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Bacterial Community Structure Along Moisture Gradients in the Parafluvial Sediments of Two Ephemeral Desert Streams

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Abstract Microorganisms inhabiting stream sediments mediate biogeochemical processes of importance to both aquatic and terrestrial ecosystems. In deserts, the lateral margins of ephemeral stream channels (parafluvial sediments) are dried and rewetted, creating periodically wet conditions that typically enhance microbial activity. However, the influence of water content on microbial community composition and diversity in desert stream sediments is unclear. We sampled stream margins along gradients of wet to dry sediments, measuring geochemistry and bacterial 16S rRNA gene composition, at streams in both a cold (McMurdo Dry Valleys, Antarctica) and hot (Chihuahuan Desert, New Mexico, USA) desert. Across the gradients, sediment water content spanned a wide range (1.6–37.9% *w*/*w*), and conductivity was highly variable (12.3–1,380 μS cm^{-2}). Bacterial diversity (at 97% sequence similarity) was high and variable, but did not differ significantly between the hot and cold desert and was not correlated with sediment water content. Instead, conductivity was most strongly related to diversity. Water content was strongly related to bacterial 16S rRNA gene community composition, though samples were distributed in wet and dry clusters rather than as assemblages shifting along a gradient. Phylogenetic analyses showed that many taxa from wet sediments at the hot and cold desert site were related to, respectively, halotolerant *Gammaproteobacteria*, and one family within the *Sphingobacteriales* (*Bacteroidetes*), while dry sediments at both sites contained a high proportion of taxa related to the *Acidobacteria*. These results suggest that bacterial diversity and composition in desert stream sediments is more strongly affected by hydrology and conductivity than temperature.

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Introduction

Microbes living in stream and riparian sediments drive many biogeochemical processes and mediate nutrient exchange between terrestrial and aquatic ecosystems. Diverse benthic (sediment–water interface) and subsurface microbial communities have been studied in temperate streams around the world, with regards to seasonality [26, 41], litter decomposition [34, 66], biofilm formation [10], and denitrification [45]. However, few such studies have taken place in desert streams.

Biological activity in deserts is commonly limited by the availability of water. This is true in both temperate regions [58, 70] and polar regions [9, 44]. As precipitation events and stream flows are highly variable in timing and volume, wetting and drying of stream sediments is common. Microbial activity responds very quickly to rewetting of

sediments: for example, cyanobacterial mats inhabiting streambeds in the McMurdo Dry Valleys of Antarctica recover from desiccation rapidly, exhibiting high photosynthetic rates only minutes after rewetting [50, 76]. Also, sediment nutrient uptake in Sonoran Desert stream sediments is high during the first hours of rewetting [33].

The products of microbial activity in stream sediments are important to the entire landscape [5], particularly in desert regions [11]. In the McMurdo Dry Valleys, where vascular plants do not grow, respiration is highest in wetted sediments at the edges of waterbodies [32], and the relatively high productivity in these areas supports more complex food webs [53, 75]. Desiccated mat material is transported from stream beds by wind, providing a carbon source to biota in soils with no autotrophic activity [28, 38]. In vegetated deserts, microbial nitrogen (N) mineralization controls plant available N concentrations in stream riparian areas [68] and nitrification and denitrification processes in stream sediments affect the form and concentration of nutrients transported downstream [36, 37, 43]. In ephemeral desert streams, the lateral extent of the stream channel (termed the parafluvial zone), and thus the moist sediments that support high microbial activity, is highly variable over time and space. It is currently unclear whether microbial community composition of desert stream sediments is, like microbial activity, sensitive to water availability. In desert soils and cryptoendoliths, there are differences in community structure relative to soil moisture content or total annual precipitation [1, 62]. For example, molecular fingerprinting techniques showed differences in the sediment bacterial community of an Australian ephemeral stream before and after sediment rewetting [65], but the identity of the organisms is still unknown. In general, the microbial community composition of parafluvial sediments remains largely unexplored.

The goal of this study was to determine how sediment microbial (in particular, bacterial) community structure changes across gradients of sediment moisture content at both a hot and a cold ephemeral desert stream. While some evidence indicates increased diversity with higher water content in both hot and cold desert soils [1, 62], a mechanism has been proposed for the opposite pattern: wet soils may have lower spatial heterogeneity which in turn limits bacterial diversity [85]. It is not clear which of these patterns will prevail in ephemeral stream sediments, which regularly experience cycles of wetting and drying. Also, while macrobiological diversity is strongly and positively correlated with environmental temperature [2], temperate soil bacterial diversity appears to vary more with pH than mean annual temperature [27]. However, the bacterial diversity of similarly high pH soils with widely varying mean ambient temperatures has not been examined, to our knowledge. This cross-site comparative study was initiated to determine how water content or ambient temperature was related to bacterial community diversity and composition in parafluvial stream sediments.

We sampled parafluvial sediments across moisture gradients in stream–soil transition zones adjacent to the Onyx River, Wright Valley, Antarctica and the Rio Salado, New Mexico. Both streams have ephemeral flow dependent on local climatic conditions. The Onyx River flows only when summer radiation melts glacial ice, and the Rio Salado flows due to spring-fed base flow and summer monsoonal thunderstorms. Both streams have visible moisture gradients in the parafluvial zone, i.e., a strip of wetted sediment is visible at the margin of each stream. Despite these similarities, average seasonal temperature differs by approximately 20–40°C. To elucidate patterns of microbial diversity and community structure in hot and cold, wet and dry desert sediments, we measured physicochemical parameters and bacterial 16S rRNA gene community diversity and composition at four points along a sediment moisture gradient adjacent to each study stream.

Materials and Methods

Site Description and Sampling Approach

The Onyx River in Wright Valley (77°30′ S, 163°00′ E) is the longest river on the Antarctic continent. It is located within the McMurdo Dry Valleys, a 4,800 km^2 area of ice-free polar desert that receives <100 mm precipitation annually, most of which sublimates before accumulating on the surface. The McMurdo Dry Valleys have mean summer and winter temperatures of −5 in January and −30°C in July [20]. The Onyx River is fed solely by glacial melt, with an average flow season of 8–10 weeks and a flow season daily mean discharge of 490 L/s (range 1–1,900 L/s) [30]. Two sites were sampled in the McMurdo Dry Valleys: (1) the Upper Onyx River site (UOX) was approximately 1 km below the river source, glacial Lake Brownsworth, and (2) the Lower Onyx River site (LOX) was approximately 25 km downstream, 3 km above the river's outflow into Lake Vanda. More information on the study sites [57] and on the region is available online (http://mcmlter.org).

The Rio Salado (33.75° N, 111.51° W), located within the Sevilleta National Wildlife Refuge in central New Mexico, USA, lies at the northern extent of the Chihuahuan Desert. The mean winter and summer temperatures are −4.2°C in January and 34.5°C in July, and annual precipitation is approximately 250 mm, about 60% of which falls in episodic monsoon events during the summer months [31]. The Rio Salado drains a catchment of ~400 km^2 extending from the northern Datil Mountains in the west to its outflow into the Rio Grande. A short reach of this river carries perennial flow

where the near-surface bedrock upthrust of the Ladron Mountains creates a constriction and strong upwelling of groundwater [52]. However, the river flows ephemerally along most of its length, with large storm flow pulses primarily during the summer. The Rio Salado sampling site (SAL) was located in an ephemeral spring-fed reach approximately 10 km below the point of groundwater upwelling. More information on the site is available online (http://sev.lternet.edu).

Sediments were sampled from transects established perpendicular to the direction of stream flow following the onset of spring discharge, during periods of typical base flow at each stream. There were no high-flow events (i.e., storms) at either site during the flow year prior to the sampling period, thus we sampled a base-flow microbial community, not a post-disturbance community. At the Onyx River, samples were collected in December 2005 at both sites. At the Rio Salado, samples were collected in April 2006. Sediments from four replicate transects (1–4) across the gradient were sampled at four points (A–D from wet to dry) to 10 cm depth for chemical analyses (n=4 total) for each of the three sampling sites (Fig. 1). Initially, we performed bacterial 16S rRNA gene denaturing gradient gel electrophoresis (DGGE) analyses on sediment from all points along each field replicated transect and at sub-depths of 0–3 cm, 3–6 cm, and 6–10 cm, but we observed no significant DGGE pattern dissimilarity in the longitudinal (between transect) or vertical (by depth) direction (P>0.1) [14, 83]. Therefore, we proceeded with one clone library analysis at each of the four points along one median transect for the combined 0–10 cm sediment depths.

The sediments utilized for chemical and nutrient analyses were collected into WhirlPac™ bags and stored at −20°C until analysis. Sediments for bacterial community analysis were collected using a flame-sterilized soil corer and preserved immediately in an equal volume of sucrose lysis buffer (SLB: 20 mM ethylenediaminetetraacetic acid, 400 mM NaCl, 0.7 M sucrose, and 50 mM tris(hydroxymethyl)aminomethane (TRIS); pH 9.0). SLB is a high-concentration sugar solution that lyses cells immediately, preserving nucleic acids present at the time of sample collection [51]. These sediments were frozen at −20°C (UOX, LOX) or placed on ice (SAL) and immediately transported to the laboratory and stored at −80°C until analysis.

Sediment Chemical and Nutrient Analyses

Each of 16 sediment samples per site was analyzed for sediment water content, electrical conductivity (a proxy for salinity), and KCl-extractable NO_3–N and NH_4–N. Water content was measured as mass loss upon drying overnight at 100°C, conductivity was measured in a 1:5 sediment/deionized water solution and pH was measured in a 1:1 sediment/deionized water solution. For all samples, inorganic nitrogen ions were extracted for 1 h in 1 M KCl from 10 g of sediment; NO_3–N concentration was measured on a Dionex Ion Chromatograph and NH_4–N concentration was measured colorimetrically using a Technicon Autoanalyzer. Organic matter content was measured via mass loss on ignition of 3–5 g of sediment on a subset of the samples due to limited sample volume (n=3 for available Upper and Lower Onyx River samples; n=4 for each Rio Salado sample). Biomass C was measured by chloroform fumigation, but many samples fell below a detectable limit of 10 μg C g^{-1} dry soil, preventing statistical evaluation of biomass data.

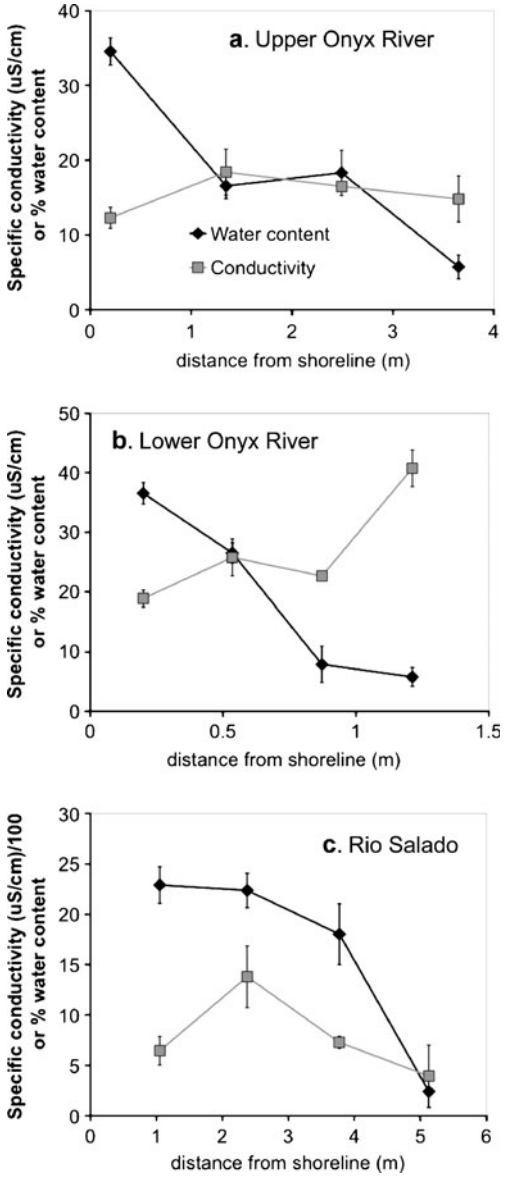

Figure 1 Profiles of sediment moisture gradients and salinity (as conductivity) by distance from water at each site. Note the differences in scale on each graph, and the 1/100 transformation of conductivity data at **c** Rio Salado, where values ranged from 266 to 1,870 μS/cm

Bacterial Community Analysis

Whole community genomic DNA was extracted from 0.2 to 0.3 g of sediment sample from each point along one transect using a MoBio (Carlsbad, CA, USA) PowerSoil extraction kit, eluted in 10 mM TRIS and stored at −20°C during analysis. One step in the MoBio protocol was modified: instead of vortex bead-beating, the samples were shaken by hand to prevent excessive DNA shearing. Bacterial 16S rRNA genes were amplified by PCR with the domain-specific primer 8F (5′-AGAGTTTGATCCTG GCTCAG-3′) [3] and universal primers 1391R (5′-GACGG GCGGTGTGTRCA-3′ for UOX and LOX) or 1492R (5′-GGTTACCTTGTTACGACTT-3′ for SAL) [46]. Of all bacterial sequences in the SILVA non-redundant 16S rRNA database, 63,630 sequences match 1492R and 63,215 of those match 1391R; none of the 415 sequences which 1391R misses is related to any sequence found in our clone libraries: thus, results acquired using the different primers are directly comparable. Each 50 μL reaction included 5.0 μL of 10*X* buffer, 0.8 μL of 12.5 mM dNTPs, 1 U of *Taq* polymerase (Promega, Madison, WI, USA), 2 μL of each 10 mM primer, 2 μL of 2% BSA, and 50 ng of genomic DNA. PCR conditions for all reactions were as follows: 5 min at 94°C; 30 cycles of 30 s at 94°C, 30 s at 50°C, and 90 s at 72°C; final extension at 72°C for 7 min. Full-length 16S rRNA gene PCR products were cloned using the TOPO TA and TA kits (Invitrogen, Carlsbad, CA, USA) and 96 clones per library were sequenced on an ABI 3730 capillary sequencer using the 8F primer. We also produced 3,000 200-bp 454 FLX 16S rRNA gene sequences (V1–V3 region [22]) for amplicons produced using each reverse primer from genomic DNA from one Lower Onyx River and one Rio Salado sample to ascertain that data acquired using different primers were in fact comparable.

Between 52 and 75 high-quality 16S rRNA gene sequences from the first 500–800 bp of the 5′ end of the gene (forward sequences) were produced per library (contained more than 500 bases with PHRED scores >20), which were then edited, aligned (using CodonCode Aligner) and used for community composition and diversity analysis. All 817 forward sequences were grouped into site-specific OTUs of 97% similarity, and one representative clone of each OTU (556 in total) was targeted for complete sequencing using the internal primers 519R (5′-ATTAC CGCGGCTGCTGG-3′), 515F (5′-GTGCCAGCMGCCG CGGTAA-3′), 1100R (5′-AGGGTTGCGCTCGTTG-3′), 1114F (5′-GCAACGAGCGCAACCC-3′), and 1492R (5′-GGTTACCTTGTTACGACTT-3′, just SAL) [46]. Sequences were edited and assembled to 2*X* coverage using CodonCode, scanned for chimeras using Bellerophon version 3 [39] and aligned using the NAST alignment tool at the GreenGenes website [18]. Because not every internal primer sequence was high quality enough to assemble, despite repeated attempts to sequence, only 257 16S rRNA genes were assembled to 2*X* coverage (800–1,000 bp, UOX and LOX; 1,200–1,400 bp, SAL). These sequences were utilized for phylogenetic analysis and are accessible at GenBank (EU869545–EU869802).

Statistical, Diversity, and Phylogenetic Analyses

Analysis of variance (ANOVA) was used to evaluate differences in biogeochemical characteristics between points along each gradient, with significant groups identified based on Bonferroni post-hoc multiple comparisons. To compare total richness between sites, ANOVA (n=4, each clone library as one replicate) was used. Correlations of biogeochemical, diversity, and ordination variables were evaluated using Pearson's R statistic and two-tailed significance values. All data fit the assumptions of normality and equal variances associated with these statistical analyses. ANOVA and correlation analyses were performed using SPSS 11 for Mac. Rarefaction curves, Chao1 richness estimates, Simpson's and Shannon's diversity were calculated using DOTUR [69]. Good's coverage statistic, the proportion of sequences that are represented more than once in the library, was calculated as $(1-n/N)\times 100$, where n is the number of singletons and N is the total number of sequences per library [29].

Arlequin (2.000) was used to evaluate the level (F_{st}) and significance (P) of differences in 16S rRNA gene sequence composition among all samples. Taxonomic affiliation of each 97% similar OTU was derived from each sequence's placement in the bacterial 16S rRNA gene tree [40]; this placement was accomplished using ARB quick add using parsimony [48]. Using the final bacterial domain topology and sequence frequency for each clone library, UniFrac was used to identify clades enriched in sequences from certain sites and to plot phylogenetic similarity between samples [47]. UniFrac output reported here includes (1) Martin's P Test Significance, for which significant pairwise comparisons indicate different phylogenetic distribution between samples, (2) lineage-specific analysis, which tests whether certain clades are "enriched" in taxa from certain samples (i.e., have a greater number of sequences from one sample than expected from random reshuffling of all terminal taxa (P<0.05)), and (3) principal coordinates analysis (PCA), an ordination of phylogenetic distance between samples, weighted for the relative abundance of each sequence in each library.

Phylogenetic analysis on all 257 2*X* sequences (800–1,200 bp) was performed using PAUP 4.0 [73]. Before input into PAUP, hypervariable regions of the 16S rRNA gene were masked using domain and phyla-specific masks [40]. Trees containing reference isolate and environmental

sequences and sequences collected in this study were built using the neighbor-joining algorithm, with the general-time reversible model of nucleotide evolution (gamma=0.6) as indicated by running ModelTest [63] on our dataset. Trees were bootstrapped by resampling 1,000 times using stepwise addition and tree bisection replacement.

Results and Discussion

Geochemical Characteristics of Sediments Across Moisture Gradients

Moisture gradients at hot and cold desert sites spanned a range of sediment water content, conductivity, and extractable nitrate in a qualitatively similar pattern (Table 1, Fig. 1). Water content decreased with increasing distance from the shoreline at each stream (Pearson's correlation between distance and water content: Onyx River, $R=-0.539$, $P<0.001$; Rio Salado, $R=-0.537$, $P=0.002$). There was no statistically significant variability in geochemistry between transects. Conductivity was generally lowest in wet sediments (Fig. 1), and extractable nitrate was generally highest in dry sediments (Table 1). These patterns are typical of hydrological margin gradients across the McMurdo Dry Valleys landscape, where evapo-concentration can cause solutes to accumulate at the distal ends of these hydrological gradients [8, 57].

Inorganic nitrogen concentration, organic matter content, pH, and conductivity in parafluvial sediments varied significantly between hot and cold desert sites (Table 1). Sediments from Rio Salado, the hot desert stream, had statistically significant higher conductivity and ammonium concentration than Onyx River sediments (ammonium at Onyx River (0.14 μg g^{-1} dry sediment)<Rio Salado (0.93 μg g^{-1} dry sediment), $P<0.05$; OM content at Onyx River (2.3 mg g^{-1} dry sediment)<Rio Salado (7.7 mg g^{-1} dry sediment), $P<0.01$; pH at Onyx River (7.81)<Rio Salado (7.43), $P<0.001$; conductivity at Onyx River (21.3 μS cm^{-1})<< Rio Salado (787 μS cm^{-1}), $P<0.001$). While all sites are very low nutrient habitats, Onyx River sediments are more nutrient poor and on average 37 times less saline than Rio Salado sediments. Thus conditions related to nutrient availability and baseline osmotic status, in addition to temperature and water content, may affect site differences in bacterial community composition.

Bacterial Diversity

16S rRNA gene diversity was high and variable in both hot and cold desert parafluvial sediments (Table 2), and the rarefaction curve of only one clone library, Rio Salado B, approached saturation (data not shown). There was no difference in Good's coverage, Shannon's diversity, and Simpson's diversity or Chao1 richness between SAL, UOX, and LOX (Table 2, ANOVA results, respectively, $P=0.64$, $P=0.12$, $P=0.45$, and $P=0.34$); thus the hot desert sediment habitat did not support a higher diversity bacterial community than the cold desert. Also, there was no correlation between sediment water content and bacterial richness. Therefore, the definitive environmental conditions of our "hot desert" and "cold desert" sites, ambient temperature and water content, do not appear to be related to bacterial diversity.

Total diversity was surprisingly high, and can be attributed to the large number of singletons in all 16S

Table 1 Mean values of geochemical variables for sediments at each gradient position at both sites (SEM)

		Distance from shoreline (m)	Sediment water content (%)	Electrical conductivity (μS cm^{-1})	pH	OM content (mg g^{-1} dry sediment)	Extractable ammonium (μg g^{-1} dry sediment)	Extractable nitrate (μg g^{-1} dry sediment)	Extractable inorganic N (μg g^{-1} dry sediment)
Upper Onyx River	A	0.2 (0)	37.9^{a} (2.1)	12.3 (2.8)	7.74 (0.15)	n/a	0.043 (0.04)	0.109 (0.10)	0.152 (0.12)
	B	1.6 (0.15)	11.6^{b} (4.3)	18.4 (6.1)	7.71 (0.09)	1.0 (0.1)	0.039 (0.02)	0.244 (0.37)	0.283 (0.35)
	C	3.1 (0.25)	11.7^{b} (8.0)	16.5 (1.2)	7.68 (0.08)	n/a	0.023 (0.03)	0.096 (0.14)	0.125 (0.14)
	D	4.5 (0.45)	3.42^{b} (1.9)	14.8 (6.2)	7.79 (0.13)	1.0 (0.1)	0.38 (0.04)	0.078 (0.06)	0.115 (0.07)
Lower Onyx River	A	0.2 (0)	34.6^{a} (2.1)	18.9^{a} (4.2)	7.71^{a} (0.05)	n/a	0.194 (0.22)	0.404 (0.50)	0.598 (0.60)
	B	0.6 (0.03)	22.0^{ab} (10)	25.8^{ab} (10)	8.16^{b} (0.07)	4.0 (0.1)	0.180 (0.22)	0.334 (0.31)	0.514 (0.51)
	C	1.1 (0.05)	10.5^{bc} (7.7)	22.6^{ab} (10)	7.89^{ab} (0.08)	n/a	0.134 (0.17)	0.373 (0.42)	0.507 (0.39)
	D	1.7 (0.08)	1.63^{c} (0.66)	40.7^{b} (14)	7.85^{ab} (0.13)	3.0 (2.0)	0.139 (0.12)	0.927 (0.28)	1.07 (0.35)
Rio Salado	A	1.1 (0.05)	23.0^{a} (2.6)	646^{a} (270)	7.26 (0.08)	10.9 (1.8)	0.821 (0.17)	0.100^{a} (0.00)	0.921^{a} (0.17)
	B	2.4 (0.07)	22.4^{a} (1.5)	$1{,}380^{b}$ (450)	7.54 (0.08)	6.8 (1.0)	1.09 (0.61)	0.099^{a} (0.00)	1.19^{a} (0.61)
	C	3.8 (0.13)	18.0^{a} (3.6)	728^{a} (204)	7.54 (0.06)	6.5 (0.8)	0.945 (0.10)	0.124^{a} (0.05)	1.07^{a} (0.13)
	D	5.1 (0.18)	2.40^{b} (1.0)	393^{a} (155)	7.39 (0.08)	6.6 (1.4)	0.847 (0.06)	1.25^{b} (0.47)	2.09^{b} (0.42)

Superscripts denote differences across each gradient within a site, ANOVA with Bonferroni post-hoc

Table 2 Diversity estimates for all sediment 16S rRNA gene communities from clone library sequence data for this and comparable studies

		Clones per library	OTUs (97% similarity)	Good's coverage (%)	Shannon's Diversity (H′)	Simpson's Diversity (1/D)	Estimated Chao1 Richness
Upper Onyx River	A	60	50	30.0	3.85	148	173
	B	72	53	43.1	3.82	69	128
	C	64	54	23.4	3.89	119	446
	D	60	51	23.3	3.85	126	396
Lower Onyx River	A	75	56	42.7	3.90	90	138
	B	64	51	32.8	3.82	96	202
	C	64	51	32.8	3.82	96	202
	D	52	46	11.5	3.78	190	210
Rio Salado	A	67	50	38.8	3.73	55	167
	B	44	26[a]	56.8	2.99	21	69
	C	66	38	56.1	3.41	36	103
	D	66	63	9.1	4.13	715	506
McKelvey Valley, Antarctica [61]		180	48	87	3.3	1	44
Miers Valley, Pennance Pass, Antarctica [71]		na	na	na	1.33–1.60	na	na
Luther Vale, Antarctica [55]		67–92	na	na	3.32–4.04	na	na
Near Lake Vanda, Wright Valley, Antarctica [1][c]		113	na	70	3.27	na	na
Sevilleta NWR, USA upland soil [67][d]		17–27	2–13	70.8–100	0.65–2.39	1.8–9.3	na
Sevilleta NWR, USA upland soil [27][e]		na	41–43	na	3.5–3.6	na	na
Salton Sea, USA sediment[b] [19]		109	78	28.4	4.18	51.6	204
Lake Tebenquiche, Salar de Atacama, Chile water [17]		14–53	8–15	16.7–53.3	1.9–2.4	5.4–10.9	na
Cuatros Cienegas, Chihuahuan Desert, Mexico water and sediment [72]		76	38	28.9	3.22	15.4	na

[a] Rarefaction curve nearing plateau

[b] OTUs calculated at 99% similarity

[c] OTUs calculated at 100% similarity

[d] OTU defined by restriction fragment length polymorphism (RFLP) type

[e] OTU defined by terminal-RFLP type

rRNA gene clone libraries (Table 2). The mean Good's coverage of our clone libraries was 33%, indicating that on average only one-third of the OTUs we collected were found more than once in any sample. This level of diversity is notable: bacterial communities in these desert stream sediments have a similar or higher diversity than communities from comparable extreme environments, such as other Antarctic Dry Valleys soils, desert soils, and saline desert waters and sediments (Table 2).

The lowest diversity samples in our study, Rio Salado B and C, were also geochemical outliers with high conductivity (1,870 and 935 μS cm^{-2}). While neither nutrient content nor pH was significantly correlated with any diversity metric, Shannon's diversity index (H′) and conductivity were negatively correlated (Pearson's R=0.899, P<0.001). Assuming conductivity is a good proxy for salinity, high conductivity could negatively affect bacterial sequence diversity by selecting against organisms that are not halotolerant. Other studies have documented strong relationships between conductivity and microbial community composition in estuarine, wet sediment, and hypersaline environments that are driven by changes in abundance of halotolerant and non-halotolerant bacterial clades [12, 13, 77].

Bacterial Community Composition

Bacterial 16S rRNA gene community structure differed between hot and cold desert sediments, and between wet and dry sediments. All between-sample F_{st} comparisons (Arlequin) were significant (F_{st} ranged from 0.003 to 0.03, pairwise P values were all <0.01), indicating that all clone libraries were distinct in their raw sequence composition. UniFrac's phylogenetically explicit analysis showed that at Rio Salado, dry sediment (gradient position D) differed from wet sediment (gradient positions A, B, and C) 16S gene clone library composition (P≤0.01). Also, Onyx River dry sediments were phylogenetically distinct from wet sediment samples (differences across all samples: UOX-D ≠ (LOX-A, B, and C), LOX-D ≠ UOX-C (P≤0.04)). In fact, the difference between wet and dry

sediment community composition was greater than the difference between corresponding gradient positions at UOX and LOX (i.e., A=A, B=B, C=C, and D=D; $P \geq 0.49$). The PCA of phylogenetic distance between all samples reflects these patterns visually: Rio Salado A, B, and C sediments cluster together, Rio Salado and Onyx River D sediments cluster together, and Onyx River A, B, and C sediments cluster together (Fig. 2). PC1 separated the hot from the cold desert sediments and was significantly correlated ($P \leq 0.05$) with extractable ammonium ($R=-0.933$), conductivity ($R=-0.871$) and pH ($R=0.734$), and PC2 separated the dry from the wet sediment samples and was significantly correlated with extractable nitrate ($R=0.619$) and water content ($R=-0.569$).

Interestingly, there was not a smooth transition of community composition from wet to dry sediments along each gradient; instead, bacterial communities from the driest sediments (position "D") were clearly distinct from the moist sediments at each gradient, and were in fact more similar to dry sediments from the other sites than to moist sediments at the same site. Two mechanisms could explain the difference in bacterial community composition in wet and dry sediments. Because water stimulates microbial activity [11, 44], wet sediment clone libraries may reflect primarily active bacterial cells while dry sediment clone libraries contain a "seed bank" of sequences from dormant or inactive cells [64]. Alternatively, if there were unique aquatic and terrestrial source pools of bacterial taxa, and water provided a dispersal vector for aquatic taxa [85], the wet and dry sediments might reflect aquatic- and terrestrial-dominated communities. If the "seed bank" idea was the sole explanation for the variability in our data, then

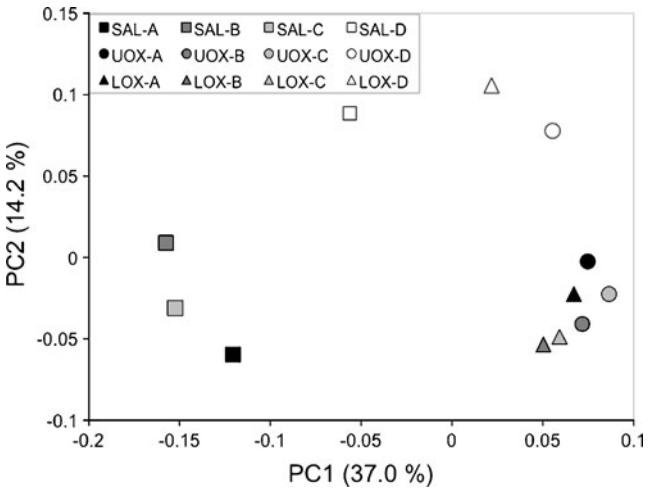

Figure 2 Principal coordinates analysis (UniFrac, weighted) of 16S rRNA gene OTU (97% DNA sequence similarity) occurrence and abundance from clone libraries of 8F reads for all samples in the study. The first two axes explained a total of 51.2% of the variability in the whole dataset

bacterial taxa in the wet sediments would contain a subset of the sequences in the dry sediment clone libraries, following a nested subset pattern [56]. This was not the case: the nestedness temperature of 74.52° indicates a high entropy in community assembly [4], suggesting either a random mechanism for OTU occurrence or a mixing of bacterial taxa with differing histories [60]. Hypotheses like these are rarely addressed in microbial communities, and would be better served with more thorough surveys of diversity, e.g., 454 "deep sequencing" of the 16S rRNA gene. However, the "two pool" hypothesis can explain microbial community composition in at least one other stream ecosystem: in an Austrian glacial fed stream, upstream waters contained a higher proportion of subglacial associated bacterial taxa than downstream waters [10].

Phylogenetic Analysis

Seventeen bacterial phyla were represented in the 16S rRNA gene clone libraries (Fig. 3). Abundant groups at both sites included *Acidobacteria* and *Proteobacteria*, which were particularly common at the Rio Salado, and *Bacteroidetes*, which were particularly common at the Onyx River. Onyx River sediments also consistently contained *Actinobacteria*, *Cyanobacteria*, *Gemmatimonadetes*, and *Verrucomicrobia*. Rio Salado sediments also included *Verrucomicrobia* in all but one sample, but overall fewer phyla were consistently represented at this site. UniFrac's lineage-specific analysis was used to identify the phylogenetic groups that contributed to differences in community composition, i.e., clades with significantly more terminal taxa in one sample than predicted by randomly sampling taxa from the total pool of sequences ($P<0.05$). Clone libraries from wet sediments at Rio Salado (positions A, B, and C) contained an over-abundance of sequences from the *Gammaproteobacteria* subphylum. The Rio Salado dry sediment sample (position D) had a high proportion of *Acidobacteria* sequences. In all Onyx River clone libraries, *Bacteroidetes* and *Acidobacteria* sequences were more numerous than expected.

In addition, a comparison of the bacterial community composition to other Antarctic Dry Valleys soils, hot desert soils, water and sediment from desert lakes and springs, and global composite soil [42] shows that these sediment communities are distinct from those in comparable environments (Fig. 3). Interestingly, bacterial community composition in Onyx River sediments was most similar to a soil sample collected near Lake Vanda, in the same drainage basin (Wright Valley, Antarctica) [1], and Rio Salado sediments were most similar to water and sediment samples collected at Cuatro Cienegas, in the Chihuahuan Desert [72]; i.e., there may be some regional similarity in bacterial community composition even between studies. While the bacterial composition of Rio Salado sediments appears to

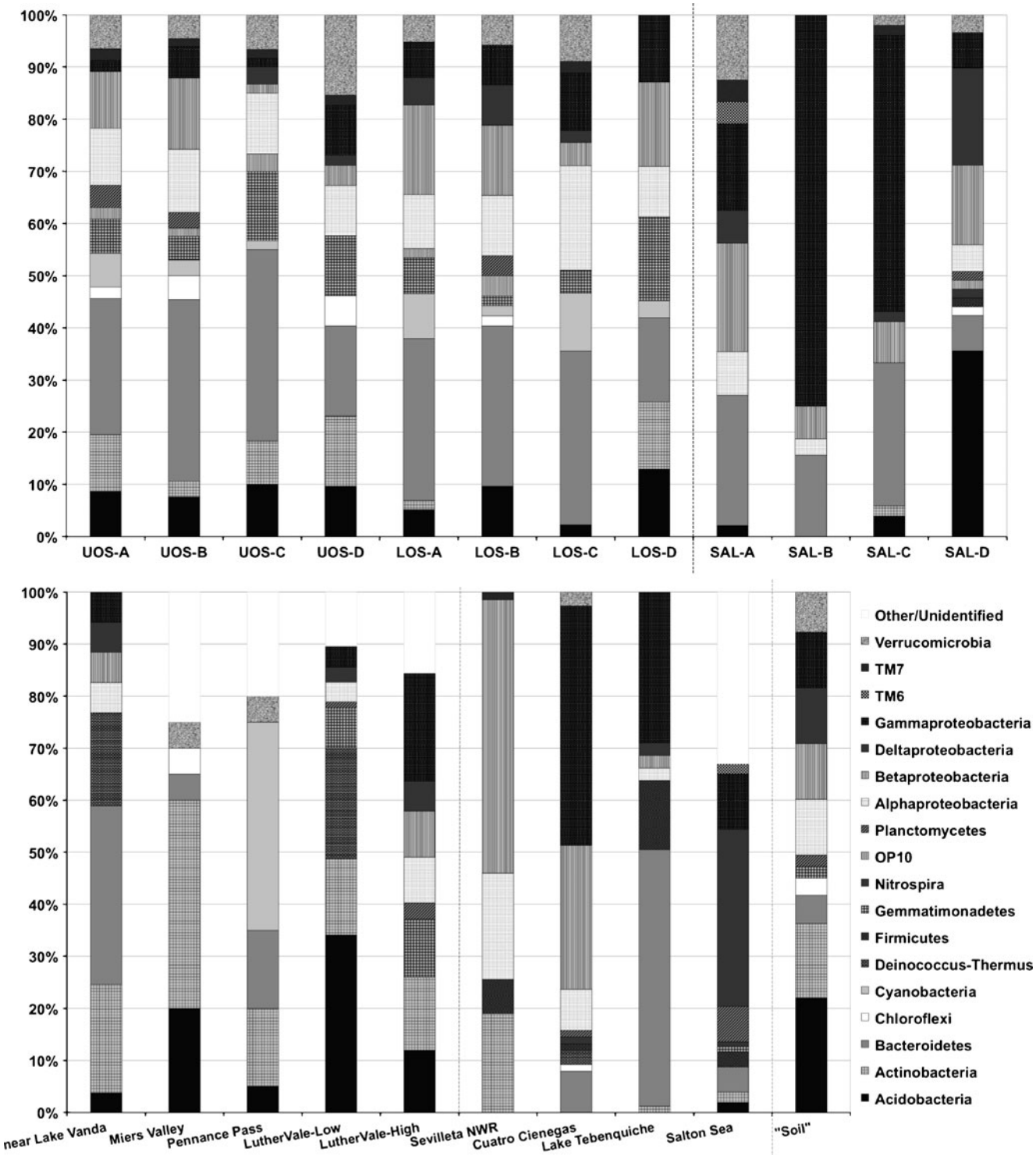

Figure 3 Phylogenetic placement of all 16S rRNA clone library sequences from all Rio Salado and Onyx River sediment samples, plus the taxonomic composition of a number of comparable samples (the same samples as described in Table 2, plus the "average" cosmopolitan soil bacterial community [42])

be quite different from upland Sevilleta NWR soils, the only study available for comparison used a very different method of defining OTUs (RFLP type) [67], so further comparison is necessary to confirm this difference.

While 16S rRNA gene sequences from the *Acidobacteria* phylum were most common in dry sediments at both sites, there was little phylogenetic overlap between Onyx River and Rio Salado *Acidobacterial* representatives (Figs. 3 and

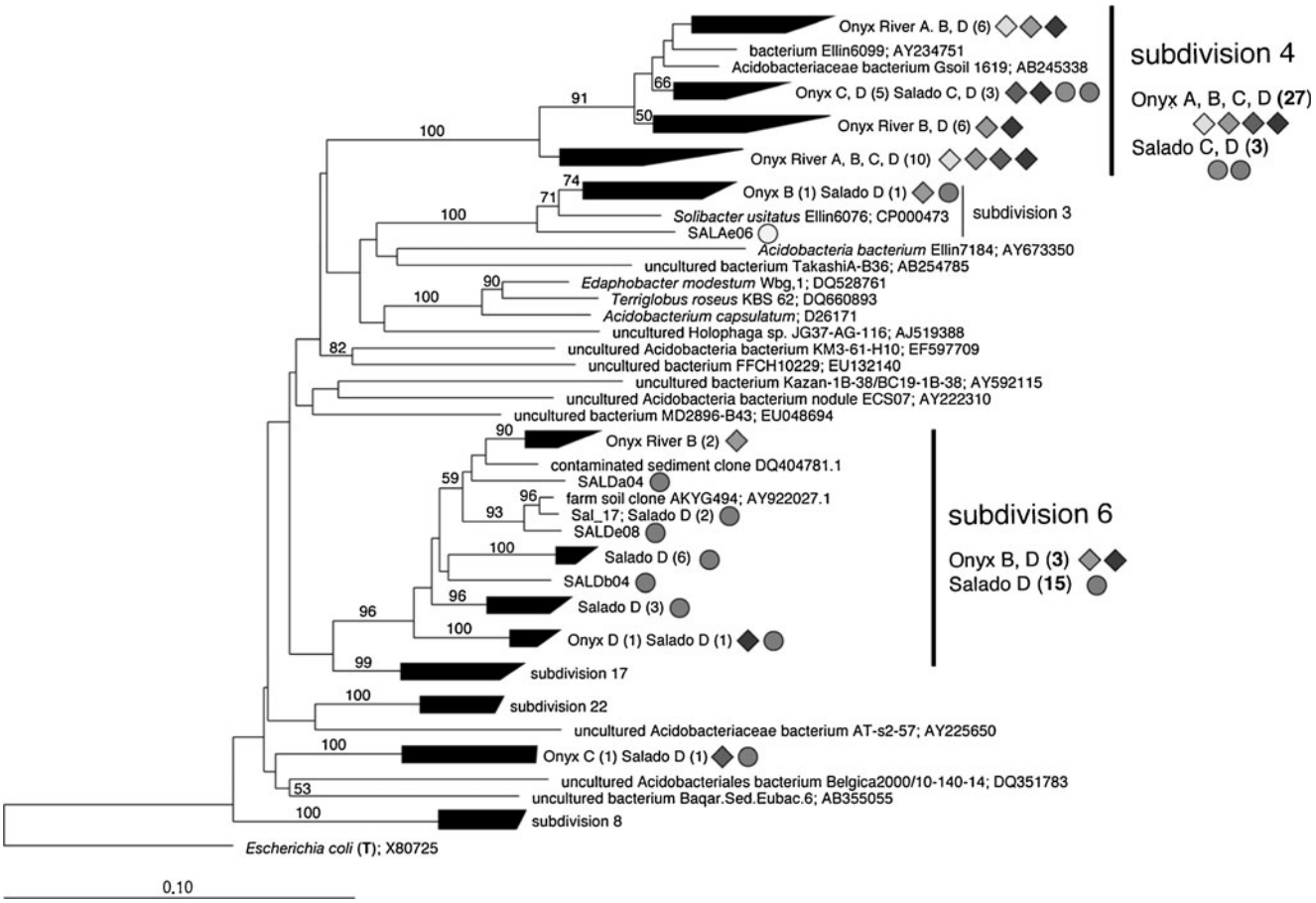

Figure 4 Bootstrapped neighbor joining tree of the 16S rRNA gene, *Acidobacteria* phylum (*Bacteria*, *Acidobacteria*), including full sequences from this study and type and reference sequences from GenBank (clone or isolate name, accession number). The abundance of sequences from each Rio Salado and Onyx River sample in each bootstrapped clade is noted

4). Sequences from Rio Salado generally fell into subdivision 6, and those from Onyx River were commonly found in subdivision 4. 16S rRNA gene sequences from these two *Acidobacteria* subdivisions are abundant [7, 42], but also two of the least successfully cultured. Because subdivision 6 *Acidobacteria* are also common in uranium-containing sediments [6], and desiccation tolerance and radiation tolerance are related in their necessary DNA repair physiology [49], subdivision 6 *Acidobacteria* may have adapted an efficient method to repair DNA or other essential cellular components. There are few cultured representatives of the phylum *Acidobacteria*, but the group is generally thought to contain oligo-heterotrophic organisms that are prevalent in soil habitats [7, 24, 42], such as the nutrient poor dry sediment of these desert streams.

A large proportion of Rio Salado 16S rRNA sequences, but no Onyx River sequences, fell within the *Gammaproteobacteria* subphylum (Figs. 3 and 5). The hot desert bacterial sequences grouped with three distinct genera (*Rheinheimera*, *Idiomarina*, and *Saccharospirillum*). Type species from these clades are halotolerant marine organisms like *Idiomarina* sp., *Rheinheimeria* sp., and *Oceanospirales* sp. [15, 81]. At least one other Chihuahuan Desert stream system fed by saline groundwaters, Cuatro Cienegas, has a high diversity of marine-related bacterial sequences [72]. There is evidence to suggest that Cuatro Cienegas source waters have an ancient marine origin [72]. However, high conductivity at the Rio Salado is more likely related to deep groundwater interactions with sedimentary brines [35] and tectonic activity in the Rio Grande Rift [54]. The bacteria represented by these sequences may have descended from relict marine bacterial populations in the subsurface or from cells transported via summer monsoonal precipitation systems that originate over the Gulf of California and Gulf of Mexico. In either case, the phylogenetic data suggest that the high conductivity of Rio Salado stream sediments has promoted a unique diversification of halotolerant bacteria.

Finally, 16S rRNA gene sequences from the *Bacteroidetes* phylum were most common in wet sediments at the Onyx River. *Bacteroidetes* is a diverse phylum, and phylogenetic analysis was restricted to the *Sphingobacteriales* order. A very high number of sequences from Onyx River clone libraries fell in this clade (Figs. 3 and 6): in fact, approximately one-sixth (88/554, or 16%) of all Onyx River

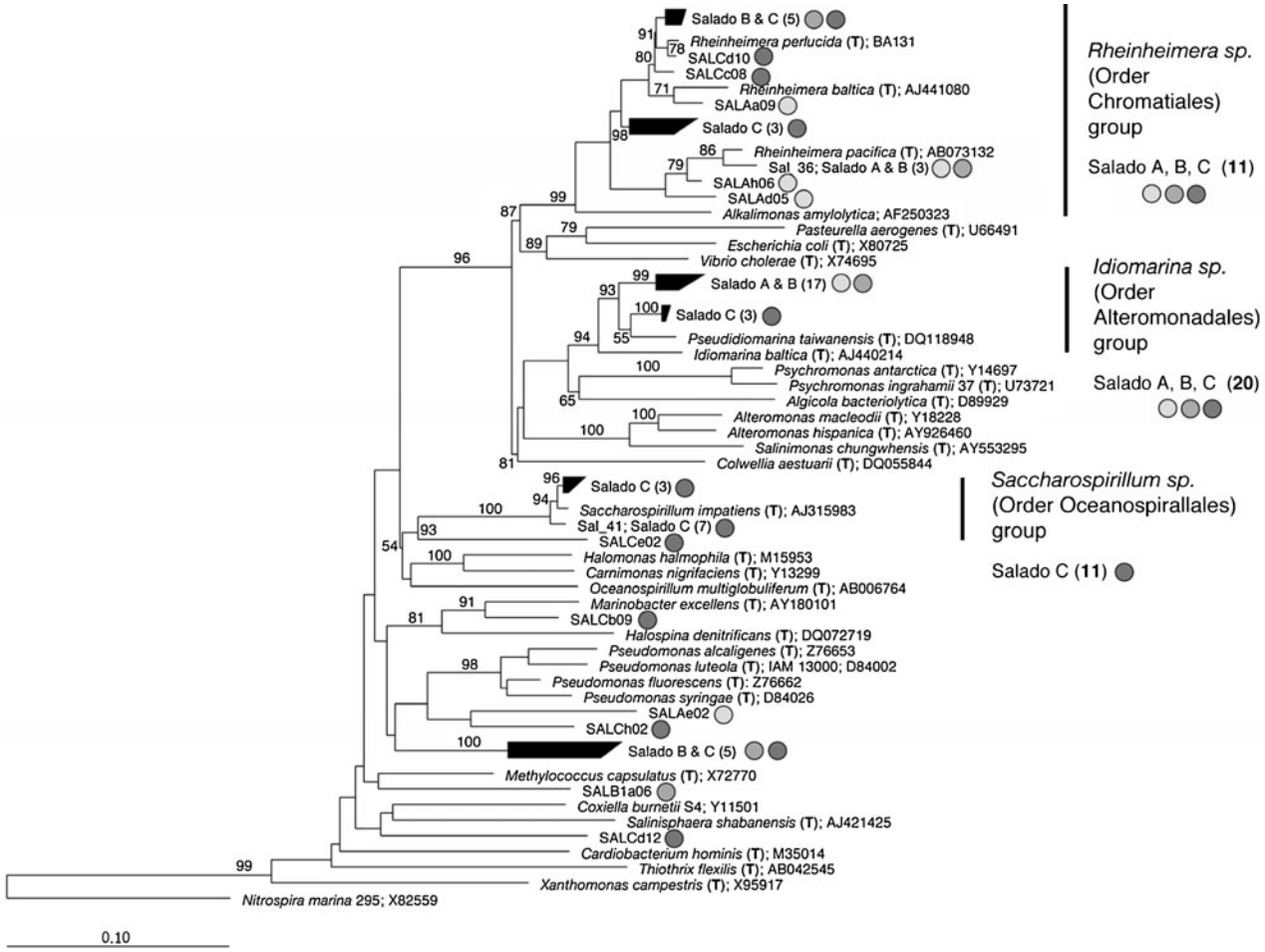

Figure 5 Bootstrapped neighbor joining tree of the 16S rRNA gene, *Gammaproteobacteria* subphylum (*Bacteria*, *Proteobacteria*, *Gammaproteobacteria*), including full sequences from this study and type and reference sequences from GenBank (clone or isolate name, accession number). The abundance of sequences from each Rio Salado and Onyx River sample in each bootstrapped clade is noted

sequences grouped within the *Chitinophagaceae* family. The characterized isolates from this group are aerobic heterotrophs with versatile metabolic capabilities [79, 82]. As many uncultured sequences from various habitats appear to group within this genus, these bacteria may be generalist heterotrophs that can thrive in numerous soil habitats. At the least, the high microdiversity of this group in Onyx River and other nearby sediments (sequences from this clade comprise 25% of a clone library collected near Lake Vanda [1]), suggests that "*Chitinophagacae*" bacteria have successfully colonized and diversified in Antarctic sediments.

Conclusion

Diverse bacterial communities exist in the parafluvial sediments of hot and cold desert streams. This high diversity was particularly surprising in Antarctic sediments, since cold Antarctic soils are traditionally viewed as low in diversity [71]. However, several modern surveys using molecular methods have shown that Antarctic Dry Valleys microbial communities are diverse [55, 61], not simply composed of easily cultivable, cosmopolitan microbes, and thus possibly endemic to the continent [16, 74]. The uncultured taxa represented by sequences within the "*Chitinophagacae*" and *Acidobacteria* subdivision 4 clades in our clone libraries may be candidates for locally adapted Antarctic bacterial types. Similarly, the prevalence of novel diversity at the hot desert site, Rio Salado, in the subdivision 6 *Acidobacteria* and halotolerant clades of the *Gammaproteobacteria* suggests that local adaptation may be important in the hot desert ecosystem as well. Physical isolation and allopatric speciation can drive patterns of microbial biogeography [59, 78]. Our data suggest that wetted stream sediments in desert environments may be habitats that promote distinct, unique patterns of microbial diversity.

Liquid water strongly affected bacterial 16S rRNA gene community composition in parafluvial sediments of these desert streams, as in other arid ecosystems [23, 44, 62]. However, the relationship was binary (wet/dry) rather than gradient-driven, suggesting a mechanism based on dispersal

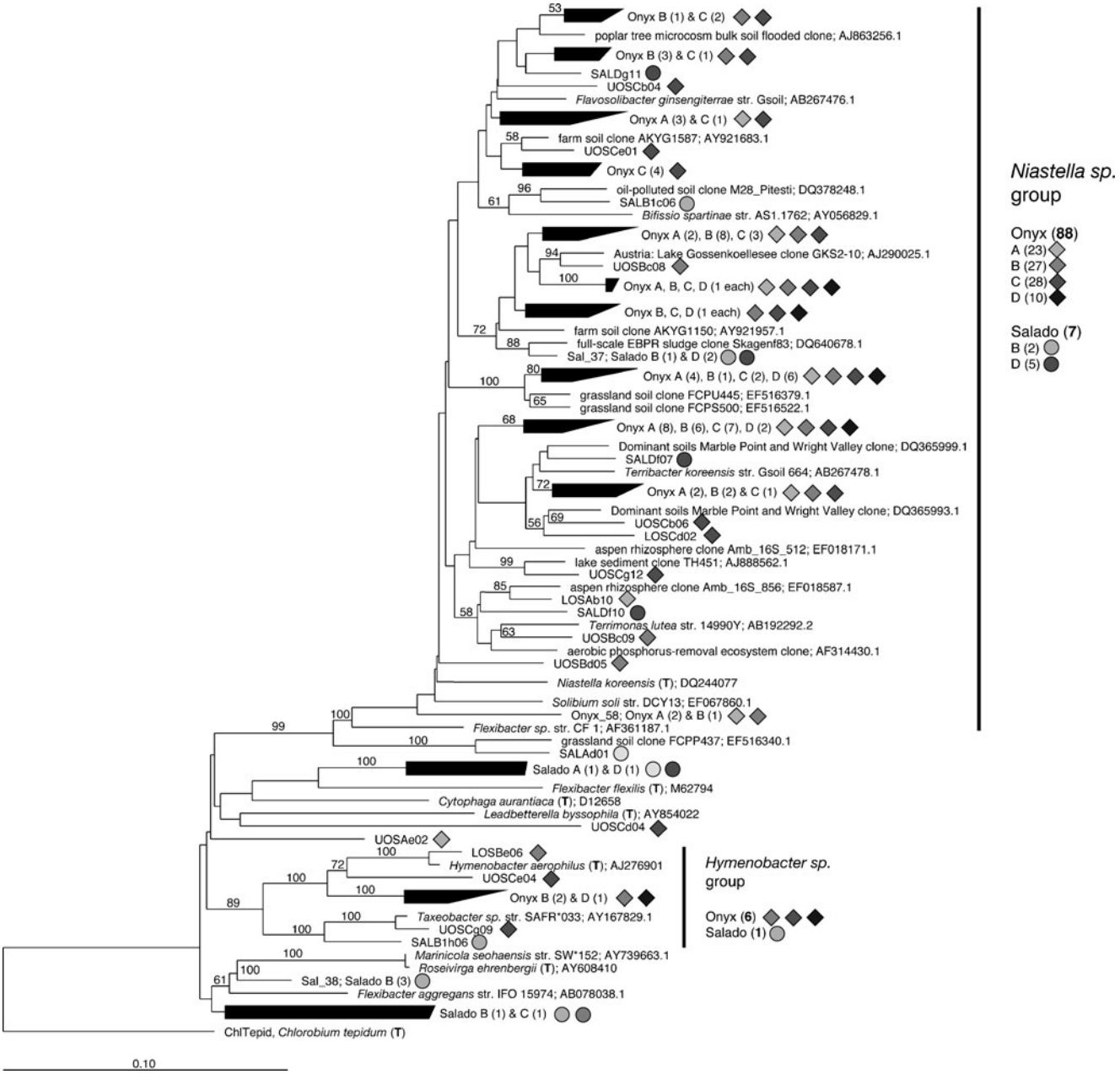

Figure 6 Bootstrapped neighbor joining tree of the 16S rRNA gene, *Sphingobacteriales* order (*Bacteria*, *Bacteroidetes*, *Sphingobacteria*, *Sphingobacteriales*), including full sequences from this study and type and reference sequences from GenBank (clone or isolate name, accession number). The abundance of sequences from each Rio Salado and Onyx River sample in each bootstrapped clade is noted

or release from dormancy. Conductivity, which is linked to evaporative processes in these parafluvial stream sediments, was more strongly related to bacterial diversity than temperature or water content. It remains to be seen whether the conclusions of this study, conducted at a single time point and a limited sampling resolution, will be applicable to patterns of bacterial diversity across greater ranges of spatial and temporal variability. However, it is clear that microbial community structure and diversity in cold and hot desert environments are not influenced solely by temperature [80]; hydrologic patterns and geochemical characteristics can also play key roles. It may be interesting to consider the mechanisms driving these patterns of microbial biodiversity in the context of a changing climate, as desert stream microbial activity [84] and biotic diversity [25, 65] are linked to hydrologic variability, which in turn is particularly sensitive to temperature and precipitation regime [21, 52]. [17, 19]

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References

1. Aislabie JM, Chhour KL, Saul DJ, Miyauchi S, Ayton J, Paetzold RF, Balks MR (2006) Dominant bacteria in soils of Marble Point and Wright Valley, Victoria Land, Antarctica. Soil Biol Biochem 38:3041–3056
2. Allen AP, Brown JH, Gillooly JF (2002) Global biodiversity, biochemical kinetics, and the energetic-equivalence rule. Science 297:1545–1548
3. Amann RI, Ludwig W, Schleifer KH (1995) Phylogenetic identification and in-situ detection of individual microbial-cells without cultivation. Microbiol Rev 59:143–169
4. Atmar W, Patterson BD (1993) The measure of order and disorder in the distribution of species in fragmented habitat. Oecologia 96:373–382
5. Bardgett RD, Anderson JM, Behan-Pelletier V, Brussaard L, Coleman DC, Ettema C, Moldenke A, Schimel JP, Wall DH (2001) The influence of soil biodiversity on hydrological pathways and the transfer of materials between terrestrial and aquatic ecosystems. Ecosystems 4:421–429
6. Barns SM, Cain EC, Sommerville L, Kuske CR (2007) *Acidobacteria* phylum sequences in uranium-contaminated subsurface sediments greatly expand the known diversity within the phylum. Appl Environ Microbiol 73:3113–3116
7. Barns SM, Takala SL, Kuske CR (1999) Wide distribution and diversity of members of the bacterial kingdom *Acidobacterium* in the environment. Appl Environ Microbiol 65:1731–1737
8. Barrett JE, Gooseff MN, Takacs-Vesbach C (2009) Spatial variation in soil active-layer geochemistry across hydrologic margins in polar desert ecosystems. Hydrol Earth Syst Sci Discussion 6:3725–3751
9. Barrett JE, Virginia RA, Wall DH, Doran PT, Fountain AG, Welch KA, Lyons WB (2008) Persistent effects of a discrete warming event on a polar desert ecosystem. Glob Chang Biol 14:2249–2261
10. Battin TJ, Wille A, Sattler B, Psenner R (2001) Phylogenetic and functional heterogeneity of sediment biofilms along environmental gradients in a glacial stream. Appl Environ Microbiol 67:799–807
11. Belnap J, Welter JR, Grimm NB, Barger N, Ludwig JA (2005) Linkages between microbial and hydrologic processes in arid and semiarid watersheds. Ecology 86:298–307
12. Benlloch S, Lopez-Lopez A, Casamayor EO, Ovreas L, Goddard V, Daae FL, Smerdon G, Massana R, Joint I, Thingstad F, Pedros-Alio C, Rodriguez-Valera F (2002) Prokaryotic genetic diversity throughout the salinity gradient of a coastal solar saltern. Environ Microbiol 4:349–360
13. Bernhard AE, Donn T, Giblin AE, Stahl DA (2005) Loss of diversity of ammonia-oxidizing bacteria correlates with increasing salinity in an estuary system. Environ Microbiol 7:1289–1297
14. Bobb M (2005) Spatial patterns of bacterial diversity in cold desert riparian zones. M.S. Thesis. Department of Biology, University of New Mexico, Albuquerque, NM, USA
15. Brettar I, Christen R, Hofle MG (2006) *Rheinheimera perlucida* sp nov., a marine bacterium of the *Gammaproteobacteria* isolated from surface water of the central Baltic Sea. Int J Syst Evol Microbiol 56:2177–2183
16. Cowan DA, Tow LA (2004) Endangered Antarctic environments. Annu Rev Microbiol 58:649–690
17. Demergasso C, Escudero L, Casamayor EO, Chong G, Balague V, Pedros-Alio C (2008) Novelty and spatio-temporal heterogeneity in the bacterial diversity of hypersaline Lake Tebenquiche (Salar de Atacama). Extremophiles 12:491–504
18. DeSantis TZ, Hugenholtz P, Keller K, Brodie EL, Larsen N, Piceno YM, Phan R, Andersen GL (2006) NAST: a multiple sequence alignment server for comparative analysis of 16S rRNA genes. Nucleic Acids Res 34:W394–W399
19. Dillon JG, McMath LM, Trout AL (2009) Seasonal changes in bacterial diversity in the Salton Sea. Hydrobiologia 632:49–64
20. Doran PT, McKay CP, Clow GD, Dana GL, Fountain AG, Nylen T, Lyons WB (2002) Valley floor climate observations from the McMurdo Dry Valleys, Antarctica, 1986–2000. J Geophys Res Atmos 107:4772
21. Doran PT, Priscu JC, Lyons WB, Walsh JE, Fountain AG, McKnight DM, Moorhead DL, Virginia RA, Wall DH, Clow GD, Fritsen CH, McKay CP, Parsons AN (2002) Antarctic climate cooling and terrestrial ecosystem response. Nature 415:517–520
22. Dowd SE, Callaway TR, Wolcott RD, Sun Y, McKeehan T, Hagevoort RG, Edrington TS (2008) Evaluation of the bacterial diversity in the feces of cattle using 16S rDNA bacterial tag-encoded FLX amplicon pyrosequencing (bTEFAP). BMC Microbiol 8:125
23. Drees KP, Neilson JW, Betancourt JL, Quade J, Henderson DA, Pryor BM, Maier RM (2006) Bacterial community structure in the hyperarid core of the Atacama Desert, Chile. Appl Environ Microbiol 72:7902–7908
24. Eichorst SA, Breznak JA, Schmidt TM (2007) Isolation and characterization of soil bacteria that define *Terriglobus* gen. nov., in the phylum *Acidobacteria*. Appl Environ Microbiol 73:2708–2717
25. Esposito RMM, Horn SL, McKnight DM, Cox MJ, Grant MC, Spaulding SA, Doran PT, Cozzetto KD (2006) Antarctic climate cooling and response of diatoms in glacial meltwater streams. Geophys Res Lett 33:L07406
26. Feris KP, Ramsey PW, Frazar C, Rillig M, Moore JN, Gannon JE, Holben WE (2004) Seasonal dynamics of shallow-hyporheic-zone microbial community structure along a heavy-metal contamination gradient. Appl Environ Microbiol 70:2323–2331
27. Fierer N, Jackson RB (2006) The diversity and biogeography of soil bacterial communities. Proc Natl Acad Sci U S A 103:626–631
28. Fritsen CH, Grue AM, Priscu JC (2000) Distribution of organic carbon and nitrogen in surface soils in the McMurdo Dry Valleys, Antarctica. Polar Biol 23:121–128
29. Good IJ (1953) The population frequencies of species and the estimation of population parameters. Biometrika 40:237–264
30. Gooseff MN, McKnight DM, Doran PT, Lyons WB (2007) Trends in discharge and flow season timing of the Onyx River, Wright Valley, Antarctica since 1969. US Geological Survey and The National Academies, Short Research Paper USGS: OF-2007-1047
31. Gosz JR, Moore DI, Shore GA, Grover HD, Rison W, Rison C (1995) Lightning estimates of precipitation location and quantity on the Sevilleta LTER, New Mexico. Ecol Appl 5:1141–1150
32. Gregorich EG, Hopkins DW, Elberling B, Sparrow AD, Novis P, Greenfield LG, Rochette P (2006) Emission of CO_2, CH_4 and N_2O from lakeshore soils in an Antarctic dry valley. Soil Biol Biochem 38:3120–3129
33. Heffernan JB, Sponseller RA (2004) Nutrient mobilization and processing in Sonoran desert riparian soils following artificial re-wetting. Biogeochemistry 70:117–134
34. Hieber M, Gessner MO (2002) Contribution of stream detritivores, fungi, and bacteria to leaf breakdown based on biomass estimates. Ecology 83:1026–1038

35. Hogan JF, Phillips FM, Mills SK, Hendrickx JMH, Ruiz J, Chesley JT, Asmerom Y (2007) Geologic origins of salinization in a semi-arid river: the role of sedimentary basin brines. Geology 35:1063–1066
36. Holmes RM, Fisher SG, Grimm NB (1994) Parafluvial nitrogen dynamics in a desert stream ecosystem. J North Am Benthol Soc 13:468–478
37. Holmes RM, Jones JBJ, Fisher SG, Grimm NB (1996) Denitrification in a nitrogen-limited stream ecosystem. Biogeochemistry 33:125–146
38. Hopkins DW, Sparrow AD, Novis PM, Grogorich EG, Elberling B, Greenfield LG (2006) Controls on the distribution of productivity and organic resources in Antarctic Dry Valley soils. Proc R Soc B 273:2687–2695
39. Huber T, Faulkner G, Hugenholtz P (2004) Bellerophon: a program to detect chimeric sequences in multiple sequence alignments. Bioinformatics 20:2317–2319
40. Hugenholtz P (2002) Exploring prokaryotic diversity in the genomic era. Genome Biol 3:1–8
41. Hullar MAJ, Kaplan LA, Stahl DA (2006) Recurring seasonal dynamics of microbial communities in stream habitats. Appl Environ Microbiol 72:713–722
42. Janssen PH (2006) Identifying the dominant soil bacterial taxa in libraries of 16S rRNA and 16S rRNA genes. Appl Environ Microbiol 72:1719–1728
43. Jones JB, Fisher SG, Grimm NB (1995) Nitrification in the hyporheic zone of a desert stream ecosystem. J North Am Benthol Soc 14:249–258
44. Kennedy AD (1993) Water as a limiting factor in the Antarctic terrestrial environment—a biogeographical synthesis. Arct Alpine Res 25:308–315
45. Knapp CW, Dodds WK, Wilson KC, O'Brien JM, Graham DW (2009) Spatial heterogeneity of denitrification genes in a highly homogeneous urban stream. Environ Sci Technol 43:4273–4279
46. Lane DJ (1991) 16S/12S rRNA sequencing. In: Stackebrant E, Goodfellow M (eds) Nucleic acid techniques in bacterial systematics. Wiley, London, pp 115–175
47. Lozupone C, Hamady M, Knight R (2006) UniFrac—an online tool for comparing microbial community diversity in a phylogenetic context. BMC Bioinform 7:371–385
48. Ludwig W, Strunk O, Westram R, Richter L, Meier H, Yadhukumar BA, Lai T, Steppi S, Jobb G, Forster W, Brettske I, Gerber S, Ginhart AW, Gross O, Grumann S, Hermann S, Jost R, Konig A, Liss T, Lussmann R, May M, Nonhoff B, Reichel B, Strehlow R, Stamatakis A, Stuckmann N, Vilbig A, Lenke M, Ludwig T, Bode A, Schleifer KH (2004) ARB: a software environment for sequence data. Nucleic Acids Res 32:1363–1371
49. Mattimore V, Battista JR (1996) Radioresistance of *Deinococcus radiodurans*: functions necessary to survive ionizing radiation are also necessary to survive prolonged desiccation. J Bacteriol 178:633–637
50. McKnight DM, Niyogi DK, Alger AS, Bomblies A, Conovitz PA, Tate CM (1999) Dry valley streams in Antarctica: ecosystems waiting for water. Bioscience 49:985–995
51. Mitchell KR, Takacs-Vesbach CD (2008) A comparison of methods for total community DNA preservation and extraction from various thermal environments. J Ind Microbiol Biotechnol 35:1139–1147
52. Molles MC Jr, Dahm CN, Crocker MT (1992) Climatic variability and streams and rivers in semi-arid regions. In: Roberts RD, Bothwell ML (eds) Aquatic ecosystems in semi-arid regions: implications for resource management. The Institute, Saskatoon, pp 197–201
53. Moorhead DL, Barrett JE, Virginia RA, Wall DH, Proazinska D (2003) Organic matter and soil biota of upland wetlands in Taylor Valley, Antarctica. Polar Biol 26:567–576
54. Newell DL, Crossey LJ, Karlstrom KE, Fischer TP, Hilton DR (2005) Continental-scale links between the mantle and groundwater systems of the western United States: evidence from travertine springs and regional He isotope data. GSA Today 15:4–10
55. Niederberger TD, McDonald IR, Hacker AL, Soo RM, Barrett JE, Wall DH, Cary SC (2008) Microbial community composition in soils of Northern Victoria Land, Antarctica. Environ Microbiol 10:1713–1724
56. Noguez AM, Arita HT, Escalante AE, Forney LJ, Garcia-Oliva F, Souza V (2005) Microbial macroecology: highly structured prokaryotic soil assemblages in a tropical deciduous forest. Glob Ecol Biogeogr 14:241–248
57. Northcott ML, Gooseff MN, Barrett JE, Zeglin LH, Takacs-Vesbach CD, Humphrey J (2009) Hydrologic characteristic of lake- and stream-side riparian wetted margins in the McMurdo Dry Valleys, Antarctica. Hydrol Process 23:1255–1267
58. Noy-Meir I (1973) Desert ecosystems: environment and producers. Annu Rev Ecol Syst 4:25–51
59. Papke RT, Ward DM (2004) The importance of physical isolation to microbial diversification. FEMS Microbiol Ecol 48:293–303
60. Patterson BD (1999) Contingency and determinism in mammalian biogeography: the role of history. J Mammal 80:345–360
61. Pointing SB, Chan Y, Lacap DC, Lau MCY, Jurgens JA, Farrell RL (2010) Highly specialized microbial diversity in hyper-arid polar desert. Proc Natl Acad Sci U S A 107:1254–1254
62. Pointing SB, Warren-Rhodes KA, Lacap DC, Rhodes KL, McKay CP (2007) Hypolithic community shifts occur as a result of liquid water availability along environmental gradients in China's hot and cold hyperarid deserts. Environ Microbiol 9:414–424
63. Posada D, Crandall KA (1998) Modeltest: testing the model of DNA substitution. Bioinformatics 14:817–818
64. Prosser JI, Bohannan BJM, Curtis TP, Ellis RJ, Firestone MK, Freckleton RP, Green JL, Green LE, Killham K, Lennon JJ, Osborn AM, Solan M, van der Gast CJ, Young JPW (2007) Essay—the role of ecological theory in microbial ecology. Nat Rev Microbiol 5:384–392
65. Rees GN, Watson GO, Baldwin DS, Mitchell AM (2006) Variability in sediment microbial communities in a semipermanent stream: impact of drought. J North Am Benthol Soc 25:370–378
66. Romani AM, Fischer H, Mille-Lindbloom C, Travnik LJ (2006) Interactions of bacteria and fungi on decomposing litter: differential extracellular enzyme activities. Ecology 87:2559–2569
67. Rutz BA, Kieft TL (2004) Phylogenetic characterization of dwarf archaea and bacteria from a semiarid soil. Soil Biol Biochem 36:825–833
68. Schade JD, Marti E, Welter JR, Fisher SG, Grimm NB (2002) Sources of nitrogen to the riparian zone of a desert stream: implications for riparian vegetation and nitrogen retention. Ecosystems 5:68–79
69. Schloss PD, Handelsman J (2005) Introducting DOTUR, a computer program for defining operational taxonomic units and estimating species richness. Appl Environ Microbiol 71:1501–1506
70. Schwinning S, Sala OE (2004) Hierarchy of responses to resource pulses in arid and semi-arid ecosystems. Oecologia 141:221–220
71. Smith JJ, Tow LA, Stafford W, Cary C, Cowan DA (2006) Bacterial diversity in three different Antarctic cold desert mineral soils. Microb Ecol 51:413–421
72. Souza V, Espinosa-Asuar L, Escalante AE, Eguiarte LE, Farmer J, Forney L, Lloret L, Rodriguez-Martinez JM, Soberon X, Dirzo R, Elser JJ (2006) An endangered oasis of aquatic microbial biodiversity in the Chihuahuan desert. Proc Natl Acad Sci U S A 103:6565–6570
73. Swofford DL (2003) Phylogenetic analysis using parsimony. Version 4. Sinauer Associates, Sunderland

74. Takacs-Vesbach C, Zeglin LH, Barrett JE, Gooseff MN, Priscu JC (2010) Factors promoting microbial diversity in the McMurdo Dry Valleys, Antarctica. In: Doran PT, Lyons WB, McKnight DM (eds) Life in antarctic deserts and other cold dry environments. Cambridge University Press, Cambridge
75. Treonis AM, Wall DH, Virginia RA (1999) Invertebrate biodiversity in Antarctic Dry Valley soils and sediments. Ecosystems 2:482–492
76. Vincent WF, Howard-Williams C (1986) Antarctic stream ecosystems: physiological ecology of a blue-green algal epilithon. Freshw Biol 16:219–233
77. Walsh DA, Papke RT, Doolittle WF (2005) Archaeal diversity along a soil salinity gradient prone to disturbance. Environ Microbiol 7:1655–1666
78. Whitaker RJ (2006) Allopatric origins of microbial species. Philos Trans R Soc Lond B Biol Sci 361:1975–1984
79. Xie CH, Yokota A (2006) Reclassification of *Flavobacterium ferrugineum* as *Terrimonas ferruginea* gen. nov., comb. nov., and description of *Terrimonas lutea* sp nov., isolated from soil. Int J Syst Evol Microbiol 56:1117–1121
80. Yergeau E, Kowalchuk GA (2008) Responses of Antarctic soil microbial communities and associated functions to temperature and freeze-thaw cycle frequency. Environ Microbiol 10:2223–2235
81. Yoon JH, Kang SJ, Lee CH, Oh TK (2005) *Marinicola seohaensis* gen. nov., sp nov., isolated from sea water of the Yellow Sea, Korea. Int J Syst Evol Microbiol 55:859–863
82. Yoon MH, Im WT (2007) *Flavisolibacter ginsengiterrae* gen. nov., sp nov and *Flavisolibacter ginsengisoli* sp nov., isolated from ginseng cultivating soil. Int J Syst Evol Microbiol 57:1834–1839
83. Zeglin LH (2008) Microbial diversity and function at aquatic-terrestrial interfaces in desert ecosystems. Ph.D. Dissertation. Department of Biology, University of New Mexico, Albuquerque, NM, USA
84. Zeglin LH, Sinsabaugh RL, Barrett JE, Gooseff MN, Takacs-Vesbach CD (2009) Landscape distribution of microbial activity in the McMurdo Dry Valleys: linked biotic processes, hydrology and geochemistry in a cold desert ecosystem. Ecosystems 12:562–573
85. Zhou J, Xia B, Treves DS, Wu L-Y, Marsh TL, O'Neill RV, Palumbo AV, Tiedje JM (2002) Spatial and resource factors influencing high microbial diversity in soil. Appl Environ Microbiol 68:326–334