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ORIGINAL PAPER

Limits to the three domains of life: lessons from community assembly along an Antarctic salinity gradient

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Abstract

Extremophiles exist among all three domains of life; however, physiological mechanisms for surviving harsh environmental conditions differ among Bacteria, Archaea and Eukarya. Consequently, we expect that domain-specific variation of diversity and community assembly patterns exist along environmental gradients in extreme environments. We investigated inter-domain community compositional differences along a high-elevation salinity gradient in the McMurdo Dry Valleys, Antarctica. Conductivity for 24 soil samples collected along the gradient ranged widely from 50 to 8355 µS cm^{-1}. Taxonomic richness varied among domains, with a total of 359 bacterial, 2 archaeal, 56 fungal, and 69 non-fungal eukaryotic operational taxonomic units (OTUs). Richness for bacteria, archaea, fungi, and non-fungal eukaryotes declined with increasing conductivity (all $P < 0.05$). Principal coordinate ordination analysis (PCoA) revealed significant (ANOSIM $R = 0.97$) groupings of low/high salinity bacterial OTUs, while OTUs from other domains were not significantly clustered. Bacterial beta diversity was unimodally distributed along the gradient and had a nested structure driven by species losses, whereas in fungi and non-fungal eukaryotes beta diversity declined monotonically without strong evidence of nestedness. Thus, while increased salinity acts as a stressor in all domains, the mechanisms driving community assembly along the gradient differ substantially between the domains.

Keywords Species richness patterns · Inter-domain response · Salinity · McMurdo Dry Valleys · Antarctica

Introduction

Extreme environments and their endemic organisms have drawn considerable attention from biologists in an effort to shed light on the basic physiochemical limits to biology, the origins of life on a hostile primitive-earth, and the potential structure of extraterrestrial communities (Cavicchioli 2002; Cavicchioli et al. 2011; Doran et al. 1998; Rothschild and Mancinelli 2001; Wharton et al. 1995). All three domains of life contain extremophile organisms; however, inter-domain comparisons reveal varying molecular, physiological, and ecological adaptations (Clarke 2003; Rothschild and Mancinelli 2001). Extremophiles vary in their ability to exploit a diversity of metabolic pathways (Rothschild and Mancinelli 2001), and are capable of persisting under differing levels of physicochemical stress (Baker-Austin and Dopson 2007; Clarke 2003; Kashefi and Lovley 2003; Oren 2002a). These differences may lead to inter-domain variation in patterns of diversity, distribution, and community assembly along environmental gradients in extreme environments (Colman et al. 2018; Valentine 2007); however, to date, few studies have simultaneously considered the response of organisms from all three domains to varying stress.

The McMurdo Dry Valleys (MDV) region is the largest ice-free area in Antarctica (Levy 2013) and, as one of the

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most extreme terrestrial environments on Earth, provides an ideal habitat to study inter-domain microbial community structure and function under extreme stress. Average annual temperatures on the valley floors range from − 15 to − 30 ºC (Doran et al. 2002; Fountain et al. 1999) and annual precipitation, which is comprised entirely of snow, ranges from 3 to 50 mm liquid water equivalent (Fountain et al. 2010) with high rates of sublimation (Clow et al. 1988). The MDV are also characterized by low nutrient availability with average soil organic carbon and total nitrogen values of 0.19 g/kg and 0.025 g/kg, respectively (Barrett et al. 2004). Thus, limited water resources, low organic matter (OM), variable conductivity, low temperature, high UV radiation and high pH are common features of soil habitats in the MDV, which lack macroscopic animals and vascular plants, and are dominated by microorganisms (Bamforth et al. 2005; Cary et al. 2010; Fell et al. 2006; Van Horn et al. 2013; Virginia and Wall 1999).

Culture-independent 16S rRNA gene-based sequencing techniques have revealed relatively high diversity in MDV soil bacterial communities in spite of the extreme nature of the environment (Cary et al. 2010; Lee et al. 2012; Van Horn et al. 2013). In contrast, the diversity of protozoans (Bamforth et al. 2005; Fell et al. 2006) and invertebrates (e.g., rotifers, tardigrades and nematodes) (Bamforth et al. 2005; Freckman and Virginia 1997; Treonis et al. 1999) endemic to this region are orders of magnitude lower (Adams et al. 2006; Poage et al. 2008). Although it has likely been not fully described, fungal diversity also appears to be limited, with filamentous fungi dominating communities in high soil moisture areas and non-filamentous taxa being widely distributed throughout the MDV (Connell et al. 2006). Finally, while Archaea are widespread in MDV soils, their abundances and richness are limited to a few species compared to Bacteria (Richter et al. 2014) and soil habitats in other regions (Bintrim et al. 1997; Høj et al. 2008; Isobe et al. 2018; Kent and Triplett 2002).

Strong linkages exist between the composition and diversity of these MDV communities and abiotic factors including moisture (Niederberger et al. 2015; Zeglin et al. 2011), salinity (Feeser et al. 2018; Lee et al. 2012; Poage et al. 2008; Van Horn et al. 2014), organic carbon availability (Aislabie et al. 2009; Geyer et al. 2013; Tiao et al. 2012), temperature (Okie et al. 2015) and combinations of multiple factors (Feeser et al. 2018; Niederberger et al. 2008; Richter et al. 2014; Smith et al. 2010; Stomeo et al. 2012; Van Horn et al. 2013). In addition, these abiotic/biotic relationships are highly contextual at multiple scales, suggesting complex controls on life in this polar desert environment (Van Horn et al. 2013). Of these abiotic factors, salinity is a key determinant of bacterial community assemblages in the MDV, with decreases in soil microbial diversity (Feeser et al. 2018; Okie et al. 2015), a shift in dominant bacterial phyla (Feeser et al. 2018; Van Horn et al. 2014), and differential responses to water and organic matter additions (Buelow et al. 2016; Schwartz et al. 2014; Van Horn et al. 2014) along salinity gradients. Similarly, there is a significant negative correlation between the abundance of nematodes and salinity in soils of the MDV (Poage et al. 2008). These results agree with the global-scale paradigm that salinity is an important variable structuring microbial communities (Lozupone and Knight 2007). Finally, since soil communities in the MDV region experience numerous stressors, elevated salinity, even at relatively low levels as compared to extreme saline environments such as brines or hypersaline lakes, may elicit a community tipping-point due to synergistic stressor interactions.

To date, a comprehensive description of the molecular diversity of all three domains of life in response to a range of salinity in MDV is lacking. This comparison will provide information about the impacts of an important stress in an already extreme polar desert with implications for elucidating how communities are structured and function at the edge of habitability. The specific objectives of this study were to utilize a steep, naturally occurring salinity gradient to: (1) investigate the community diversity and assembly responses from all three domains of life to an environmental stress gradient, and (2) explore changes in the taxonomic profile of the community along this gradient to infer possible physiological mechanisms underlying this distribution.

Materials and methods

Site description and sample collection

Bull Pass (BP) is a glacially carved valley connecting Victoria and Wright Valleys (Fig. 1), with a roughly northwest to southeast orientation. The valley floor is covered by coarse-textured soils containing soil polygons created by freeze–thaw cycles (Mellon et al. 2014). Stone surface pavement formed from the long-term weathering of Ferrar dolerite and granite covers much of the sandy soil (Conca and Astor 1987). It has been proposed that BP and the adjacent central Wright Valley share a common geomorphologic history (Hall et al. 2001; Prentice et al. 1993); however, the influence of historical events on current edaphic chemistry remains unclear (Poage et al. 2008).

In the present study, we chose an experimental design based on the regression approach to sampling (Schweiger et al. 2016) to maximize our ability to detect threshold changes, limits to species ranges, and nestedness in communities along a gradient. A single sample was taken from 24 sites located along a natural salinity gradient that had been used previously in a nematode survey of Bull Pass (Poage et al. 2008) (Table 1). Sites were located using the

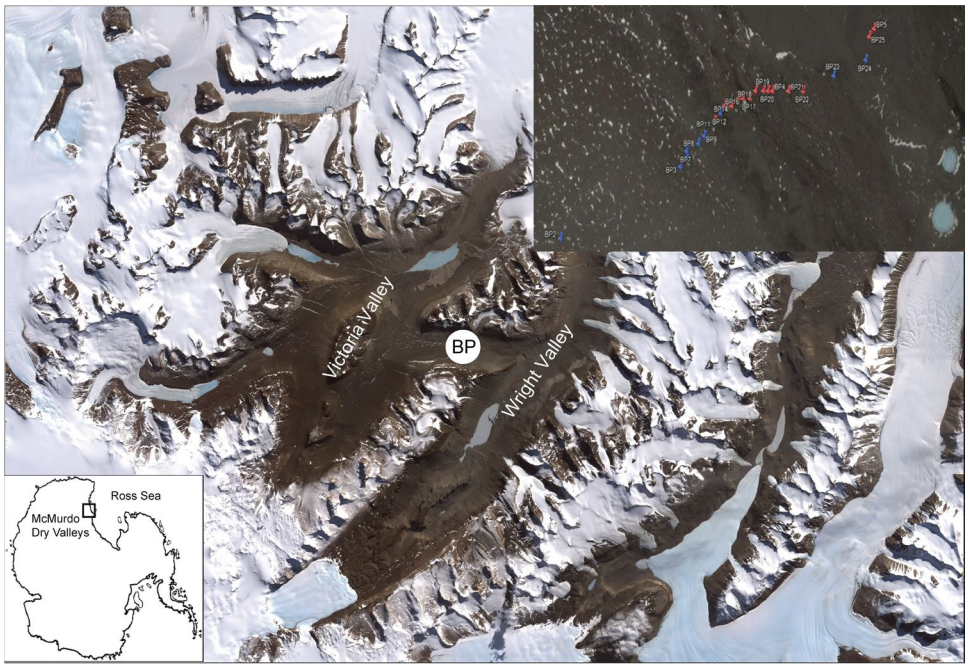

Fig. 1 Geographic maps showing sampling locations

Table 1 Sample location and edaphic chemistry

Sample ID	Lat. (South)	Long. (East)	pH	Conductivity (μS cm^{-1})	ATP (RLU)
BP1	77° 28.779′	161° 44.439′	7.90	52	789
BP2	77° 28.719′	161° 45.229′	8.60	50	299
BP3	77° 28.629′	161° 46.179′	7.72	74	563
BP4	77° 28.529′	161° 46.979′	8.09	2359	128
BP5	77° 28.449′	161° 47.869′	8.60	383	1524
BP6	77° 28.619′	161° 46.229′	8.51	73	754
BP7	77° 28.609′	161° 46.229′	8.95	129	526
BP8	77° 28.599′	161° 46.329′	8.31	119	1113
BP9	77° 28.589′	161° 46.379′	8.80	121	680
BP11	77° 28.569′	161° 46.469′	9.17	173	847
BP12	77° 28.559′	161° 46.519′	8.65	148	436
BP13	77° 28.549′	161° 46.559′	8.51	1293	77
BP14	77° 28.549′	161° 46.619′	8.16	1429	267
BP15	77° 28.539′	161° 46.679′	8.02	8355	6
BP16	77° 28.539′	161° 46.719′	7.93	3000	60
BP17	77° 28.539′	161° 46.779′	7.85	8200	0
BP18	77° 28.529′	161° 46.829′	7.97	2025	79
BP19	77° 28.529′	161° 46.899′	8.06	3102	17
BP20	77° 28.529′	161° 46.939′	8.15	2955	160
BP21	77° 28.529′	161° 47.119′	7.96	3022	11
BP22	77° 28.529′	161° 47.249′	8.34	1645	55
BP23	77° 28.509′	161° 47.519′	8.47	219	139
BP24	77° 28.489′	161° 47.799′	8.30	172	346
BP25	77° 28.459′	161° 47.829′	8.26	772	69

coordinates given in Poage et al. (2008). The elevation of the sites ranges from 635 to 832 m. At each location a ~ 250 g sample of soil was collected to a depth of 10 cm from the top of the soil, or until the ice cement was encountered, using

a sterilized spatula and sealed in sterile bags. In the field, large stones and pebbles (> 0.5 cm diameter) were removed and each sample was homogenized and split into two portions. Samples were transported at − 20 ºC from the field to the laboratory, where one portion was immediately used for pH, electrical conductivity (EC) and ATP measurements and the other portion was stored at − 80 ºC for DNA extraction in sucrose lysis buffer (Giovannoni et al. 1990). EC and pH were the edaphic characteristics selected for analysis due to their importance in structuring microbial communities in the MDV (Bottos et al. 2020; Feeser et al. 2018; Van Horn et al. 2013).

Edaphic characteristics

Soil pH was measured on 1:2 soil/DI water extracts using an Orion pH meter (Thermo Scientific™). Electrical conductivity was measured on 1:5 DI water extracts and determined with a Yellow Springs Instrument 3100 conductivity meter. ATP concentrations were estimated using the commercially available luminometric assay kit (Hygiena, Camarillo CA) following the manufacturer's protocols.

DNA extraction, PCR, pyrosequencing and illumina sequencing

Community DNA was extracted from 0.75 g of soil for bacteria, archaea, fungi and other eukaryotes using bead-beating disruption in a cetyltrimethylammonium bromide (CTAB) buffer (1% CTAB, 0.75 M NaCl, 50 mM Tris pH 8, 10 mM EDTA) and subsequent phenol–chloroform purification steps as previously described (Mitchell and Takacs-Vesbach 2008). Amplicon sequencing was performed by pyrosequencing for Bacteria and Archaea, and with Illumina sequencing for fungi and other eukaryotes. For Bacteria, barcoded amplicon pyrosequencing of 16S rRNA genes was performed as described previously (Andreotti et al. 2011; Dowd et al. 2008; Jiang and Takacs-Vesbach 2017; Van Horn et al. 2013, 2016) using universal bacterial primers 939F (5′-TTGACGGGGGCCCGCACAAG-3′) and 1492R (5′-GTTTACCTTGTTACGACTT-3′) targeting the V6–V9 regions. Archaeal 16S rRNA genes were amplified with archaeal-specific primers 349F (5′-GYGCASCAGKCGMGAAW-3′) and 806R (5′-GGACTACVSGGGTATCTAAT-3′) targeting the V3–V4 regions, which are effective at capturing a wide range of Archaea as described previously (Colman et al. 2015). Triplicate reaction mixtures of each sample were combined and subsequently purified with an UltraClean™ GelSpin™ DNA Extraction Kit (MoBio Laboratories, Carlsbad, CA, USA). The purified amplicons were quantified using a Nanodrop ND-2000c spectrophotometer (Thermo Fisher Scientific, Wilmington, DE, USA) and pooled in equimolar concentrations for pyrosequencing, using Roche titanium reagents and titanium procedures on a Roche 454 GS FLX instrument (454 Life Sciences, Branford, CT, USA) at the Molecular Biology Facility, in the Biology Department at the University of New Mexico.

Fungal diversity was determined using the fungal ITS primers ITS1-F (5′-CTTGGTCATTTAGAGGAAGTAA-3′) and ITS4 (5′-TCCTCCGCTTATTGATATGC-3′) (White et al. 1990). Eukaryotic 18S rRNA gene primers euk1390F (5′-GTACACACCGCCCGTC-3′) and EukB-Rev (5′-TGATCCTTCTGCAGGTTCACCTAC-3′) (Amaral-Zettler et al. 2009) were used following protocols from the Earth microbiome project (http://www.earthmicrobiome.org/emp-standard-protocols/18s/). After amplification, samples were purified using AMPure XP beads (Beckman Coulter, Brea, CA, USA) and pooled in equimolar concentrations. The purified PCR products of fungal and eukaryotic 18S rRNA genes were used to prepare DNA libraries following the Illumina TruSeq DNA library preparation protocol. Illumina sequencing was performed at MR DNA (www.mrdnalab.com, Shallowater, TX, USA) on a MiSeq platform following the manufacturer's guidelines.

DNA sequence data processing

The 16S rRNA gene sequences (generated by pyrosequencing) were quality filtered, denoised, and checked for chimeras using AmpliconNoise and Perseus (Quince et al. 2011) within Quantitative Insights into Microbial Ecology (QIIME, Ver. 1.9.0) (Caporaso et al. 2010b). Adapters, multiplex identifiers and primers were trimmed from denoised data. In QIIME, species level operational taxonomic units (OTUs) were identified at the 97% DNA similarity criterion (Blaxter et al. 2005) using UCLUST (Edgar 2010). The most abundant sequence was picked from each OTU as a representative sequence and aligned using the PyNAST aligner (Ver. 1.2.2) (Caporaso et al. 2010a) and Greengenes database (GG 13_5) (DeSantis et al. 2006). Taxonomic affiliations were assigned by the Ribosomal Database Classifier program (Ver. 2.2) (Wang et al. 2007). The archaeal data set was further curated by removing OTUs classified as belonging to the bacterial domain. All measurements of bacterial and archaeal community structure were performed with randomly drawn subsets of sequences from each sample to standardize for varying sequencing efforts across samples. Bacterial and archaeal data sets were rarified to 570 and 181 sequences per sample, respectively.

Demultiplexing and quality filtering of Illumina (fungal ITS and eukaryotic 18S rRNA) data were performed in QIIME (split_libraries_fastq.py). OTUs were identified at the 97% DNA similarity level (pick_open_reference_otus.py). Fungal OTUs were taxonomically assigned by BLAST against the QIIME/UNITE reference OTUs database (alpha version 12_11). All measurements of fungal community

structure were performed by randomly subsampling each data set to a depth of 3,470 sequences. Taxonomic affiliations of eukaryotic OTUs were determined by BLAST against the SILVA 119 SSU database for QIIME (Quast et al. 2013). All downstream eukaryotic data analyses were conducted using a subset of this data set further curated by removing fungal OTUs to focus on the diversity of non-fungal eukaryotes. The raw pyrosequencing and Illumina sequencing reads were deposited into the Short Read Archive database at NCBI with accession ids SAMN04696062 through SAMN04696132 under Bioproject PRJNA318249.

Alpha diversity and community composition analyses

Statistical analyses were conducted using QIIME and/or R (R Development Core Team 2011) using the 'cluster' (Maechler et al. 2013) and 'vegan' (Oksanen et al. 2013) packages and libraries, unless otherwise noted. To assess differences in community composition, a principal coordinates analysis (PCoA) was constructed from unweighted UniFrac distance (Lozupone et al. 2011) using the rarified OTU table. Groupings apparent in PCoA analysis were verified by the unweighted pair group method with arithmetic mean (UPGMA) hierarchical clustering. ANOSIM (Clarke 1993) was used to determine the strength and statistical significance of groupings in PCoA and clustering. Partial Mantel tests were employed to assess correlations between bacterial community differences and specific environmental variables. Analysis of covariance (ANCOVA) was used to compare the impact of salinity on alpha diversity across domains. To identify potentially halophilic taxa, representative sequences of OTUs exclusively present in the high salinity sites (EC > 300 µS cm^{-1}) were given taxonomic assignments using BLASTn (Altschul et al. 1997) against the NCBI nucleotide (NT) database.

Community structure and beta diversity analyses

While alpha diversity measures quantify the species richness at a given site, beta diversity measures interrogate differences in species presence and/or abundance between sites (species turnover). This information can be used to determine the factors that structure community composition along environmental gradients. One component of community structure is the extent to which communities vary due to species turnover (species replacement) and nestedness (species loss) (Leibold and Mikkelson 2002). Turnover occurs when one species replaces another species along a gradient, while nested subset structure occurs when a diverse community becomes increasingly depauperate. We used both a graphical qualitative and a quantitative approach to assess these characteristics. The qualitative assessment involved creating a presence/absence matrix of the OTUs found in each sample with samples organized from low to high salinity (note that singletons and doubletons were removed from the bacterial data set for this analysis to tractably visualize these data). The quantitative method leverages differences inherent in the various common beta diversity indices: Sorensen's (Bsor) index measures total/overall changes in beta diversity, while Simpson's (Bsim) index measures turnover, and thus the difference between them (i.e., Sorensen's minus Simpson's index) indicates dissimilarity due to nestedness (Bnes) (Baselga 2010; Baselga and Leprieur 2015). This analysis was performed using the betapart package in R (Baselga and Orme 2012).

An additional beta diversity analysis was performed by calculating Jaccard distances between pairwise comparisons of sites varying by no more than 0.3 log conductivity (µS cm^{-1}) values. We then plotted these Jaccard beta diversity values versus the mean log-conductivity for each of these pairwise comparisons. Least-squares regression analysis with second-order interaction (i.e., quadratic) terms and backward elimination of terms with $\alpha = 0.1$ were used within each taxonomic group to evaluate the effects of conductivity on beta diversity and determine whether the relationship, if any, is best explained by a linear or quadratic model. All alpha and beta analyses were performed using rarified OTU tables unless otherwise specified.

Results

Edaphic characteristics

Soil conductivity ranged from 50 to 8,355 µS cm^{-1}, ATP values ranged from 0 to 1524 RLU, and pH values ranged from near circumneutral (7.72) to alkaline (9.17) (Table 1). The magnitude of these geochemical measurements is consistent with measurements of soils from across the MDV (Barrett et al. 2004; Courtright et al. 2001; Nkem et al. 2006) including from a previous study along this same salinity transect (Poage et al. 2008).

Sequencing results and taxonomic composition

Bacterial 16S rRNA gene pyrosequencing resulted in 32,294 sequences from 24 samples after denoising and removal of low-quality sequences and chimeras. Three samples that had an insufficient number of sequencing reads were excluded from further analyses. The number of sequences in each sample ranged from 572 to 3711 with a mean of 1516. A total of 359 bacterial OTUs were found at the 97% nucleotide similarity level. Good's coverage (Good 1953), which provides an estimate of sampling completeness, ranged between 94.4 and 99.8% (mean of 97.9%). The bacterial

assemblages varied across the salinity gradient with the detection of fifteen major phyla and candidate divisions. High salinity sites were primarily comprised of Bacteroidetes (~41.5%) and Proteobacteria (~52.9%), while low salinity site communities were dominated by Acidobacteria (~44.2%, Fig. 2A). Low abundances of 16S rRNA gene sequences (less than 2.0% of 16S rRNA gene sequences) from the Actinobacteria, BRC1, Chloroflexi, Cyanobacteria, FBP, Firmicutes, Gemmatimonadetes, Nitrospirae, Planctomycetes, TM7, Verrucomicrobia, Deinococcus-Thermus (Fig. 2A) were also found at both high and low salinity sites.

Archaeal 16S rRNA gene sequencing resulted in 5304 16S rRNA gene sequences from seven samples after quality filtering and removal of bacterial sequences. The number of archaeal 16S rRNA gene sequences in the seven samples ranged from 181 to 1619 with a mean of 758. The remaining 17 samples did not produce PCR amplification products despite varying DNA and reagent concentrations. Tests to determine if the PCR was inhibited by potential co-extracts in the DNA were negative. A total of two archaeal OTUs were found at the 97% similarity level. One sample (BP8) contained two OTUs, while the other six samples contained a single OTU. Coverage of archaeal diversity was consequently complete in the data set as noted by Good's coverage values of 100 ± 0% for all seven samples, even at a minimal sequence subsampling depth of 181 16S rRNA gene sequences. Both archaeal OTUs were classified as Group 1.1b Thaumarchaeota in the genus *Nitrososphaera* (Fig. 2B).

Fungal ITS gene sequencing resulted in 460,138 sequences from 21 samples. The number of sequences in each sample ranged from 3479 to 44,162 with a mean of 21,911. A total of 56 fungal OTUs were found at the 97% similarity level. Good's coverage values of all samples were greater than 99.9%. The majority of sequences (97.5%) were classified as *Aureobasidium pullulans* within the phylum Ascomycota (Fig. 2C).

Overall, eukaryotic 18S rRNA gene sequencing generated 38,324 quality sequences from 22 samples, ranging from 368 to 3633 among samples, with an average of 1742. After quality control, a total of 69 eukaryotic OTUs were found at the 97% similarity level, with Good's coverage values of all samples greater than 99.9%. Since the primary goal of our 18S rRNA gene sequencing was to target non-fungal eukaryotes, we filtered all fungal sequences from the data

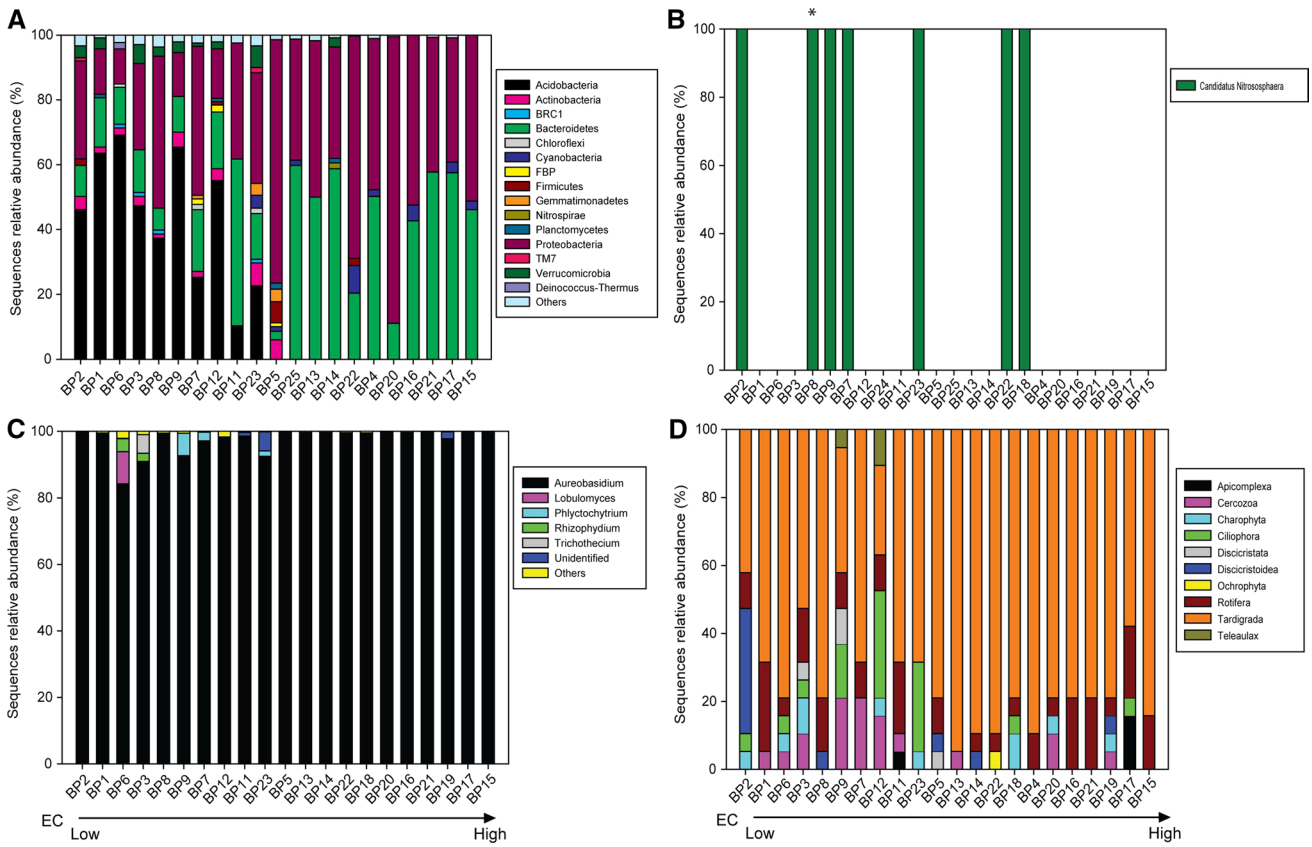

Fig. 2 Taxonomic bar charts. **A** Bacterial community composition at the phylum level. The phyla with < 1% abundance are included as 'Others'. **B** Archaeal community composition at the genus level. "*", two unique OTUs are found in this site. **C** Fungal community composition at the genus level. The genera with < 1% abundance are included as 'Others'. **D** Non-fungal eukaryotic community composition at the phylum level

set, after which only 1529 sequences remained from 22 samples. The number of sequences in each sample ranged from 19 to 245, with an average of 70. A total of 42 non-fungal eukaryotic OTUs were found at the 97% similarity level. The non-fungal 18S rRNA gene sequences were mostly classified as Apicomplexa, Cercozoa, Charophyta, Ciliophora, Discicristata, Discicristoidea, Charophyta, Rotifera, Tardigrada and Teleaulax (Fig. 2D).

Alpha diversity, beta diversity, and community structure

Alpha diversity (log of the observed number of species) was significantly ($P < 0.05$) negatively correlated with increasing EC (log) for bacteria ($R^2 = 0.83$), archaea ($R^2 = 0.35$), fungi ($R^2 = 0.26$), and non-fungal eukaryotes ($R^2 = 0.26$), as shown in Fig. 5. The slopes of these relationships differed significantly (ANCOVA test of equal slopes; $P < 0.001$), from −0.41 for bacteria to −0.06 for fungi. The presence/absence of bacterial OTUs varied considerably above and below an EC value of ~ 300 µS cm^{-1} (Fig. 5), although a group of ~ 5 bacterial OTUs was present across the majority of the sampling sites. For fungi and non-fungal eukaryotes, the total richness of OTUs declined with increasing salinity. The consistent group of fungal and non-fungal eukaryote OTUs found at most sites comprised ~ 25 and ~ 10% of the total number of OTUs, respectively (Fig. 5).

The PCoA ordination and UPGMA clustering revealed relationships between bacterial community structure and edaphic variables (Figs. 3A and 4A). The majority of the bacterial samples clustered into two groups that corresponded to soils with electrical conductivity (EC) values greater than 300 µS cm^{-1} and EC values less than 200 µS cm^{-1} (Figs. 3A, 4A, and Table 1), hereafter referred

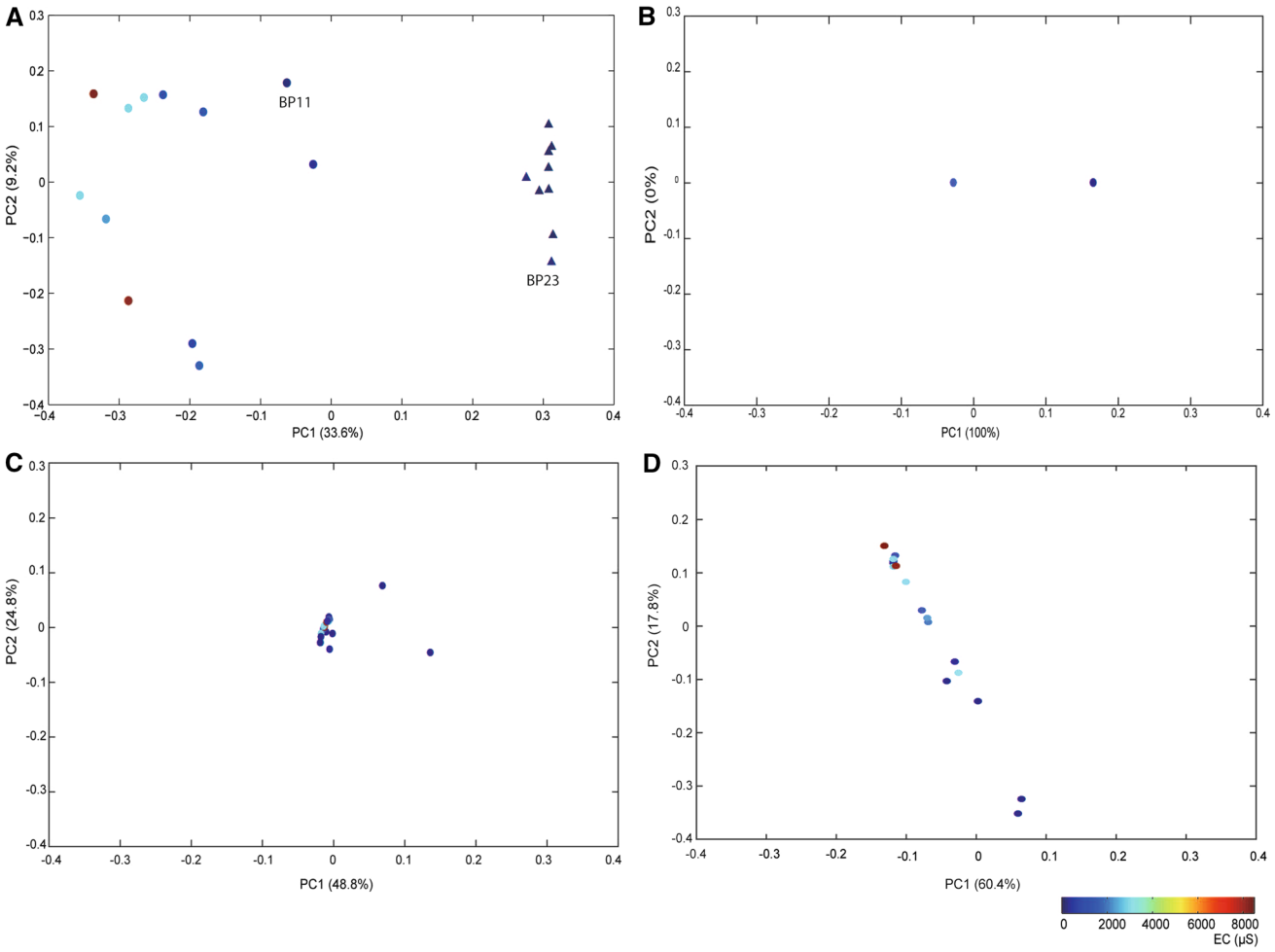

Fig. 3 Principal coordinates analysis. Color coding of samples indicates the EC values of sampling locations. **A** Bacterial PCoA plot built with unweighted UniFrac distance. The dots and triangles represent samples from high salinity and low salinity groups, respectively. **B** Archaeal PCoA plot built with Bray–Curtis distance. **C** Fungal PCoA plot built with Bray–Curtis distance. **D** Non-fungal eukaryotic PCoA plot built with Bray–Curtis distance

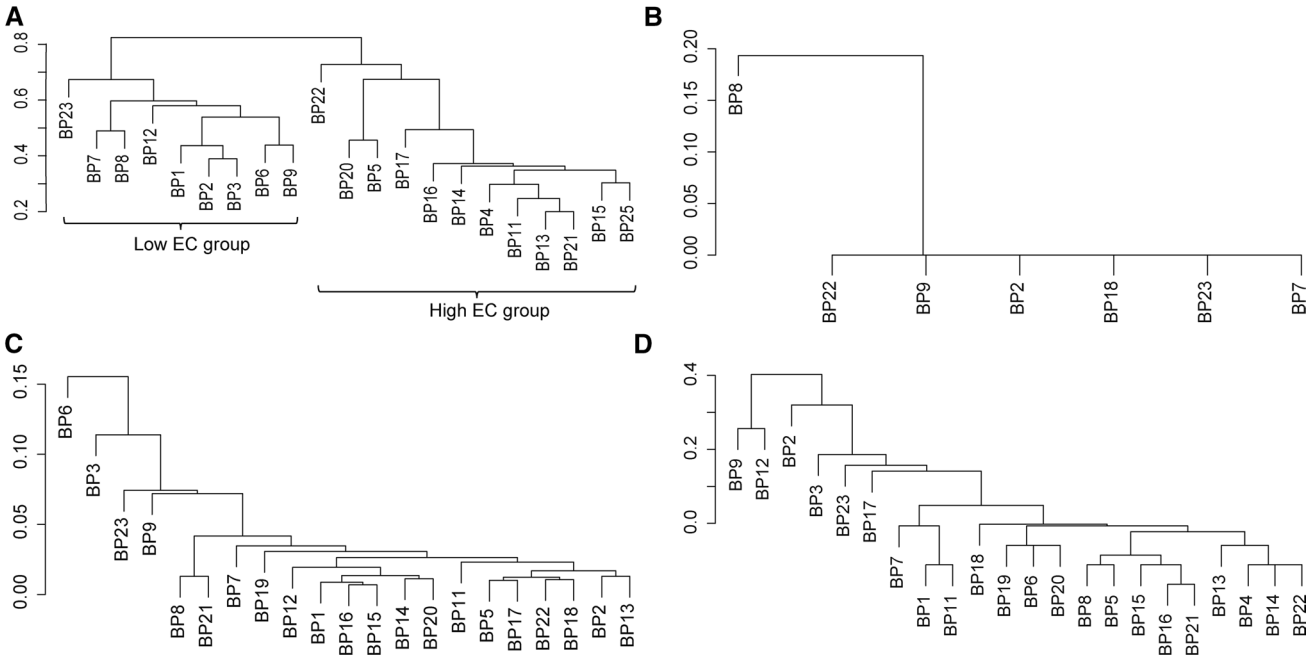

Fig. 4 UPGMA cluster analysis using Bray–Curtis dissimilarity. **A** Bacterial communities. **B** Archaea communities. **C** Fungal communities. **D** Non-fungal eukaryotic communities

to as high and low salinity sites. Two samples with EC of ~ 200–300 µS cm^{-1} displayed a community composition in the transition from high salinity to low salinity. An ANOSIM test ($R = 0.97$ and $P = 0.001$) confirmed that the high and low salinity groups were significantly different. A significant linear relationship was observed between the first principal coordinate (log PC1) and log EC ($R^2 = 0.87$, $P < 0.001$). The strength of correlation from the partial Mantel test remained high between bacterial community similarity and salinity ($r = 0.50$, $P = 0.001$) when controlling for the effect of geographic distance among sampling sites. Compared to bacterial community composition, archaeal, ITS fungal, and 18S rRNA eukaryotic OTUs did not separate into clear groups based on soil salinity (Figs. 3 and 4).

The beta diversity nestedness versus turnover analysis found strong support for nestedness ($R^2 = 0.45$, $P = 0.001$), but not turnover, along the salinity gradient for bacterial communities, and evidence of significant ($P < 0.05$) but very weak nestedness patterns for fungal ($R^2 < 0.026$) and non-fungal eukaryote communities ($R^2 < 0.035$). A unimodal relationship was found for pairwise comparisons of bacterial community Jaccard distances among sites varying no more than 0.3 log conductivity (µS cm^{-1}) values ($P = 0.007$, $R^2 = 21\%$, Fig. 5, see Table S2 for statistical details), with beta diversity clearly increasing steeply from 1.7 to 2.5 log conductivity units ($r^2 = 72\%$) and showing high variation among samples with high conductivities ($r^2 = 0.003\%$). In contrast, both fungal and non-fungal eukaryote community beta diversity values decreased monotonically with increasing conductivity ($P < 0.001$, $R^2 = 37\%$; $P = 0.012$, $R^2 = 14\%$, respectively, Tables S3 and S4).

Discussion

Previous research related to biodiversity in MDV soils has primarily focused on within-domain diversity and how environmental variables influence this diversity (Aislabie et al. 2008; Connell et al. 2006; Courtright et al. 2001; Freckman and Virginia 1997; Niederberger et al. 2008, 2015; Poage et al. 2008; Richter et al. 2014; Stomeo et al. 2012). There has been limited exploration of variation in biodiversity and taxonomic composition among domains in response to the same environmental gradient (Boey et al. 2021; Hendershot et al. 2017; Rath et al. 2019; Sang et al. 2018; Vander Vorste et al. 2019). In this study, we conducted the first comparative study of the response of members from the three domains of life to a wide range of soil conductivity values, from low to high salinity, in an extreme, resource limited, hyper-arid, polar desert, finding disparate patterns that suggest strong inter-domain differences in community assembly.

Alpha diversity patterns

The observed negative correlation between soil salinity and alpha diversity within all domains corroborates similar findings from both field observations and theoretical predictions for MDV soils. Surveys and experiments in the MDV

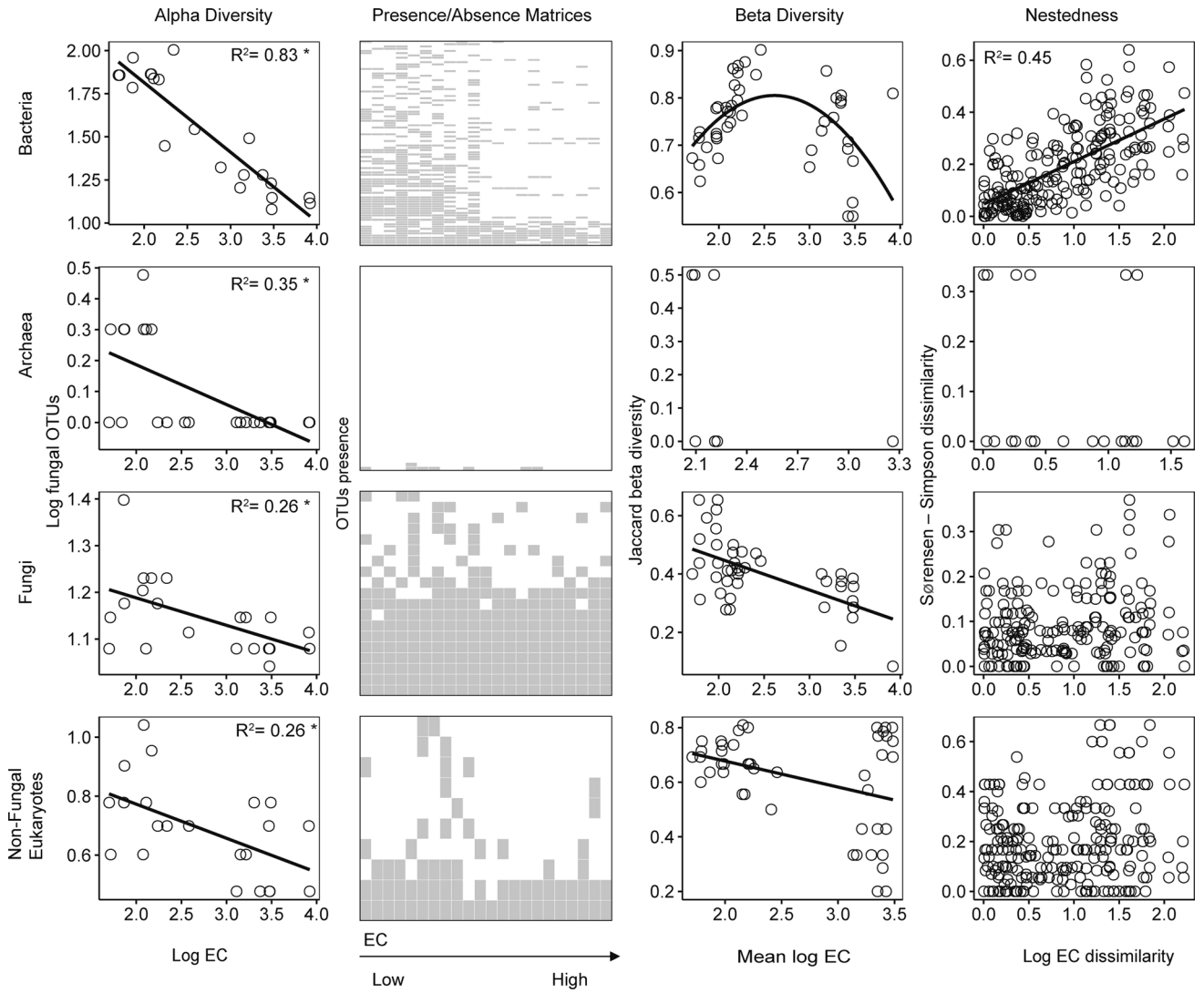

Fig. 5 Results of alpha diversity (linear regression between EC and the number of observed OTUs for each site), OTU presence and absence table, beta diversity and nestedness analyses. Bacterial, archaeal, fungal, and non-fungal eukaryotic communities are arranged from top to bottom, respectively

suggest that soil salinity is a primary driver of bacterial (Feeser et al. 2018; Lee et al. 2012; Okie et al. 2015; Van Horn et al. 2014), nematode (Poage et al. 2008), and fungal (Arenz and Blanchette 2011; Connell et al. 2006) abundance and diversity, with negative relationships observed for all three groups of organisms. This negative relationship was not reported for archaeal diversity in the single study of MDV archaeal communities, which found very low overall archaeal diversity and a single positive relationship between diversity and soil moisture (Richter et al. 2014). Our results also support the recently developed theory suggesting that as environmental stress increases, the challenges associated with maintaining physiological homeostasis and obtaining sufficient resources also increases, leading to a decline in rates of growth (Okie et al. 2015). As rates decline, the niche widths of organisms living in these environments are reduced, leading to a predicted decline in alpha diversity due to fewer taxa having niches overlapping with local conditions (Okie et al. 2015). Empirical confirmation of this theoretical prediction is provided by recent findings of a decline in bacterial growth rates and biomass along an increasing salinity gradient in non-polar soils (Bernhard et al. 2005, 2007; Egamberdieva et al. 2010; Li et al. 2021), and that Antarctic species of *Arthrobacter* have narrower salinity tolerance ranges than species from temperate environments (Dsouza et al. 2015). Thus, the decrease we observed in alpha diversity in all three domains appears to result from increasing environmental filtering at higher salinities reflecting the challenges associated with life in low-temperature, high salinity soils.

While the alpha diversity of all three domains decreased with increasing salinity, the significant differences in the slopes and strengths of this relationship (e.g., slopes of −0.41 for bacteria to −0.06 for fungi, and R^2 values of 0.83 for bacteria to 0.25 for fungi, Fig. 5), suggests variation in response among the domains (ANCOVA test of equal slopes; $P < 0.001$). The stronger correlation between salinity and alpha diversity for bacterial as compared to archaeal and eukaryotic communities may be related to the greater overall diversity of this domain in MDV (Fig. 5). The high bacterial diversity supports the observation of fine-scale environmental filtering and niche partitioning for bacterial taxa along the gradient, creating a continuous distribution of OTUs that is not apparent in the much lower diversity fungal and non-fungal eukaryotic communities. The steeper alpha diversity versus salinity slope observed for bacteria as compared to the other domains suggests that in the MDV, salinity is a more important environmental filter in controlling bacterial diversity. This result differs from studies in solar salterns in which steeper declines in eukaryotic, as opposed to bacterial or archaeal alpha diversity were observed with increasing salinity (Casamayor et al. 2002), and in Tibetan lakes, where bacterial diversity increased concurrently with salinity (Wang et al. 2011). These contrasting results suggest that domain-specific responses of richness to salinity may differ between habitats or be influenced by other confounding variables.

Beta diversity patterns

The beta diversity patterns explored by examining the dissimilarity of all samples within a sliding window of salinity, and using a nestedness analysis, also suggest strong inter-domain differences in community assembly. For Bacteria, the observed increase in beta diversity with the initial increase in salinity (from ~ 50 to 300 µS, Fig. 5) is in agreement with the environmental filtering diversity theory discussed above (Okie et al. 2015) and in another recent study that tested this prediction (Wu et al. 2018). This theory suggests that a reduction in rates of growth due to increasing physiological harshness should lead to increasing beta diversity. However, at higher soil salinities, bacterial community beta diversity decreased leading to an overall unimodal beta diversity pattern. The maximum between-sample dissimilarity at intermediate soil salinities appears to be a result of the diversity threshold that occurs between sample conductivities of 219 and 383 µS cm^{-1}: below this threshold, samples have relatively high alpha diversity and abundant rare taxa, both of which decline dramatically above the threshold (Fig. 5). The subsequent decline in beta diversity above this threshold is not predicted by baseline environmental filtering diversity theory (Okie et al. 2015), suggesting that additional factors are governing diversity and distribution at higher soil salinities. In contrast, the lack of clear patterns in beta diversity for the fungi and non-fungal eukaryotes is likely due to the very low observed alpha diversity for these domains at high salinities.

We found strong evidence of nested subset structure in bacteria, with higher salinity communities representing subsets of the communities at lower salinities. However, fungi and non-fungal eukaryotes did not exhibit a strong nestedness pattern (Fig. 5). The evidence of nestedness rather than turnover for Bacteria supports predictions and observations that nestedness beta diversity patterns are common at high latitudes due to increased local extinctions associated with extreme conditions and low biomass (Castro-Insua et al. 2016; Soininen et al. 2018). The between-domain difference in nestedness/turnover patterns likely reflects the decline in alpha diversity and the existence of a stable, high-occurrence community for Bacteria versus the more stochastic assembly of the other domains. Furthermore, the nested subset structure is a factor not incorporated into the baseline predictions presented in Okie et al. 2015, which assumed that the salinity niche width of taxa is invariant of salinity. The nested structure of bacteria in this study indicates that the Bacteria that can grow at high conductivities tend to have higher salinity niche widths, as they tend to also be present at the low salinity sites. Further exploration of this pattern and how to integrate it into the environmental filtering diversity theory and other community assembly theories is needed.

Taxonomy

The shift in bacterial taxonomy observed along the salinity gradient from an Acidobacteria to a Bacteroidetes and Proteobacteria-dominated community is consistent with other MDV studies. A decline in Acidobacteria with increasing salinity was also observed along transects in soil polygons encompassing low salinities at the edge (~ 200 µS/cm) to higher salinities at the center (~ 1500 µS/cm) (Feeser et al. 2018) and in an experimental manipulation performed along a soil salinity gradient (105 to 4,800 µS/cm) (Van Horn et al. 2014), and in other non-polar soils (Guo et al. 2019; Li et al. 2021). Of the bacterial taxa found exclusively in high salinity sites at BP, several are known for their ability to survive under multiple stressors. For example, one such OTU (denovo139, Table S1) is highly similar to *Halomonas* sp. SYO J52, a halophilic and oligotrophic bacterium (Keshtacher-Liebso et al. 1995), that grows in a wide range of salt concentrations (Ventosa et al. 1998) and is adapted to wide thermal fluctuations and desiccation (Oren 2002b). These results suggest that one mechanism of bacterial survival in BP high salinity sites may involve the expression of polyextremotolerant capabilities.

In contrast to the observed diverse bacterial communities, we detected only two archaeal OTUs, both of which

were related to the genus *Nitrososphaera* (Stieglmeier et al. 2014) within the phylum Thaumarchaeota that globally distribute in a variety of soils (Bouali et al. 2012; Wang et al. 2019; Zhalnina et al. 2014). These results are supported by a broader survey of archaea in three MDV valleys that reported a total of 18 archaeal OTUs and communities dominated by Thaumarchaeota (Richter et al. 2014).

The majority of fungal ITS sequences we observed in BP were identified as *Aureobasidium pullulans*, an oligotrophic and polyextremotolerant black yeast fungus from the fungal division Ascomycota (Arenz and Blanchette 2011; Gostincar et al. 2011; Lawley et al. 2004). These organisms are known for their adaptations to salinity and desiccation (Gorbushina et al. 2008; Kogej et al. 2006, 2005; Turk et al. 2007).

Similar to the fungal communities, the vast majority of non-fungal eukaryote sequences belonged to a single tardigrade species, *Acutuncus antarcticus*, which is known for resistance to multiple stressors including low temperature (− 253 ºC), high dosages of radiation, and low and high pressures (Rothschild and Mancinelli 2001; Seki and Toyoshima 1998). The ubiquity and dominance of *Aureobasidium pullulans* and *Acutuncus antarcticus* in BP communities suggest that polyextremophiles may be the dominant organisms in this habitat, in agreement with the hypothesis that multiple stressors prohibit the growth of most microbial taxa (Power et al. 2018).

It should be noted that the taxonomic assignments and patterns of diversity discussed above rely on sequences derived from bulk DNA and do not necessarily represent the active community. While this may affect some of the results reported here, studies using stable isotope probing and mRNA analyses in the MDV (Buelow et al. 2016; Schwartz et al. 2014) suggest that a large percentage of the bulk community is active and thus our findings are likely robust to the potential confounding effect of the persistence of legacy DNA in MDV soils.

Conclusions

There are fundamental differences in the metabolic strategies, susceptibility to extreme conditions, and energetic niches between Archaea, Bacteria, unicellular eukaryotes, and multicellular eukaryotes (e.g., Rothschild and Mancinelli, 2001; Valentine, 2007; DeLong et al., 2010). However, the degree to which these differences affect basic patterns of diversity and distribution along environmental gradients is not well understood. Antarctic soil is a model system for determining how the fundamental differences among the three domains of life and unicellular and multicellular life alter biogeographic patterns of diversity and distribution in extreme environments. Examining the diversity and distribution of all three domains of life along a gradient spanning over two orders of magnitude variation in conductivity, our study suggests that despite the fundamental organismal differences among the domains, species richness patterns were similar. However, there were also important differences among domains in the patterns of beta diversity and species distributions that suggest mechanisms of community assembly varied at highest taxonomic levels in this extreme environment. This work highlights the need for more theoretical and empirical research exploring how variation in basic physiological characteristics of organisms scales up to shape diversity patterns in extreme environments. This study is the first step towards understanding the impacts of stressors on the three domains of life in extreme environments. Future work to extend these results should include surveys along multiple gradients in polar environments to determine the consistency of the patterns observed here and to explore interactions between salinity and other abiotic variables. In addition, functional surveys should be included in future research to determine how salinity as an extra stressor affects community function in addition to patterns of diversity in already extreme polar deserts.

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