LIMNOLOGY
and
OCEANOGRAPHY LETTERS

Open Access

Limnology and Oceanography Letters 11, 2026, e70088

doi: 10.1002/lol2.70088

LETTER

A matter of salt: Global assessment of the effect of salt ionic composition as a driver of aquatic bacterial diversity

Attila Szabó,[1,2,3]* **Anna J. Székely**,[1] **Emil Boros**,[2] **Zsuzsanna Márton**,[2,3] **Bianka Csitári**,[3,4]
Natalie Barteneva,[5] **Dóra Anda**,[2] **Péter Dobosy**,[2] **Alexander Eiler**,[6] **Stefan Bertilsson**,[1] **Tamás Felföldi**[2,3,7]

[1]Department of Aquatic Sciences and Assessment, Science for Life Laboratory, Swedish University of Agricultural Sciences, Uppsala, Sweden; [2]Institute of Aquatic Ecology, HUN-REN Centre for Ecological Research, Budapest, Hungary; [3]Department of Microbiology, ELTE Eötvös Loránd University, Budapest, Hungary; [4]Department of Microbiology, Tumor and Cell Biology, Karolinska Institutet, Stockholm, Sweden; [5]Department of Biology, Nazarbayev University, Astana, Kazakhstan; [6]Department of Biosciences, University of Oslo, Oslo, Norway; [7]National Multidisciplinary Laboratory for Climate Change, HUN-REN Centre for Ecological Research, Budapest, Hungary

Scientific Significance Statement

This study explores the drivers of bacterial diversity in inland saline lakes lacking marine connection, focusing on the "matter of salt"—how different salt compositions influence planktonic microbial community composition. Despite their global abundance and ecological importance, these aquatic systems remain much less studied than marine-related saline water bodies. To address this knowledge gap, we generated a comprehensive dataset from published and unpublished studies, as well as conducted targeted sampling campaigns in underexplored systems, with a particular focus on endorheic soda lakes. Our findings provide novel insights into how the anionic composition of dissolved salts shapes microbial diversity in inland waters, clearly distinguishing carbonate ion-dominated systems.

Abstract

While the influence of salinity on microbial diversity is well documented in marine and brackish ecosystems, the impact of different dissolved inorganic ion types remains largely unexplored. In this study, we assessed how ionic composition shapes planktonic bacterial community structure in inland saline aquatic habitats, compared to the effects of salinity alone, spatial factors, and other environmental variables. We collected and analyzed 16S rRNA gene amplicon datasets from freshwater to hypersaline aquatic environments worldwide (375 samples from 130 lakes). The composition of major ions explained more variability in bacterioplankton structure than bulk salinity. Taxa contributing the most to the observed dissimilarity between communities included lineages characteristic of specific habitat types, such as Actinobacteria acI in freshwater, Halomonadaceae in saline waters, or Nitriliruptorales in soda- and soda-saline systems. Many of these indicator lineages for specific habitat types were monophyletic, further underpinning ionic composition as a crucial eco-evolutionary driver of aquatic microbial diversity.

---

*Correspondence: attila.szabo@slu.se

Associate editor: Meryem Beklioglu

Saline lakes are globally significant habitats, with a total water volume comparable to all freshwater lakes and with a surface area comprising 23% of all lakes (Messager et al. 2016). While thalassic saline systems (i.e., waters of recent marine origin) are relatively uniform in ionic composition—dominated by Na^+ and Cl^-—and therefore can be adequately characterized by overall salt concentration, athalassic saline waters exhibit broad variability in ionic composition and can thus be further classified based on the relative ratio of major ions (Hammer 1986; Saccò et al. 2021). Many of these systems are situated in closed drainage (endorheic) basins, where salt composition is primarily influenced by weathering of local rocks and soils, rather than the remnants of marine salts (Bayly 1967; Hammer 1986). The cation composition of saline lakes is typically dominated by Na^+, and dominance of Mg^{2+} or Ca^{2+} is rare. In contrast, there is a notable diversity in anion composition, and while Cl^- and ${SO_4}^{2-}$ are prevalent in most saline inland waters, alkaline soda waters feature a dominance of carbonate ions (${HCO_3}^-/{CO_3}^{2-}$) (Williams 1998; Boros and Kolpakova 2018). Elevated carbonate content leads to alkaline pH and low Ca^{2+} availability, which promotes high concentration of bioavailable phosphates (Toner and Catling 2020) that enhance primary production (Grant and Sorokin 2011; Boros et al. 2025). Additionally, the often remarkably high dissolved organic carbon content can make these systems hotspots for microbial organic carbon processing (Eiler et al. 2003; Boros et al. 2020).

Microbial community assembly in aquatic ecosystems is governed by a combination of deterministic (environmental selection) and stochastic (dispersal, drift, speciation) processes that shape diversity patterns across spatial and environmental gradients (Vellend 2010; Zhou and Ning 2017; Langenheder and Székely 2011). For aquatic bacteria, external osmotic stress constitutes one of the most cardinal environmental selective factors that not only drives species sorting processes but also adaptive evolutionary processes and, consequently, microbial diversity (Gunde-Cimerman et al. 2018; Paver et al. 2018; Jurdzinski et al. 2023). As we previously demonstrated for bacterial isolates (Csitári et al. 2022), the requirement for distinct adaptive mechanisms to cope with the salinity stress imposed by different ions (Banciu and Muntyan 2015) underscores the significance of ionic composition as a critical selective force, even at low salt concentrations. Nevertheless, in contrast to the extensive body of literature on how salinity influences microbial diversity (e.g., Lozupone and Knight 2007; Tamames et al. 2010; Thompson et al. 2017) or how community composition is structured along salinity gradients in thalassic systems (e.g., Herlemann et al. 2011; Campbell and Kirchman 2013; Paver et al. 2018), the influence of ionic composition on community assembly processes has not yet been systematically explored.

To address this knowledge gap, we analyzed bacterial 16S rRNA gene amplicon datasets from a range of inland aquatic systems with varying salt content, with a particular focus on soda lakes. Using multiple statistical approaches, we tested the hypothesis that beyond total salt concentration, ionic composition is a major environmental filtering factor structuring planktonic bacterial communities.

Materials and methods

Data collection and sampling

To ensure comprehensive data collection, we utilized two complementary strategies: (1) data retrieval from sequence databases and literature sources, and (2) additional sampling from various athalassic saline aquatic environments (Table 1; Supporting Information Table S1; Supporting Information Fig. S1). The comprehensive search of publicly available databases was performed by querying the NCBI, EBI, and IMG/M databases with terms "saline lake," "alkaline lake," "soda lake,"

Table 1. Geographic origin, ionic composition type, and source studies for 16S rRNA gene datasets used in this study. Source studies: 1: Kambura 2017; 2: Lavrentyeva et al. 2020; 3: Matyugina et al. 2018; 4: Ji et al. 2019; 5–12: Sinclair et al. 2015; Szabó et al. 2017, 2020, 2022; Mentes et al. 2018; Korponai et al. 2019; Szuróczki et al. 2020; Márton et al. 2023b; 13: Zorz et al. 2019; 14: Edwardson and Hollibaugh 2018; 15: Phillips et al. 2021.

Geographic region	Ionic composition type	No. of samples	Source
Great Rift Valley (Africa)	Soda	5	1
North Kazakhstan (Asia)	Saline, freshwater	14	This study
Balkhash-Alakol Basin (Asia)	Saline, soda, soda-saline	34	This study
West and South Kazakhstan (Asia)	Saline, soda-saline	9	This study
Barguzin Valley (Asia)	Saline	1	2
Transbaikalia (Asia)	Soda	6	3
Tibetan Plateau (Asia)	Freshwater, soda, soda-saline, saline	20	4
Pannonian Basin (Europe)	Freshwater, soda, soda-saline, saline	262	This study, 5–12
Cariboo Plateau (North America)	Soda	15	13
Great Basin (North America)	Soda	10	14, 15

"soda pan," "soda," "saline," and "alkaline." Additionally, we manually reviewed the results and searched for peer-reviewed publications that referred to sequence data in Google Scholar and Web of Science databases. From the hits evaluated as of 15th November 2022, we excluded entries without available sequences that lacked proper metadata description or contained too few sequences (< 2500 reads) after pipeline processing. For deeper water bodies, we included only sequences obtained above the chemo- and oxycline. Detailed descriptions of the source study sites are provided in Supporting Information Text S1 and Supporting Information Table S1.

We limited our analyses to sequence data generated by PCR amplification of the V4 or V3–V4 regions of the bacterial 16S rRNA gene, as these were the most commonly targeted regions. We used the V4 dataset for broader site representation and the V3–V4 dataset to provide more highly resolved taxonomic affiliation.

In addition to data retrieval, from 2012 to 2021, we conducted extensive sampling campaigns across several inland aquatic systems in Central and Eastern Europe, as well as in Central Asia (Supporting Information Table S1). The sampling sites were selected to encompass a diverse range of saline conditions, from freshwater lakes to hypersaline environments, with salinities spanning from < 0.5 to > 150 g/L and pH values ranging from 7.0 to 10.7. Water samples were collected from the near-surface layer of the water columns.

Ionic composition classification of sampling sites

Freshwater sites were provided as low salinity references, and their collection was limited to lakes sampled during the same campaigns as nearby saline systems. Freshwater habitats were defined as aquatic environments with low salinity, typically below 1 g/L (Saccò et al. 2021) based on previously published data. However, salinity thresholds reported in the literature may vary depending on classification criteria (Supporting Information Fig. S2). Saline sites were categorized as described in Boros and Kolpakova (2018) according to their dominant anion equivalent percentage (e%). Accordingly, sodium brines were classified into the following categories: (1) soda type: carbonate ions have > 25 e% with this species being first in the rank of anions; (2) soda-saline type: carbonate ions > 25 e%, but with other anions in higher rank; (3) saline type: chloride or sulfate dominate with carbonates < 25 e% (Supporting Information Figs. S2, S3).

Description of sampling sites

We specifically targeted underrepresented sites such as saline lakes in Kazakhstan and soda and saline waters of Austria, Hungary, Romania, and Serbia.

Kazakhstan is the 9th largest country in the world, featuring an extraordinary diversity of aquatic habitats and wetlands (Boros et al. 2017), yet planktonic prokaryotic communities of its saline-alkaline lakes remain scarcely studied. We targeted four regions of the country. In Northern Kazakhstan, during April–May 2015, 2 freshwater and 12 saline lakes were sampled (Boros et al. 2017). Seven samples were collected from different sites of Lake Balkhash in September 2018. In 2021, 27 additional sites were sampled along the southeastern shore of Lake Balkhash, as well as from Lake Alakol and adjacent saline lakes (Boros et al. 2025). Finally, in 2018–2019, we collected nine samples from saline-alkaline water bodies in West and South Kazakhstan.

The Pannonian Steppe, the westernmost part of the Eurasian steppe and one of the largest grasslands in Europe, features numerous soda lakes, pans (shallow lakes with a high area-to-volume ratio), and a few saline waters. Between 2012 and 2021, several sampling campaigns have been conducted to investigate the spatiotemporal diversity of their planktonic microbial communities (Felföldi 2020; Somogyi et al. 2022). The present study incorporated samples collected during this period from various locations, including soda pans in the Kiskunság National Park in Hungary (Szabó et al. 2017, 2020; Márton et al. 2023a), Lake Neusiedler/Fertő (Szuróczki et al. 2020), and the Seewinkel/Fertőzug region (Sinclair et al. 2015; Szabó et al. 2022; Márton et al. 2023b). Additional samples were collected from a transect spanning Austria to Serbia (2018), during a monitoring program of soda and saline lakes in Hungary (2021) (Boros et al. 2025), from Lacul Ursu and Lacul "Plus" hypersaline lakes in Romania (2015), and 25 freshwater sites from the Pannonian (Carpathian) Basin (Anda et al. 2025) were also included to compare bacterial communities within the same biogeographic region. Details of sample collection and processing are given in the Supporting Information Text S2.

Bioinformatic and statistical analyses

Raw sequence data from various platforms were processed with mothur (Schloss et al. 2009) to generate a unified operational taxonomic unit (OTU) table with reads clustered at 99% sequence identity, minimizing inherent biases in diversity estimates for data originating from diverse sources (Johnson et al. 2019; Schloss 2021). Quality filtering, adapter removal, and chimera check were performed, with subsequent taxonomic assignments based on Silva SSU 138 (Quast et al. 2012) and the FreshTrain database (Rohwer et al. 2018). Non-target sequences (e.g., Archaea, chloroplasts) were removed, and OTUs were clustered using OptiClust (Westcott and Schloss 2017). Rarefaction was applied to standardize sequencing depth across samples. OTUs responsible for dissimilarity among samples of contrasting ionic composition type were identified using similarity percentage (SIMPER) analysis based on Bray–Curtis similarity. The PAST3 software (Hammer 2001) was used to determine which OTUs were responsible for the dissimilarity among ionic composition sample types. Ordination and statistical analyses were conducted in R 4.3.0 (R Core Team 2023). The "ggplot2" package (Wickham et al. 2016) was used for data visualization. Ternary plots were generated by "ggtern" (Hamilton and Ferry 2018), while nonmetric multidimensional scaling (NMDS), "envfit," PERMANOVA (using "adonis2" function), and variance partitioning analyses were carried out by the "vegan" package (Oksanen 2022). A Procrustes test was employed to assess dissimilarities in the ordination patterns between the V4 and V3–V4 datasets. Distance-decay relationships were investigated based on Bray–Curtis similarity, enabling the examination of community similarity as a function of geographic distances between sampling sites, calculated using the Haversine formula from the "geosphere" library (Hijmans et al. 2017). A Mantel test was conducted to test for correlations between community dissimilarity and geographic distance. Three-way PERMANOVA tested differences in planktonic bacterial community composition across salinities, ionic types, and geographic regions, while variance partitioning estimated the relative contributions of environmental, spatial, and methodological factors to variation in community composition (Supporting Information Text S2). Variance inflation factors (VIF) were calculated for samples with complete metadata to assess collinearity among environmental parameters and ion equivalent percentages using the "vif.cca" function. Significant Pearson correlations ($p < 0.05$) were identified between environmental parameters and visualized with "corrplot" (Wei et al. 2017). Indicator OTUs characteristic of specific ionic composition types were identified using the "indicspecies" package (Cáceres and Legendre 2009). A phylogenetic tree was constructed for indicator OTUs using "clearcut" (Sheneman et al. 2006) implemented in the mothur program and visualized with "ggtree" and "ggtreeExtra" (Yu et al. 2017). Further details of the analyses are provided in Supporting Information Text S2, S3 and Szabó (2025).

Results and discussion

High-quality amplicon sequences were obtained from 375 samples collected at 130 sites in ten geographic regions on four continents (Africa: 4, Asia: 84, Europe: 262, and North America: 25) (Fig. 1A; Table 1; Supporting Information Fig. S1). Thirty-five samples were collected from lakes classified as freshwater according to Saccò et al. (2021) (< 1.0 g/L salinity), while 340 samples were from athalassic saline lakes (1.0–248 g/L). Based on their anionic composition, the saline sites could be further classified as soda ($n = 246$, Na^+-HCO_3^--CO_3^{2-}), soda-saline ($n = 28$, Na^+-Cl^- or Na^+-$SO_4^{2-} > HCO_3^-$-$CO_3^{2-} > 25$ e%) or saline lakes ($n = 66$, Na^+-Cl^- or Na^+-SO_4^{2-}) (Fig. 1; Supporting Information Fig. S2; Supporting Information Table S1).

VIF calculated for a data subset with detailed available environmental variables ($n = 115$) showed no collinearity between ionic composition and environmental parameters such as depth, temperature, pH, salinity, dissolved oxygen, chlorophyll-a, and dissolved organic carbon (DOC). Strong collinearity was observed among the different dissolved ions, particularly between Na^+ and Mg^{2+}, as well as between the concentration of dissolved ions and salinity. However, no collinearity was detected between salinity and ion equivalent percentages. Correlation analysis failed to detect any strong ($|r| > 0.7$) correlation between ion equivalent percentages and environmental parameters, and only identified one moderate ($0.5 \le |r| < 0.7$) correlation between pH and Na + e%. Overall, these results suggest that ionic composition is largely independent of other environmental variables typically associated with driving microbial diversity (e.g., nutrients, DOC, pH), underpinning its importance as a major community structuring selective factor.

Despite the global distribution of sampling sites, bacterial community composition was primarily structured by the specific ionic composition of the waters (Fig. 2; Supporting Information Figs. S4, S7). Communities were also influenced by the salinity gradient (Fig. 2A,B; Supporting Information Fig. S6), with salinity identified as a significant factor by the PERMANOVA, even though it only explained 1.2% of the variance in community composition (Fig. 3A). Soda lake communities from the American continent and, to some extent, from Africa, tended to separate from Eurasian sites along the salinity gradient (Fig. 2; Supporting Information Figs. S6, S7), reflecting their generally higher salinities, site-specific features such as the dominance of mat-forming cyanobacteria (e.g., *Nodosilinea* in the Cariboo Plateau samples), with a possible additional contribution of geographic distance (Supporting Information Fig. S8). In contrast, despite distances of several thousands of kilometers, certain soda lake communities from Africa, Asia, and Europe were similar in composition, indicating that geographic distance alone does not fully explain community separation. Other environmental factors such as pH, DOC, water temperature, and depth were also significantly fitted on the NMDS plot, and according to the variance partitioning analysis (VPA), the three parameters which had been reported for all samples (salinity, pH, sampling depth) explained 3.1% of the total variance (Fig. 3B). Overall, these results suggest a primary role of deterministic processes in the assembly of bacterial communities in inland saline lakes.

Geographic region explained a large part of the variance in community composition when using PERMANOVA (10.9%, Fig. 3A) and to a minor part using VPA, where spatial vectors explained merely 3.1% variance (Fig. 3B), or by the distance decay analyses (Supporting Information Fig. S8). The latter showed only a weak positive correlation (Mantel $r_{\text{all}} = 0.33$, $p < 0.01$) with geographic distance and often showed greater similarity between samples from distant sites than between time series samples from the same site. This is supported by the previously reported high seasonal turnover of bacterial communities in these habitats (Szabó et al. 2020; Márton et al. 2023b; Pellegrinetti et al. 2024). A likely explanation for the contrasting results of the PERMANOVA could be methodological differences, as samples from the same region were often processed within the same project or by the same group, suggesting that these regional differences might reflect variations in sampling and sample processing (e.g., sample

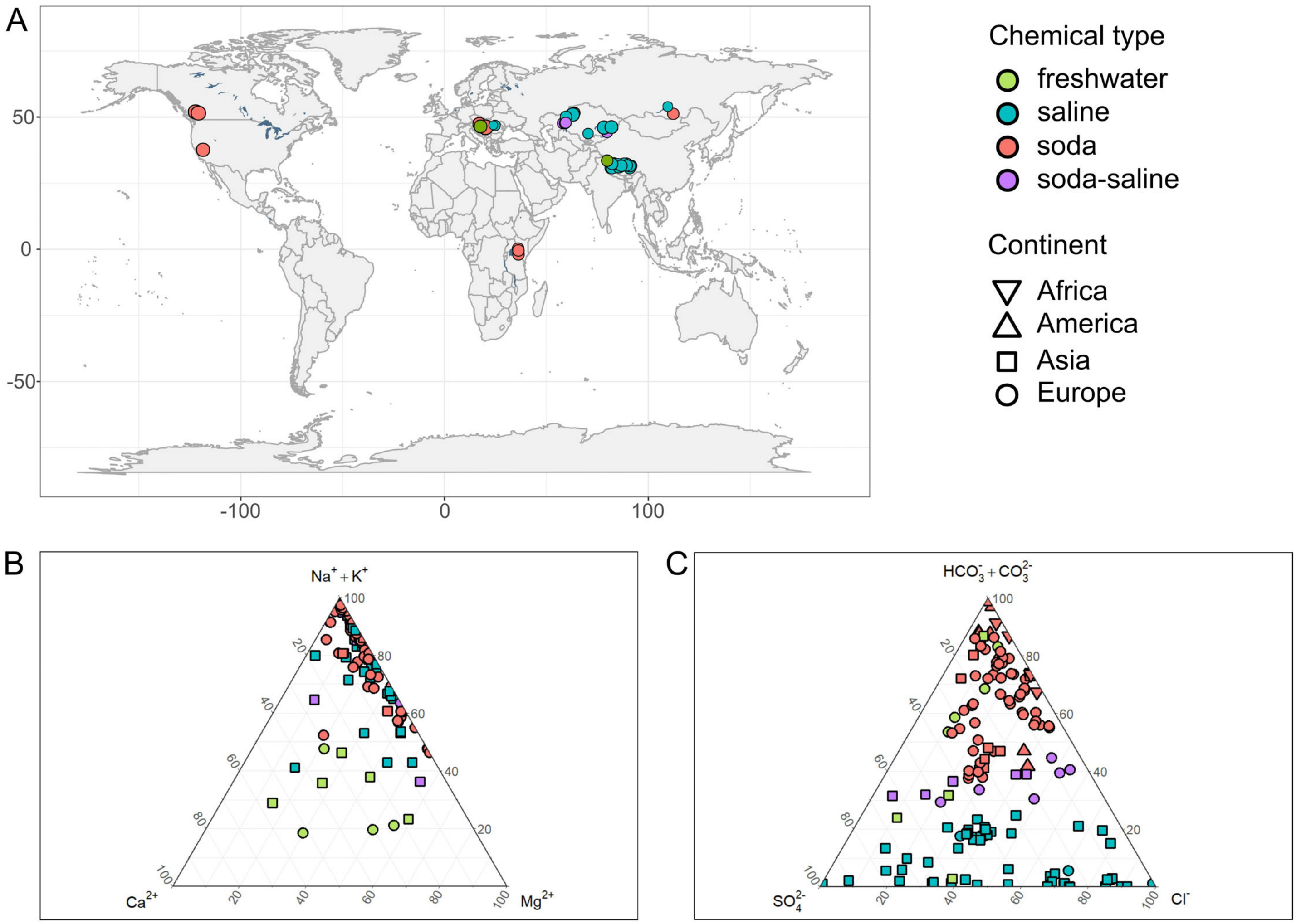

Fig. 1. Ionic composition and geographic location of samples. (**A**) Map showing the geographic origins of the samples. (**B**, **C**) Ternary diagrams of the equivalent percentage (e%) contribution of major dissolved ions to total ion content in the samples.

collection, DNA extraction, PCR amplification) rather than true spatial processes such as dispersal. In addition, we note that PERMANOVA tests categorical differences, in contrast to variance partitioning or distance-decay analyses, which assess continuous environmental or spatial contributions to community variation. No differences in community structure were observed between the V3–V4 and V4 datasets, as shown by the Procrustes test (Supporting Information Fig. S9), which indicated a strong and significant similarity ($r = 0.989$, $p < 0.01$), and only a minimal fraction of the variance ($R^2 = 0.014$, $p < 0.01$) was explained by primer choice indicating a negligible effect of primer choice in this study. Future efforts should aim to employ standardized methods to facilitate more comprehensive comparisons.

The equivalent percentage (e%) of all major ions (Na^+, K^+, Ca^{2+}, Mg^{2+}, Cl^-, SO_4^{2-}, $HCO_3^- + CO_3^{2-}$) was significantly fitted on the NMDS plot. As expected, soda and soda-saline communities aligned along Na^+, and $HCO_3^- + CO_3^{2-}$ vectors, while saline lakes aligned along Cl^- and SO_4^{2-} vectors (Fig. 2B). The ionic composition of the samples consistently explained a significant and high proportion of community variance, whether considered as ionic composition type (PERMANOVA: 5.8%, Fig. 3A) or as ion equivalent percentages (VPA: 4.1%, Fig. 3B).

Our findings emphasize that bacterial community composition is influenced not only by salinity, as a measure of total dissolved salts, but also by the ionic composition of the salts, independently of other environmental factors and geographic distance. In athalassic saline systems, variable amounts of specific dissolved ions require distinct cellular adaptation strategies, creating selective barriers for microorganisms adapted to similar salinity levels but different ionic compositions (Stevens and Cockell 2020; Waajen et al. 2020; Csitári et al. 2022). Such adaptations may include modifications in cell wall composition

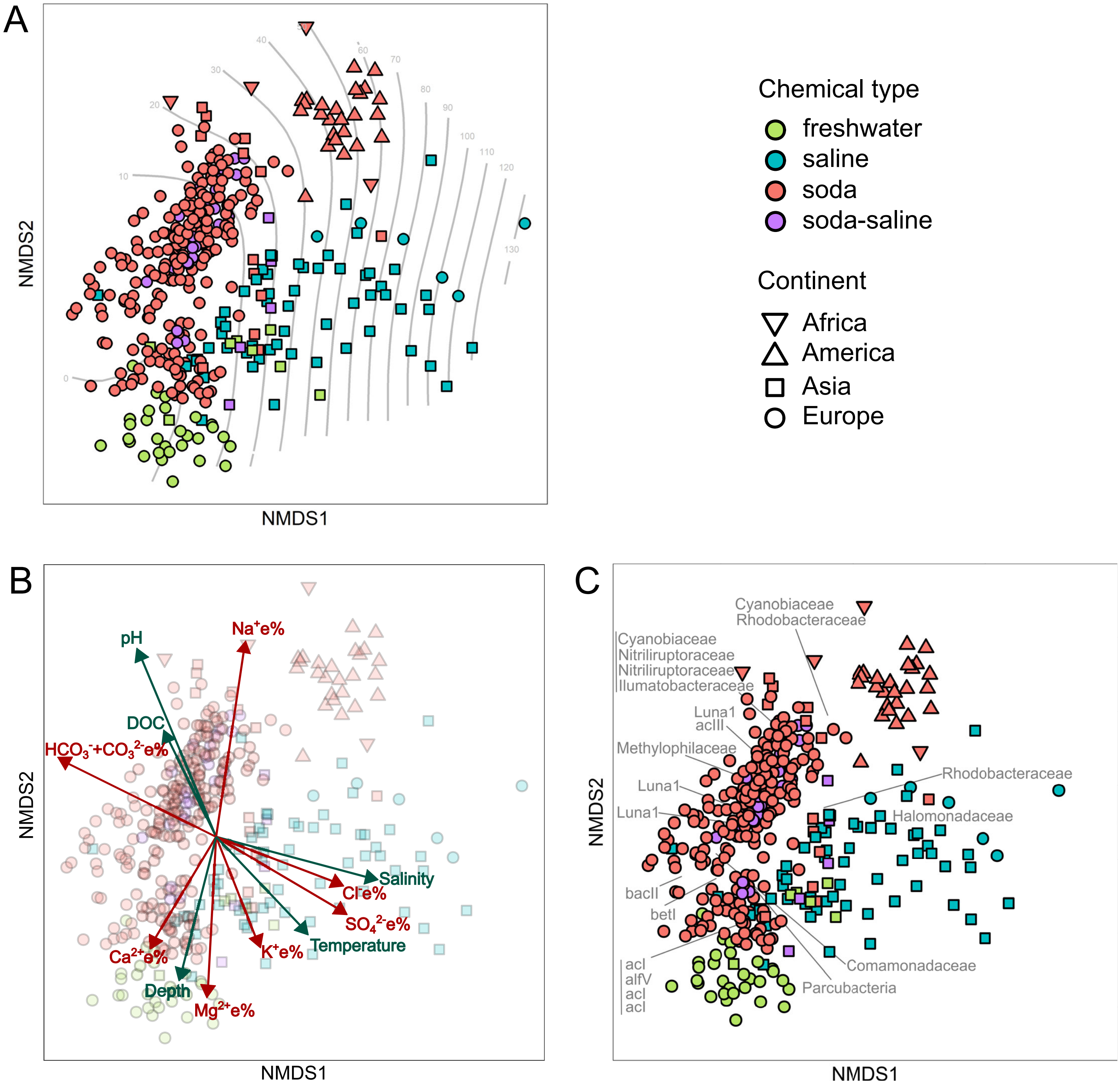

Fig. 2. Comparison of planktonic freshwater and different athalassic saline inland water bacterial communities. NMDS ordination of bacterial OTUs (stress 0.19), defined at 99% sequence identity for the V4 region of the 16S rRNA gene and rotated along the salinity gradient. (**A**) Salinity (in g/L) is projected as gray contours. (**B**) Significantly fitted ($p < 0.05$) environmental variables are represented by green vectors, while significantly fitted ion equivalent percentages are depicted in red. (**C**) OTUs responsible for 20% dissimilarity between ionic composition types were identified according to SIMPER analysis and shown in gray by the name of the closest affiliated taxa (family level or above).

to enhance or inhibit ion attraction, plasma membrane lipid composition to regulate ion permeability, and membrane proteins that selectively bind specific ions (Banciu and Muntyan 2015). Specialized ion transporters are also crucial for preventing toxic ion accumulation, balancing internal pH, and regulating osmotic pressure. Additionally, the ability to utilize sodium-motive force for bioenergetics and different osmoregulation strategies—such as intracellular K^+ accumulation or

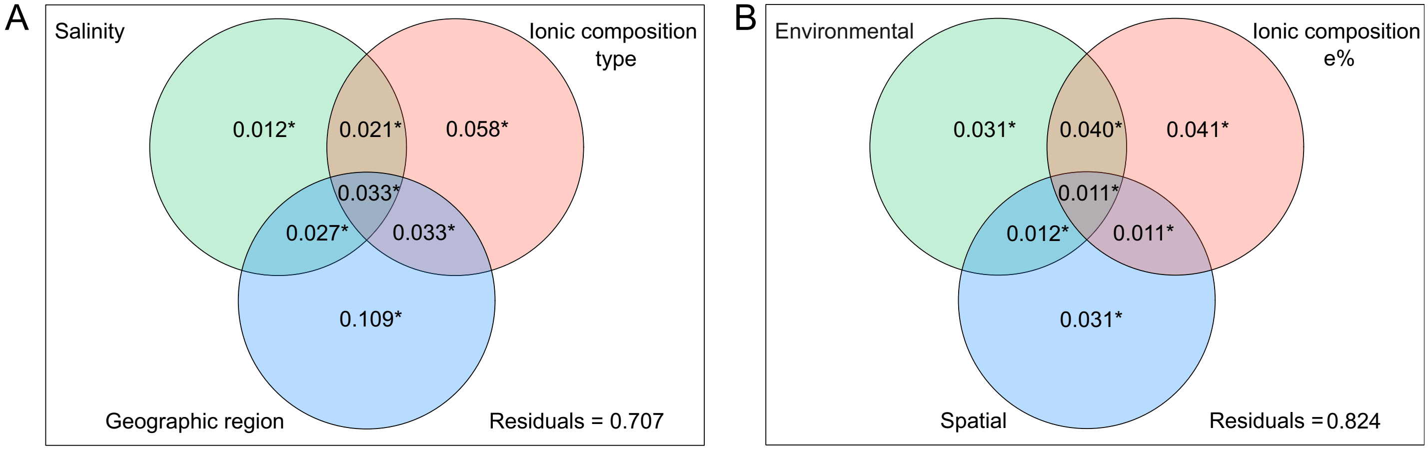

Fig. 3. Variance in bacterial community composition explained by ionic composition and other parameters. (**A**) Variance significantly explained by salinity, ionic composition types, and geographic regions based on R^2 of PERMANOVA tests ($p < 0.01$). (**B**) Variance explained according to VPA by significant environmental parameters (salinity, pH, and sampling depth), ion equivalent percentages, and geographic distance represented by positive significant eigenvectors derived from a distance-based Moran's eigenvector maps analysis.

the synthesis and uptake of organic compatible solutes—determine which microorganisms can persist under given ionic conditions (Banciu and Sorokin 2013; Banciu and Muntyan 2015). The similarity of bacterial communities in geographically distant sites that feature comparable ionic compositions (Supporting Information Fig. S5) implies strong species sorting processes and unrestricted dispersal of aquatic bacteria as shown in previous studies (Jurdzinski et al. 2023). Our dataset predominantly featured sites with Na^+ as the dominant cation, with limited representation of Mg^{2+}-dominated lakes due to the scarcity of such samples in databases. We assume that $CaCl_2$ and $MgCl_2$ rich inland saline sites (Saccò et al. 2021) are also distinct in bacterial community composition compared to Na^+ dominated waters, as chaotropic salts, such as Mg^{2+} and Ca^{2+} chloride salts, are known to destabilize macromolecules and disrupt cellular functions (Hallsworth et al. 2007; Ball and Hallsworth 2015; Gutiérrez-Preciado et al. 2024). These further underpin the pivotal role of ionic composition in shaping microbial diversity.

More than 80% (385 out of 470) of the indicator OTUs were specific to a single environment type (freshwater, soda, soda-saline, or saline). In contrast, less than 20% (85 OTUs) were associated with multiple environment types, with most (74 OTUs) shared between soda and soda-saline environments. Monophyletic bacterial lineages were identified in association with specific ionic composition types. The principal taxa driving the observed community differences were acI-related actinobacteria in freshwaters and Halomonadaceae in saline samples (Figs. 2C, 4), both well-known characteristic groups of these respective habitats (Ghylin et al. 2014; de la Haba et al. 2023). Soda and soda-saline lakes were distinguished by other planktonic actinobacteria (e.g., acIII, Luna1, Nitriliruptoraceae) as well as by "Cyanobiaceae," Methylophilaceae, and Rhodobacteraceae, all of which are lineages previously described from these habitats (Vavourakis et al. 2019; Szabó et al. 2020; Fazi et al. 2021) (Fig. 2C; Supporting Information Fig. S7). Some saline and freshwater indicator OTUs were monophyletic, exemplified in freshwaters by the betI lineage (Pseudomonadota) and Frankiales (Actinomycetota), and in saline waters by Flavobacteriaceae, Idiomarinaceae, and Alteromonadaceae (Fig. 4). In contrast, there were no monophyletic lineages exclusively comprising taxa from soda or soda-saline lakes. However, several monophyletic lineages such as Nitriliruptorales, Rubritaleaceae, Gemmatimonadota, and Cyclobacteriaceae contained representatives only from soda and soda-saline types (Fig. 4). Our study did not incorporate 16S rRNA gene composition data on Archaea, due to the limited availability of such datasets. However, Archaea, especially the class Halobacteria, are well-known to be key members of microbial communities in hypersaline environments, often thriving under extreme ionic and osmotic conditions (Oren 2024). Future endeavors to more broadly assess the composition of the entire prokaryotic community could shed further light on differences between sites with varying ionic compositions.

In conclusion, our comprehensive analysis of 16S rRNA gene amplicon datasets supports the hypothesis that the composition of major dissolved ions is a substantial selective factor that influences the assembly of planktonic microbial communities in athalassic habitats, potentially surpassing the importance of total salinity. Samples with different ionic composition were distinguished by characteristic microbial taxa, often represented by monophyletic lineages, highlighting ionic composition as a strong selective force with evolutionary implications. Our findings provide a foundation for future studies on the genomic and

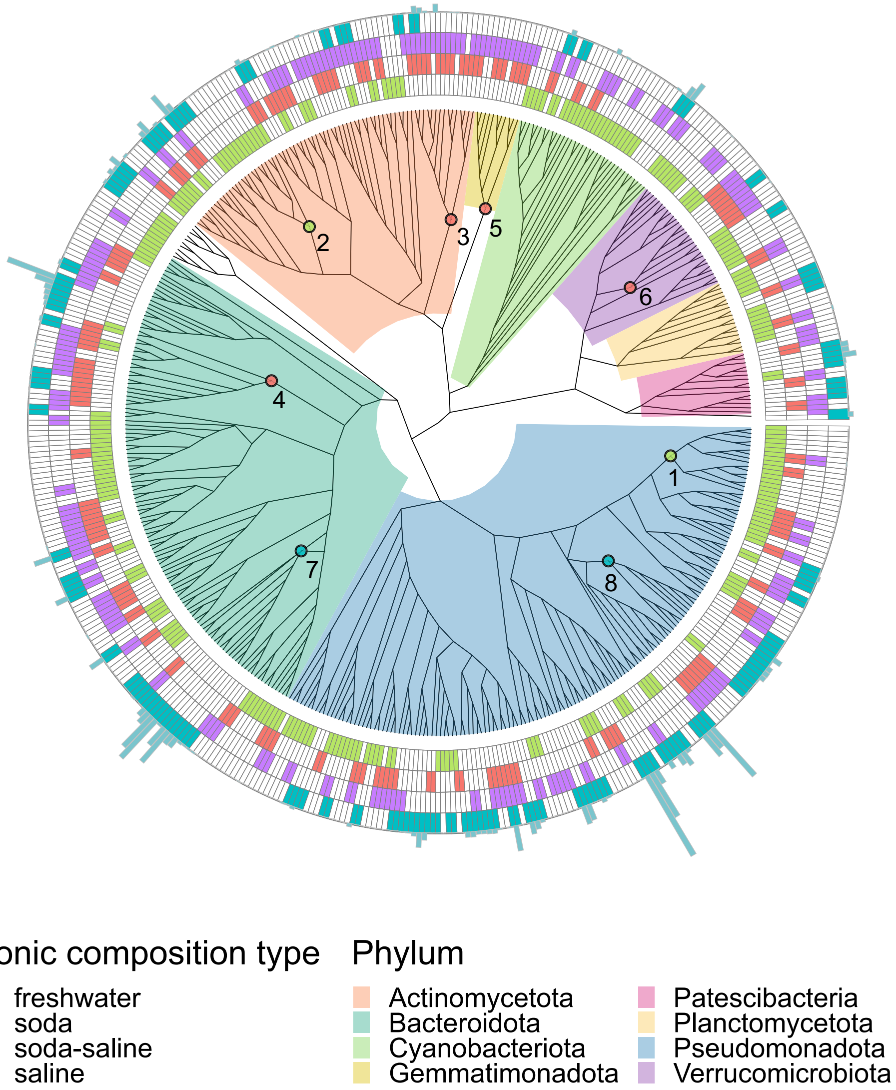

Fig. 4. Phylogenetic tree of the OTUs indicative of different ionic composition types of inland waters. Colors in the tree and heatmap correspond to bacterial phyla and ionic composition types, respectively, as detailed in the figure legend. Colored inner nodes represent monophyletic lineages associated with distinct ionic composition types (> 70% of indicator OTUs align with a given environment type: freshwater, soda and soda-saline, saline), where less than 20% of the indicator OTUs are affiliated with any other category. Key lineages include (1) betI (Pseudomonadota) and (2) Frankiales (including acI, Actinomycetota) for freshwater, (3) Nitriliruptorales (Actinomycetota), (4) Cytophagales (Bacteroidota), (5) Gemmatimonadota, and (6) Verrucomicrobiales (Verrucomicrobiota) for soda and soda-saline, and (7) Flavobacteriaceae (Bacteriodota) and (8) Alteromonadales (Pseudomonadota) for saline aquatic habitats. The heatmap in the outer circle illustrates the ionic composition type associated with each indicator OTUs. The mean salinity of samples, weighted by the abundance of each indicator is represented by greenish-blue bars in the outermost circle.

physiological adaptations to ionic stress and underscore the importance of considering ionic composition alongside salinity, particularly when studying saline systems of non-marine origin.

Author Contributions

Attila Szabó, Anna J. Székely, and Tamás Felföldi conceptualized the research. Sampling campaigns were conducted by Attila Szabó, Anna J. Székely, Emil Boros, Zsuzsanna Márton, Bianka Csitári, Natalie Barteneva, Alexander Eiler, and Tamás Felföldi. Péter Dobosy provided DOC and ion composition data. Attila Szabó, Zsuzsanna Márton, Bianka Csitári, Dóra Anda, Alexander Eiler performed DNA extraction and amplicon library preparations. Data collection and bioinformatic analyses were carried out by Attila Szabó. Data curation and validation were conducted by Attila Szabó and Dóra Anda. Statistical analyses and visualizations were performed

by Attila Szabó and Anna J. Székely. Funding acquisition was accomplished by Anna J. Székely, Emil Boros, Natalie Barteneva, Stefan Bertilsson, and Tamás Felföldi. Resources were provided by Anna J. Székely, Emil Boros, Natalie Barteneva, Alexander Eiler, Stefan Bertilsson, and Tamás Felföldi. Attila Szabó, Anna J. Székely, Stefan Bertilsson, and Tamás Felföldi supervised the project. Attila Szabó, Anna J. Székely, and Tamás Felföldi wrote the original draft, and all authors contributed to editing the manuscript.

Acknowledgments

The authors are thankful for the assistance in sample collections to Aidyn Abilkas, Zarina Inelova, Kristóf Korponai, Gergely Krett, István Máthé, Csaba Romsics, and Tamás Sápi. Processing of the samples was aided by Marina Ádler, Balázs József Nagy, Izabel Siszler, and Sára Szuróczki. Csaba Vad advised on statistical analyses. The authors express gratitude to Károly Márialigeti for providing funding for a part of the project. Computations and data handling were enabled by the resources of the ELTE Eötvös Loránd University and computing projects NAISS 2023/6-388 and NAISS 2023/5-574, provided by the Swedish Research Council (Vetenskapsrådet) at UPPMAX, funded by the Swedish Research Council through grant agreement no. 2022-06725. Attila Szabó and Anna J. Székely were supported by the Wenner-Gren Foundations. Anna J. Székely and Stefan Bertilsson were supported by startup funds from the Swedish University of Agricultural Sciences. Attila Szabó was supported by the Swedish Research Council for Sustainable Development—Formas (2024-00727). Anna J. Székely was also supported through the Knut and Alice Wallenberg Foundation [NP00052] and by the Swedish Research Council Formas (FR-2016/0005). Alexander Eiler was supported by Stiftelsen för Strategisk Forskning through grant agreement no. ICA10-0015. Tamás Felföldi was supported by the National Multidisciplinary Laboratory for Climate Change project (grant ID: RRF-2.3.1-21-2022-00014) within the framework of Hungary's National Recovery and Resilience Plan supported by the Recovery and Resilience Facility of the European Union. This work was partially supported by the National Research, Development and Innovation Office, Hungary (grant ID: OTKA FK 138789). Emil Boros was supported through the project "Assessment of the ecological state of unique soda-saline ecosystems in Kazakhstan (AP08856160)" by the Ministry of Education and Science of the Republic of Kazakhstan.

Conflicts of Interest

None declared.

Data Availability Statement

Comprehensive information on sequence sets' accession in the NCBI SRA and available metadata is given in Supporting Information Table S1, which provides references for environmental parameters and ionic composition of the sites. Data, analysis codes, and metadata are archived in the Zenodo repository and available at https://doi.org/10.5281/zenodo.17546049. Detailed scripts for data analysis and for reproducing the manuscript's figures are also available as quarto documents using the knitr engine on the GitHub repository "MatterOfSalt" (https://github.com/attiszabo/MatterOfSalt).

References

Anda, D., T. Felföldi, Z. Márton, et al. 2025. "Assessment of Bacterioplankton Community Structure in Relation to Macrophyte Cover in Shallow Lakes of the Carpathian Basin (Central Europe)." Available at SSRN 5580660. https://doi.org/10.2139/ssrn.5580660.

Ball, P., and J. E. Hallsworth. 2015. "Water Structure and Chaotropicity: Their Uses, Abuses and Biological Implications." *Physical Chemistry Chemical Physics* 17: 8297–8305. https://doi.org/10.1039/C4CP04564E.

Banciu, H. L., and M. S. Muntyan. 2015. "Adaptive Strategies in the Double-Extremophilic Prokaryotes Inhabiting Soda Lakes." *Current Opinion in Microbiology* 25: 73–79. https://doi.org/10.1016/j.mib.2015.05.003.

Banciu, H. L., and D. Y. Sorokin. 2013. "Adaptation in Haloalkaliphiles and Natronophilic Bacteria." In *Polyextremophiles: Life Under Multiple Forms of Stress*, edited by J. Seckbach, A. Oren, and H. Stan-Lotter, 121–178. Netherlands: Springer.

Bayly, I. A. E. 1967. "The General Biological Classification of Aquatic Environments With Special Reference to Those of Australia." In *Australian Inland Waters and Their Fauna*, edited by A. H. Weatherley, 78–104. Canberra: Australian National University Press.

Boros, E., L. Jurecska, E. Tatár, L. Vörös, and M. Kolpakova. 2017. "Chemical Composition and Trophic State of Shallow Saline Steppe Lakes in Central Asia (North Kazakhstan)." *Environmental Monitoring and Assessment* 189: 1–12. https://doi.org/10.1007/s10661-017-6242-6.

Boros, E., and M. Kolpakova. 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: e0202205. https://doi.org/10.1371/journal.pone.0202205.

Boros, E., K. V.-Balogh, B. Csitári, L. Vörös, and A. J. Székely. 2020. "Macrophytes and Groundwater Drive Extremely High Organic Carbon Concentration of Soda Pans." *Freshwater Biology* 65: 1555–1568. https://doi.org/10.1111/fwb.13521.

Boros, E., Z. Végvári, A. Kiss, et al. 2025. "Waterbirds as Ecosystem Flagships of Eurasian Inland Saline Waters: Dual Control Indicators of Trophic Structure." *Ecological Indicators* 172: 113197. https://doi.org/10.1016/j.ecolind.2025.113197.

Cáceres, M. D., and P. Legendre. 2009. "Associations Between Species and Groups of Sites: Indices and Statistical Inference." *Ecology* 90: 3566–3574. https://doi.org/10.1890/08-1823.1.

Campbell, B. J., and D. L. Kirchman. 2013. "Bacterial Diversity, Community Structure and Potential Growth Rates Along an Estuarine Salinity Gradient." *ISME Journal* 7: 210–220. https://doi.org/10.1038/ismej.2012.93.

Csitári, B., A. Bedics, T. Felföldi, et al. 2022. "Anion-Type Modulates the Effect of Salt Stress on Saline Lake Bacteria." *Extremophiles* 26: 12. https://doi.org/10.1007/s00792-022-01260-5.

de la Haba, R. R., D. R. Arahal, C. Sánchez-Porro, et al. 2023. "A Long-Awaited Taxogenomic Investigation of the Family Halomonadaceae." *Frontiers in Microbiology* 14: 1293707. https://doi.org/10.3389/fmicb.2023.1293707.

Edwardson, C. F., and J. T. Hollibaugh. 2018. "Composition and Activity of Microbial Communities along the Redox Gradient of an Alkaline, Hypersaline, Lake." *Frontiers in Microbiology* 9: 14. https://doi.org/10.3389/fmicb.2018.00014.

Eiler, A., A. H. Farnleitner, T. C. Zechmeister, et al. 2003. "Factors Controlling Extremely Productive Heterotrophic Bacterial Communities in Shallow Soda Pools." *Microbial Ecology* 46: 43–54. https://doi.org/10.1007/s00248-002-2041-9.

Fazi, S., S. Amalfitano, S. Venturi, et al. 2021. "High Concentrations of Dissolved Biogenic Methane Associated With Cyanobacterial Blooms in East African Lake Surface Water." *Communications Biology* 4: 845. https://doi.org/10.1038/s42003-021-02365-x.

Felföldi, T. 2020. "Microbial Communities of Soda Lakes and Pans in the Carpathian Basin: A Review." *Biologia Futura* 71: 393–404. https://doi.org/10.1007/s42977-020-00034-4.

Ghylin, T. W., S. L. Garcia, F. Moya, et al. 2014. "Comparative Single-Cell Genomics Reveals Potential Ecological Niches for the Freshwater ACI Actinobacteria Lineage." *ISME Journal* 8: 2503–2516. https://doi.org/10.1038/ismej.2014.135.

Grant, W. D., and D. Y. Sorokin. 2011. "Distribution and Diversity of Soda Lake Alkaliphiles." In *Extremophiles Handbook*, edited by K. Horiskoshi, 27–54. Tokyo: Springer. https://doi.org/10.1007/978-4-431-53898-1_3.

Gunde-Cimerman, N., A. Plemenitaš, and A. Oren. 2018. "Strategies of Adaptation of Microorganisms of the Three Domains of Life to High Salt Concentrations." *FEMS Microbiology Reviews* 42: 353–375. https://doi.org/10.1093/femsre/fuy009.

Gutiérrez-Preciado, A., B. Dede, B. A. Baker, L. Eme, D. Moreira, and P. López-García. 2024. "Extremely Acidic Proteomes and Metabolic Flexibility in Bacteria and Highly Diversified Archaea Thriving in Geothermal Chaotropic Brines." *Nature Ecology & Evolution* 8: 1856–1869. https://doi.org/10.1038/s41559-024-02505-6.

Hallsworth, J. E., M. M. Yakimov, P. N. Golyshin, et al. 2007. "Limits of Life in $MgCl_2$-Containing Environments: Chaotropicity Defines the Window." *Environmental Microbiology* 9: 801–813. https://doi.org/10.1111/j.1462-2920.2006.01212.x.

Hamilton, N., and M. Ferry. 2018. "Ggtern: Ternary Diagrams Using ggplot2." *Journal of Statistical Software* 87: 1–17. https://doi.org/10.18637/jss.v087.c03.

Hammer, Ø., D. A. T. Harper, and P. D. Ryan. 2001. "PAST: Paleontological Statistics Software Package for Education and Data Analysis." *Palaeontologia Electronica* 4: 1–9. https://palaeo-electronica.org/2001_1/past/issue1_01.htm.

Hammer, U. T. 1986. *Saline Lake Ecosystems of the World*. Springer Science & Business Media.

Herlemann, D. P., M. Labrenz, K. Jürgens, S. Bertilsson, J. J. Waniek, and A. F. Andersson. 2011. "Transitions in Bacterial Communities Along the 2000 Km Salinity Gradient of the Baltic Sea." *ISME Journal* 5: 1571–1579. https://doi.org/10.1038/ismej.2011.41.

Hijmans, R. J., E. Williams, C. Vennes, and M. R. J. Hijmans. 2017. "Package 'geosphere'." *Spherical Trigonometry* 1: 1–45. https://cran.r-project.org/web/packages/geosphere/index.html.

Ji, M., W. Kong, L. Yue, J. Wang, Y. Deng, and L. Zhu. 2019. "Salinity Reduces Bacterial Diversity, But Increases Network Complexity in Tibetan Plateau Lakes." *FEMS Microbiology Ecology* 95: fiz190. https://doi.org/10.1093/femsec/fiz190.

Johnson, J. S., D. J. Spakowicz, B. Y. Hong, et al. 2019. "Evaluation of 16S rRNA Gene Sequencing for Species and Strain-Level Microbiome Analysis." *Nature Communications* 10: 5029. https://doi.org/10.1038/s41467-019-13036-1.

Jurdzinski, K. T., M. Mehrshad, L. F. Delgado, Z. Deng, S. Bertilsson, and A. F. Andersson. 2023. "Large-Scale Phylogenomics of Aquatic Bacteria Reveal Molecular Mechanisms for Adaptation to Salinity." *Science Advances* 9: eadg2059. https://doi.org/10.1126/sciadv.adg2059.

Kambura, A. K. 2017. "Metagenomic and Metatranscriptomic Analysis of Bacterial, Archaeal and Fungal Communities Within the Hot Springs of Lake Magadi in Kenya." PhD Thesis, Institute of Biotechnology Research, Jomo Kenyatta University of Agriculture and Technology. http://ir.jkuat.ac.ke/handle/123456789/2403?show=full.

Korponai, K., A. Szabó, B. Somogyi, et al. 2019. "Dual Bloom of Green Algae and Purple Bacteria in an Extremely Shallow Soda Pan." *Extremophiles* 23: 467–477. https://doi.org/10.1007/s00792-019-01098-4.

Langenheder, S., and A. J. Székely. 2011. "Species Sorting and Neutral Processes Are Both Important During the Initial Assembly of Bacterial Communities." *ISME Journal* 5: 1086–1094. https://doi.org/10.1038/ismej.2010.207.

Lavrentyeva, E. V., E. B. Erdyneeva, T. G. Banzaraktsaeva, et al. 2020. "Prokaryotic Diversity in the Biotopes of the Gudzhirganskoe Saline Lake (Barguzin Valley, Russia)." *Microbiology* 89: 359–368. https://doi.org/10.1134/S0026261720030157.

Lozupone, C. A., and R. Knight. 2007. "Global Patterns in Bacterial Diversity." *Proceedings of the National Academy of*

Sciences 104: 11436–11440. https://doi.org/10.1073/pnas.0611525104.

Márton, Z., B. Csitári, T. Felföldi, et al. 2023*a*. "Contrasting Response of Microeukaryotic and Bacterial Communities to the Interplay of Seasonality and Local Stressors in Shallow Soda Lakes." *FEMS Microbiology Ecology* 99: fiad095. https://doi.org/10.1093/femsec/fiad095.

Márton, Z., B. Szabó, C. F. Vad, K. Pálffy, and Z. Horváth. 2023*b*. "Environmental Changes Associated With Drying Climate Are Expected to Affect Functional Groups of Pro- and Microeukaryotes Differently in Temporary Saline Waters." *Scientific Reports* 13: 3243. https://doi.org/10.1038/s41598-023-30385-6.

Matyugina, E., N. Belkova, S. Borzenko, et al. 2018. "Structure and Diversity Dynamics of Microbial Communities at Day and Night: Investigation of Meromictic Lake Doroninskoe, Transbaikalia, Russia." *Journal of Oceanology and Limnology* 36: 1978–1992. https://doi.org/10.1007/s003?43-018-7332-1.

Mentes, A., A. Szabó, B. Somogyi, et al. 2018. "Differences in Planktonic Microbial Communities Associated With Three Types of Macrophyte Stands in a Shallow Lake." *FEMS Microbiology Ecology* 94: fix164. https://doi.org/10.1093/femsec/fix164.

Messager, M. L., B. Lehner, G. Grill, I. Nedeva, and O. Schmitt. 2016. "Estimating the Volume and Age of Water Stored in Global Lakes Using a Geo-Statistical Approach." *Nature Communications* 7: 13603. https://doi.org/10.1038/ncomms13603.

Oksanen, J. 2022. "vegan: Community Ecology Package." R package version 2.6-4. https://CRAN.R-project.org/package=vegan.

Oren, A. 2024. "Novel Insights Into the Diversity of Halophilic Microorganisms and Their Functioning in Hypersaline Ecosystems." *npj Biodiversity* 3: 18. https://doi.org/10.1038/s44185-024-00050-w.

Paver, S. F., D. Muratore, R. J. Newton, and M. L. Coleman. 2018. "Reevaluating the Salty Divide: Phylogenetic Specificity of Transitions Between Marine and Freshwater Systems." *mSystems* 3: 10–1128. https://doi.org/10.1128/msystems.00232-18.

Pellegrinetti, T. A., Y. B. Cotta, P. L. Feitosa, et al. 2024. "The Role of Microbial Communities in Biogeochemical Cycles and Greenhouse Gas Emissions Within Tropical Soda Lakes." *Science of the Total Environment* 947: 174646. https://doi.org/10.1016/j.scitotenv.2024.174646.

Phillips, A. A., D. R. Speth, L. G. Miller, et al. 2021. "Microbial Succession and Dynamics in Meromictic Mono Lake, California." *Geobiology* 19: 376–393. https://doi.org/10.1111/gbi.12437.

Quast, C., E. Pruesse, P. Yilmaz, et al. 2012. "The SILVA Ribosomal RNA Gene Database Project: Improved Data Processing and Web-Based Tools." *Nucleic Acids Research* 41: D590–D596. https://doi.org/10.1093/nar/gks1219.

R Core Team. 2023. *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing. https://www.R-project.org/.

Rohwer, R. R., J. J. Hamilton, R. J. Newton, and K. D. McMahon. 2018. "TaxAss: Leveraging a Custom Freshwater Database Achieves Fine-Scale Taxonomic Resolution." *mSphere* 3: e00327-18. https://doi.org/10.1128/mSphere.00327-18.

Saccò, M., N. E. White, C. Harrod, et al. 2021. "Salt to Conserve: A Review on the Ecology and Preservation of Hypersaline Ecosystems." *Biological Reviews* 96: 2828–2850. https://doi.org/10.1111/brv.12780.

Schloss, P. D. 2021. "Amplicon Sequence Variants Artificially Split Bacterial Genomes into Separate Clusters." *mSphere* 6: e00191-21. https://doi.org/10.1128/mSphere.00191-21.

Schloss, P. D., S. L. Westcott, T. Ryabin, et al. 2009. "Introducing Mothur: Open-Source, Platform-Independent, Community-Supported Software for Describing and Comparing Microbial Communities." *Applied and Environmental Microbiology* 75: 7537–7541. https://doi.org/10.1128/AEM.01541-09.

Sheneman, L., J. Evans, and J. A. Foster. 2006. "Clearcut: A Fast Implementation of Relaxed Neighbor Joining." *Bioinformatics* 22: 2823–2824. https://doi.org/10.1093/bioinformatics/btl478.

Sinclair, L., O. A. Osman, S. Bertilsson, and A. Eiler. 2015. "Microbial Community Composition and Diversity via 16S rRNA Gene Amplicons: Evaluating the Illumina Platform." *PLoS One* 10: e0116955. https://doi.org/10.1371/journal.pone.0116955.

Somogyi, B., T. Felföldi, E. Boros, A. Szabó, and L. Vörös. 2022. "Where the Little Ones Play the Main Role—Picophytoplankton Predominance in the Soda and Hypersaline Lakes of the Carpathian Basin." *Microorganisms* 10: 818. https://doi.org/10.3390/microorganisms10040818.

Stevens, A. H., and C. S. Cockell. 2020. "A Systematic Study of the Limits of Life in Mixed Ion Solutions: Physicochemical Parameters Do Not Predict Habitability." *Frontiers in Microbiology* 11: 1478. https://doi.org/10.3389/fmicb.2020.01478.

Szabó, A. 2025. *Data, Metadata and Analysis Scripts Used for the Global Assessment of the Effect of Salt Ionic Composition as a Driver of Aquatic Bacterial Diversity*. Zenodo. https://doi.org/10.5281/zenodo.17546050.

Szabó, A., B. K. Korponai, B. Somogyi, et al. 2020. "Grazing Pressure-Induced Shift in Planktonic Bacterial Communities With the Dominance of acIII-A1 Actinobacterial Lineage in Soda Pans." *Scientific Reports* 10: 19871. https://doi.org/10.1038/s41598-020-76822-8.

Szabó, A., K. Korponai, C. Kerepesi, et al. 2017. "Soda Pans of the Pannonian Steppe Harbor Unique Bacterial Communities Adapted to Multiple Extreme Conditions."

Extremophiles 21: 639–649. https://doi.org/10.1007/s00792-017-0932-4.

Szabó, B., A. Szabó, C. F. Vad, et al. 2022. "Microbial Stowaways: Waterbirds as Dispersal Vectors of Aquatic Pro- and Microeukaryotic Communities." *Journal of Biogeography* 49: 1286–1298. https://doi.org/10.1111/jbi.14381.

Szuróczki, S., A. Szabó, K. Korponai, et al. 2020. "Prokaryotic Community Composition in a Great Shallow Soda Lake Covered by Large Reed Stands (Neusiedler See/Lake Fertő) as Revealed by Cultivation- and DNA-Based Analyses." *FEMS Microbiology Ecology* 96: fiaa159. https://doi.org/10.1093/femsec/fiaa159.

Tamames, J., J. J. Abellan, M. Pignatelli, A. Camacho, and A. Moya. 2010. "Environmental Distribution of Prokaryotic Taxa." *BMC Microbiology* 10: 85. https://doi.org/10.1186/1471-2180-10-85.

Thompson, L. R., J. G. Sanders, D. McDonald, et al. 2017. "A Communal Catalogue Reveals Earth's Multiscale Microbial Diversity." *Nature* 551: 457–463. https://doi.org/10.1038/nature24621.

Toner, J. D., and D. C. Catling. 2020. "A Carbonate-Rich Lake Solution to the Phosphate Problem of the Origin of Life." *Proceedings of the National Academy of Sciences* 117: 883–888. https://doi.org/10.1073/pnas.1916109117.

Vavourakis, C. D., M. Mehrshad, C. Balkema, et al. 2019. "Metagenomes and Metatranscriptomes Shed New Light on the Microbial-Mediated Sulfur Cycle in a Siberian Soda Lake." *BMC Biology* 17: 69. https://doi.org/10.1186/s12915-019-0688-7.

Vellend, M. 2010. "Conceptual Synthesis in Community Ecology." *Quarterly Review of Biology* 85: 183–206. https://doi.org/10.1086/652373.

Waajen, A. C., J. Heinz, A. Airo, and D. Schulze-Makuch. 2020. "Physicochemical Salt Solution Parameters Limit the Survival of *Planococcus halocryophilus* in Martian Cryobrines." *Frontiers in Microbiology* 11: 1284. https://doi.org/10.3389/fmicb.2020.01284.

Wei, T., V. Simko, M. Levy, Y. Xie, Y. Jin, and J. Zemla. 2017. "Package 'corrplot'." *Statistician* 56: e24. https://cran.r-project.org/web/packages/corrplot/index.html.

Westcott, S. L., and P. D. Schloss. 2017. "OptiClust, an Improved Method for Assigning Amplicon-Based Sequence Data to Operational Taxonomic Units." *mSphere* 2: e00073-17. https://doi.org/10.1128/mSphereDirect.00073-17.

Wickham, H., W. Chang, and M. H. Wickham. 2016. "Package 'ggplot2'." Create Elegant Data Visualisations Using the Grammar of Graphics. Version 2: 1–189.

Williams, W. D. 1998. "Management of Inland Saline Waters." In *Guidlines of Lake Management*, edited by S. E. Jorgensen and R. A. Vollenweider, 6. Japan: ILEC.

Yu, G., D. K. Smith, H. Zhu, Y. Guan, and T. T. Lam. 2017. "ggtree: An R Package for Visualization and Annotation of Phylogenetic Trees With Their Covariates and Other Associated Data." *Methods in Ecology and Evolution* 8: 28–36. https://doi.org/10.1111/2041-210X.12628.

Zhou, J., and D. Ning. 2017. "Stochastic Community Assembly: Does It Matter in Microbial Ecology?" *Microbiology and Molecular Biology Reviews* 81: 1–32. https://doi.org/10.1128/mmbr.00002-17.

Zorz, J. K., C. Sharp, M. Kleiner, et al. 2019. "A Shared Core Microbiome in Soda Lakes Separated by Large Distances." *Nature Communications* 10: 4230. https://doi.org/10.1038/s41467-019-12195-5.

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Submitted 26 February 2025
Revised 17 November 2025
Accepted 29 November 2025