

Bacterial and archaeal communities within the alkaline Na₂CO₃-type Langaco Lake in the Qinghai-Tibet Plateau

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Abstract

Purpose: Langaco Lake (LGL) is a strong Na₂CO₃-type lake that sits at an altitude of 4,548 m in the Qinghai-Tibet Plateau of China. LGL exhibits unique hydrochemical characteristics among Na₂CO₃-type lakes, but little is known about the microbial diversity of LGL and their interactions with environmental factors.

Methods: The water samples were filtered by chemical-grade cellulose acetate membrane (pore size 0.45 μm), and analyzed the Hydrochemical characteristics. Community DNA was extracted then high-throughput sequencing of 16S rRNA genes were used to evaluate the microbial community composition.

Results: Here, high-throughput sequencing of 16S rRNA genes revealed that LGL bacterial diversity comprised 327 genera in 24 phyla (4,871 operational taxonomic units [OTUs]; Shannon index values of 5.20–6.07) that represented significantly higher diversity than that of Archaea (eight phyla and 29 genera comprising 1,008 OTUs; Shannon index values of 2.98–3.30). The bacterial communities were dominated by Proteobacteria (42.79–53.70% relative abundances), followed by Bacteroidetes (11.13–15.18%), Planctomycetes (4.20–12.82%), Acidobacteria (5.91–9.50%), Actinobacteria (2.60–5.80%), and Verrucomicrobia (2.11–4.08%). Further, archaeal communities were dominated by Crenarchaeota (35.97–58.29%), Euryarchaeota (33.02–39.89%), and Woeisearchaeota (6.50–21.57%). The dominant bacterial genus was *Thiobacillus* (8.92–16.78%), whose abundances were most correlated with total phosphorus (TP), pH, CO₃²⁻ concentrations, and temperature. The most abundant archaeal genus was *Methanoregula* (21.40–28.29%), whose abundances were most highly correlated with TOC and TS in addition to the concentrations of K⁺, and Na⁺.

Conclusions: Taken together, these results provide valuable insights towards a more comprehensive understanding of microbial diversity in these unique carbonate alkaline environments, in addition to a better understanding of microbial resources in the Qinghai-Tibet Plateau.

Introduction

Na₂CO₃-type lakes are exceptional among aquatic ecosystems because they simultaneously exhibit high productivity rates and high pH (9.5–11.0) (Banda et al. 2019; Paul et al. 2015). The lakes are naturally occurring alkaline environments that contain high concentrations of sodium carbonate due to evaporative concentration in addition to high concentrations of other salts that can also accumulate (especially sodium chloride), leading to the formation of alkaline saline lakes (Namsaraev et al. 2015). Na₂CO₃-type lakes have likely massively contributed to global primary productivity in Earth's geological past and these “soda lake” environments represent examples of contemporary extreme environments. Generally, they are inland lakes and have a propensity to become meromictic due to regional and local hydrologic events. In addition they are highly productive due to elevated temperatures, high sunlight incidence, and large supplies of CO₂. Further, diverse microbial populations are abundant in Na₂CO₃-type lakes (Lanzen et al. 2013). Many regional examples of soda lakes are known including in the East African Rift Zone, rain-shadowed regions of California and Nevada, the Kulunda steppe in South Russia, and on the Cariboo Plateau in Canada. Likewise, many microorganisms have been isolated from such lakes including *Cyanobacteria*, chemolithoautotrophic sulfide oxidizing bacteria, sulfating/nitrifying/denitrifying bacteria, aerobic heterotrophic bacteria, fermentative methanotrophs and methanogens (Zorz et al. 2019; Tiodjio et al. 2014).

Underlying basaltic rocks in some areas of these plateaus originate from volcanic activity during the Miocene and Pliocene eras and lead to ideal conditions for the formation of Na₂CO₃-type lakes, owing to the low solubility of calcium and magnesium from the basaltic formations. Thus, Na₂CO₃-type lakes are important components of terrestrial ecosystems and contain abundant microbial resources while playing critical roles in geochemical cycles by promoting material exchange, as in the Qinghai-Tibet Plateau of China (Xing et al. 2019). Na₂CO₃-type lakes are widely distributed in terrestrial plateau ecosystems that exhibit extreme environmental conditions like the persistence of extreme drought, intense solar ultraviolet radiation, extreme daily temperature changes, and low partial pressures of dissolved and atmospheric oxygen (Namsaraev et al. 2015; Lanzen et al. 2013). Consequently, changes in these environmental conditions in association with elevation can lead to changes in bacterial or archaeal lake community diversity in high altitude areas (Liu et al. 2010).

Langaco Lake (LGL) is one of the highest typical Na₂CO₃-type lakes in the Qinghai-Tibet Plateau. However, the microbial structure and diversity of LGL have not been previously investigated. LGL is also minimally directly affected by human activities and thus remains ecologically intact, thereby providing a natural laboratory for scientific studies. These rarely explored lakes may harbor new microbial species, and thus, an understanding of the bacterial diversity in these high-altitude lakes is critical for informing species protection and ecosystem conservation (Mesbah et al. 2007). High-throughput sequencing has been extensively used to investigate microbial communities in recent years via 16S rRNA gene compositional analysis in natural environments. These methodologies have become increasingly used to determine differences in microbial community diversity and structure among environments, thereby helping to reveal interactions among microorganisms in environments, in addition to their adaptations towards specific environment (Paul et al. 2015). Here, Illumina high-throughput sequencing analysis of community 16S rRNA genes was used to comprehensively investigate the bacterial and archaeal communities of LGL, while also exploring the dominant genera of LGL and their associations with environmental factors. This study therefore provides a theoretical framework for understanding the relationships among microorganisms and environments in alkaline conditions on plateaus.

Materials And Methods

Sample Sites and Sample Collection

Langaco Lake (LGL) is located in the northwestern margin of the Tibet Plateau (30°40'30.6"N, 81°18'32.3"E) in Pulan County of the Ngari Region at an altitude of 4,548 m. LGL comprises an area of 256.2 km² and experiences a frigid semi-arid plateau climate (Zheng 1997). The lake is shaped irregularly and is slightly spoon-shaped, with several islands exposed within the lake. The northern portion of the lake is a smaller open lake area that is connected to the open south by

a narrow channel, while the center is flat (Wang et al. 2013). The lake features a sodium concentration of 106.24 mg/L, a total salinity of 1.00 mg/L, and a pH of 8.62 (Zheng 1997). The total area of the lake has decreased since the 1970's and especially in the northwest, while temperatures have generally risen, and precipitation has significantly dropped in the region (Dai 2020). Consequently, lake water is primarily replenished by meltwater from northern glaciers (Wang et al. 2013).

Four samples were collected from LGL in mid-July 2018 from a sediment depth of 30–40 cm and included a mixture of water and sediment (about 4 L total). The distance between the two samples was greater than 4 km (Fig. 1) and they were all collected about 5 m from the coastline. In addition, approximately 2 L of water was immediately filtered through a 0.22 µm filter (Millipore, USA) on site for subsequent DNA extraction. A portable pH meter (LEICI/PHBJ-261L, Shanghai) was used to measure pH in the field. The filters were taken back to the laboratory on ice while water samples for physicochemical analysis were stored at 4°C.

Hydrochemical Analyses

Water samples were filtered with chemical-grade cellulose acetate membrane (pore size 0.45 µm), while total salinity and major cation concentrations (Na^+ , K^+ , Ca^{2+} , and Mg^{2+}) were measured using atomic absorption spectrometry (CE 3000 series spectrometer, Thermo Scientific). Anion (Cl^- and SO_4^{2-}) concentrations were measured on an ion chromatographer (Dionex/ICS-6000, Thermo Scientific, USA). Total salinity (TS) was measured using the dry gravimetric method, while total organic carbon (TOC) and total nitrogen (TN) were measured at Xi'an United Nations Quality Detection Technology CO., Ltd (China). Finally, the double-indicator titration method was used to measure total phosphate (TP), CO_3^{2-} , and HCO_3^- anion concentrations.

Microbial Community Dna Extraction And Pcr Amplification

The 0.22 µm filter membranes used to filter microbial community samples via vacuum filtration were sectioned according to the manufacturer's instructions. Community DNA was then extracted using an E.Z.N.A Mag-Bind Soil DNA Kit (Omega Bio-Tek, USA). The integrity of extracted DNA was evaluated with 1% agarose gel electrophoresis and a Qubit® 2.0 Fluorometer Q32866 type (Invitrogen, USA) was used to determine DNA concentrations followed by storage at -80°C.

To evaluate microbial community composition, bacterial and archaeal 16S rRNA genes were amplified from the water DNA extracts using PCR with universal domain specific primers. PCR amplifications of the V3-V4 hypervariable regions of bacterial 16S rRNA genes were conducted with the primers 341F (5'-ACTCCTACGGGAGCAGCA-3') and 805R (5'-GGACTACHVGGGTWTCTAAT-3'), in addition to multiplex barcodes (Han et al. 2017). Likewise, the universal primers 349F (5'-ACGGGGYGCAGCAGGCGCA-3') and 806R (5'-GACTGGAGTTCCTTGGCACCGAGAAT-3') (Deng et al. 2012) were used to amplify the V3-V4 hypervariable regions of archaeal 16S rRNA genes using barcoded primers. PCR mixtures (30 µL volume) consisted of 15 µL of 2×Taq master mixture (containing 0.1 U/µL Taq DNA polymerase EP0406 [Thermo, USA], 0.4 mM per dNTP, and 2×Taq buffer), 10–20 ng of community genomic DNA, 1 µL of each primer at 10 µM concentrations, and 12 µL of ultrapure H₂O. PCRs were repeated in triplicate for each sample on a T100™ thermal circulator PCR system (Bio-RAD, USA). PCR conditions comprised 95°C for 3 min followed by 32 cycles of denaturation at 95°C for 30 s, annealing at 55°C for 30 s, and extension at 72°C for 45 s; all followed by an extension at 72°C for 10 min. Amplified PCR fragments were purified with an Agencourt AMPure XP Kit (A63882, Beckman, USA) and then quantified with the Qubit 2.0 DNA quantification Kit (InvitGen, USA). Paired-end 16S rRNA gene sequencing was conducted on the Illumina MiSeq 300PE platform of Sangong Biotechnology Co., Ltd., Shanghai, China.

Processing Of Raw Sequence Reads And Statistical Analyses

The raw 16S rRNA gene sequences (ranging from 45,000 to 55,000 sequences per sample) were processed and analyzed as described previously (Han et al. 2017). Briefly, the Cutadapt software program (v.1.2.1) was used to combine the original paired-end sequences into overlapping contig sequences (Edgar et al. 2011). The Uchime software program (v.4.2.40) was then used to detect and remove chimeric sequences (Martin 2011), along with the Usearch (v.5.2.236) program (Edgar 2010) that was also used to detect chimeric sequences by comparison against the SILVA (release 132; <https://www.arb-silva.de/>) and RDP (v.11.3; <https://rdp.cme.msu.edu/misc/resources.jsp>) databases. Taxonomic classification of OTUs was conducted using the Quantitative Insights into Microbial Ecology (QIIME; V.1.8.0) pipeline with the RDP Bayesian classification method (v.2.12) and a 97% classification confidence level threshold (Wang et al. 2007; Caporaso et al. 2010).

Community alpha-diversity was calculated using the Mothur software package (v.1.30.1) (Schloss et al. 2009) and included the abundance-based coverage estimation (ACE), terminal richness estimation (Chao1), the Simpson index, the Shannon-Weiner index, rarefaction analysis, and Good's coverage estimation. Venn diagrams were used to assess the numbers of shared and unique OTUs among samples. Beta-diversity was measured based on Bray-Curtis distances between samples, and overall community differences were evaluated with full linkage cluster analysis of Bray-Curtis distances. Canonical correspondence analysis (CCA) was performed using the CCA function in the vegetarian R package, using the community distance matrix and hydrochemical factors. Variables that significantly explained differences in community composition were evaluated using permutation tests under a simplified model.

Taxonomic Classification Analysis

The relative abundances of bacterial and archaeal communities were summarized at the phylum, class, and genus levels. The R software suite was used to construct boxplots of taxonomic relative abundances among samples, while the GraPhlAn software package (Asnicar et al. 2015) and the online Tree Of Life

interactive tool (ITOL, v.3.2.1) (Letunic et al. 2015) were used for phylogenetic tree visualization for the 100 most abundant OTUs.

Sequence Accession Numbers

Raw 16S rRNA gene sequences were deposited in the NCBI database under the BioSample accession Nos. SAMN20703607 to SAMN20703610 for *Bacteria*, and SAMN20703611 to SAMN20703614 for *Archaea*.

Results

Hydrochemical Characteristics

LGL is a sodium carbonate type lake that exhibits major water cations of Na⁺ (105.90–106.62 mg/L) and Ca²⁺ (84.24–85.80 mg/L), while the major anions are HCO₃⁻ (472.34–476.17 mg/L) and CO₃²⁻ (75.97–76.43 mg/L). The average water temperature in mid-July was 16.7°C, while the pH of the water was alkaline, ranging from 8.54 to 8.62. The average values of TOC, TN, and TP were 6.21 mg/L, 104.21 mg/L and 1.91 mg/L, respectively (Table 1).

Table 1

Chemical characteristics of surface water and sediment samples from Langaco Lake. Table 2: Operational taxonomic unit (OTU) richness and diversity measures from Langaco Lake communities. Table 3: Hydrochemical characteristics and dominant genera within worldwide soda lakes. Table 1. Chemical characteristics of surface water and sediment samples from Langaco lake.

Samples	Temp (°C)	pH	TOC (%)	TN (µg/L)	TS (g/L)	TP (µg/L)	Major ions (mg/L)							
							Na ⁺	K ⁺	Ca ²⁺	Mg ²⁺	Cl ⁻	SO ₄ ²⁻	CO ₃ ²⁻	HCO ₃ ⁻
L1, L1a	16.70	8.62	6.20	102.70	1.00	1.92	106.24	15.24	85.08	74.34	56.08	75.73	76.30	475.56
L2, L2a	16.51	8.54	6.18	106.37	1.02	1.91	106.40	15.84	85.80	73.46	56.57	79.02	76.10	472.34
L3, L3a	16.32	8.61	6.22	107.56	1.03	1.93	105.90	16.24	84.24	75.13	55.89	76.35	75.97	476.17
L4, L4a	17.30	8.59	6.25	100.24	0.99	1.90	106.62	16.00	84.80	74.87	56.28	73.47	76.43	473.79

Note: TOC, total organic carbon; TN, total nitrogen; TP, total phosphorus.

Bacterial And Archaeal Community Diversity

Bacterial and archaeal community composition was investigated among the four LGL samples using high-throughput Illumina sequencing of community 16S rRNA genes (Table 2). A total of 5,879 OTUs were recovered that comprised 4,871 bacterial OTUs and 1,008 archaeal OTUs. Among bacterial samples, the richness and diversity of L2 and L4 were slightly higher than those of the L1 and L3 samples. The observed bacterial community OTU richness, Shannon index, and ACE values ranged from 1,025–1,293, 5.20–6.07, and 2,148.23–2,376.17, respectively. In contrast, archaeal diversity (221–269 observed OTUs, Shannon index values of 2.98–3.30, and ACE index values of 417.63–536.42) was significantly lower than that of the bacterial communities.

Table 2

Operational taxonomic unit (OTU) richness and diversity measures from Langaco Lake communities.

Sample-ID	Sequence reads	Richness and diversity metric					
		OTUs	Shannon	ACE	Chao1	Coverage	Simpson
Bacteria							
L1	9,377	1,025	5.20	2,148.23	1,668.18	0.95	0.03
L2	9,424	1,287	6.07	2,359.52	1,990.62	0.94	0.01
L3	9,356	1,266	5.92	2,243.30	1,912.93	0.94	0.01
L4	9,354	1,293	5.96	2,376.17	1,995.66	0.94	0.01
Archaea							
L1a	16,316	269	2.98	536.42	390.27	0.99	0.12
L2a	16,465	221	3.16	417.63	336.62	0.99	0.09
L3a	16,415	250	3.27	434.32	395.25	0.99	0.10
L4a	16,403	268	3.30	497.65	418.19	0.99	0.09

Note: ACE, abundance-based coverage estimator.

Taxonomic Composition Of Lgl Microbial Communities

Venn diagrams were used to visualize the overlap in the OTUs among the lake water samples (Fig S1). Total unique bacterial genera observed in the four samples were 219 (L1), 270 (L2), 291 (L3), and 271 (L4), while unique archaeal genera were significantly lower at 77 (L1a), 56 (L2a), 72 (L3a), and 74 (L4a). There were 472 and 81 shared bacterial genera among the two communities. The most abundant sequences were selected as representative sequences of OTUs, and the relative abundances of bacterial and archaeal populations among communities were compared at the phylum, class, and genus taxonomic levels (Fig. 2 and Fig S2). In addition, community clustering based on community compositional differences indicated that there were three different bacterial community groups, with L3 and L1 each comprising single branches, and L4 and L2 clustering together. In contrast, the archaeal communities comprised two groups with L4 and L1 comprising one group, while L3 and L2 comprised the other group. Overall, twenty-four bacterial phyla were detected in the LGL microbial communities, comprising 50 classes and 327 genera. Additionally, eight archaeal phyla were detected that comprised nine classes and 29 genera (Table S1, S2, S3).

At the phylum level, the predominant bacteria (> 1% relative abundance) were Proteobacteria (42.79–53.70% relative abundance), Bacteroidetes (11.13–15.18%), Planctomycetes (4.20–12.82%), and Acidobacteria (5.91–9.50%), followed by Actinobacteria (2.60–5.80%), Verrucomicrobia (2.11–4.08%), Chloroflexi (2.00–2.54%), Parcubacteria (0.83–2.16%), Firmicutes (0.63–1.14%), and Nitrospirae (0.21–1.53%). The dominant archaeal phyla among all samples were Crenarchaeota (35.97–58.29%), Euryarchaeota (33.02–39.89%), and Woesearchaeota (6.50–21.57%). In addition, Pacearchaeota (0.63–1.13%) and Acidobacteria (0.01%) were detected in the L1a and L3a samples. The relative abundances of Woesearchaeota were greater than 20% in the L2a, L3a, and L4a samples, but only 6.50% in L1a.

At the class level, the dominant *Bacteria* (> 1% relative abundance) among the four samples were Betaproteobacteria (21.46–28.52%), followed by Alphaproteobacteria (9.13–12.34%), Gammaproteobacteria (7.91–10.70%), Sphingobacteriia (5.90–7.61%), Actinobacteria (2.60–5.76%), Deltaproteobacteria (1.87–2.95%), and Planctomycetia (3.97–12.00%). The dominant *Archaea* among the four samples were Thermoprotei (35.97–58.29%), Methanomicrobia (24.08–32.84%), Thermoplasmata (6.94–8.86%), and unclassified Woesearchaeota groups (6.50–21.57%).

At the genus level, the dominant bacterial genera (excluding unclassified genera) among the four samples were *Thiobacillus* (8.92–16.78%), *Hydrogenophaga* (1.76–3.71%), *Gemmobacter* (1.38–3.56%), *Algoriphagus* (0.87–3.15%), *Pirellula* (1.07–2.44%), *Parcubacteria*-genera-incertae-sedis (0.83–2.16%), *Ilumatobacter* (1.25–1.70%), *Sphingorhabdus* (0.69–1.74%), *Phaeodactylibacter* (1.07–1.40%), and the acidobacterial groups GP16, GP6, GP3, and GP7 (0.67–2.42%). In addition to the above bacterial genera, other *Bacteria* exhibited higher abundances in individual samples including *Lacibacter* (1.15%) in L1, Saccharibacterial genera incertae-sedis (0.59–0.80%) in L2 and L3, *Thermomonas* (1.03–3.21%) in L1 and L3, and *Litorilinea* (0.55–0.68%) in the L2 and L4 samples. The dominant archaeal genera were *Methanoregula* (21.40–28.29%), *Thermocladium* (4.17–12.75%), *Methanomassiliococcus* (6.92–8.77%), Woesearchaeota incertae-sedis-AR16 group (2.46–5.96%), and *Methanotherix* (1.02–1.91%). Each of the four samples exhibited unique archaeal genera including *Aridibacter* (0.01%) in L1a, *Aquisphaera* (0.01%) in L4a, and *Halovenus* (0.01%) in L3a and L4a.

Associations Between Environmental Factors And Dominant Genera

Differences in abundances among samples were investigated (Fig. 3) while considering the twelve and nine most abundant bacterial and archaeal phyla, respectively. The most abundant (> 1% relative abundance) bacterial genera among the four communities were the betaproteobacterial genera *Thiobacillus* and *Hydrogenophaga*, the alphaproteobacterial genus *Gemmobacter*, and the gammaproteobacterial genus *Thermomonas*. In addition, *Methanoregula* was the most abundant archaeal genus, and other archaeal genera exhibited higher abundances in individual samples including *Thermocladium* and *Methanomassiliococcus*.

CCA was conducted to evaluate the relationships among community structures and environmental parameters, yielding numerous associations of overall community composition with several environmental parameters. Consequently, environmental parameters were analyzed in context of representative genera (Fig. 4). The abundances of the dominant bacterial genus *Thiobacillus* were most correlated with TP, followed by pH, CO_3^{2-} concentrations, and temperature. The abundances of the next most dominant bacterial genera *Hydrogenophaga* and *Gemmobacter* were associated with TP and HCO_3^- concentrations. The Moderately abundant (1.50–4.00%) bacterial genera *Thermomonas*, *Algoriphagus*, and *Sphingorhabdus* in the L1 samples were correlated with TP, pH, and HCO_3^- concentrations. The abundances of the Parcubacteria genera incertae sedis and GP16 groups were strongly correlated with pH and Cl^- concentrations, respectively. The minorly abundant (1.5–2.5%) genera of *Rheinheimeria*, *Nitrospira*, and Gp6 in the L2 samples were significantly correlated with TN, in addition to the concentrations of Ca^{2+} , SO_4^{2-} , and Cl^- . Furthermore, the abundances of the genera *Pirellula*, *Gimesia*, and *Spartobacteria* genera incertae sedis were related to K^+ and Na^+ concentrations, in addition to TOC and TS in the L3 and L4 samples. The abundances of the dominant (> 20%) archaeal genera *Methanoregula*, *Methanotherix*, *Methanomassiliococcus*, Pacearchaeota incertae sedis-AR13, and Woesearchaeota incertae sedis-AR16 were highly correlated with TOC and TS in addition to the concentrations of K^+ and Na^+ . In addition, *Thermocladium* abundances were particularly highly associated with HCO_3^- concentrations.

Discussion

Characteristics of the LGL Soda Lake

Soda lakes are globally distributed and are predominantly found in arid and semi-arid environments including in the Rift Valley in East Africa, the rain-shadowed regions of California and Nevada, and the Kulunda Steppe in South Russia (Namsaraev et al. 2018), in addition to throughout Europe, Egypt, North America and China (Namsaraev et al. 2015; Patricia et al. 2018). Soda lakes have recently been classified into “soda” and “soda-salt” types based on differences in carbonate and bicarbonate content. “Soda” types are those that are dominated by sodium, bicarbonate, and carbonate ions, while “soda-salt” types are those with ions dominated by sodium, in addition to others besides bicarbonate/carbonate (Boros et al. 2018). Soda lakes generally form in hydrologically closed lake basins, with waters featuring high concentrations of Na^+ , in addition to CO_3^{2-} (0.023–63.20 g/L) or HCO_3^- (0.11–20.40 g/L) (Table 3), although their waters may contain some abundant and variable concentrations of SO_4^{2-} , K^+ , or Cl^- (Boros et al. 2018; Schagerl et al. 2016). LGL is an example of an extreme soda lake with lower ionic content, with CO_3^{2-} , and HCO_3^- concentrations of 76.30, and 475.56 mg/L, respectively. Soda waters also usually contains high concentrations of Cl^- , as in the alkaline-saline (soda) lakes of tropical Africa (L. Nakuru and L. Simbi. Kenya) that exhibit Cl^- concentrations of 1,167 mg/L (Finlay et al. 1987), contrasting with that of LGL, which was 55 mg/L. Thus, LGL is considered a weakly ionic soda lake. The formation of alkalinity is closely related to hydrology, climate, and regional geology, which ultimately affect the diversity of microorganisms within these systems. The pH of LGL was 8.62, but is greater than 9.00 in most other soda lakes (Table 3). Due to the extreme conditions within these systems, the characteristics of soda lakes (including high pH) provide unique environments for microbial communities (Table 3). Thus, a predominance of carbonate and bicarbonate, (in addition to associated alkalinity) are hallmarks of soda lake ecosystems, although diversity has been observed in their hydrochemical characteristics.

Table 3
hydrochemical characteristics and dominant genera within worldwide soda lakes.

Lake name	N	E	pH	Salinity (g/L)	CO ₃ ²⁻ (g/L)	HCO ₃ ⁻ (g/L)	OTU	Shannon	Dominant <i>Bacteria</i>	Dominant <i>Archaea</i>	Ref.
Badong, Baxi, Xiaoshazao, Zhongnao, and Sangenjilin Lakes (China)*	39°55'–39°94'	101°59'–102°37'	9.69–10.83	2.1–397.3	0.04–31.67	0.60–16.82	16,381 ^a	1.15–3.24	<i>Spiribacter</i> , <i>Halomonas</i> , <i>Burkholderia</i>	<i>Halobellus</i> , <i>Halohasta</i> , <i>Halorubrum</i>	[1]
Khilganta, Dabasa Nur, Solenoye, Gurvany Nuur, <i>ect</i> (Mongolia)*	No	No	8.10–10.4	1.8–360.0	0.09–63.2	0.21–7.49	No	No	<i>Geitlerinema</i> , <i>Coleofasciculus</i>	No	[3]
Zabuye Lake (China)*	31°23'	84°04'	9.00	230.0	11.20	11.20	127 ^g	No	<i>Pseudomonas</i> , <i>Alkalimonas</i> , <i>Nitricola</i>	No	[39]
Isabel Lake (Mexico)*	21°52'	W 105°54'	9.00–10.00	94.5	No	No	2,799 ^{b, d, e}	1.15–5.48	<i>Salegentibacter</i> , <i>Formosa</i> , <i>Muricauda</i>	No	[29]
Bitter-1 Lake (Russia)	51°67'	79°91'	9.60–10.50	85.0	60.00	No	No	No	<i>Ectothiorhodospira</i>	No	[23]
Beseka, Arenguadi, Chitu, Abijata, and Shalla Lakes (Ethiopian)*	7°40'–8°90'	38°42'–39°87'	9.60–10.40	2.1–58.0	No	No	2,704 ^a	2.30–4.70	<i>Ectothiorhodospira</i> , <i>Rhodobaca</i> , <i>Rhodobacter</i>	<i>Thaumarchaeota</i> , <i>Methanocalculus</i>	[4]
Doroninskoe Lake (Russia)*	51°14'	112°14'	9.93–10.09	22.2–36.0	5.73	6.62	2,254 ^a	1.49–3.46	<i>Serratia</i> , <i>Achromobacter</i> , <i>Rhodobaca</i>	Pacearchaeota, Woesearchaeota ¹	[29]
Van Lake (Turkey)	38°38'	42°57'	9.70–9.80	23.0	3.50	2.40	No	No	Proteobacteria, Firmicutes ¹	No	[40]
Qinghai Lake (China)*	36°32'–37°15'	99°36'–100°16'	8.80–8.86	10.1–12.8	0.32	0.71	B:743; A:592 ^a	2.48–4.56	<i>Loktanelia</i> , <i>Pseudarthrobacter</i> , <i>Nitricola</i>	<i>Woesearchaeota</i> , <i>Methanosarcina</i>	[41]
Mono Lake (USA)*	37°56'	W119°13'	9.40–10.0	10.8–11.2	18.90	11.20	No	0.85–4.86	<i>Rhodoplanes</i> , <i>Spiribacter</i>	<i>Methanocalculus</i> , <i>Methanosarcina</i>	[24]
Lonar Lake (India)*	19°97'–19°98'	76°50'–76°51'	9.50–10.00	1.7–3.9	0.17–0.26	No	1,568 ^a	6.82–10.93	Proteobacteria, Actinobacteria, Firmicutes	No	[2]
Namco Lake (China)*	30°30'–30°35'	90°16'–91°03'	9.21	1.1	0.023	0.55	83 ^f	No	<i>Polynucleobacter</i> , <i>Rhodoferax</i> , <i>Acinetobacter</i>	No	[8]
Langaco Lake (China)*	30°67'	81°30'	8.62	0.001	0.076	0.48	B:4,871; A:1,008 ^a	2.98–6.07	<i>Thiobacillus</i> , <i>Hydrogenophaga</i> , <i>Gemmobacter</i>	<i>Methanoregula</i> , <i>Thermocladium</i>	This stud ¹
Last Chance, Probe, Deer, and Goodenough Lake (Canada)*	51°32'–51°45'	121°25'–121°64'	10.10–10.70	No	3.42–16.44	2.07–20.4	1,662 ^c	No	<i>Gemmatirosa</i> , <i>Rhodobacter</i>	No	[5]
Nyos Lake (Cameroon)*	06°26'	10°18'	6.90–7.30	No	No	0.11–2.37	61 ^d	1.50–2.70	Firmicutes, Actinobacteria ¹	Thaumarchaeota, Euryarchaeota ¹	[6]

Note N, northern latitude; E, east longitude; W, west longitude; B, Bacteria; A, Archaea;

a, high throughput sequencing; b, pyrosequencing; c, shotgun metagenome; d, DGGE; e, cultivation; f, flow cytometer; g, culture-independent;

1, The dominant genus has not been described in the literature; *, The lake located in the plateau.

Lake name	N	E	pH	Salinity (g/L)	CO ₃ ²⁻ (g/L)	HCO ₃ ⁻ (g/L)	OTU	Shannon	Dominant <i>Bacteria</i>	Dominant <i>Archaea</i>	Ref.
Soda lake in Hoh Xil Basin (China)*	35°11'–35°41'	92°12'–93°29'	7.64–8.01	No	No	No	289 ^a	9.16	<i>Bacillus</i> , <i>Psychrobacter</i>	No	[7]
Fazda, UmRisha, and Hamra Lakes (Kyrgyzstan)	30°19'–30°23'	30°19'–30°24'	8.50–9.80	No	No	No	B:345; A:198 ^e	1.85–3.92	Firmicutes, Proteobacteria, Bacteroidetes ¹	Halobacteriales, Methanosarcinales ¹	[9]
Note N, northern latitude; E, east longitude; W, west longitude; B, Bacteria; A, Archaea;											
a, high throughput sequencing; b, pyrosequencing; c, shotgun metagenome; d, DGGE; e, cultivation; f, flow cytometer; g, culture-independent;											
1, The dominant genus has not been described in the literature; *, The lake located in the plateau.											

Bacterial And Archaeal Diversity Within Lgl

Despite the extreme environments within soda lakes, they harbor high levels of microbial diversity, as evinced by the 327 and 29 bacterial and archaeal genera respectively, within LGL that corresponded to 4,871 and 1,008 16S rRNA gene OTUs, respectively. Under the condition of using same sequencing method, LGL exhibited higher diversity than other soda lakes that have been investigated previously including four alkaline soda lakes of the Cariboo Plateau (bacterial OTUs: 1,662), Doroninskoe Lake (bacterial OTUs: 2,254), and Lonar Lake (bacterial OTUs: 1,568) (Table 3). Furthermore, the Shannon diversity index values observed here (*Bacteria*: 5.20–6.07; *Archaea*: 2.98–3.30) were higher than previously observed in soda lakes, including Doroninskoe Lake (*Bacteria*: 1.49–3.46) five soda lakes of the Badain Jaran Desert (*Bacteria*: 1.15–3.24) (Table 3). Thus, the microbial diversity in LGL appears to be considerably higher than in other previously studied soda lakes.

Microbial Community Structure Of Lgl

High-throughput sequencing of community 16S rRNA genes was used to conduct a comprehensive investigation of the microbial community diversity in LGL. Twenty-four bacterial phyla, and 50 classes were detected in LGL microbial communities, representing a significantly higher level of taxonomic diversity than in other soda lakes including 17 bacterial phyla in Mono Lake (CA, USA) and 11 bacterial phyla in Doroninskoe Lake (Transbaikalia, Russia) (Patricia et al. 2018; Matyugina et al. 2018). Proteobacteria (42.79–53.70%) was the most dominant bacterial phylum, followed by Bacteroidetes (11.13–15.18%), Planctomycetes (4.20–12.82%) and Acidobacteria (5.91–9.50%). Proteobacteria, Bacteroidetes, and Firmicutes, are typically dominant bacterial taxa in soda lakes (Paul et al. 2015; Mesbah et al. 2007). The unique sodium carbonate may be one of the factors affecting differences in microbial diversity in LGL relative to other soda lakes. As indicated above, Proteobacteria and Bacteroidetes have been detected in many soda lakes (Paul et al. 2015; Mesbah et al. 2007), but their relative abundances considerably vary in these systems. The relative abundance of Proteobacteria was 29.5% in Lonar Lake (India) (Paul et al. 2015), which is significantly lower than observed in LGL and also in the Soda Lake of Inner Mongolia (Namsaraev et al. 2015). In addition, the abundances of some bacterial groups were lower than observed in LGL, including for the Bacteroidetes (8.25%) and Planctomycetes (6.8%) (Banda et al. 2019). Planctomycetes and Acidobacteria are rarely observed in other soda lakes (Namsaraev et al. 2015; Aguirre-Garrido et al. 2016). Our results indicate that the compositions of the LGL bacterial communities were primarily affected by environmental factors, likely due to the long hydraulic retention time in the lake. These effects are likely reflected in the differences in the dominant taxonomic classes within LGL relative to those in other soda lakes. Cytophagia and Flavobacteria (phylum: Bacteroidetes) are the dominant classes in other soda lakes (Szabó et al. 2017), while the most abundant class of Bacteroidetes in LGL was Sphingobacteria, which may be related to the unique hydrochemical characteristics of LGL. Likewise, Alphaproteobacteria are typically the dominant proteobacterial class among soda lakes (Szabó et al. 2017), although the Gammaproteobacteria class was dominant in LGL. Thus, LGL bacterial communities exhibit unique compositional differences relative to other soda lakes.

Archaeal diversity in LGL was much lower than that observed for the bacterial communities but was unique among soda lakes. A total of eight archaeal phyla were detected in LGL comprising nine classes and 29 genera. LGL archaeal communities exhibited higher diversity than in other soda lakes. For example, only three archaeal phyla were detected in Doroninskoe Lake (Matyugina et al. 2018). Dominant archaeal phyla also interestingly vary with sediment salinity in some salt lakes. For example, Crenarchaeota are generally dominant in hyposaline sediments, while Halobacteriales (phylum Euryarchaeota) are dominant in hypersaline sediments (Jiang et al. 2007). Methanogens and other Euryarchaeota *Archaea* are important contributors to global organic carbon cycling (Vavourakis et al. 2016). The relative abundances of *Archaea* in LGL also varied compared to other soda lakes. Crenarchaeota were dominant (43.96%), followed by Euryarchaeota (36.56%). In contrast, Crenarchaeota have been either undetected (Matyugina et al. 2018) or at very low levels (Patricia et al. 2018) in other soda lakes. Similar to levels observed in LGL, Euryarchaeota (35.15%) was the most abundant phylum in soda lakes of the Badain Jaran Desert (Banda et al. 2019). Nevertheless, the overall microbial diversity in LGL was relatively higher than observed in other studies, and the unique hydrochemical characteristics of LGL may be an important factor contributing to this high diversity and unique microbial community structure.

In addition to the above, unclassified *Bacteria* and *Archaea* accounted for a considerable proportion of the LGL communities, contributing to 12.67% and 18.31% of the overall communities, respectively. Unclassified *Bacteria* included the groups GP6, GP16, GP7, GP3, GP4 of the Acidobacteria and unclassified Parcubacteria. Acidobacteria are one of the most abundant phyla in soils, where their OTU richness, phylogenetic diversity, and community composition can

be significantly related to soil pH (Wei et al. 2018). Previous studies indicated that human disturbance and activity can reduce the abundances of soil Acidobacteria (Qin et al. 2019). Moreover, sediment bacterial communities, including Acidobacteria, have been shown to be sensitive to fluctuations in environments, especially from external input water sources.

Dominant Bacterial Genera Unique To The Lgl

The most dominant bacterial genus of the LGL communities was *Thiobacillus* (8.92–16.78%), which featured uniquely higher abundances than in other soda lakes (e.g., those in eastern China: 1.39–2.47%) (Duan et al. 2020). The abundances of *Thiobacillus* have also been negatively correlated with the sedimentary sulfate, total sulfur (Duan et al. 2020). *Thiobacillus* can be one of the most dominant groups in freshwater sediments, where it can be used as a biomarker to predict the intensity of subsequent blooms (Chen et al. 2015). Further, *Thiobacillus* can also be detected in some typical habitat types (e.g., soil, water, in addition to duck and fish farm) (Yi et al. 2021) and has been observed as a unique member of coastal bacterial benthic communities (Sherysheva et al. 2020). Intriguingly, *Thiobacillus* has rarely been observed in other soda lakes (Table 3).

Thiobacillus is an autotrophic bacterium, and is one of the primary iron-reducing bacterial taxa in lake sediments, where its abundances and diversity are closely related to the degree of water eutrophication (Fan et al. 2018). Through these processes, *Thiobacillus* participates in redox cycling of heavy metals by producing ferrous iron and accelerating the oxidation of ferric iron in localized areas like anaerobic sedimentary environments with high concentrations of heavy metals, where they contribute to a large proportion of communities (Ding et al. 2017). Additionally, *Thiobacillus* can be a key mediator of S^{2-} oxidation coupled to denitrification, thereby playing an important role in NO_3^- reduction during S^{2-} enrichment conditions when organic carbon is lacking (Pang et al. 2021). Our CCA analysis of LGL communities also indicated that *Thiobacillus* abundances were most highly correlated to variation in pH, CO_3^{2-} concentrations, TP, and temperature. The association of *Thiobacillus* with these factors thus warrants further investigation.

Dominant Archaeal Genera Unique To The Lgl

Members of the archaeal family Methanoregulaceae, have been isolated from various habitats, including acidic peat bogs, anaerobic organic waste treatment reactors, sunken sinkhole ecosystems (e.g., oil fields, paddy soils, and mud volcanoes), and freshwater lakes (Savvichev et al. 2021). *Methanoregula* was the most abundant taxa in LGL (21.40–28.29%), despite that it has low sodium requirements (E. Rosenberg et al. 2014). Further, CCA indicated that *Methanoregula* abundances were significantly correlated with TOC and TS in addition to the concentrations of K^+ , and Na^+ . *Methanoregula* is a nitrogen fixing archaeal taxon that dominates freshwater lakes (Stoeva et al. 2014) and is a dominant methane producer within communities. Other studies have shown significant genetic potential for nitrogen metabolism (e.g., nitrate transport, denitrification, nitrite assimilation, and nitrogen fixation) in methyl-methanogenesis bacterial genomes (Biderre-Petit et al. 2019). In addition, *Methanoregula* can be detected at different temperatures in wetland soils near alkali lakes (Deng et al. 2019), but has not been detected in most soda lakes, because it has an optimal pH growth range of 4.50 to 5.55 (E. Rosenberg et al. 2014). Lastly, *Methanoregula* was also the dominant member of a methanogenic community, and is well adapted to hypoxic conditions (Savvichev et al. 2021).

Conclusions

The LGL soda lake, is a unique sodium carbonate ecosystem that may serve as an excellent model for understanding microbial diversity and its adaptation to carbonate habitats. Here, high-throughput 16S rRNA gene sequencing was used to comprehensively characterize the bacterial and archaeal communities of LGL. LGL bacterial diversity was significantly higher than that of *Archaea* and was mostly dominated by Proteobacteria, Bacteroidetes, and Planctomycetes, in addition to the archaeal groups Crenarchaeota, and Euryarchaeota. The presence and high abundances of Crenarchaeota were uniquely different relative to other soda lakes. Moreover, the characteristics and metabolism of *Thiobacillus* provide more possibilities for bacterial diversity, and their abundances were most correlated with environmental pH, CO_3^{2-} concentrations, TP, and temperature. The high abundance of *Methanoregula* in LGL was also a unique observation for the LGL archaeal communities and their abundances were correlated to TOC and TS, in addition to the concentrations of K^+ and Na^+ . Finally, the minimal anthropogenic effects on LGL and its extreme environmental conditions provide a unique context for understanding interactions between microorganisms and extreme soda environments, while also furthering our understanding of microbial resources on the Tibetan Plateau.

Declarations

Compliance with Ethical Standards

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Author contributions MW performed most of the experiments, and wrote the manuscript. XZ and ZS supervised the execution of the experiments, and analyzed the data. DZ, GS, YT, and ZW performed the sample collection. DZ, CL and GS provided the bioinformatics technical assistance, and evaluated the data. All authors read and approved the final version of manuscript.

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Figures



Figure 1
 Geographic location of Langaco Lake and the location of the four sampling sites in the lake. Map is sourced from Esri, Digital Globe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community.

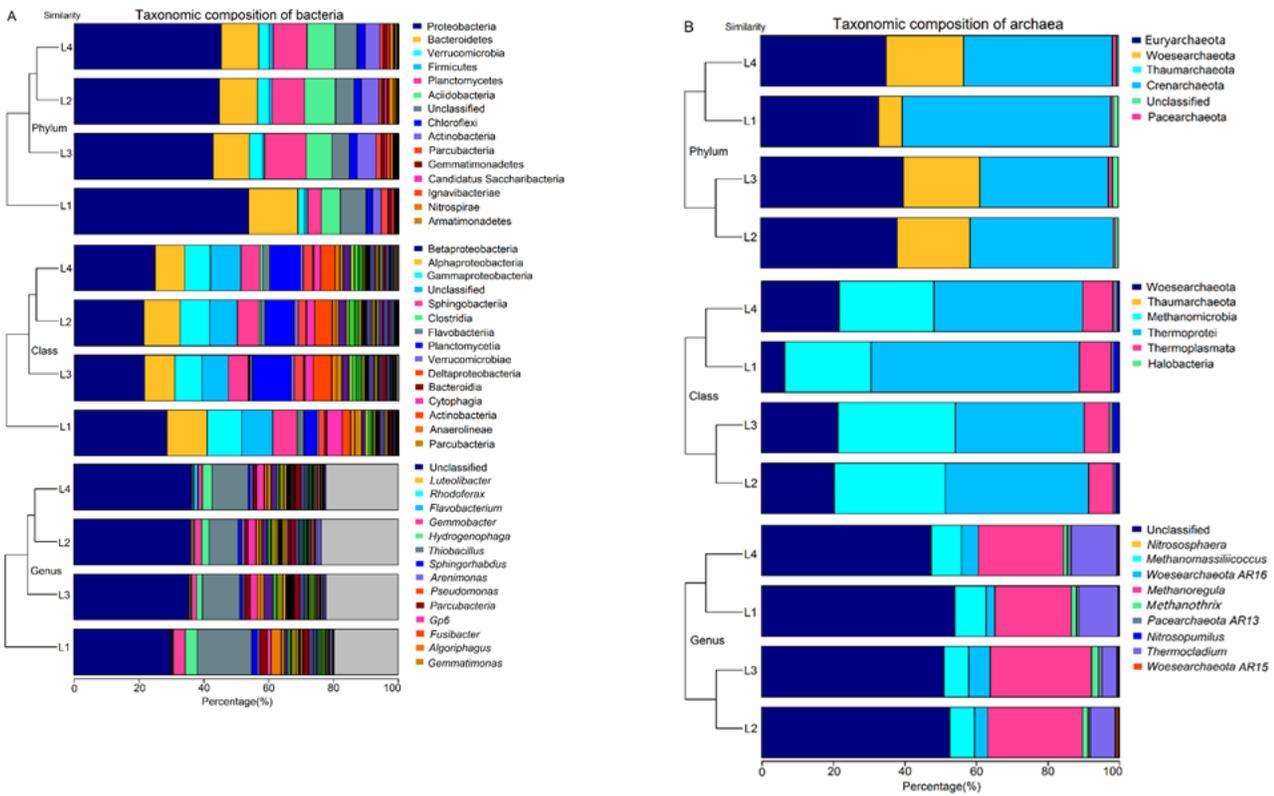


Figure 2
 Taxonomic classification and community clustering of LGL bacterial (A) and archaeal (B) communities. The top, middle, and bottom panels show taxonomic distributions at the phylum, class, and genus levels, respectively.

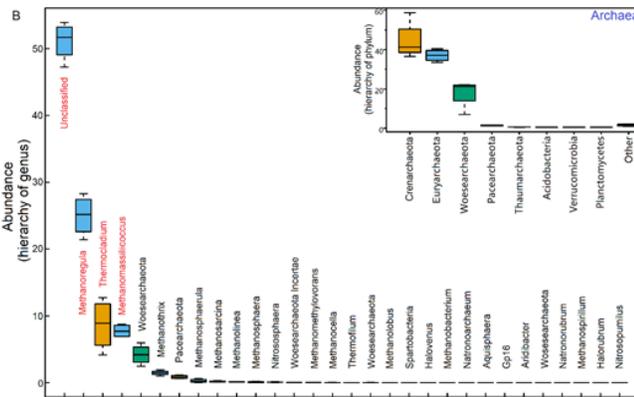
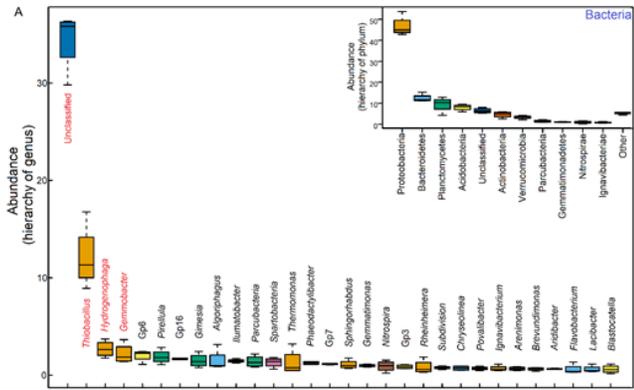


Figure 3
 Boxplots showing the distributions of dominant bacterial (A) and archaeal (B) genera abundances among LGL sites. Different phyla are indicated by different colors (as indicated in the top right corner), while genera within the same phylum are indicated with the same colors. Dominant taxa are indicated in red font.

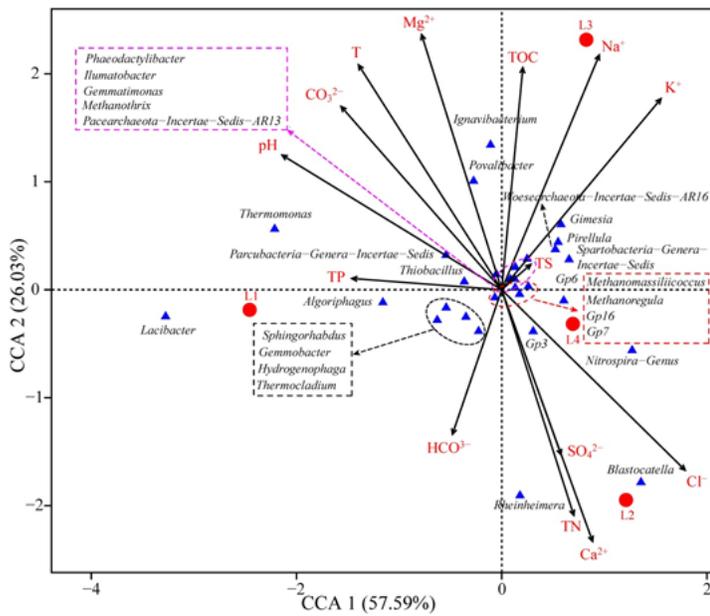


Figure 4

Canonical correspondence analysis (CCA) showing the relationships among dominant genera and hydrochemical variables in LGL. Samples are indicated by red circles, while genera are indicated by blue triangles, and environmental variables are indicated by arrows. TS, TOC, TN, and TP correspond to total salinity, total organic carbon, total nitrogen, and total phosphate, respectively.

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