Annamox genes were detected only among planctomycetes. Two-letter codes denote microbial phyla as follows: *Ad* Acidobacteria, *Ag* Agaricomycetes, *Ap* Alphaproteobacteria, *Aq* Aquificae, *Ar* Archaeoglobi, *As* Ascomycota, *At* Actinobacteria, *Ba* Basidiomycota, *Bd* Bacteriodetes, *Bp* Betaproteobacteria, *Cb* Chlorobi, *Cd* Chlamydiae, *Cf* Chloroflexi, *Ck* Candidatus korarchaeum, *Cr* Crenarchaeota, *Cy* Cyanobacteria, *Da* Dacrymycetes, *Df* Deferribacteres, *Dg* Dictyoglomi, *Do* Dothidiomycetes, *Dp* Deltaproteobacteria, *DT* Deinococcus-Thermus, *En* Entomophthoromycota, *Em* Elusimicrobia, *Ep* Epsilonproteobacteria, *Eu* Eurotiomycetes, *Ex* Exobasidiomycetes, *Ey* Euryarchaea, *Fb* Fibrobacteres, *Fc* Firmicutes, *Fu* Fusobacteria, *Gm* Gemmatimonadetes, *Hb* Halobacteria, *Ko* Korarchaeota, *Le* Leotiomycetes, *Ls* Lentisphaerae, *Mb* Methanobacteria, *Mc* Methanococci, *Mm* Methanomicrobia, *Mp* Methanopyri, *My* Mycetozoa, *Na* Neocallimastigomycota, *Ns* Nitrospirae, *Pe* Pezizomycetes, *Pm* Planctomycetes, *Sa* Saccharomycetes, *Sc* Schizosaccharomycetes, *So* Sordariomycetes, *Sp* Spirochaetes, *Sy* Synergistetes, *Ta* Thaumarchaeota, *Tb* Thermobaculum, *Tc* Thermococci, *Tg* Thermotogae, *Tm* Thermoplamsata, *Tn* Tenericutes, *Tp* Thermoprotei, *Tr* Tremellomycetes, *Ub* Unknown bacteria, *Uc* Unknown Crenarchaeota, *Ue* Unknown Euryarchaeota, *Uf* Unknown fungus, *Un* unknown, *Up* Unknown proteobacteria, *Us* Ustilaginomycetes, *Vm* Verrucomicrobia, *Zp* Zetaproteobacteria, *Zy* Zygomycota. (Color figure online)

A SIMPER analysis was performed to identify which group(s) of pathway-specific genes was primarily responsible for the observed difference between the two niches. Overall, the most striking differences (24 % of variation) between chasmoendoliths and soils were due to catabolic pathways for aromatic compounds.

Carbon utilization

The potential for autotrophy (photoautotrophy and chemoautotrophy) was indicated among 26 phyla (Fig. 2a). The strongest signal intensities were detected among the archaea and proteobacteria. Autotrophic signatures were more abundant in chasmoendoliths than soils, and some phylum-specific differences were apparent, notably the strong contribution from Zeta Proteobacteria in soils but their absence in chasmoendoliths where cyanobacteria were more common. We identified 8 phyla capable of acetogenesis (Fig. 2b) and dominant phyla for this pathway were different in chasmoendoliths (Actinobacteria, alpha proteobacteria and firmicutes) and soils (Bacteriodetes, Crenarchaea and Gamma Proteobacteria). In C1 metabolism the Methanococci dominated methanogenesis (Fig. 2c), whereas methane oxidation was indicated by seven phyla dominated by proteobacteria (Fig. 2d). The ability to carry out simple and complex carbohydrate catabolism was present in 48 bacterial, archaeal and fungal phyla in both substrates, with strongest signatures from ascomycete and basidiomycete fungi (Fig. 2e). Catabolism of complex aromatic compounds was a less widespread trait and dominated by the fungi (Fig. 2f). This was notably more abundant among soil phyla. We also recovered signals indicating the Korarchaeota may be involved in transformation of aromatic compounds (Fig. 2f).

Nitrogen utilization

The ability to fix nitrogen was indicated by a large number of phyla (Fig. 3a). Archaeal signals were more abundant and largely due to Halobacteria and Methanopyri; whereas bacterial signals were dominated by alpha proteobacteria, Cyanobacteria and Fusobacteria. Most abundant nitrifiers (oxidation of ammonium ions from nitrogen fixation and ammonification into nitrate) were Alpha and Delta Proteobacteria, Cyanobacteria and Deinococci and (Fig. 3b). The potential for soil nitrate removal via denitrification was also indicated for 15 bacterial and archaeal phyla, and differences in the dominant phyla between chasmoendoliths and soils were observed (Fig. 3c). Annamox genes were detected among only one phylum (Planctomycetes). Ammonification (introduction of nitrate via decomposition) was indicated and strongest signals in chasmoendoliths were fungal, whereas in soils bacterial signals predominated (Fig. 3d). Anoxic nitrogen assimilation was largely indicated for Firmicutes and Verrucomicrobia (Fig. 3e). Strongest dissimilatory nitrate reduction signals were from Bacteriodetes, Delta Proteobacteria and Firmicutes (Fig. 3f).

Stress response

In all stress tolerance categories overall community responses were greater in chasmoendoliths than in soils. Twelve phyla displayed pathways for osmotic shock tolerance, accounted for largely by Actinobacteria, Bacteriodetes and Delta Proteobacteria (Fig. 4a). Radiation stress responses were widespread, with proportionally greater cyanobacterial and fungal signals. Strongest overall signals were among Deinococci, Nitrospirae and Proteobacteria (Fig. 4b). Heat shock pathways were very widespread, indicating possession by 36 phyla (Fig. 4c). Among chamsoendoliths strongest signals were from Acidobacteria, Proteobacteria and basidiomycete fungi. Cold shock pathways were indicated by relatively few bacterial and archeal phyla (Fig. 4d). Pathways for nutrient nitrogen and phosphate limitation were widespread among almost all phyla, with relatively higher signals in chasmoendoliths due to fungal contribution (Fig. 4e–f).

Discussion

The Miers Valley is a relatively simple system where microbial communities account for most of the standing

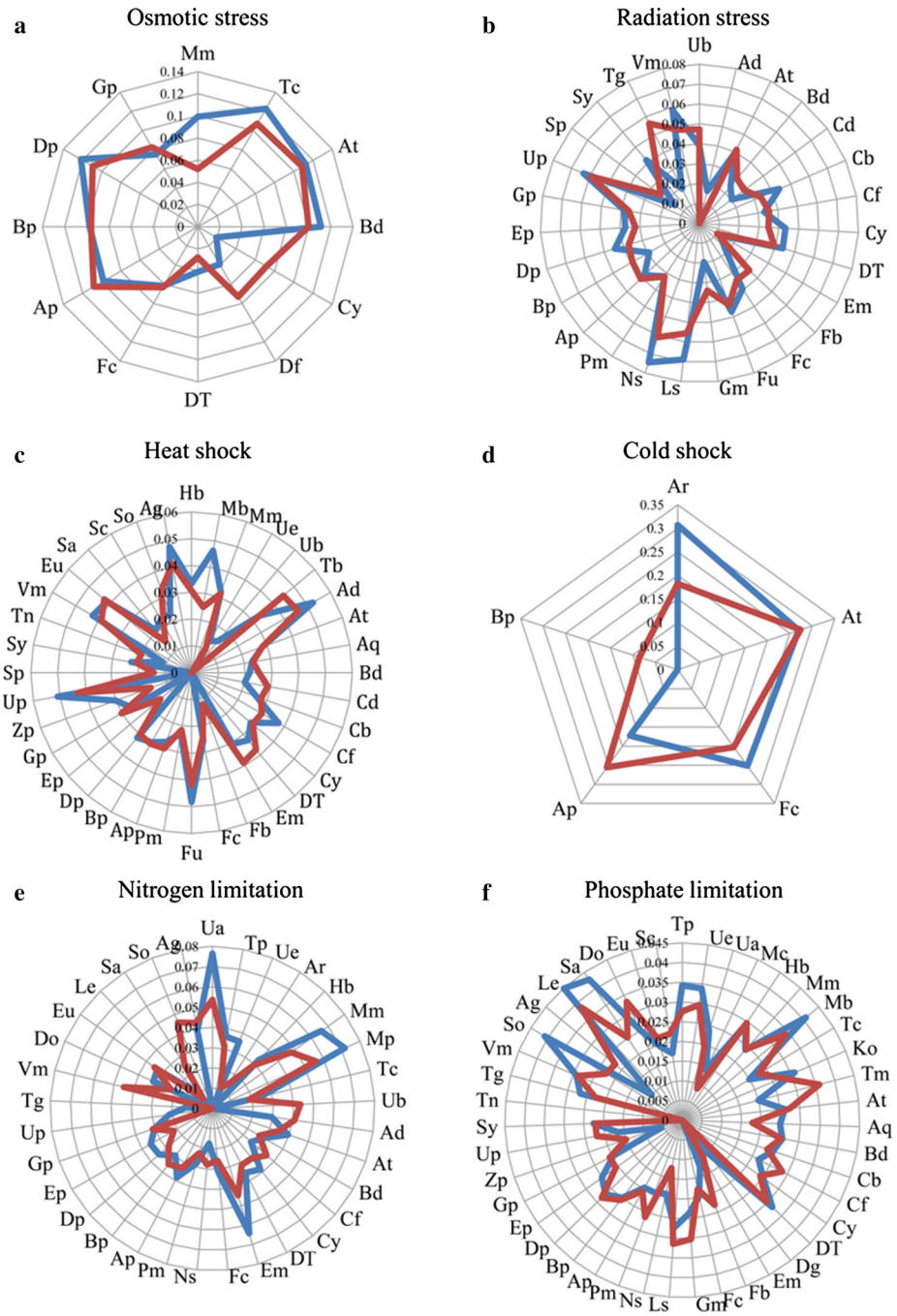

Fig. 4 Taxa-function relationships for stress response genes. The relative signal intensity was normalized for the number of probes per taxon. Mean values of samples from respective niches (chasmoendoliths [*blue*] and soils [*red*]) were plotted for the genes responsive to **a** osmotic stress, **b** radiation (desiccation) stress, **c** heat shock, **d** cold shock, **e** nitrogen limitation, **f** phosphate limitation. Two-letter codes denote microbial phyla as follows: *Ad* Acidobacteria, *Ag* Agaricomycetes, *Ap* Alphaproteobacteria, *Aq* Aquificae, *Ar* Archaeoglobi, *As* Ascomycota, *At* Actinobacteria, *Ba* Basidiomycota, *Bd* Bacteriodetes, *Bp* Betaproteobacteria, *Cb* Chlorobi, *Cd* Chlamydiae, *Cf* Chloroflexi, *Ck* Candidatus korarchaeum, *Cr* Crenarchaeota, *Cy* Cyanobacteria, *Da* Dacrymycetes, *Df* Deferribacteres, *Dg* Dictyoglomi, *Do* Dothidiomycetes, *Dp* Deltaproteobacteria, *DT* Deinococcus-Thermus, *En* Entomophthoromycota, *Em* Elusimicrobia, *Ep* Epsilonproteobacteria, *Eu* Eurotiomycetes, *Ex* Exobasidiomycetes, *Ey* Euryarchaea, *Fb* Fibrobacteres, *Fc* Firmicutes, *Fu* Fusobacteria, *Gm* Gemmatimonadetes, *Hb* Halobacteria, *Ko* Korarchaeota, *Le* Leotiomycetes, *Ls* Lentisphaerae, *Mb* Methanobacteria, *Mc* Methanococci, *Mm* Methanomicrobia, *Mp* Methanopyri, *My* Mycetozoa, *Na* Neocallimastigomycota, *Ns* Nitrospirae, *Pe* Pezizomycetes, *Pm* Planctomycetes, *Sa* Saccharomycetes, *Sc* Schizosaccharomycetes, *So* Sordariomycetes, *Sp* Spirochaetes, *Sy* Synergistetes, *Ta* Thaumarchaeota, *Tb* Thermobaculum, *Tc* Thermococci, *Tg* Thermotogae, *Tm* Thermoplamsata, *Tn* Tenericutes, *Tp* Thermoprotei, *Tr* Tremellomycetes, *Ub* Unknown bacteria, *Uc* Unknown Crenarchaeota, *Ue* Unknown Euryarchaeota, *Uf* Unknown fungus, *Un* unknown, *Up* Unknown proteobacteria, *Us* Ustilaginomycetes, *Vm* Verrucomicrobia, *Zp* Zetaproteobacteria, *Zy* Zygomycota. (Color figure online)

biomass. This study links biodiversity to functional traits in the two major terrestrial substrates within this system, and thus provides an inventory of potential geobiological contributions by Miers Valley microorganisms. Future landscape-scale studies will allow elucidation of the actual contributions to ecosystem processes.

The diversity estimates obtained using the *gyrB* marker yielded taxonomic resolution at the species-strain level and thus generally provided higher biodiversity estimates than rRNA gene-based estimates of this valley system (Lee et al. 2012; Yung et al. 2014). This may have resulted in some over-estimation, but the different biases associated with PCR primers versus oligonucleotide microarray specificity make direct comparison difficult. Biodiversity estimates using GeoChip are less informative than sequence-based data and are not truly quantitative, yet offer an important triangulation using an alternate molecular approach for environmental samples. The inherent heterogeneity of desert microbial communities must also be a consideration in studies such as these (Caruso et al. 2011; Lee et al. 2012). An interesting finding was that the *gyrB* estimates imply the salt-tolerant Halobacteria (Archaea) may be far more abundant in both soil and granite than previously appreciated. This may reflect the osmotic stresses that are thought to be a major force in shaping bacterial assemblages in the region (Pointing et al. 2009; Maghales et al. 2012; Lee et al. 2012). The array also revealed greater fungal diversity than was previously acknowledged, and this is congruent with predictions from earlier biodiversity studies that fungi may emerge as a major force in Dry Valleys ecology (Arenz et al. 2006; Pointing et al. 2009; Rao et al. 2011) and also in other extreme cold deserts (Wong et al. 2010b). Of interest was the recovery of basidiomycetous fungal signatures and their putative involvement in a range of mineral transformations, since most Antarctic fungi described to date have been ascomycetes and mitosporic fungi (Arenz et al. 2006).

The major focus of the array was bacteria. In this regard the diversity data was largely consistent with rRNA estimates from cloning (Pointing et al. 2009) and high-throughput sequencing studies (Lee et al. 2012). This taxonomic marker revealed some interesting differences between the two substrates and these support our delineation of putative differences in their contribution to carbon and nitrogen transformations based upon functional gene categories. Although the ability to both sequester inorganic carbon and nitrogen and carry out complete mineralization was detected in both substrates, the taxa within each phylum involved appear strikingly different and frequency of recovery implies relative contributions may vary.

Chasmoendoliths supported slightly higher overall levels of primary producers than soil in this study, and so we envisage granite communities are major sites of carbon fixation to the system along with soils. This is supported by productivity estimates for cryptoendolithic communities in Antarctica (Friedmann et al. 1993). Interestingly, the recovery of signatures for chemo-autotrophic carbon fixation suggest that non-photosynthetic inputs may also occur in this system. The abundance of signals for aromatic compound transformation in soil relative to chasmoendolith suggests that soil communities have evolved to utilize recalcitrant carbon reservoirs whilst in rocks this is not an important substrate (Chan et al. 2013). Soils supported a higher overall abundance of nitrogen-fixing proteobacteria compared to chasmoendoliths. This raises an interesting paradigm as to whether biological carbon and nitrogen inputs to this ecosystem are to some extent spatially discreet, with greater carbon fixation in granite and greater nitrogen fixation in soils. The basis for this may lie in terms of substrate geochemistry, where rocky substrates have been estimated as nitrogen sufficient for slow-growing endolithic colonization (Friedmann and Kibler 1980), whilst soils are ultra-oligotrophic but do possess organic carbon at levels above those of granite substrates (Lee et al. 2012).

Nitrogen fixation was largely attributed to the known diazotrophic cyanobacterial and Alpha Proteobacterial taxa, and is consistent with signatures for diazotrophy obtained in hyporrheic and extreme inland Antarctic soils (Niederberger et al. 2012; Chan et al. 2013). The potential for a complete pathway for nitrogen transformation was evident, and so under conditions favorable to annamox and denitrification pathways, the microbially mediated loss of nitrogen from the system may occur. It is not clear how cyanobacterial nitrogen fixation may be regulated under a 24-hr daylight scenario during the austral summer, since it is usually a dark reaction inhibited by oxygenic photosynthesis (Fay 1992). Circadian controls on primary metabolism may emerge as important in this regard (Ng et al. 2013). Overall these findings support the notion of a continuous soil-rock surface community (SRSC) forming a 'blanket' of surface biological activity in arid landscapes (Pointing and Belnap 2012), and these cryptogamic covers are likely globally important sources of carbon and nitrogen fixation (Elbert et al. 2012).

The only other geochip-based metagenomic study of Dry Valleys soil and rock communities was made at a colder drier inland site (McKelvey Valley et al. 2013). General patterns in the abundance of overall carbon and nitrogen fixation genes were similar, although the less extreme Miers Valley location in this study supported considerably greater diversity in all pathways. This implies less selective pressure may actually introduce multiple redundancies in metabolic pathways at the community level. Conversely the number of phyla possessing osmotic, radiation-desiccation, heat shock and nutrient limitation

stress response pathways was greater at the inland site (Chan et al. 2013). This strongly suggests that environmental stress adaptation has been a major driver of microbial diversity in the Dry Valleys. A further consideration is that this may also indicate a more profound difference in the way community stress tolerance is mediated: with individual taxa eliciting their own responses under more extreme stress, but community-wide benefits accruing from responses among fewer taxa in less extreme locations. Of course a caveat is that some important stress tolerance mechanisms may not be detectable using this microarray approach. One such response is the secretion by cyanobacteria of extracellular polymeric substances, which have been implicated in moisture retention that benefits the entire community within rocks (de los Rios et al. 2004).

Overall, we conclude that the granite substrate is an important site for key geobiological transformations, and likely fulfils complimentary ecosystem services to the surrounding soils, involving a discreet community of microbial taxa. Further insight will be gained by landscape-scale studies obtaining in situ estimates of actual geobiological transformations, and interrogation of the cellular basis for stress tolerance.

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