Archives of Microbiology (2022) 204:317
https://doi.org/10.1007/s00203-022-02925-7

ORIGINAL PAPER

Composition and key-influencing factors of bacterial communities active in sulfur cycling of soda lake sediments

Xiangyuan Li[1,2] · Maohua Yang[1] · Tingzhen Mu[1] · Delu Miao[1] · Jinlong Liu[2] · Jianmin Xing[1]

Received: 2 December 2021 / Revised: 20 January 2022 / Accepted: 15 April 2022 / Published online: 14 May 2022

Abstract

Bacteria are important participants in sulfur cycle of the extremely haloalkaline environment, e.g. soda lake. The effects of physicochemical factors on the composition of sulfide-oxidizing bacteria (SOB) and sulfate-reducing bacteria (SRB) in soda lake have remained elusive. Here, we surveyed the community structure of total bacteria, SOB and SRB based on 16S rRNA, *sox*B and *dsr*B gene sequencing, respectively, in five soda lakes with different physicochemical factors. The results showed that the dominant bacteria belonged to the phyla Proteobacteria, Bacteroidetes, Halanaerobiaeota, Firmicutes and Actinobacteria. SOB and SRB were widely distributed in lakes with different physicochemical characteristics, and the community composition were different. In general, salinity and inorganic nitrogen sources (NH_4^+-N, NO_3^--N) were the most significant factors. Specifically, the communities of SOB, mainly including *Thioalkalivibrio*, *Burkholderia*, *Paracoccus*, *Bradyrhizobium*, and *Hydrogenophaga* genera, were remarkably influenced by the levels of NH_4^+-N and salinity. Yet, for SRB communities, including *Desulfurivibrio*, *Candidatus Electrothrix*, *Desulfonatronospira*, *Desulfonatronum*, *Desulfonatronovibrio*, *Desulfonatronobacter* and so on, the most significant determinants were salinity and NO_3^--N. Besides, *Rhodoplanes* played a significant role in the interaction between SOB and SRB. From our results, the knowledge regarding the community structures of SOB and SRB in extremely haloalkaline environment was extended.

Keywords Soda lake · Sulfur cycle · Haloalkaliphiles · Sulfide-oxidizing bacteria · Sulfate-reducing bacteria

Introduction

Soda lake is a unique ecosystem with both high salinity and high pH, in which the total salt concentration exceeds 50 g/L, and the pH value can reach 10 (Schagerl and Renaut 2016; Furian et al. 2013). Despite these double extreme conditions, most lakes have high productivity and contain fully functional microbial systems. Due to the presence of high concentration of inorganic sulfur compounds, microbial sulfur cycle is one of the most active cycles in soda lake, which provides sufficient energy for microorganisms to cope with costly life at double extreme conditions (Sorokin 2017; Sorokin et al. 2015).

Haloalkalophilic sulfur oxidizing bacteria (SOB) participate in the oxidation part of the sulfur cycle in soda lake. The majority of detected SOB in soda lakes belong to Gammaproteobacteria and Alphaproteobacteria classes, which can be divided into the following three categories: chemoautotrophic (colorless) sulfur bacteria, purple sulfur bacteria, and purple non-sulfur bacteria (Berben 2019). Up to now, the following four genera of chemolithotrophic SOB have been found in soda lakes: *Thioalkalimicrobium*, *Thioalkalispira*, *Thioalkalivibrio* and *Thioalkalibacter*. They can utilize reduced sulfur compounds, such as sulfide, polysulfide, thiosulfate, polythionates, and elemental sulfur as e-donor (Sorokin 2017; Sorokin et al. 2015). The purple sulfur bacteria mainly include canoxygenic phototrophs in soda lakes,

Communicated by Erko Stackebrandt.

✉ Maohua Yang
mhyang@ipe.ac.cn

Jinlong Liu
jlliu18@126.com

Jianmin Xing
jmxing@ipe.ac.cn

[1] CAS Key Laboratory of Green Process and Engineering, Institute of Process Engineering, Chinese Academy of Sciences, Beijing 100190, China

[2] College of Bioscience and Bioengineering, Hebei University of Science and Technology, Shijiazhuang 050018, Hebei, China

such as the genera *Ecthothiorhodospira*, *Halorhodospira*, *Thiorhodospira*, *Thioalkalicoccus*, and *Ectothiorhodosinus* (Gorlenko 2007). The sulfate-reducing bacteria (SRB) found in the anoxic layer of soda lake sediments belong to the Deltaproteobacteria class (Sorokin 2017; Sorokin et al. 2015). Members of the deltaproteobacterial haloalkaliphilic genera *Desulfonatronum*, *Desulfonatronovibrio*, *Desulfonatronospira* and *Desulfohalophilus* have been detected in soda lakes. They can grow either by oxidizing hydrogen, formate or small organic molecules using sulfate, thiosulfate or sulfite as electron acceptor, or by thiosulfate or sulfite disproportionation (Sorokin et al. 2011a, b).

Previous studies have shown that the structure of SOB and SRB communities could be affected by the environmental factors. For instance, Edwardson et al. compared the composition of microbial communities along the redox gradient of Mono Lake, California, USA at five depths. They found that the prokaryotic community was dominated by bacteria and the community diversity increased with depth (Edwardson and Hollibaugh 2018). In petroleum reservoirs, the SRB and SOB communities were closely associated with temperature of a reservoir, pH of formation brine, and sulfate concentration (Tian et al. 2017). And several scholars demonstrated that environmental parameters, such as depth, dissolved inorganic nitrogen concentrations, and the sedimentary dynamic environment, can significantly influence the community structures of total bacteria, SOB and SRB in sea (Zhang et al. 2017). However, the effects of physicochemical characteristics on the composition of SOB and SRB in haloalkaline environment have remained elusive. Therefore, the present study aimed to assess the diversity and structures of bacteria associated with sulfur cycle in soda lakes with different physicochemical characteristics in Inner Mongolia, China (Fig. 1).

Due to the high phylogenetic diversity of SOB and SRB, we used high-throughput sequencing of 16 s rRNA gene coupled to clone libraries of the functional genes to determine the community structures of SOB and SRB. The soxB gene, encoding sulfate thiohydrolase, a key enzyme of the Sox pathway, had been detected in sulfur oxidizers irrespective of the pathway, and thus it was selected as the biomarker of SOB in our study (Zhang et al. 2017; Meyer et al. 2007). The *dsr*B gene is the main subunit of isomerization (bi) sulfite reductase (DsrB) which is highly essential for the reduction of sulfite to sulfide. This gene had been used as a phylogenetic marker for SRB identification (Giloteaux et al. 2013; Gao et al. 2015). In this study, the combination of 16S rRNA gene and functional genes sequencing would improve our ability to analyze these microbial populations in detail.

Materials and methods

Sites description and sampling

The sampling sites were located in Ordos, Inner Mongolia Autonomous Region, China. This region has a temperate continental climate with an annual average temperature of 5.3–8.7 °C. The annual rainfall in this region is 170–450 mm, which primarily falls from July to September.

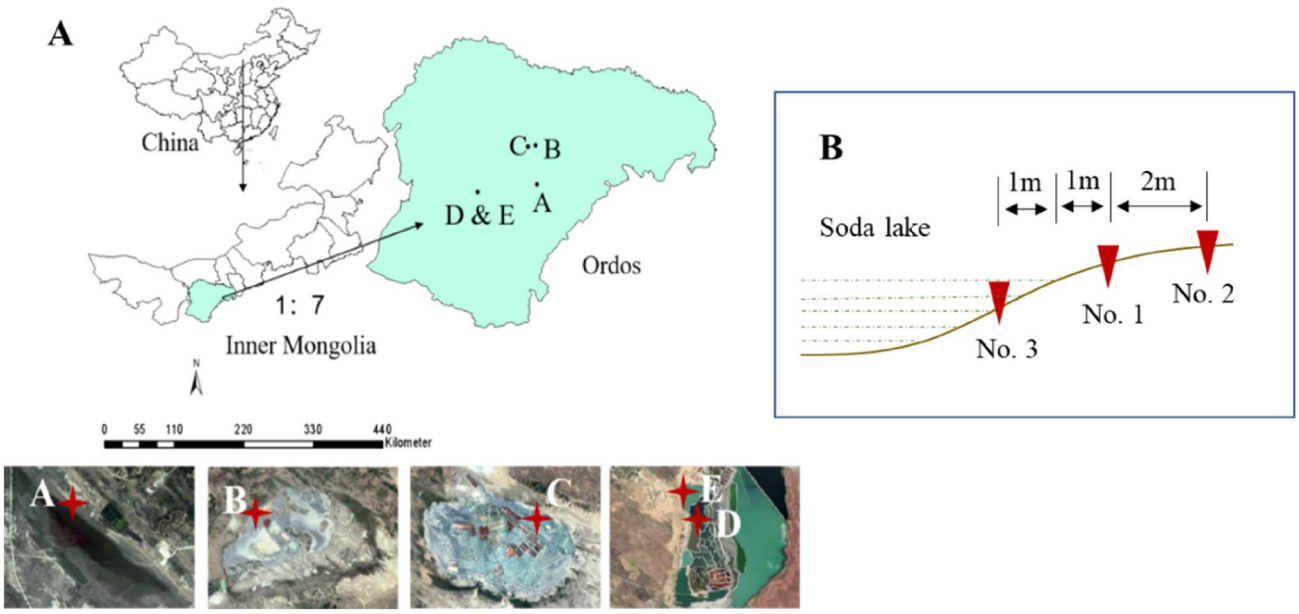

Fig. 1 **A** Locations of the soda lakes. **A** Haole Baoji Nao, **B** Xiaohu, **C** Bayin Naoer, **D** Hama Rige Tainao Er, Salt Pond No. 1, **E** Hama Rige Tainao Er, Salt Pond No. 2; **B** Locations of three sampling points for each lake

The evaporation is remarkable, with annual evaporation of 2000–3000 mm (Xu et al. 2010). The details of five sampling sites are as follows: soda lake A (Haole Baoji Nao; E108°54′07″, N38°73′49″), soda lake B (Xiaohu; E108°52′69″, N39°39′83″), soda lake C (Bayin Naoer; E108°46′30″, N39°38′86″), soda lake D (Hama Rige Tainao Er; Salt Pond No. 1, E108°03′16″, N39°09′07″), and soda lake E (Hama Rige Tainao Er; Salt Pond No. 2, E108°03′16″, N39°09′07″). Sediment samples (50 cm^3) of five soda lakes were collected at July 25, 2019. For each lake, three sediment samples (depth of 0–10 cm) were taken, as shown in Fig. 1A. All the samples were placed in sterile plastic bags and were transported to the laboratory in a portable ice bag at 4 ℃. In the laboratory, the sediment samples were divided into two parts: one part was for subsequent microbial DNA extraction, and the other was for physicochemical tests (Rastogi et al. 2009).

Chemical analyses of soda lake sediments

To measure the sediment pH and conductivity, the sediment was suspended in ultrapure water at a ratio of 1:5 (w/w) and then the suspension was vortexed. Following the centrifugation at 21,500 ×*g* for 1 min at 4 °C, pH and electrical conductivity of the supernatant were measured with a multiparameter probe (Mettler Toledo Delta 320, Switzerland). The concentrations of NO_3^- and NH_4^+ were analyzed by spectrophotometry (Perkin-Elmer Lambda 35, USA) (Sheibley et al. 2003). The concentrations of SO_4^{2-}, Cl^-, and Na^+ were determined by ion chromatography (DIONEX ICS-1000) using a cation-exchange column (DIONEX ICs-1000) and an anion-exchange column (Shim-Pack IC-C3). The sediment was dried at 105 °C until the weight became constant to calculate the moisture concentration (MC). After that, the dried sediment was heated in a muffle furnace at 550 °C for 5 h to measure the total organic matter (TOM) (Santisteban et al. 2004). All analyses were performed in triplicate, and the mean values with standard deviations (SD) were given.

Genome extraction and high-throughput sequencing of 16S rRNA, *sox*B, and *dsr*B genes

Total DNA was extracted from sediment samples using FastDNA® SPIN Kit for Soil (MP Biomedicals, Santa Ana, CA, USA) according to manufacturer's instructions. The DNA extract was checked on 1% agarose gel, while concentration and purity of DNA were detected with NanoDrop 2000 UV–vis spectrophotometer (Thermo Fisher Scientific, Waltham, MA, USA). V3-V4 hypervariable region of 16S rRNA, *sox*B gene and *dsr*B gene were amplified by an ABI GeneAmp® 9700 PCR thermocycler (ABI, CA, USA). The primer sequences are shown in Table 1 (Tian et al. 2017). The PCR product was extracted from 2% agarose gel and then purified using the AxyPrep DNA Gel Extraction Kit (Axygen Biosciences, Union City, CA, USA) according to the manufacturer's instructions and quantified by using Quantus™ Fluorometer (Promega Corp., Madison, WI, USA). Purified amplicons were pooled in an equimolar and paired-end sequenced on an Illumina MiSeq PE300 platform (Illumina, San Diego, CA, USA) according to the standard protocols provided by Majorbio Bio-Pharm Technology Co. Ltd. (Shanghai, China). The raw reads were deposited into the NCBI Sequence Read Archive (SRA) database (Accession Number: PRJNA678019).

Table 1 Primer sequences used for PCR

Gene	Primer sequence
16S rRNA	338F: (5'- ACTCCTACGGGAGGCAGCAG-3') 806R: (5'- GGACTACHVGGGTWTCTAAT-3')
*sox*B	710F:(5'-ATCGGYCAGGCYTTYCCSTA-3') 1184R:(5'-MAVGTGCCGTTGAARTTGC-3')
*dsr*B	DSRp2060F:(5'-CAACATCGTYCAYACCCAGGG-3') DSR4R:(5'-GTGTAGCAGTTACCGCA-3')

Sequence analysis of the 16S rRNA, *sox*B, and *dsr*B genes

Microbiome bioinformatics were performed with QIIME2 2019.4C (Bokulich et al. 2018) with slight modification according to the official tutorials (https://docs.qiime2.org/2019.4/tutorials/). Briefly, raw sequence data were demultiplexed using the demux plugin following by primers cutting with cutadapt plugin (Martin 2011). Sequences were then merged, quality filtered and dereplicated using functions of fastq_mergepairs, fastq_filter and derep fullength in Vsearch plugen. All the unique sequences were then clustered at 98% (via cluster_size) followed by chimera removing (via uchime_denovo). At last, the non_chimera sequences were re_clustered at 97% to generate OTU representative sequences and OTU table. Non-singleton amplicon sequence variants (OTUs) were aligned with mafft (Katoh et al. 2002) and used to construct a phylogeny with fasttree2 (Price et al. 2009). Alpha-diversity metrics Chao1, Shannon, Simpson, Pielou's evenness and Good's coverage were estimated using the diversity plugin. SOB and SRB samples were rarefied to 2293 and 707 sequences per sample, respectively. Taxonomy was assigned to OTUs using the classify-sklearn naïve Bayes taxonomy classifier in feature-classifier plugin (Bokulich et al. 2018) against the SILVA Release 132 and NCBI Database (Koljalg et al. 2013).

Bioinformatics and statistical analysis

Sequence data analyses were mainly performed using QIIME2 and R packages (v3.2.0). The taxonomy

compositions and abundances were visualized using MEGAN (Koljalg et al. 2013) and GraPhlAn software (Asnicar et al. 2015). The abundance comparison among groups at the phylum and genus levels was performed by Metastats analysis (White et al. 2009) and then visualized as a histogram. R programming language (Ihaka and Gentleman 1996) was used to analyze and draw Heatmap graphs, and Gephi 0.9.2 (Bastian et al. 2009) was employed to analyze and draw microbial interaction networks. SPSS 21.0 software (IBM, Armonk, NY, USA) was used for correlation analysis via Spearman's correlation analysis. The redundancy analysis (RDA) was carried out by Canoco 5 software.

Results

Physicochemical characteristics of five soda lakes

The physicochemical parameters of the samples collected from five soda lakes were significantly different (Table 2). The salinity (Na^+) of the samples ranged from 7.99 g/L to 68.45 g/L. The salinity (Na^+) was as high as 60.00 g/L and 68.45 g/L in samples of lakes B and D, respectively, while it was medium in samples of lakes C and E and very low in lake A (7.99 g/L), which were consistent with the conductivity data of water samples. In the samples, CO_3^{2-}, Cl^- and SO_4^{2-} were the main anions, and their concentrations were positively correlated with salinity (Na^+), which were significantly higher than those of freshwater lakes. The color of water samples of lakes B and D was pink, and other lakes were colorless. The pink lake could be explained by dense blooms of halophilic microorganism, which synthesized lots of carotenoid to adapt to the environment of low dissolved oxygen and high light intensity (Grant and Sorokin 2011).

Nitrogen content and total organic matter were also considered (Table 2). There were significant differences in concentrations of NH_4^+-N and NO_3^--N ($P < 0.05$, $n = 3$), in which the NH_4^+-N concentration in the samples of lake A was obviously higher than that in other lakes, and the NO_3^--N concentration in the samples of lake B was markedly higher. The total organic matter (TOM) of the three sampling points in the same lake was significantly different, but no obvious regularity was found. The pH of sediment samples was between 9.0 and 10.0. There was no significant difference in moisture content (MC) of sediment samples in the five lakes.

Bacteria diversity in sediment samples

High-throughput sequencing sample description and alpha-diversity index of total bacteria (16S rRNA), SOB (*sox*B gene), and SRB (*dsr*B gene) in sediment samples were shown in Supplementary Table 1. The coverage of the sequencing libraries of all samples is over 96%, most of which reached over 99%, which could reflect the microbial community in each sample. Shannon index and Chao index were calculated. The results showed that the diversity of bacteria in most samples had little difference. However, there were some exceptions. The diversity of SOB in A1 and D3 samples and SRB in A3 sample was significantly lower than that in other samples. Table 3 summarized the correlation between diversity index and physicochemical characteristics of the samples. In all the samples, the α-diversity index of total bacteria, SOB and SRB was highly correlated with the salinity ($Na^+/SO_4^{2-}/Cl^-$) and concentration of NO_3^--N,

Table 2 Physicochemical parameters of sediment samples from five soda lakes

Sample	pH	SO_4^{2-}(g/L)	Cl^- (g/L)	Na^+(g/L)	NO_3^--N (mg/kg)	NH_4^+-N (mg/kg)	MC (%)	TOM (mg/kg)
A1	9.22 (±0.03)	0.54 (±0.01)	1.63 (±0.08)	8.28 (±0.06)	2.85 (±0.10)	15.14 (±0.09)	25.21 (±0.06)	40.92 (±0.16)
A2	9.63 (±0.12)	0.68 (±0.03)	1.36 (±0.18)	8.00 (±0.22)	2.17 (±0.03)	6.79 (±0.11)	14.40 (±0.06)	9.86 (±0.11)
A3	9.33 (±0.33)	0.61 (±0.01)	1.70 (±0.10)	7.99 (±0.09)	8.40 (±0.09)	19.28 (±0.14)	23.50 (±0.11)	14.28 (±0.03)
B1	9.69 (±0.23)	11.16 (±0.04)	52.16 (±0.06)	58.65 (±0.11)	6.55 (±0.02)	4.10 (±0.06)	14.97 (±0.03)	28.53 (±0.06)
B2	9.49 (±0.13)	9.23 (±0.11)	55.34 (±0.06)	60.00 (±0.03)	20.02 (±0.01)	6.32 (±0.14)	21.44 (±0.04)	72.01 (±0.09)
B3	9.57 (±0.07)	13.12 (±0.24)	53.44 (±0.06)	59.15 (±0.19)	20.35 (±0.02)	5.65 (±0.18)	11.51 (±0.02)	4.38 (±0.03)
C1	9.36 (±0.02)	7.03 (±0.05)	15.43 (±0.03)	28.29 (±0.07)	4.02 (±0.06)	0.13 (±0.10)	10.94 (±0.23)	4.74 (±0.17)
C2	9.05 (±0.01)	5.93 (±0.09)	13.34 (±0.03)	25.20 (±0.45)	5.03 (±0.03)	0.13 (±0.03)	12.07 (±0.22)	23.08 (±0.01)
C3	9.35 (±0.09)	7.71(±0.12)	17.81 (±0.03)	29.92 (±0.17)	3.18 (±0.04)	0.13 (±0.03)	14.32 (±0.19)	107.93 (±0.02)
D1	10.05(±0.0)	23.03 (±0.03)	70.14 (±0.07)	66.47 (±0.08)	5.37 (±0.09)	0.31 (±0.05)	15.02 (±0.05)	28.22 (±0.02)
D2	9.12 (±0.02)	21.00 (±0.01)	65.17 (±0.07)	64.49 (±0.11)	0.1 (±0.12)	5.00 (±0.06)	9.75 (±0.17)	28.39 (±0.04)
D3	9.49 (±0.13)	25.03 (±0.17)	71.12 (±0.07)	68.45 (±0.23)	6.38 (±0.18)	0.17 (±0.01)	13.48 (±0.03)	14.60 (±0.11)
E1	9.79 (±0.12)	2.77 (±0.16)	5.55 (±0.13)	21.62 (±0.04)	1.50 (±0.12)	6.88 (±0.01)	17.31 (±0.08)	5.09 (±0.16)
E2	9.71 (±0.08)	2.13 (±0.06)	5.02 (±0.02)	20.01 (±0.05)	0.82 (±0.02)	3.95 (±0.03)	16.07 (±0.04)	54.90 (±0.09)
E3	9.38 (±0.10)	3.49 (±0.18)	6.15 (±0.14)	22.65 (±0.07)	5.20 (±0.04)	7.69 (±0.07)	17.30 (±0.06)	9.48 (±0.09)

Table 3 Correlation analysis between alpha-diversity and physicochemical parameters of soda lakes

Alpha-diversity	$Na^+/SO_4^{2-}/Cl^-$	NH_4^+-N	NO_3^--N	TOM	pH	MC
16 s rRNA						
Shannon index	− 0.491	− 0.269	− 0.636*	0.011	− 0.09	− 0.139
Chao index	− 0.633*	0.007	− 0.568	0.29	− 0.306	− 0.057
SOB						
Shannon index	− 0.316	− 0.280	− 0.361	− 0.032	− 0.088	− 0.286
Chao index	− 0.196	− 0.358	− 0.561	0.032	0.241	− 0.343
SRB						
Shannon index	0.302	− 0.364	− 0.650*	0.056	0.462	− 0.203
Chao index	0.151	− 0.203	− 0.727*	0.091	0.256	− 0.154

*Represents significant correlation, *$P < 0.05$

while it had a low correlation with other parameters. Shannon and Chao indexs of total bacteria and SOB were negatively correlated with the salinity and concentration of NO_3^--N. The Shannon and Chao indexs of SRB were positively correlated with salinity, while were negatively correlated with NO_3^--N concentration. These results indicated that the diversity of total bacteria and SOB decreased with the increase of salinity, especially the total bacteria. With the increase of NO_3^--N concentration, the diversity of total bacteria, SOB and SRB all decreased.

Total bacterial community in sediment samples

We compared and annotated sequencing results of 16 s rRNA and performed taxonomic analysis on phylum level (Fig. 2A). Total bacterial community mainly included phyla Proteobacteria (11.34–46.00%), Bacteroidetes (10.10–45.24%), Halanaerobiaeota (0.03–53.53%), Firmicutes (0.73–21.95%), Actinobacteria (0.75–16.31%) and Gemmatimonadetes (0.1–17.59%). The results showed that there were extreme differences in bacterial composition among the samples from different lakes. However, three samples from the same lake, with similar physicochemical parameters, had similar bacterial composition, which indicated that the physicochemical parameters were important factors affecting the bacterial composition. Meanwhile, it should be noted that the bacterial diversity of samples B and D with high salinity was lower than that of other samples, and the content of phyla Haloanaerobiaeota, which was famous for its salt tolerance and anaerobic characteristics, was significantly higher than that of other samples.

SOB community in sediment samples

Many microorganisms, including obligate anaerobes, facultative anaerobes and aerobic bacteria, play roles in sulfur oxidation (Ghosh and Dam 2009; Jung et al. 2010). Based on the results of high-throughput sequencing of *sox*B gene, the taxonomic composition of SOB was analyzed on genus level (Fig. 2B, Supplementary Fig. 1A), in which 26 SOB genera were detected, including *Thioalkalivibrio* (Gammaproteobacteria), *Burkholderia*, *Hydrogenophaga* (Betaproteobacteria), *Paracoccus*, *Bradyrhizobium* (Alphaproteobacteria) and so on. The compositions of SOB were different in the sediment samples of five soda lakes. However, the cluster of bacteria was basically consistent with the sampling sites, i.e., the samples from the same lake had similar composition and proportion of SOB. On the whole, based on the annotated results, the diversity of SOB was relatively low. *Thioalkalivibrio* was found dominant in the majority of samples with relative abundances ranging from 0.9 to 81.7%. *Burkholderia* was only detected in the sediment samples of lakes A and E with a low salinity, and the relative abundance was the highest in the sediment samples of lake E3, which was as high as 10.3%. *Paracoccus* was found in a small amount of the majority of samples, while it was relatively high in lakes A and E with a low salinity, which reached 5.92%, and the abundance of *Hydrogenophaga* was 4.51% only in lake C. Purple non-sulfur bacteria and purple sulfur bacteria, including *Rhodoplanes* (0.94%) and *Halorhodospira* (0.58%), were detected in lake D with a high salinity.

SRB community in sediment samples

Based on the results of high-throughput sequencing of *dsr*B gene, the taxonomic composition of SRB was analyzed at the genus level (Fig. 2C, Supplementary Fig. 1B), and it was revealed that 39 SRB genera, including *Desulfurivibrio*, *Candidatus Electrothrix*, *Desulfonatronum*, *Desulfonatronovibrio*, *Desulfonatronobacter*, *Desulfohalophilus*, *Desulfonatronospira* and so on, all belong to the deltaproteobacteria class. It was observed that the community structure of the SRB varied across the different soda lakes. Similar to SOB, the cluster of SRB was consistent with the sampling sites. However, compared with SOB, the diversity of SRB was higher in all samples. *Desulfunvibno* was detected in the majority of the samples, while it was dominant only in lake D with a high-salinity,

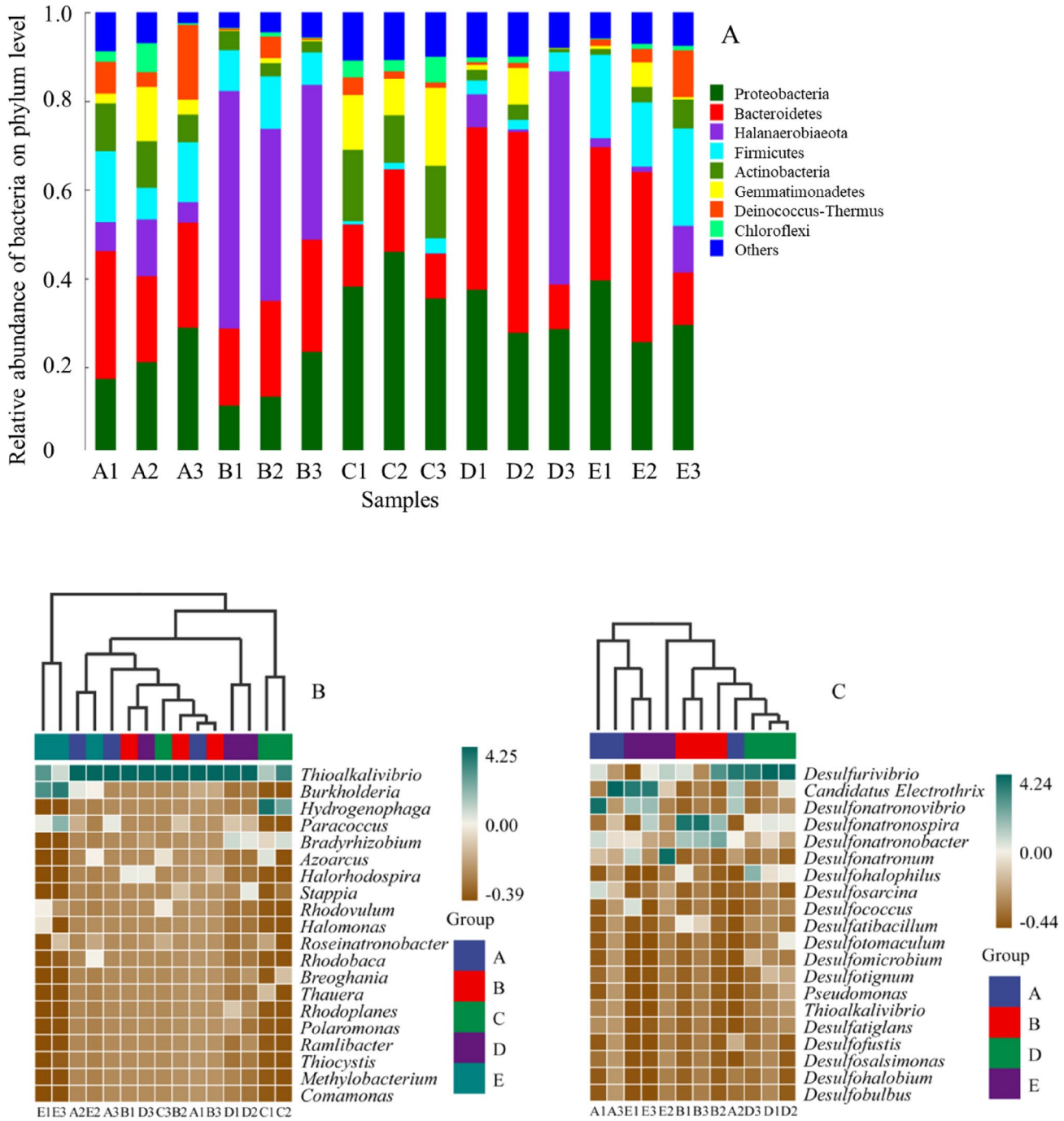

Fig. 2 Microbial community structures in soda lakes. **A** Total bacteria on phylum level, **B** SOB on genus level, **C** SRB on genus level. Due to the technical error, the extraction of *dsr*B gene from the lake C sediment samples was not completed. Thus, the *dsr*B gene sequencing results derived from four lakes were analyzed

and the relative abundance was as high as 28.09%. The relative abundances of *Candidatus Electrothrix*, *Desulfonatronum* and *Desulfonatronovibrio* were relatively high in lakes A and E with a low-salinity, and the highest abundance was 38.58, 43.20, and 17.45%, respectively. *Desulfonatronospira* and *Desulfohalophilus* were found to have higher abundance only in lakes B and D with a high salinity, which reached 18.69 and 8.79%, respectively. *Desulfonatronobacter* was detected to have a higher abundance in lake B, which was as high as 22.70%.

Effects of physicochemical factors on the SOB and SRB community

To illustrate the relationship between the microbial communities and physicochemical characteristics in soda lakes, Spearman's correlation analysis and Redundant analysis (RDA) were conducted. Spearman correlation analysis showed that most of the dominant SOB were highly correlated with the concentrations of NH_4^+-N and salinity (Na^+) (Table 4). Specifically, *Bradyrhizobium*, *stappia* and *rhodoplanes* were positively correlated with salinity. *Burkholderia* and *Paracoccus* were positively correlated with NH_4^+-N concentration, while *Bradyrhizobium* and *Hydrogenophaga* were the opposite. In addition, *Bradyrhizobium* and *Hydrogenophaga* were significantly affected by MC. As the main SOB in the soda lake, *Thioalkalivibrio* was not significantly affected by the factors investigated, which indicated that *Thioalkalivibrio* had a wide range of adaptability. Overall, as shown in Fig. 3A, NH_4^+-N was the most

Table 4 Correlation analysis between SOB, SRB and physicochemical parameters of soda lakes

Bacteria	$Na^+/SO_4^{2-}/Cl^-$	NH_4^+-N	NO_3^--N	TOM	pH	MC
SOB						
Thioalkalivibrio	0.164	0.409	0.196	0.268	− 0.111	0.261
Burkholderia	− 0.497	0.608*	− 0.436	− 0.364	− 0.192	0.234
Paracoccus	− 0.065	0.552*	0.062	− 0.153	0.044	0.366
Bradyrhizobium	0.611*	− 0.574*	− 0.130	− 0.077	0.082	− 0.576*
Hydrogenophaga	0.364	− 0.566*	− 0.165	− 0.133	− 0.023	− 0.545*
Stappia	0.560*	− 0.189	− 0.005	0.335	0.046	− 0.183
Halorhodospira	0.484	− 0.179	0.516*	− 0.161	− 0.014	− 0.296
Rhodoplanes	0.553*	− 0.145	− 0.199	0.133	0.211	− 0.248
SRB						
Desulfurivibrio	0.367	− 0.524	− 0.091	0.448	0.312	− 0.259
Candidatus electrothrix	− 0.674*	0.711*	− 0.458	− 0.366	− 0.095	0.394
Desulfonatronospira	0.583*	− 0.399	0.657*	0.084	− 0.291	− 0.343
Desulfonatronum	− 0.725**	0.495	− 0.605*	− 0.011	0.152	0.470
Desulfonatronovibrio	− 0.429	0.502	− 0.573	− 0.011	0.027	0.431
Desulfonatronobacter	− 0.194	0.245	0.490	0.028	− 0.091	0.273
Desulfohalophilus	0.758**	− 0.741**	0.046	0.183	0.294	− 0.528

*Represents significant correlation, $*P < 0.05$, $**P < 0.01$

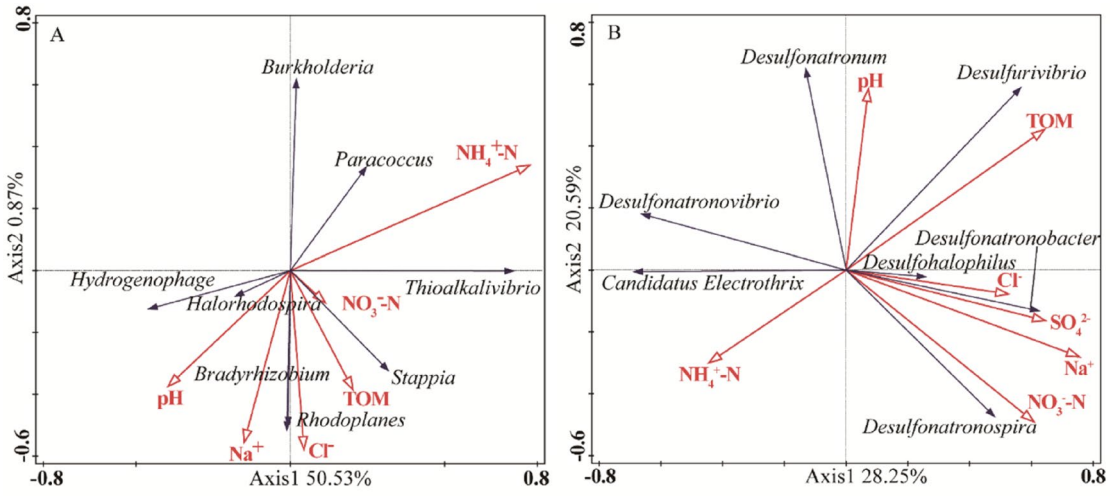

Fig. 3 Redundant analysis (RDA) of the distribution of dominant genera with respect to physicochemical characteristics. The purple arrows represent the bacterium, and the red arrows denote the physicochemical characteristics. Arrow vector length corresponds to the strength of the correlation with the axes. (**A** SOB, **B** SRB)

important factor influencing the composition of SOB in the soda lake, followed by salinity.

As shown in Table 4 and Fig. 3B, the influence of physicochemical factors on SRB composition was analyzed. Similar to SOB, salinity and NH_4^+-N had significant effects on SRB. *Candidatus electrothrix* and *Desulfonatronum* were negatively correlated with salinity, while *Desulfonatronospira* and *Desulfonalophilus* were on the contrary. For the effect of NH_4^+-N, it was found that the significant effect of NH_4^+-N on *Candidatus electrotherix* was positively correlated, while the effect on *Desulfohalophilus* was negatively correlated. Different from SOB analysis, the effect of NO_3^--N concentration on SRB was more obvious, especially on *Desulfonatronospira* and *Desulfonatronum*. *Desulfurivibrio* was the main SRB bacteria in soda lakes, which had strong adaptability and was not affected by environmental factors, which was similar to *Thioalkalivibrio*. In short, salinity was noted as the most important factor that influenced the composition of SRB, followed by the NO_3^--N and NH_4^+-N. In addition, it can be seen from the above data that TOM, pH and MC had no significant effect on the composition of SOB and SRB.

Co-occurences of SOB and SRB

In order to study the interaction between SOB and SRB, we used R programming language and Gephi 0.9.2 software to analyze and draw a network diagram. As shown in Fig. 4, there were 65 nodes (bacteria) and 309 edges in the graph. A group of closely associated microorganisms in the microbial network were divided into the same module. The bacterium in the same module had similar niches. The colors of different nodes denoted different modules. As shown in Fig. 4, there were five modules (I–V), and the proportion of each module was 29.23, 18.46, 18.46, 15.38 and 6.15%. The network diagram showed the complex relationship between sulfur metabolizing bacteria in soda lake sediments. Most SRB were distributed in the same module (module IV), which indicated that their functions were similar and had relatively close niche. Similar to SRB, photophilic sulfur oxidizing bacteria were mostly found in module III. However, as the highest abundance of SOB, *Thioalkalivibrio* occupied a less important position, which implied the diversity of sulfur oxidizers and their unimportance in determining the niche.

It can be seen that *Rhodoplanes* was highly connected with other bacteria, which was called kinless hubs, although its relative abundance was low in the samples. Previous research had shown that the relative abundance of taxa classified as kinless hubs within the ecological network were positively and significantly correlated with the abundance of functional genes (Shi et al. 2020). The demise of kinless hubs would bring huge changes to the community structure and its functions (Banerjee et al. 2018). *Rhodoplanes* had a unique position in the microbial community of this study. *Rhodoplanes* was a kind of purple non-sulfur bacteria, which belonged to Alphaproteobacteria (Okamura et al. 2009). *Rhodoplanes* could grow aerobically in the atmosphere or grow anaerobically through denitrification in the dark, but

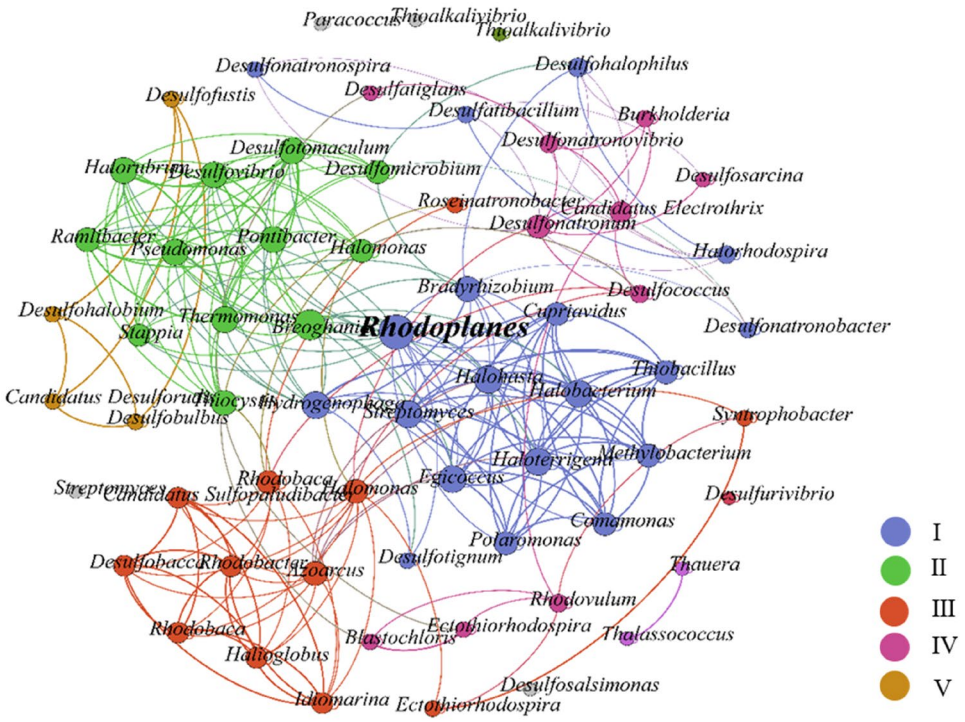

Fig. 4 Network diagram of bacterial groups associated with sulfur cycle

the preferred growth way was to use simple organic acids, such as pyruvate, for anaerobic organic growth (Chakravarthy et al. 2012). *Rhodoplanes* had been reported to have an optimal pH of 7.0 (Chakravarthy et al. 2012). However, it was found that *Rhodoplanes* play an important role in the community of soda lake sediments, indicating the existence of some haloalkalophilic *Rhodoplanes* species.

Discussion

Diversity of the sulfur bacteria community in soda lakes

For the first time, we depended on high-throughput sequencing of 16S rRNA, *sox*B and *dsr*B genes to accurately estimate phylogenetic richness and composition in five soda lakes with different physicochemical factors, located in Ordos, Inner Mongolia Autonomous Region, China. A surprisingly diverse bacterial community was discovered in five lake sediments. The bacterial community was dominated by the phyla Proteobacteria, Bacteroidetes, Halanaerobiaeota, Firmicutes, Actinobacteria and Gemmatimonadetes. From the results, it was found that chemolithoautotrophic genus *Thioalkalivibrio* covered the whole spectrum of salinity, NO_3^-, NH_4^+ conditions present in soda lakes. *Thioalkalivibrio* presented the obvious physiological diversity, the most prominent of which was that, the dominant subgroup of this genus was able to grow in saturated soda brines containing 4 M total Na^+ (Sorokin et al. 2011a, b). Due to its strong contribution in biological desulfurization process, the growth characteristics of *Thioalkalivibrio* have been studied in depth (Mu et al. 2016; Grant and Sorokin 2011), and the genome editing methods for *Thioalkalivibrio* have been established (Sharshar et al. 2020). Important genes related to sulfur oxidation, such as *fcc*, *sox*, and *sat/apr*, have been detected in most of *Thioalkalivibrio* genus that have been sequenced, indicating that the genus has rich sulfur oxidation pathways, showing that it can adapt to more complex environments and contribute to the sulfur cycling process, which was consistent with the results of the present study (Foti et al. 2006; Liu et al. 2021).

Although our data highlighted the importance of *Thioalkalivibrio* to sulfur biogeochemistry in soda lakes, purple non-sulfur bacteria and purple sulfur bacteria, including *Rhodoplanes* (0.94%) and *Halorhodospira* (0.58%), were detected in lake D with a high salinity. Photoheterotrophic bacteria could oxidize sulfide, thiosulfate and sulfur to sulfate during heterotrophic growth with additional energy benefit and occupy the niche rapidly, which placed them in a favorable position in the rapidly changing environment of soda lakes (Tourova et al. 2013). In addition, heterotrophic sulfur oxidizing bacteria *Halomonas* was also detected by *sox*B gene. The most remarkable feature of the bacteria was their ability to grow and concomitantly oxidize sulfide and polysulfide to elemental sulfur anaerobically under denitrifying conditions (Sorokin and Kuenen 2005).

The reductive part of the sulfur cycle was active in the anoxic layers of the sediments of soda lakes. Microbiological analysis indicated a domination of haloalkaliphilic SRB, including *Desulfurivibrio*, *Candidatus Electrothrix*, *Desulfonatronovibrio*, *Desulfonatronum* and *Desulfonatronospira*. At present, 15 genera of haloalkaliphilic SRB had been isolated, of which 11 strains have completed genome sequencing. Most of these bacteria were isolated from soda lakes in Russia, the United States and Kenya (Sorokin et al. 2015). *Desulfurivibrio* had the characteristics of elemental sulfur disproportionation to adapt to the environment and became the dominant bacteria (Poser et al. 2013). Recent studies suggested that *Desulfurivibrio* might have the potential of extracellular electron transfer, because similar conductive pili synthesis genes responsible for electron transfer had been detected in the genome of *D. alkaliphiles* (Melton et al. 2016; Ni et al. 2019). Although as to whether *Desulfurivibrio* could carry out extracellular electron transfer still needed further verification, it was speculated that *Desulfurivibrio* played an important role in the electron sharing of anaerobic bacterial community.

In addition, a great number of *Candidatus Electrothrix* were firstly detected in the sediment samples of soda lakes with a low salinity. *Candidatus Electrothrix* was a kind of filamentous multicellular microorganism, which can electrically couple the oxygen reduction on the surface of the sediment with the oxidation of sulfide in the deep hypoxic layer through long-distance electron transmission (Trojan et al. 2016). *Candidatus Electrothrix* can also use nitrate or nitrite as an electron acceptor to couple nitrate reduction and sulfide oxidation to transfer electrons over a long distance (Bjerg et al. 2018). Uniquely, it can perform sulfide oxidation and sulfate reduction at the same time (Nielsen et al. 2010), but in this study, *Candidatus Electrothrix* was not detected with *sox*B as the marker gene. It should be because most strains of this genus use opposite pathway of classical sulfur reduction to complete sulfur oxidation (Müller et al. 2020).

Salinity, NH_4^+-N and NO_3^--N were the significant factors

We compared the effects of salinity, nitrogen and other physicochemical parameters on the diversity and composition of total bacteria, SOB and SRB. In general, salinity, NH_4^+ and NO_3^- concentration were the most important factors. The diversity of total bacteria and SOB was negatively correlated with salinity. It has been proved that salinity can cause

changes in the sulfur cycle. There were two sulfur cycles in soda lakes mainly depending on the salinity of the lake water. At medium salinity, a complete sulfur cycle, namely "long" sulfur cycle, is more likely between HS^- and SO_4^{2-}, where HS^- is completely oxidized to SO_4^{2-}, and $SO_4^{2-}$is reduced to HS^- by SRB. Under saturation salinity, the cycle may be shortened due to the presence of sulfur intermediate products such as S^0, Sn^{2-}, $S_2O_3^{2-}$, namely "short" sulfur cycle. In this cycle, HS^- is not completely oxidized to $S_2O_3^{2-}$ and then formed HS^- by sulfur reduction reaction (Sorokin et al. 2011a, b).

Additionally, it was showed that the diversity of total bacteria and SRB was significantly correlated with NO_3^-, and the RDA analysis revealed that NO_3^- was the second important factor influencing the composition of SRB. This could be related to the high NO_3^- concentration contributing to the growth of denitrifying bacteria (DNB), because the intermediate products of denitrifying, e.g. NO and N_2O, could inhibit the growth of SRB (Zumft 1993). Moreover, studies demonstrated that DNB could preferentially use matrix and thus, it possessed an advantage compared with SRB (Chidthaisong and Conrad 2000). In addition, NO_3^- is an important electron acceptor for SOB, especially in oxygen deficient environment. Now, three out of nine *Thioalkalivibrio* species had been confirmed to be able to grow anaerobically with NO_3^- as electron acceptor.

Rhodoplanes was the core bacterium

In the process of sulfur cycle in soda lakes, there were complex relationships between sulfur-related bacteria. Many species of bacteria were located in the same niche, which indicated the complexity of sulfur cycle in soda lakes and the redundancy of the same functional bacteria, which ensured the stability of the system to the maximum extent. According to the co-occurences of SOB and SRB, it was found that the bacteria with high abundance was not the kinless hubs. The most representative example was *Thioalkalivibrio*, which had little contact with other bacteria. The results showed that *Rhodoplanes* was the core bacterium, which may be related to its metabolic diversity. This genus comprised purple non-sulfur bacteria expressing preferably photoheterotrophic growth in the light under anoxic conditions, whereas chemoorganotrophic growth was possible in the dark under both oxic and anoxic conditions. Due to its metabolic versatility, *Rhodoplanes* has been isolated from very diverse aquatic environments, ranging from freshwater through to activated sludge in wastewater treatment plants (Rojas et al. 2018).

Conclusions

In this paper, the high-throughput sequencing of 16 s rRNA, *dsr*B, and *sox*B genes was carried out, and the microbial communities in different soda lakes were analyzed. The results showed that most of the total bacteria in soda lakes belong to phyla Proteobacteria, Bacteroidetes, Halanaerobiaeota, Firmicutes, and Actinobacteria. SOB and SRB were broadly distributed in soda lakes. The detected SOB was affiliated to Alpha-, Beta- and Gamma-proteobacteria populations, while most of SRB was affiliated to Deltaproteobacteria. The distribution of SOB and SRB was significantly affected by levels of salinity and inorganic nitrogen. The communities of SOB, mainly including *Thioalkalivibrio*, *Burkholderia*, *Paracoccus*, *Bradyrhizobium*, and *Hydrogenophaga* genera, were remarkably influenced by the levels of NH_4^+-N and salinity. For SRB communities, including *Desulfurivibrio*, *Candidatus Electrothrix*, *Desulfonatronospira*, *Desulfonatronum*, *Desulfonatronovibrio*, *Desulfonatronobacter* and so on, the most significant determinants were salinity and NO_3^--N. Besides, *Rhodoplanes* played a significant role in the interaction between SOB and SRB. In summary, this study extended our knowledge regarding the distribution of community structures of SOB and SRB under haloalkaline conditions.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00203-022-02925-7.

Acknowledgements This article acknowledges the funding support provided by the National Key Research and Development Program of China (No. 2020YFA0906800) and National Science Foundation of China (Nos. 31872633, 21878307 and 31800030).

Author contributions MHY and JMX designed the experiment and wrote the first draft. XYL, ZXL, TZM, DLM, and JLL collected the fecal samples and performed preliminary preparation. All authors have helped in revision and approved the final manuscript.

Funding Key Research and Development Program of Jiangxi Province, 2020YFA0906800, Jianmin Xing, National Natural Science Foundation of China, 31872633, Maohua Yang.

Declarations

Conflict of interest The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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