Wang *et al. Annals of Microbiology* (2022) 72:33
https://doi.org/10.1186/s13213-022-01691-7

Annals of Microbiology

UNIVERSITÀ DEGLI STUDI DI MILANO

ORIGINAL ARTICLE

Open Access

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

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Abstract

Purpose: Langaco Lake (LGL) is a soda lake located at an altitude of 4548 m in the Qinghai-Tibet Plateau in China. LGL exhibits unique hydrochemical characteristics among soda lakes, but little is known about the microbial diversity of LGL and the microbial interactions with environmental factors.

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

Results: The high-throughput sequencing of 16S rRNA genes revealed that the bacterial diversity in LGL consisted of 327 genera in 24 phyla (4871 operational taxonomic units (OTUs); Shannon index values of 5.20–6.07), with a significantly higher diversity than that of the *Archaea* (eight phyla and 29 genera comprising 1008 OTUs; Shannon index values of 2.98–3.30). The bacterial communities were dominated by *Proteobacteria* (relative abundances of 42.79–53.70%), 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%). Furthermore, the archaeal communities were dominated by *Crenarchaeota* (35.97–58.29%), *Euryarchaeota* (33.02–39.89%), and *Woesearchaeota* (6.50–21.57%). The dominant bacterial genus was *Thiobacillus* (8.92–16.78%), and its abundances were most strongly correlated with the total phosphorus (TP) content, pH value, CO_3^{2-} concentration, and temperature. The most abundant archaeal genus was *Methanoregula* (21.40–28.29%), and its abundances were the most highly correlated with the total organic carbon (TOC) content, total salinity (TS), and K^+ and Na^+ concentrations.

Conclusions: The results of this study provide valuable insights for developing a more comprehensive understanding of microbial diversity in these unique carbonate alkaline environments, as well as a better understanding of the microbial resources on the Qinghai-Tibet Plateau.

Keywords: Community diversity, Soda lake, High-altitude lake, Langaco Lake, Qinghai-Tibet Plateau

Introduction

Soda lakes are exceptional among aquatic ecosystems because they simultaneously exhibit high productivity rates (i.e., carbon and the large amount of dissolved organic matter produced by photosynthesis) and high pH values (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 owing to evaporation. In addition, high concentrations of other salts can also accumulate, especially sodium chloride, leading to the formation of alkaline saline lakes (Namsaraev et al. 2015). Soda lakes have likely massively contributed to global primary productivity in Earth's

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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 CO_2. Furthermore, diverse microbial populations are abundant in soda lakes (Lanzen et al. 2013). Many regional examples of soda lakes have been reported, including in the East African Rift Zone, the rain-shadowed regions in California and Nevada, the Kulunda steppe in Russia, and on the Cariboo Plateau in Canada. Similarly, many microorganisms have been isolated from such lakes, including *Cyanobacteria*, chemolithoautotrophic sulfide oxidizing bacteria, sulfate-reducing/nitrifying/denitrifying bacteria, aerobic heterotrophic bacteria, fermentative bacteria, *methanotrophs*, and *methanogens* (Zorz et al. 2019; Tiodjio et al. 2014).

The underlying basaltic rocks in some areas of these plateaus originate from Miocene and Pliocene volcanic activity and have led to ideal conditions for the formation of soda lakes owing to the low solubility of calcium and magnesium in the basaltic formations. Thus, soda lakes are important components of terrestrial ecosystems, contain abundant microbial resources, and play critical roles in geochemical cycles by promoting material exchange, such as those in the Qinghai-Tibet Plateau in China (Xing et al. 2019). Soda lakes are widely distributed in terrestrial plateau ecosystems with extreme environmental conditions, such as the persistence of extreme droughts, 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 soda 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 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 of samples from natural environments. These methodologies have become increasingly used to determine differences in microbial community diversity and structure among environments, thereby helping to reveal the interactions among microorganisms in such environments, as well as their adaptions to specific environments (Paul et al. 2015). In this study, Illumina high-throughput sequencing analysis of community 16S rRNA genes was used to comprehensively investigate the bacterial and archaeal communities in LGL, and to explore the dominant genera in LGL and their associations with environmental factors. Therefore, the results of this study provide a theoretical framework for understanding the relationships among microorganisms and environments under alkaline conditions on plateaus.

Materials and methods

Sample sites and sample collection

Langaco Lake is located in the northwestern margin of the Tibetan Plateau (30°40′30.6″N, 81°18′32.3″E) in Pulan County in the Ngari Region at an altitude of 4548 m. LGL has an area of 256.2 km^2 and experiences a frigid semi-arid plateau climate (Mianping 1997). The lake is irregularly, slightly spoon-shaped. There are several islands exposed within the lake, and the terrain around the islands is very steep. The northern portion of the lake is a smaller open lake area that is connected to the open southern part by a narrow channel, while the center is flat (Wang et al. 2013). The lake has a sodium concentration of 106.24 mg/L, a total salinity of 1.00 mg/L, and a pH of 8.62 (Mianping 1997). The total area of the lake has decreased since the 1970s, especially in the northwestern region, while the temperatures have generally increased and precipitation has significantly decreased in this region (Dai 2020). Consequently, the lake water is primarily replenished by meltwater from the glaciers to the north (Wang et al. 2013).

Four samples were collected from LGL in mid-July 2018 from a sediment depth of 30–40 cm. These samples were mixtures of water and sediment (about 4 L total). The distance between any 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 the pH in situ. The filters were taken back to the laboratory on ice, while the water samples collected for physicochemical analysis were stored at 4°C.

Hydrochemical analyses

The water samples were filtered through a chemical-grade cellulose acetate membrane (pore size of 0.45 μm, Millipore, USA), and the physical and chemical properties of water samples were determined according to the general rules of analytical methods (JY/T020-1996). The

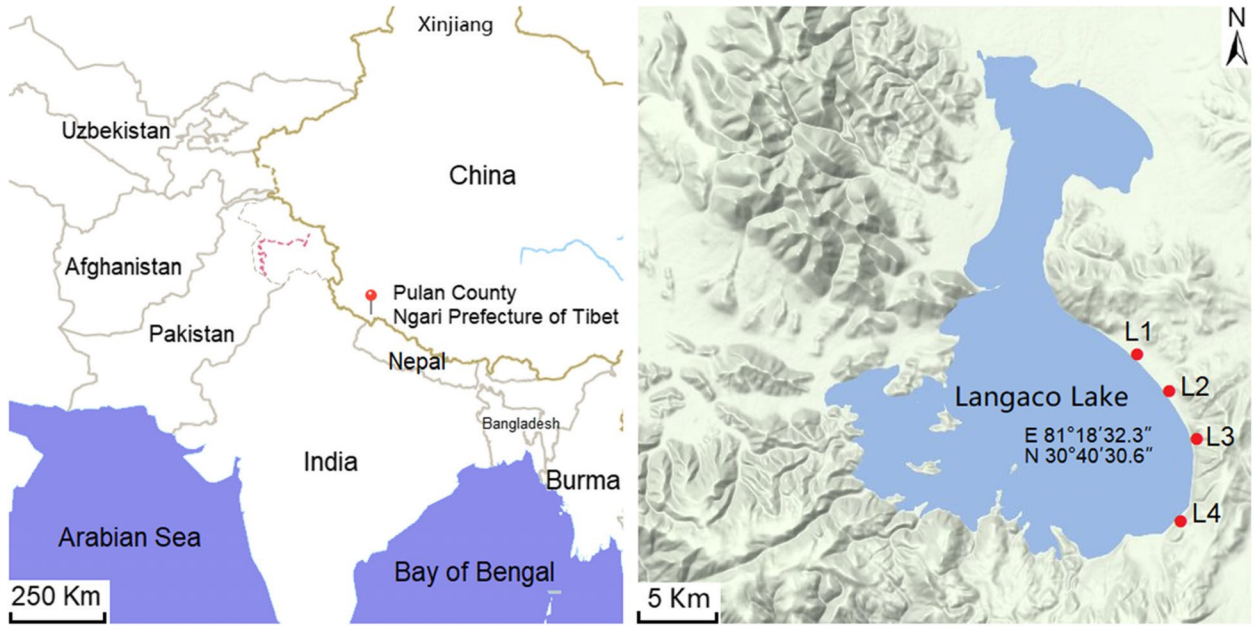

Fig. 1 Geographic location of Langaco Lake and the location of the four sampling sites in the lake. The map is sourced from Esri, Digital Globe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community

major cation concentrations (Na^+, K^+, Ca^{2+}, and Mg^{2+}) were measured using atomic absorption spectrometry (CE 3000 series spectrometer, Thermo Scientific, USA). The anion (Cl^- and SO_4^{2-}) concentrations were measured using an ion chromatograph (Dionex/ICS-6000, Thermo Scientific, USA). The concentrations of CO_3^{2-} and HCO_3^- were detected by titration. The total salinity (TS) was determined by the drying gravimetric method (HJ/T51-1999), while the total organic carbon (TOC) and total nitrogen (TN) were detected by the total organic carbon/total nitrogen analyzer (Multi N/C2100, Jena, Germany). Finally, ammonium molybdate spectrophotometry (GB11893-891) was used to determine the concentration of total phosphate (TP).

Microbial community DNA extraction and PCR amplification

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

To evaluate the microbial community's composition, the bacterial and archaeal 16S rRNA genes from the water DNA extracts were amplified using polymerase chain reaction (PCR) with domain-specific primers. The PCR amplifications of the V3–V4 hypervariable regions of the bacterial 16S rRNA genes were conducted with primers 341F (5′-ACTCCTACGGGAGCAGCA-3′) and 805R (5′-GGACTACHVGGGTWTCTAAT-3′) (Han et al. 2017). Similarly, the universal primers 349F (5′-ACGGGGYGCAGCAGGCGCGA-3′) and 806R (5′-GACTGGAGTTCCTTGGCACCCGAGAAT-3′) (Deng et al. 2012) were used to amplify the V3–V4 hypervariable regions of the archaeal 16S rRNA genes. The PCR mixtures (30 μL volume) consisted of 15 μL of 2×Taq master mixture (containing 0.1 U/μL Taq DNA polymerase EP0406 (Thermo Scientific, USA), 0.4 mM per dNTP, and 2×Taq buffer), 10–20 ng of community genomic DNA, 1 μL of each primer (10 μM concentrations), and 12 μL of ultrapure H_2O. PCRs were repeated in triplicate for each sample on a T100™ thermal cycler PCR system (Bio-RAD, USA). The PCR conditions were 95°C for 3 min, by 32 cycles of denaturation at 95°C for 30 s, annealing at 55°C for 30 s, extension at 72°C for 45 s, and extension at 72°C for 10 min. The amplified PCR fragments were purified using an Agencourt AMPure XP Kit (A63882, Beckman, USA), and then, they were quantified using a Qubit 2.0 DNA quantification Kit (InvitGen, USA). The 16S rRNA gene sequencing was conducted using the Illumina MiSeq 300PE platform (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 using the procedure described by 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). In addition, the Usearch (v.5.2.236) program (Edgar 2010) was also used to detect chimeric sequences by comparison against the SILVA (release 132; https://www.arb-silva.de/) and Ribosomal Database Project (RDP) (v.11.3; https://rdp.cme.msu.edu/misc/resources.jsp) databases. The taxonomic classification of the operational taxonomic units (OTUs) was conducted using the Quantitative Insights into Microbial Ecology (QIIME; V.1.8.0) pipeline, along with the RDP Bayesian classification method (v.2.12) and a 97% classification confidence level threshold (Wang et al. 2007; Caporaso et al. 2010).

The community alpha-diversity was calculated using the Mothur software package (v.1.30.1) (Schloss et al. 2009), including the abundance-based coverage estimation (ACE), terminal richness estimation (Chao1), Simpson index, Shannon-Weiner index, rarefaction analysis, and Good's coverage estimation. Venn diagrams were used to assess the numbers of shared and unique OTUs among the samples. The beta-diversity was measured based on the Bray-Curtis distances between the samples, and the overall community differences were evaluated through a full linkage cluster analysis of the Bray-Curtis distances. Canonical correspondence analysis (CCA) was performed using the CCA function in the vegetarian R package, the community distance matrix, and the hydrochemical factors (Han et al. 2017). The variables that significantly explained the differences in the community composition were evaluated using permutation tests under a simplified model.

Taxonomic classification analysis

The relative abundances of the bacterial and archaeal communities were summarized at the phylum, class, and genus levels. The R software suite was used to construct boxplots of the relative taxonomic abundances among the samples, while the GraPhlAn software package (Asnicar et al. 2015); and the online Tree Of Life interactive tool (ITOL, v.3.2.1) (Letunic and Bork 2015) were used for phylogenetic tree visualization of the 100 most abundant OTUs.

Sequence accession numbers

The raw 16S rRNA gene sequences were deposited in the National Center for Biotechnology Information (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. Its major water cations were Na^+ (105.90–106.62 mg/L) and Ca^{2+} (84.24–85.80 mg/L), and its major anions were HCO_3^- (472.34–476.17 mg/L) and CO_3^{2-} (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 TOC, TN, and TP values were 6.21, 104.21, and 1.91 mg/L, respectively (Table 1).

Bacterial and archaeal community diversity

The bacterial and archaeal community compositions of the four LGL samples were investigated through high-throughput Illumina sequencing of the community 16S rRNA genes (Table 2). A total of 5879 OTUs were recovered, including 4871 bacterial OTUs and 1008 archaeal OTUs. Among the bacterial samples, the richness and diversity of samples L2 and L4 were slightly higher than those of samples L1 and L3. The observed bacterial community OTU richness, Shannon index, and ACE values were 1025–1293, 5.20–6.07, and 2148.23–2376.17, respectively. In contrast, the 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 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^-	$SO4^{2-}$	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

TOC total organic carbon, *TN* total nitrogen, *TP* total phosphorus, *TS* total salinity

Table 2 Operational taxonomic unit (OTU) richness and diversity measures from Langaco Lake communities

Sample-ID	Sequence reads	Richness and diversity metric					
		OTUs	Shannon index	ACE index	Chao1 index	Coverage	Simpson index
Bacteria							
L1	9377	1025	5.20	2148.23	1668.18	0.95	0.03
L2	9424	1287	6.07	2359.52	1990.62	0.94	0.01
L3	9356	1266	5.92	2243.30	1912.93	0.94	0.01
L4	9354	1293	5.96	2376.17	1995.66	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

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). The total numbers of unique bacterial genera observed in the four samples were 219 (L1), 270 (L2), 291 (L3), and 271 (L4), while the numbers of 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 bacterial and archaeal communities. The most abundant sequences were selected as representative sequences of the OTUs, and the relative abundances of the bacterial and archaeal populations among the communities were compared at the phylum, class, and genus taxonomic levels (Fig. 2 and S2). In addition, community clustering based on community compositional differences revealed that there were three different bacterial community groups, with L3 and L1 each comprising a single community, and L4 and L2 forming a community together. In contrast, the archaeal communities included two groups with L4 and L1 comprising one group and L3 and L2 comprising the second group. Overall, 24 bacterial phyla were detected in the LGL microbial communities, including 50 classes and 327 genera. Additionally, eight archaeal phyla were detected that comprised nine classes and 29 genera (Tables S1, S2, and S3).

At the phylum level, the predominant bacteria (>1% relative abundance) were *Proteobacteria* (relative abundance of 42.79–53.70%), *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 of the samples were *Crenarchaeota* (35.97–58.29%), *Euryarchaeota* (33.02–39.89%), *Woesearchaeota* (6.50–21.57%), and *Pacearchaeota* (0.63–1.13%). The relative abundances of *Woesearchaeota* were greater than 20% in samples L2a, L3a, and L4a, but it was 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 the 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* (1.07–2.85%), *Parcubacteria-genera-incertae-sedis* (0.83–2.16%), *Ilumatobacter* (1.25–1.70%), *Sphingorhabdus* (0.69–1.74%), *Phaeodactylibacter* (1.07–1.40%), and *acidobacterial* groups GP16, GP6, GP3, and GP7 (0.67–2.42%). In addition to the above bacterial genera, other *Bacteria* exhibited higher abundances within the 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 L2 and L4. The dominant archaeal genera were *Methanoregula* (21.40–28.29%), *Thermocladium* (4.17–12.75%), *Methanomassiliicoccus* (6.92–8.77%), the *Woesearchaeota incertae-sedis-AR16* group (2.46–5.96%), and *Methanothrix* (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.

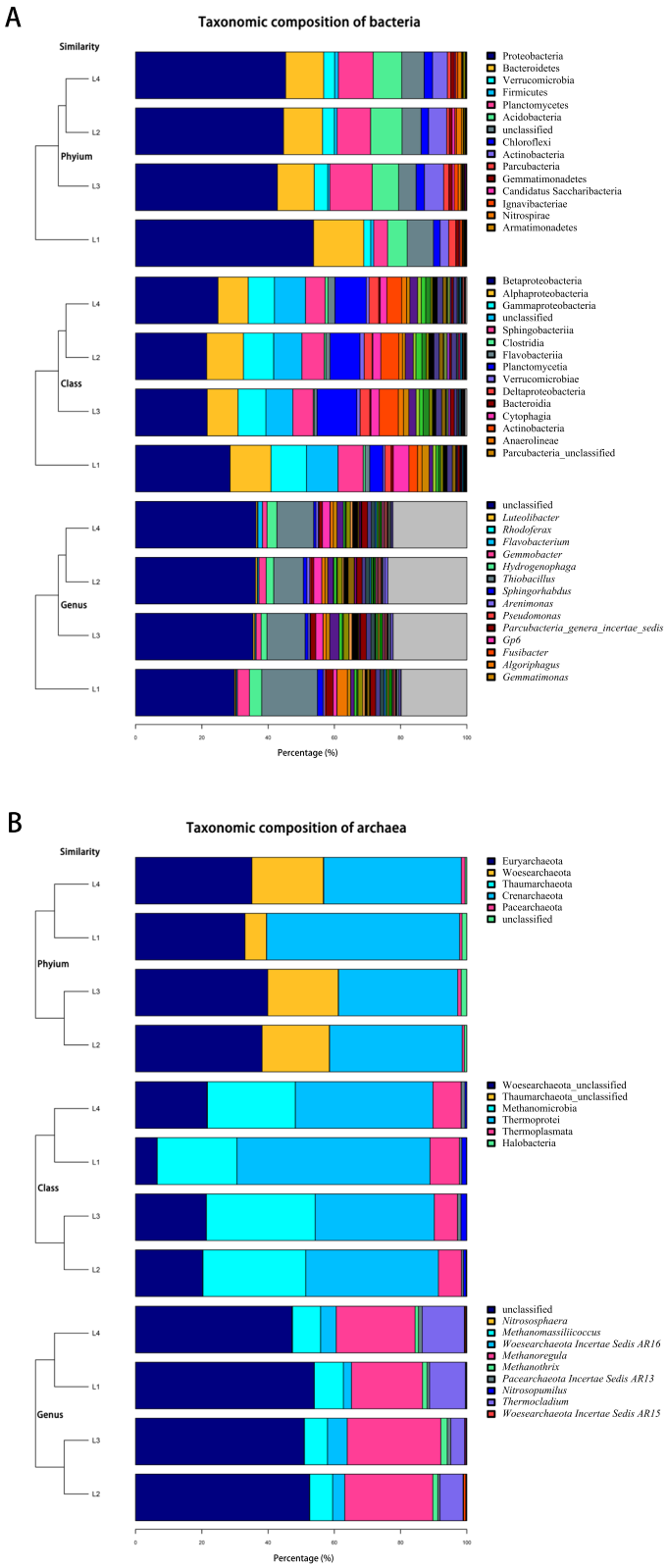

Fig. 2 Taxonomic classification and community clustering of LGL bacterial (**A**) and archaeal (**B**) communities. The top, middle, and bottom panels show taxonomic distributions at the phylum, class, and genus levels, respectively

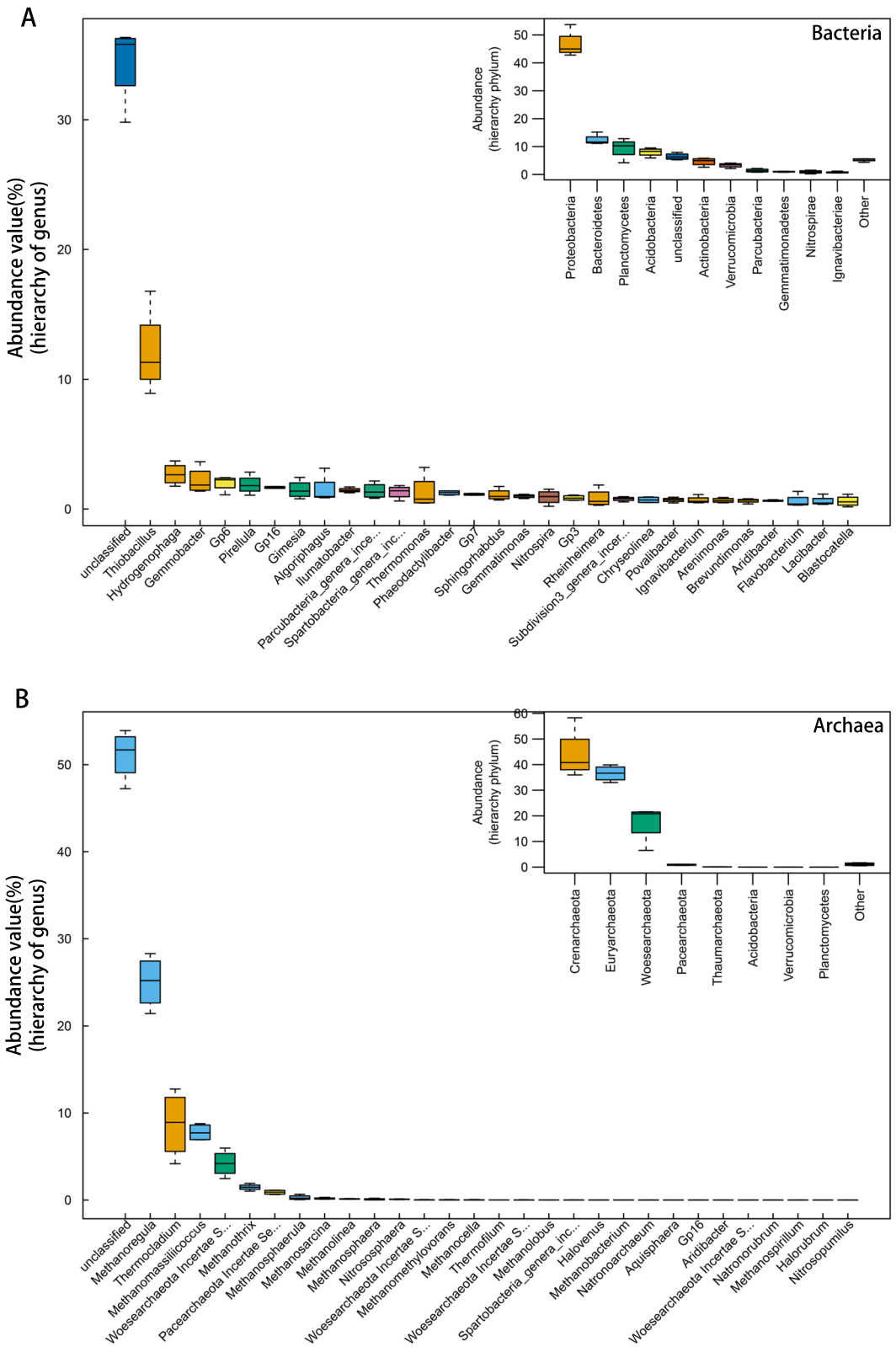

Fig. 3 Boxplots showing the distributions of dominant bacterial (**A**) and archaeal (**B**) genera abundances among LGL sites. Different phyla are indicated by different colors (as indicated in the top right corner), while genera within the same phylum are indicated with the same colors. Dominant taxa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

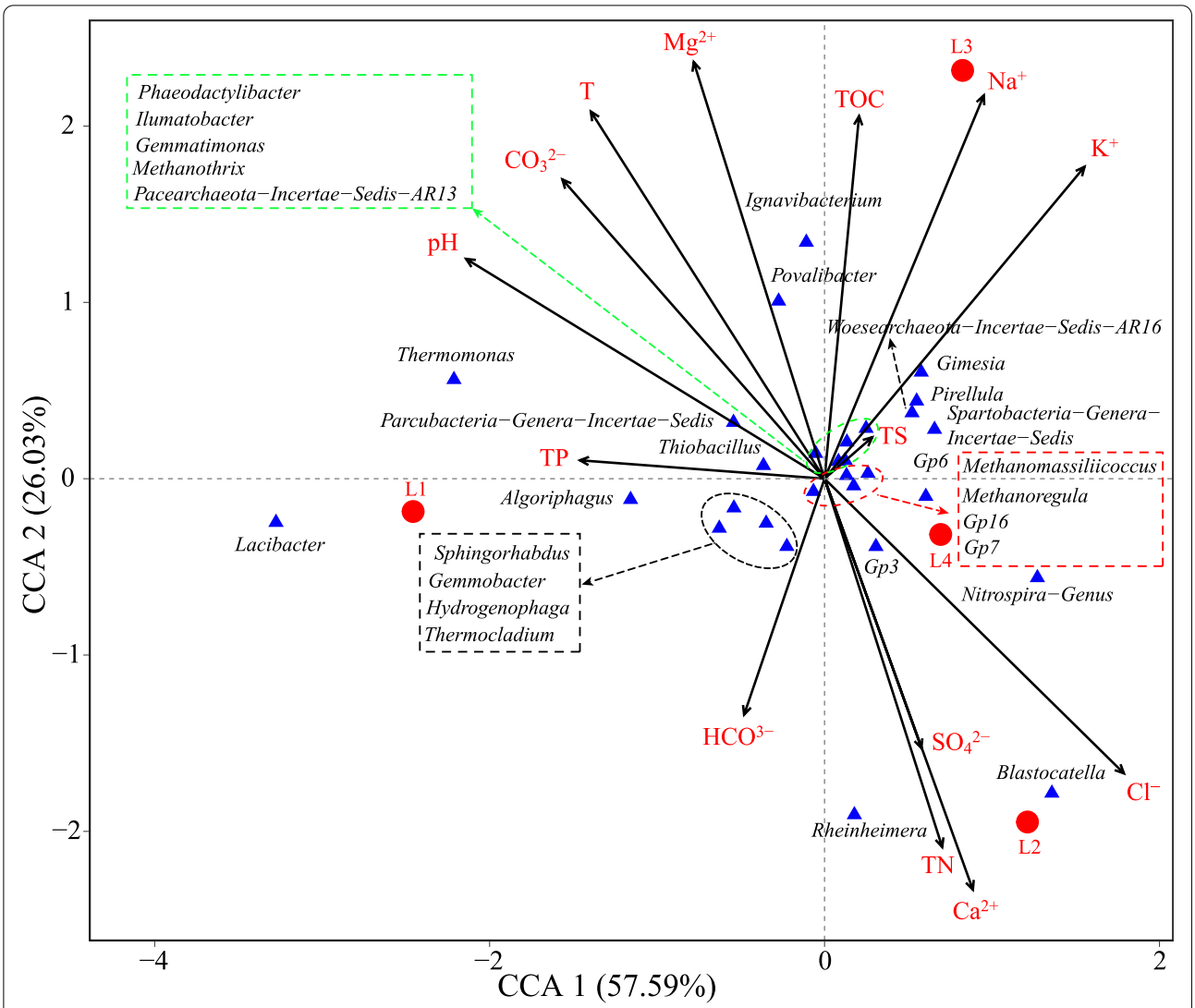

Fig. 4 Canonical correspondence analysis (CCA) showing the relationships among dominant genera and hydrochemical variables in LGL. Samples are indicated by red circles, while genera are indicated by blue triangles, and environmental variables are indicated by arrows. TS, TOC, TN, and TP correspond to total salinity, total organic carbon, total nitrogen, and total phosphate, respectively

Associations between environmental factors and dominant genera

The differences in the abundances among the samples were investigated (Fig. 3) while considering the twelve and nine most abundant bacterial and archaeal phyla. The most abundant (relative abundances of > 1%) bacterial genera among the four samples 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 *Methanomassiliicoccus*.

CCA was conducted to evaluate the relationships among community structures and environmental parameters, yielding numerous associations between the overall community composition and several environmental parameters. Consequently, the environmental parameters were analyzed in the context of the representative genera (Fig. 4). The abundances of the dominant bacterial genus *Thiobacillus* were most strongly correlated with the TP content, followed by the pH, CO_3^{2-} concentration, and temperature. The abundances of the next most dominant bacterial genera (*Hydrogenophaga* and *Gemmobacter*) were associated with the TP and HCO_3^- content. The moderately abundant (1.50–4.00%) bacterial genera *Thermomonas*,

Algoriphagus, and *Sphingorhabdus* in sample L1 were correlated with the TP content, pH, and HCO_3^- concentration. The abundances of the *Parcubacteria genera incertae sedis* and group GP16 were strongly correlated with the pH and Cl^- concentration, respectively. The less abundant (1.5–2.5%) genera *Rheinheimera*, *Nitrospira*, and Gp6 in sample L2 were significantly correlated with the TN content, as well as the Ca^{2+}, SO_4^{2-}, and Cl^- concentrations. Furthermore, the abundances of the genera *Pirellula*, *Gimesia*, and *Spartobacteria genera incertae sedis* were related to the K^+, Na^+, and TOC concentrations and the TS in samples L3 and L4. The abundances of the dominant (>20%) archaeal genera *Methanoregula*, *Methanothrix*, *Methanomassiliicoccus*, *Pacearchaeota incertae sedis-AR13*, and *Woesearchaeota incertae sedis-AR16* were highly correlated with the TOC, K^+, and Na^+ contents and TS. In addition, the *Thermocladium* abundances were particularly highly associated with the HCO_3^- concentration.

Discussion

Characteristics of the LGL soda lake

Soda lakes are globally distributed and are predominantly found in arid and semi-arid environments, including Hungary, Egypt, America, and China (Namsaraev et al. 2015; Rojas et al. 2018). Soda lakes have recently been classified into soda and soda-salt types based on differences in their carbonate and bicarbonate contents. Soda types are those that are dominated by sodium, bicarbonate, and carbonate ions, while soda-salt types are those dominated by sodium ions, as well as other ions besides bicarbonate/carbonate (Boros and Kolpakova 2018). Soda lakes generally form in hydrologically closed lake basins, and their water has high Na^+ concentrations, in addition to high CO_3^{2-} (0.023–63.20 g/L) or HCO_3^- (0.11–20.40 g/L) concentrations (Table 3); however, their water may contain abundant and variable concentrations of SO_4^{2-}, K^+, and/or Cl^- (Boros and Kolpakova 2018; Schagerl and Renaut 2016). LGL is an example of an extreme soda lake with a lower ionic content, with CO_3^{2-}, and HCO_3^- concentrations of 76.30 and 475.56 mg/L, respectively. Soda lake water also usually contains high concentrations of Cl^- (73,000 mg/L) (Schagerl and Renaut 2016). In contrast, LGL has a Cl^- concentration of 55 mg/L. Thus, LGL is considered a weakly ionic soda lake. The formation of alkalinity is closely related to the hydrology, climate, and regional geology, which ultimately affect the diversity of microorganisms within these systems. The pH of the water in LGL was 8.62; whereas it 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 values) provide unique environments for microbial communities (Table 3). Thus, a predominance of carbonate and bicarbonate (in addition to the associated alkalinity) are hallmarks of soda lake ecosystems, and diversity has been observed in their hydrochemical characteristics.

Bacterial and archaeal diversity within LGL

Despite the extreme environments within soda lakes, they have high levels of microbial diversity. This is evinced by the 327 and 29 bacterial and archaeal genera, respectively, within LGL, which corresponded to 4871 and 1008 16S rRNA gene OTUs, respectively. Under the condition of using the same sequencing method, LGL exhibited a higher diversity than other soda lakes that have been previously investigated including four alkaline soda lakes in the Cariboo Plateau (bacterial OTUs: 1662), Doroninskoe Lake (bacterial OTUs: 2254), and Lonar Lake (bacterial OTUs: 1,568) (Table 3). Furthermore, the Shannon diversity index values calculated in this study (*Bacteria*: 5.20–6.07; *Archaea*: 2.98–3.30) were higher than previously calculated for soda lakes, including Doroninskoe Lake (*Bacteria*: 1.49–3.46) and five soda lakes in the Badain Jaran Desert (*Bacteria*: 1.15–3.24) (Table 3). Thus, the microbial diversity of LGL appears to be considerably higher than those of 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 the 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) (Rojas et al. 2018; Matyugina et al. 2018). The most dominant bacterial phylum was *Proteobacteria* (42.79–53.70%), followed by *Bacteroidetes* (11.13–15.18%), *Planctomycetes* (4.20–12.82%), and *Acidobacteria* (5.91–9.50%). *Proteobacteria*, *Bacteroidetes*, and *Firmicutes* are typically the dominant bacterial taxa in soda lakes (Paul et al. 2015; Mesbah et al. 2007). The unique presence of sodium carbonate may be one of the factors affecting the differences in the microbial diversity in LGL compared to other soda lakes. As was previously mentioned, *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 reported to be 29.5% in Lonar Lake (India) (Paul et al. 2015), which is significantly lower than that observed in LGL and also in the Soda Lake of Inner Mongolia (Namsaraev et al. 2015). In addition, the

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 *Bacteria*	Dominant *Archaea*	Ref.
Badong, Baxi, Xiaoshazao, Zhongnao, and Sangenjilin Lakes (China)[i]	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	*Spiribacter*, *Halomonas*, *Burkholderia*	*Halobellus*, *Halohasta*, *Halorubrum*	(Aguirre-Garrido et al. 2016)
Khilganta, Dabasa Nur, Solenoye, Gurvany Nuur, *ect* (Mongolia)[i]	No	No	8.10–10.4	1.8–360.0	0.09–63.2	0.21–7.49	No	No	*Geitlerinema*, *Coleofasciculus*	No	(Banda et al. 2019)
Zabuye Lake (China)[i]	31°23′	84°04′	9.00	230.0	11.20	11.20	127[g]	No	*Pseudomonas*, *Alkalimonas*, *Nitrincola*	No	(Vavourakis et al. 2016)
Isabel Lake (Mexico)[i]	21°52′	W 105°54′	9.00–10.00	94.5	No	No	2799[b, d, e]	1.15–5.48	*Salegentibacter*, *Formosa*, *Muricauda*	No	(Paul et al. 2015)
Bitter–1 Lake (Russia)	51°67′	79°91′	9.60–10.50	85.0	60.00	No	No	No	*Ectothiorhodospira*	No	(Martin 2011)
Beseka, Arenguadi, Chitu, Abijata, and Shalla Lakes (Ethiopian)[i]	7°40′–8°90′	38°42′–39°87′	9.60–10.40	2.1–58.0	No	No	2704[a]	2.30–4.70	*Ectothiorhodospira*, *Rhodobaca*, *Rhodobacter*	*Thaumarchaeota*, *Methanocalculus*	(Biderre-Petit et al. 2019)
Doroninskoe Lake (Russia)[i]	51°14′	112°14′	9.93–10.09	22.2–36.0	5.73	6.62	2254[a]	1.49–3.46	*Serratia*, *Achromobacter*, *Rhodobaca*	*Pacearchaeota*, *Woesearchaeota*[h]	(Paul et al. 2015)
Van Lake (Turkey)	38°38′	42°57′	9.70–9.80	23.0	3.50	2.40	No	No	*Proteobacteria*, *Firmicutes*[h]	No	(Wang et al. 2013)
Qinghai Lake (China)[i]	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	*Loktanella*, *Pseudarthrobacter*, *Nitrincola*	*Woesearchaeota*, *Methanosarcina*	(Wang et al. 2007)
Mono Lake (USA)[i]	37°56′	W119°13′	9.40–10.0	10.8–11.2	18.90	11.20	No	0.85–4.86	*Rhodoplanes*, *Spiribacter*	*Methanocalculus*, *Methanosarcina*	(Matyugina et al. 2018)
Lonar Lake (India)[i]	19°97′–19°98′	76°50′–76°51′	9.50–10.00	1.7–3.9	0.17–0.26	No	1568[a]	6.82–10.93	*Proteobacteria*, *Actinobacteria*, *Firmicutes*	No	(Asnicar et al. 2015)
Namco Lake (China)[i]	30°30′–30°35′	90°16′–91°03′	9.21	1.1	0.023	0.55	83[f]	No	*Polynucleobacter*, *Rhodoferax*, *Acinetobacter*	No	(Dai 2020)
Langaco Lake (China)[i]	30°67′	81°30′	8.62	0.001	0.076	0.48	B:4871; A:1008[a]	2.98–6.07	*Thiobacillus*, *Hydrogenophaga*, *Gemmobacter*	*Methanoregula*, *Thermocladium*	This study

Table 3 (continued)

Lake name	N	E	pH	Salinity (g/L)	CO_3^{2-} (g/L)	HCO_3^- (g/L)	OTU	Shannon	Dominant *Bacteria*	Dominant *Archaea*	Ref.
Last Chance, Probe, Deer, and Goodenough Lake (Canada)[i]	51°32′–51°45′	121°25′–121° 64′	10.10–10.70	No	3.42–16.44	2.07–20.4	1662[c]	No	*Gemmatirosa*, *Rhodobacter*	No	(Boros and Kolpakova 2018)
Nyos Lake (Cameroon)[i]	06°26′	10°18′	6.90–7.30	No	No	0.11–2.37	61[d]	1.50–2.70	*Firmicutes*, *Actinobacteria*[h]	*Thaumacheota*, *Euryarchaeota*[h]	(Caporaso et al. 2010)
Soda lake in Hoh Xil **B**asin (China)[i]	35°11′–35°41′	92°12′–93°29′	7.64–8.01	No	No	No	289[a]	9.16	*Bacillus*, *Psychrobacter*	No	(Chen et al. 2015)
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*[h]	*Halobacteriales*, *Methanosarcinales*[h]	(Deng et al. 2019)

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

[h] The dominant genus has not been described in the literature

[i] The lake located in the plateau

abundances of some bacterial groups were lower than those observed in LGL, including *Bacteroidetes* (8.25%) and *Planctomycetes* (6.8%) (Banda et al. 2019). *Planctomycetes* and *Acidobacteria* have rarely been 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 the environmental factors, which is most likely due to the long residence time of this 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. Similarly, *Alphaproteobacteria* are typically the dominant proteobacterial class among soda lakes (Szabó et al. 2017); however, the *Gammaproteobacteria* class was dominant in LGL. Thus, the LGL bacterial communities exhibit unique compositional differences relative to other soda lakes.

The archaeal diversity in LGL was much lower than that observed for the bacterial communities, but it was unique among soda lakes. A total of eight archaeal phyla were detected in LGL comprising nine classes and 29 genera. The LGL archaeal communities exhibited a higher level of diversity than those of other soda lakes. For example, only three archaeal phyla were detected in Doroninskoe Lake (Matyugina et al. 2018). Interestingly, the dominant archaeal phyla also vary with the 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* are important contributors to global organic carbon cycling (Vavourakis et al. 2016). The relative abundances of the *Archaea* in LGL also varied compared to those in 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 had very low levels (Rojas et al. 2018) in other soda lakes. Similar to the levels observed in LGL, *Euryarchaeota* (35.15%) has been reported to be the most abundant phylum in the soda lakes in the Badain Jaran Desert (Banda et al. 2019). Nevertheless, the overall microbial diversity in LGL was higher than those reported 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, the unclassified *Bacteria* and *Archaea* accounted for a considerable proportion of the LGL communities, contributing 12.67% and 18.31% to the overall communities, respectively. The unclassified *Bacteria* included groups GP6, GP16, GP7, GP3, and GP4 of the *Acidobacteria* and the unclassified *Parcubacteria*. *Acidobacteria* are one of the most abundant phyla in soils, and their OTU richness, phylogenetic diversity, and community composition are significantly related to the pH of the soil (Wei et al. 2018). Previous studies have reported that human disturbances and activities 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 environmental factors, especially the external water supply.

Dominant Bacterial Genera Unique to LGL

The most dominant bacterial genus in 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 reported to be negatively correlated with the sedimentary sulfate and total sulfur contents (Duan et al. 2020). *Thiobacillus* can be one of the most dominant groups in freshwater sediments, and it can be used as a biomarker to predict the intensity of subsequent blooms in such environments (Chen et al. 2015). Furthermore, *Thiobacillus* has also been detected in some typical habitat types (e.g., soil, water, and duck and fish farm) (Yi et al. 2021) and has been observed to be 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. It is one of the primary iron-reducing bacterial taxa in lake sediments, and its abundances and diversity are closely related to the degree of water eutrophication (Fan et al. 2018). Through these processes, *Thiobacillus* participates in the redox cycling of heavy metals by producing ferrous iron and accelerating the oxidation of ferric ion in localized areas, such as anaerobic sedimentary environments with high concentrations of heavy metals, in which they contribute to a large proportion of the 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 under S^{2-} enrichment conditions when organic carbon is scarce (Pang et al. 2021). Our CCA analysis of the LGL communities also revealed that the *Thiobacillus* abundances were most highly correlated with the variations in the temperature, pH, and CO_3^{2-} and TP concentrations. Thus, the association of *Thiobacillus* with these factors warrants further investigation.

Dominant archaeal genera unique to LGL

Members of the archaeal family *Methanoregulaceae*, have been isolated in samples from various habitats, including acidic peat bogs, anaerobic organic waste treatment reactors, submerged 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%), even though it has low sodium requirements (Rosenberg et al. 2014). Furthermore, the CCA revealed that the *Methanoregula* abundances were significantly correlated with the TOC content and TS, in addition to the K^+ and Na^+ concentrations. *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 that it has a 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* has been detected at different temperatures in wetland soils near alkali lakes (Deng et al. 2019), but it has not been detected in most soda lakes, because it has an optimal pH growth range of 4.50 to 5.55 (Rosenberg et al. 2014). Finally, *Methanoregula* has also been reported to be 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 microbial adaptation to carbonate habitats. Here, high-throughput 16S rRNA gene sequencing was conducted to comprehensively characterize the bacterial and archaeal communities of LGL. The bacterial diversity in LGL was significantly higher than the archaeal diversity and was mostly dominated by *Proteobacteria*, *Bacteroidetes*, and *Planctomycetes*; while the dominant archaeal groups were *Crenarchaeota* and *Euryarchaeota*. The presence and high abundances of *Crenarchaeota* was uniquely different compared to other soda lakes. Moreover, the characteristics and metabolism of *Thiobacillus* provide more possibilities for bacterial diversity, and their abundances were most strongly correlated with the pH, temperature, and CO_3^{2-} and TP concentrations. The high abundance of *Methanoregula* in LGL was also a unique observation for the LGL archaeal communities, and their abundances were correlated with the TOC content, TS, and K^+ and Na^+ concentrations. Finally, the minimal anthropogenic effects on LGL and its extreme environmental conditions provide a unique context for understanding the interactions between microorganisms and extreme soda environments, while also furthering our understanding of microbial resources on the Tibetan Plateau.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s13213-022-01691-7.

Additional file 1: Fig. S1. Venn diagram of OTU sample distribution of LGL bacterial (A) and archaeal (B) communities. **Fig. S2.** Taxonomic and phylogenetic tree representations of bacterial taxa (A) and archaeal taxa (B) in LGL sample. **Table S1.** Phylum abundance percentage (%) of *Bacteria* and *Archaea* in LGL. **Table S2.** Class abundance percentage (%) of *Bacteria* and *Archaea* in LGL. **Table S3.** Genus abundance percentage (%) of *Bacteria* and *Archaea* in LGL.

Authors' contributions

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

Funding

This research was supported by the National Natural Science Foundation of China (grant numbers 21967018), the Applied Basic Research Program of Qinghai Province (grant numbers 2022ZJ771), and the Team's Research Program of Microbial Resources in Salt-lakes in the Qinghai-Tibetan Plateau grant number 2018KYT1. We thank LetPub (www.letpub.com) for providing linguistic assistance during the preparation of this manuscript.

Availability of data and materials

We have not reproduced any pre-published information/material for this study.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

Received: 1 April 2022 Accepted: 18 August 2022
Published online: 10 September 2022

References

Aguirre-Garrido JF, Ramirez-Saad HC, Toro N, Martinez-Abarca F (2016) Bacterial Diversity in the Soda Saline Crater Lake from Isabel Island, Mexico. Microb Ecol 71(1):68–77. https://doi.org/10.1007/s00248-015-0676-6

Asnicar F, Weingart G, Tickle TL, Huttenhower C, Segata N (2015) Compact graphical representation of phylogenetic data and metadata with GraPhlAn. PeerJ. 3:e1029. https://doi.org/10.7717/peerj.1029

Banda JF, Lu Y, Hao C, Pei L, Du Z, Zhang Y (2019) The Effects of Salinity and pH on Microbial Community Diversity and Distribution Pattern in the Brines of Soda Lakes in Badain Jaran Desert, China. Geomicrobiol J 37(1):1–12. https://doi.org/10.1080/01490451.2019.1654568

Biderre-Petit C, Taib N, Gardon H, Hochart C, Debroas D (2019) New insights into the pelagic microorganisms involved in the methane cycle in the meromictic Lake Pavin through metagenomics. FEMS Microbiol Ecol 95(3). https://doi.org/10.1093/femsec/fiy183

Boros E, Kolpakova M (2018) A review of the defining chemical properties of soda lakes and pans: An assessment on a large geographic scale of Eurasian inland saline surface waters. PLoS One 13(8):e0202205. https://doi.org/10.1371/journal.pone.0202205

Caporaso JG, Kuczynski J, Stombaugh J, Bittinger K, Bushman FD, Costello EK, Fierer N, Peña AG, Goodrich JK, Gordon JI, Huttley GA, Kelley ST, Knights D, Koenig JE, Ley RE, Lozupone CA, McDonald D, Muegge BD, Pirrung M, Reeder J, Sevinsky JR, Turnbaugh PJ, Walters WA, Widmann J, Yatsunenko T, Zaneveld J, Knight R (2010) QIIME allows analysis of high-throughput community sequencing data. Nat Methods 7(5):335–336. https://doi.org/10.1038/nmeth.f.303

Chen N, Yang JS, Qu JH, Li HF, Liu WJ, Li BZ, Wang ET, Yuan HL (2015) Sediment prokaryote communities in different sites of eutrophic Lake Taihu and their interactions with environmental factors. World J Microbiol Biotechnol 31(6):883–896. https://doi.org/10.1007/s11274-015-1842-1

Dai R (2020) Study on the variation of surface area of Lake Mansarovar and Lake Rakshastal from 1972 to 2018. 4(02):19–26. https://doi.org/10.16249/j.cnki.2096-4617.2020.02.004

Deng Y, Liu P, Conrad R (2019) Effect of temperature on the microbial community responsible for methane production in alkaline NamCo wetland soil. Soil Biol Biochem 132:69–79. https://doi.org/10.1016/j.soilbio.2019.01.024

Deng Y, Zhang Y, Gao Y, Li D, Liu R, Liu M, Zhang H, Hu B, Yu T, Yang M (2012) Microbial community compositional analysis for series reactors treating high level antibiotic wastewater. Environ Sci Technol 46(2):795–801. https://doi.org/10.1021/es2025998

Ding YR, Li DL, Zhang YM, Yang F, Wang LM (2017) The structure and the diversity of sediment microbialcommunities in Gehu Lake. Acta Sci Circumst 37(05):1649–1656

Duan JL, Sun JW, Ji MM, Ma Y, Cui ZT, Tian RK, Xu PC, Sun WL, Yuan XZ (2020) Indicatory bacteria and chemical composition related to sulfur distribution in the river-lake systems. Microbiol Res 236(126453). https://doi.org/10.1016/j.micres.2020.126453

Edgar R (2010) Search and clustering orders of magnitude faster than BLAST. Bioinformatics. 26(19):2460–2461. https://doi.org/10.1093/bioinformatics/btq461

Edgar RC, Haas BJ, Clemente JC, Quince C, Knight R (2011) UCHIME improves sensitivity and speed of chimera detection. Bioinformatics. 27(16):2194–2200. https://doi.org/10.1093/bioinformatics/btr381

Fan YY, Li BB, Yang ZC, Cheng YY, Liu DF, Yu HQ (2018) Abundance and diversity of iron reducing bacteria communities in the sediments of a heavily polluted freshwater lake. Appl Microbiol Biotechnol 102(24):10791–10801

Han R, Zhang X, Liu J, Long Q, Chen L, Liu D, Zhu D (2017) Microbial community structure and diversity within hypersaline Keke Salt Lake environments. Can J Microbiol 63(11):895–908. https://doi.org/10.1139/cjm-2016-0773

Jiang H, Dong H, Yu B, Liu X, Li Y, Ji S, Zhang CL (2007) Microbial response to salinity change in Lake Chaka, a hypersaline lake on Tibetan plateau. Environ Microbiol 9(10):2603–2621. https://doi.org/10.1111/j.1462-2920.2007.01377.x

Lanzen A, Simachew A, Gessesse A, Chmolowska D, Jonassen I, Ovreas L (2013) Surprising prokaryotic and eukaryotic diversity, community structure and biogeography of Ethiopian soda lakes. PLoS One 8(8):e72577. https://doi.org/10.1371/journal.pone.0072577

Letunic I, Bork P (2015) Interactive tree of life (iTOL) v3: an online tool for the display and annotation of phylogenetic and other trees. Nucleic Acids Res 44:W242–W245. https://doi.org/10.1093/nar/gkw290

Liu X, Yao T, Kang S, Jiao N, Zeng Y, Liu Y (2010) Bacterial Community of the Largest Oligosaline Lake, Namco on the Tibetan Plateau. Geomicrobiol J 27(8):669–682. https://doi.org/10.1080/01490450903528000

Martin M (2011) Cutadapt removes adapter sequences from highthroughput sequencing reads. EMBnet J 17:10–12

Matyugina E, Belkova N, Borzenko S (2018) Structure and diversity dynamics of microbial communities at day and night: investigation of meromictic Lake Doroninskoe, Transbaikalia, Russia. J Oceanol Limnol 36(6):1978–1992

Mesbah NM, Abou-El-Ela SH, Wiegel J (2007) Novel and Unexpected Prokaryotic Diversity in Water and Sediments of the Alkaline, Hypersaline Lakes of the Wadi An Natrun, Egypt. Microb Ecol 54(4):598–617. https://doi.org/10.1007/s00248-006-9193-y

Mianping Z (1997) An Introduction to Saline Lakes on the Qinghai-Tibet Plateau [M]. Springer, Dordrecht

Namsaraev ZB, Zaitseva SV, Gorlenko VM, Kozyreva LP, Namsaraev BB (2015) Microbial processes and factors controlling their activities in alkaline lakes of the Mongolian plateau. Chin J Oceanol Limnol 33(6):1391–1401. https://doi.org/10.1007/s00343-015-4373-6

Pang Y, Wang J, Li S, Ji G (2021) Long-term sulfide input enhances chemoautotrophic denitrification rather than DNRA in freshwater lake sediments. Environ Pollut 270:116201. https://doi.org/10.1016/J.ENVPOL.2020.116201

Paul D, Kumbhare SV, Mhatre SS, Chowdhury SP, Shetty SA, Marathe NP (2015) Exploration of Microbial Diversity and Community Structure of Lonar Lake: The Only Hypersaline Meteorite Crater Lake within Basalt Rock. Front Microbiol 6:1553. https://doi.org/10.3389/fmicb.2015.01553

Qin H, Cui L, Cao X, Lv Q, Chen T (2019) Evaluation of the Human Interference on the Microbial Diversity of Poyang Lake Using High-Throughput Sequencing Analyses. Int J Environ Res Public Health 16(21):4218. https://doi.org/10.3390/ijerph16214218

Rojas P, Rodríguez N, de la Fuente V, Sánchez-Mata D, Amils R, Sanz JL (2018) Microbial diversity associated to the anaerobic sediments of a soda lake (Mono Lake, CA). Can J Microbiol 64(6). https://doi.org/10.1139/cjm-2017-0657

Rosenberg E et al (2014) The Prokaryotes – Other Major Lineages of Bacteria and the Archaea, pp 253–258. https://doi.org/10.1007/978-3-642-38954-2_5

Savvichev A, Rusanov I, Dvornikov Y (2021) The water column of the Yamal tundra lakes as a microbial filter preventing methane emission. Biogeosciences. 18(9):2791–2807. https://doi.org/10.5194/BG-18-2791-2021

Schagerl M, Renaut RW (2016) Dipping into the Soda Lakes of East Africa. Soda Lakes of East Africa, pp 3–24

Schloss PD, Westcott SL, Ryabin T, Hall JR, Hartmann M, Hollister EB, Lesniewski RA, Oakley BB, Parks DH, Robinson CJ, Sahl JW, Stres B, Thallinger GG, Van Horn DJ, Weber CF (2009) Introducing mothur: open-source, platform-independent, community-supported software for describing and comparing microbial communities. Appl Environ Microbiol 75(23):7537–7541. https://doi.org/10.1128/AEM.01541-09

Sherysheva NG, Rakitina TA, Povetkina LP (2020) Taxonomic composition of the bacteriobenthos of the littoral and pelagic zones of the Lake Kandry-Kul in June and September 2010 (Natural Park "Kandry-Kul", Republic of Bashkortostan, Russia). IOP Conference Series: Earth and Environmental Science, Togljatti, Samara Region, p 607. https://doi.org/10.1088/1755-1315/607/1/012022

Stoeva MK, Aris-Brosou S, Chételat J, Hintelmann H, Pelletier P, Poulain AJ (2014) Microbial community structure in lake and wetland sediments from a high Arctic polar desert revealed by targeted transcriptomics. PLoS One 9(3):e89531. https://doi.org/10.1371/journal.pone.0089531

Szabó A, Korponai K, Kerepesi C, Somogyi B, Vörös L, Bartha D, Márialigeti K, Felföldi T (2017) Soda pans of the Pannonian steppe harbor unique bacterial communities adapted to multiple extreme conditions. Extremophiles. 21(3):639–649. https://doi.org/10.1007/s00792-017-0932-4

Tiodjio RE, Sakatoku A, Nakamura A, Tanaka D, Fantong WY, Tchakam KB (2014) Bacterial and archaeal communities in Lake Nyos (Cameroon, Central Africa). Sci Rep 4:6151. https://doi.org/10.1038/srep06151

Vavourakis CD, Ghai R, Rodriguez-Valera F, Sorokin DY, Tringe SG, Hugenholtz P, Muyzer G (2016) Metagenomic Insights into the Uncultured Diversity and Physiology of Microbes in Four Hypersaline Soda Lake Brines. Front Microbiol 7:211

Wang JB, Peng P, Ma QF, Zhu LP (2013) Investigation of water depth, water quality and modern sedimentation rate in mapam yumco and la'ang co, Tibet. J Lake Sci 25(04):609–616

Wang Q, Garrity GM, Tiedje JM, Cole JR (2007) Naive Bayesian classifier for rapid assignment of rRNA sequences into the new bacterial taxonomy. Appl Environ Microbiol 73(16):5261–5267

Wei Z, Li Y, Jiang W, Liao X (2018) Diversity of acidobacteria in rhizosphere soils ofcommon trees in Wuxi. Chin J Ecol 37(09):2649–2656. https://doi.org/10.13292/j.1000-4890.201809.025

Xing R, Gao Q-b, Zhang F-q, Wang J-l, Chen S-l (2019) Bacterial community in cold and alkaline environments of Hoh Xil basin in Qinghai–Tibet Plateau and isolation of potential sources of microbiota. Ann Microbiol 69(5):567–576. https://doi.org/10.1007/s13213-019-01447-w

Yi Y, Lin C, Wang W, Song J (2021) Habitat and seasonal variations in bacterial community structure and diversity in sediments of a Shallow lake. Ecol Indic 120. https://doi.org/10.1016/J.ECOLIND.2020.106959
Zorz JK, Sharp C, Kleiner M, Gordon PMK, Pon RT, Dong X (2019) A shared core microbiome in soda lakes separated by large distances. Nat Commun 10(1):4230. https://doi.org/10.1038/s41467-019-12195-5

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