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ORIGINAL ARTICLE

How Do Environmental and Spatial Factors Influence Beta Diversity and Composition of Abundant and Rare Bacterioplankton Communities in Lakes From the Patagonian Plateaus?

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ABSTRACT

1. Lakes in the same geographic region often exhibit outstanding differences in environmental features, as is the case in the high-altitude lakes from the basaltic plateaus of Patagonia (Argentina).
2. We analysed bacterial community composition (BCC) at local and regional scales in 37 shallow lakes on two Patagonian plateaus and evaluated the influence of environmental variables and geographic position on community structure.
3. β diversity within each plateau was the key component of regional bacterioplankton diversity. The sum of amplicon sequence variants (ASV) exclusive to each plateau was greater than 50%. Most of the exclusive ASVs corresponded to rare ones from each plateau, whereas abundant ASVs were mostly shared by both plateaus (81%), which indicates a more restricted distribution of rare and higher dispersal of abundant ASVs.
4. The lakes of the Strobel and Buenos Aires plateaus spanned a wide range of environmental conditions, which were associated with the BCC of lakes from both plateaus. Macrophyte cover, fish presence, conductivity, dissolved organic carbon, pH, and altitude were associated with BCC in these lakes. Notably, differences at the phylum and class levels were observed in lakes with contrasting limnological features. Fishless lakes had significantly greater relative abundance of *Bacteroidia* and *Gammaproteobacteria* than fish-stocked lakes. Lakes without macrophytes showed significantly higher relative abundances

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of *Cyanobacteria* and *Planctomycetota* than vegetated environments, and, conversely, vegetated lakes exhibited the highest relative abundance of *Bacteroidota*.

5. Our study shows a strong link between BCC and environmental factors, regardless of their regional or local classifications. Rare bacteria were more strongly associated with spatial factors than total or abundant bacteria, suggesting a limited dispersal capacity. Our findings highlight that variability in environmental conditions influences BCC and determines high β diversity and, consequently, high γ diversity.

1 | Introduction

Bacterioplankton are highly diverse and play a key role in freshwater ecosystems. They are critical in the decomposition of organic material into nutrients that supply higher trophic levels, which makes them the main drivers of biogeochemical cycles in aquatic systems (Cotner and Biddanda 2002; Zhang et al. 2019). Bacterial community composition (BCC) is defined by abundant bacteria—which generally represent few taxa with high abundance and are considered the active fraction of bacterioplankton—and rare bacteria—more taxa with low abundance which are considered a less active or dormant fraction usually referred to as the seed bank (Casamayor et al. 2000; Acinas et al. 2004; Pedrós-Alió 2012). Microbial rank-abundance curves are dynamic, with repeated transitions to and from the seed bank which help maintain high microbial biodiversity (Jones and Lennon 2010).

BCC is influenced by dispersal capacity, local environmental variables, and biotic interactions (e.g., competition, cooperation, and predation) (Lindström et al. 2006; Zhou and Ning 2017; Liu et al. 2019; Sadeghi et al. 2021). Bacterioplankton exhibit spatial variability, with some species showing significant local variation and high turnover in small areas and others showing changes on a larger scale and turnover only detectable in large spaces (Borcard et al. 2004; Declerck et al. 2011). The dispersal capacity of individuals strongly shapes species distribution and their relationship with the local environment and diminishes with increasing spatial scale (Beisner et al. 2006; Liu et al. 2017; Yang et al. 2018). Given their small size and high reproduction rate, bacterioplankton can disperse effectively by different agents (wind, birds, human activity, etc.), generally with a worldwide distribution and less restricted by geographical barriers (e.g., Finlay 2002). Therefore, BCC should not show spatial autocorrelation among lakes (Beisner et al. 2006). Additionally, dispersal rates may depend on whether water bodies are hydrologically connected (Ruiz-González et al. 2015). As freshwater ecosystems are highly diverse in connectivity and morphometric and limnological conditions, significant variations in BCC can be anticipated across different types of water bodies (Barberán and Casamayor 2010; Fillinger et al. 2019). The definition of abundant and rare bacteria also depends on the spatial scale, since taxa may be locally (in individual lakes) or regionally (across lakes) abundant or rare. As these components of bacterial communities may differ in dispersal capacity and the range of environmental conditions where they can proliferate, they may show different responses to environmental and spatial gradients. For instance, regionally abundant taxa may have higher dispersal rates and a broader range of suitable environmental conditions to proliferate than locally rare taxa.

Understanding the structure of bacterial communities in lakes requires considering both the local environmental conditions that shape community assembly and the broader spatial context in which lakes are embedded (Lindström and Langenheder 2012). In this sense, community diversity metrics provide valuable insights into how ecological processes operate across spatial scales (Leibold et al. 2004). Species diversity is one of the most insightful community metrics and is shaped by regional factors affecting the movement and establishment of organisms (Hubbell 2001) and local factors such as environmental conditions, area, food availability, and biotic interactions (Hutchinson 1959; Morin 1999). To study regional trends, diversity is divided into hierarchical levels α (local diversity), β (variation in species among sites), and γ (regional diversity) (Whittaker 1972). γ diversity represents the combination of α and β diversity and may help determine how α and β components contribute to regional diversity across spatial scales (Veech et al. 2002). These metrics provide a useful framework for exploring the spatial patterns of community structure in lakes from different geographic locations that exhibit contrasting environmental conditions.

The Strobel (STR) and Buenos Aires (BA) plateaus encompass many naturally fishless lakes located at varying altitudes (700–1800 m a.s.l.). These lakes exhibit considerable heterogeneity in terms of size, shape, and physical and chemical attributes, which is further influenced by factors such as the degree of macrophyte cover (predominantly *Myriophyllum quitense* Kunth), the presence or absence of introduced rainbow trout, and variations in water levels (Lancelotti 2009; Izaguirre et al. 2018; Saad et al. 2018; Porcel et al. 2019; Sabio y García et al. 2024). These environments are the habitat of several waterbird species from five families—Anatidae, Podicipedidae, Phoenicopteridae, Rallidae, and Scolopacidae (Lancelotti et al. 2009). In these harsh environments, the bacterial community endures wide fluctuations in light and temperature, transitions between ice-covered and ice-free periods, and intense exposure to high UV radiation. These factors likely act as significant filters in the colonisation process of bacteria. These variable conditions make an ideal natural system to study associations between local environmental variables and geographical position. Phytoplankton and zooplankton communities in this region are mainly constrained by macrophytes, fish, conductivity, dissolved organic carbon (DOC), altitude, and spatial factors (Porcel et al. 2020). High rates of dispersal of small organisms within plateaus tend to homogenise these communities.

In the present study, we addressed bacterial community heterogeneity in remote lakes from the Patagonian basaltic plateaus and the influence of spatial and local environmental factors on the BCC. We analysed the total species, abundant species, and fraction of rare species at both local and regional

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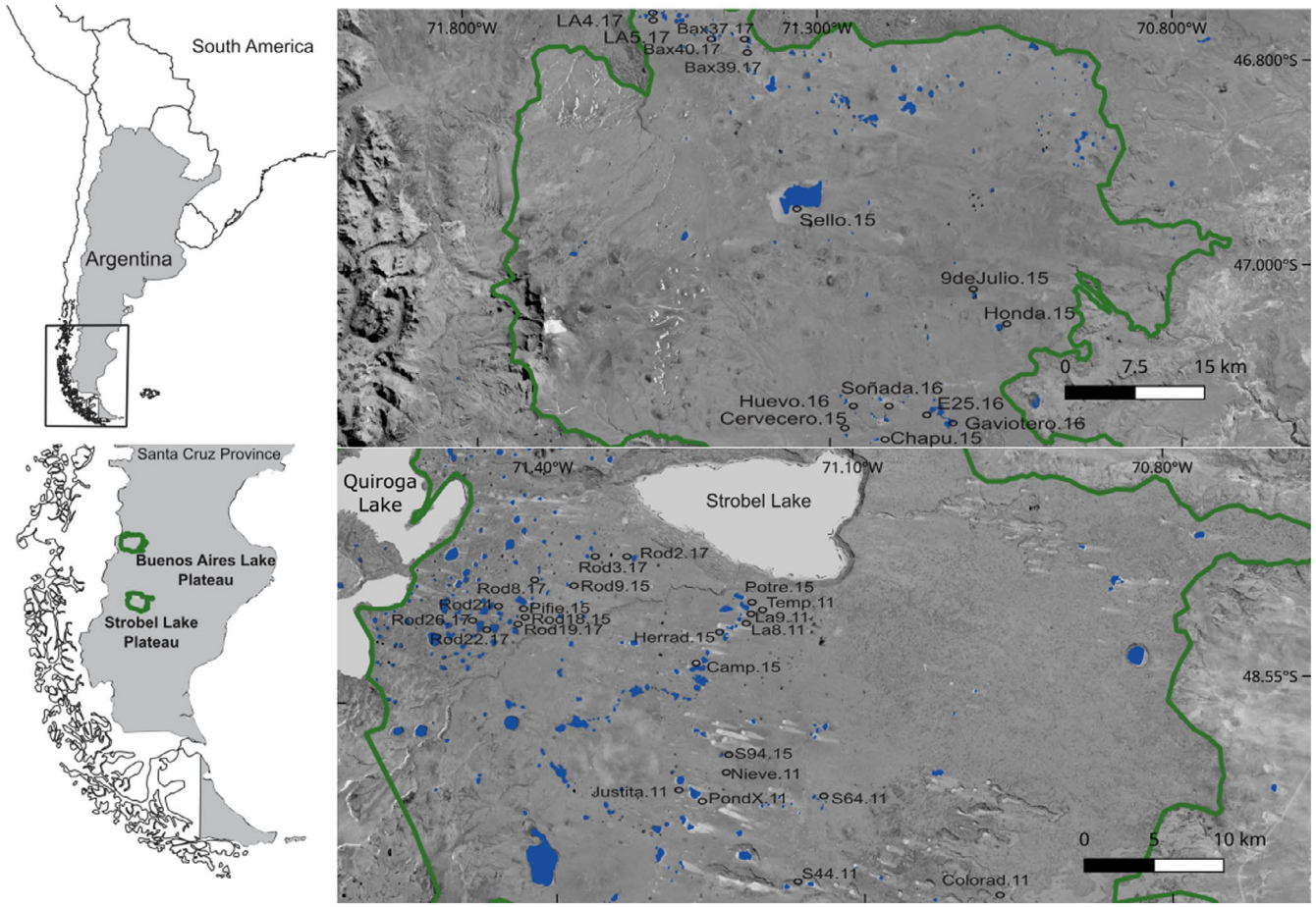


FIGURE 1 | Geographic location of the lakes studied in the Buenos Aires and Strobel plateaus (Santa Cruz Province, Argentina).

scales, with a view to collecting additional and complementary information on the BCC. We defined α as the local bacterial diversity within each lake, β reflects variations among lakes within (β1) and between (β2) plateaus, while γ corresponds to regional diversity that encompasses the total diversity across all lakes studied.

The aims of our study were: (a) to evaluate α, β, and γ bacterial diversity in the neighbouring Patagonian plateaus BA and STR, and (b) to assess the influence of local (environmental abiotic and biotic variables) and spatial (latitude and longitude) factors on lake BCC. We evaluated the BCC considering (i) lake regimes (i.e., clear vegetated, clear mesohaline, organic turbid, or inorganic turbid) which represent local environmental conditions in terms of turbidity, nutrient concentrations, and macrophyte cover (α); (ii) among-lake variations within plateaus (β1); (iii) among-lake variations between plateaus (β2); and (iv) regional diversity for both plateaus (γ).

We postulated the following hypotheses: (1) β1 and β2 bacterial diversity will largely account for regional diversity, (2) the composition of regionally abundant bacteria, which often have high dispersal rates, will be explained mainly by limnological conditions within lakes due to high variability among lakes, and (3) the composition of locally and regionally rare taxa will be more strongly influenced by the geographical position of lakes due to their low abundance, more limited dispersal rates, and therefore more restricted distribution.

2 | Methods

2.1 | Study Area and Sampling

The basaltic plateaus, originated by tectonic activity during the Tertiary and Quaternary (Panza and Franchi 2002), are in the northwestern area of Santa Cruz Province, in the arid Patagonian steppe of Argentina (Figure 1). This region is characterised by an extremely cold, windy, and dry climate (Cabrera 1976).

The BA and STR plateaus have an extent of 3650 km^2 and 3000 km^2, respectively. The BA Plateau contains more than 150 shallow lakes, with a maximum altitude ~1800 m a.s.l. in the west and a decrease to ~700 m a.s.l. toward the east (Roesler 2016). The STR Plateau reaches altitudes of 1200 m a.s.l. in the west and decreases to 700 m a.s.l. in the east. The number of lakes in the STR Plateau varies from 700 to 2000 in extreme dry and wet periods, respectively (Lancelotti 2009). Although these remote lakes are naturally fishless (Izaguirre et al. 2018), more than 40 lakes in the STR Plateau have been stocked with rainbow trout (*Oncorhynchus mykiss*; Walbaum, 1792) over the last two decades (Lancelotti 2009). In contrast, the lakes in the BA Plateau remain fishless.

A strong decrease in water levels in most arheic basins in lakes of the Patagonian plateau was observed in field studies between 2006 and 2017 (field observations), further confirmed through time series analyses of climate data and satellite images of the

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STR Plateau (Lancelotti et al. 2020). In the summer of 2016, 71% of the lakes studied in the STR Plateau showed a marked reduction in water levels (26% were dry or almost dry), compared to 50% of the lakes studied in the BA Plateau (Izaguirre et al. 2018).

In total, 37 samples were collected in four summer campaigns (December 2011, March 2015, January 2016, and February 2017), one from each of the 23 lakes in STR and the 14 lakes in BA (Figure 1). The lakes selected on both plateaus, most of them arheic basins, cover a wide range of conditions in space (latitude and longitude), topography (altitude), morphometry (lake area), and limnological variables that act as environmental filters. Due to the remoteness of the study region and logistical constraints, sampling had to be carried out in different years, which may involve temporal variability that was not addressed in the present study.

2.2 | Environmental Variables

Several physical and chemical variables were measured to characterise local conditions in each lake. The measurements of abiotic data were obtained from the euphotic zone of the lakes, ~30 cm below the surface. Temperature, pH, and conductivity were measured in situ with a Horiba D-54 (HORIBA Advanced Techno Co., Kyoto, Japan), and dissolved oxygen (DO) was measured with a HACH TM HQ30 dm portable sensor (Hach Company, Colorado, USA). The photosynthetically active radiation (PAR) was measured with a LI-COR radiometer, equipped with a submersible spherical quantum sensor (Li-Cor 3 SA Li-Cor PAR, NE, USA) at 10-cm depth intervals; then, the vertical attenuation coefficient of PAR (Kd) was calculated as the slope of the relationship between ln (irradiance) and depth (Kirk 1994). Samples for DOC, chlorophyll *a* (Chl*a*), and dissolved nutrient analyses were collected in plastic bottles cleaned with HCl 2% and rinsed with MilliQ water, and transported in cold to the field laboratory, where they were immediately filtered through glass fibre filters (0.7 μm, GF/F Whatman, Maidstone, UK). Samples for DOC determinations were acidified (pH 2) and analysed with a high-temperature Pt catalyst oxidation method (Shimadzu Analyzer TOC-L), following the recommendations of Sharp et al. (1993). Concentrations of Chl*a* (corrected for phaeopigments) were determined by spectrophotometry using acetone as solvent. The equations published by Marker et al. (1980) were used for calculations. Dissolved inorganic nutrients were measured using specific reagent kits in a HACH DR/2800 spectrophotometer, following APHA (2005). The nutrients measured were soluble reactive phosphorus (P-PO_4) and dissolved inorganic nitrogen (DIN) calculated as the sum of ammonium and nitrate.

The cover of submerged macrophytes was estimated semi-quantitatively for each water body, considering three categories: without vegetation (< 15% cover), intermediate vegetation (~50% cover) and with vegetation (> 50% cover). Fish introduction was considered a categorical variable (presence/absence of rainbow trout). In addition, "plateau" was considered a dummy variable (lakes from the BA Plateau as "1" values and lakes from the STR Plateau as "0" values).

Lake altitude, area, and depth were included in the analysis as environmental factors. The area was estimated with Google Earth tools (Google LLC, California, USA), and the altitude and geographic location of each lake were recorded with a Global Positioning System. We established two lake categories based on depth: shallow (< 10 m) and deep (≥ 10 m) lakes. Depth was estimated with a portable sounder (Speedtech, USA) and on the basis of previous data (Lancelotti et al. 2010).

2.3 | Bacterial DNA Analysis

Samples for bacterial DNA analyses were collected within the euphotic zone at the subsurface layer. Water samples were prefiltered with a 51 μm mesh and transported in cold to the field laboratory using plastic bottles washed with HCl 2% and rinsed with MilliQ water. Samples were then sequentially filtered through a net (18 μm mesh) and a 0.2 μm polycarbonate filter (Merck Millipore, Germany). The filters were maintained in liquid nitrogen during the campaigns and conserved at −80°C in the laboratory. DNA was extracted using CTAB lysis buffer and chloroform/isoamyl alcohol following the protocol described in Fernández Zenoff et al. (2006). The environmental DNA obtained was processed through Illumina Miseq 2 × 300 paired-end sequencing (in Macrogen, Korea) after amplification of the V3–V5 variable region of the 16S subunit of ribosomal RNA with the 341F-805R primer set (Herlemann et al. 2011).

2.4 | Bioinformatic Analysis

Raw paired-end Illumina MiSeq-sequenced data were analysed through the DADA2 package (2.14 version; Callahan et al. 2016) in the R environment. The analysis involved the quality filtering and trimming of forward and reverse sequences using the parameters truncLen c = (260, 190) and maxEE = c (2, 5), merging of sequences, removal of the chimera, and taxonomic assignation of the amplicon sequence variants (ASVs). The ASV table obtained was further filtered to avoid possible chimeras by excluding ASVs with less than 50 reads and present in less than three samples (Metz et al. 2022; Sabio y García et al. 2024). ASVs taxonomically affiliated to chloroplast, mitochondria, and the Archaea domain were also eliminated. The taxonomic classification was performed using the SILVA database ("https://www.arb-silva.de/documentation/release-132/"). Samples (mean reads per sample = 58,696) were then normalised to the number of reads of the sample with the least reads (Cmin = 19,659) using the SRS pipeline, which preserves the relative abundances of ASVs after normalisation as similar as possible to those of the original datasets (Beule and Karlovsky 2020). Phyloseq (McMurdie and Holmes 2013) and ggplot2 R packages were used for preliminary ASV table analysis and graphical visualisation.

We applied two classifications of ASVs to assess abundance patterns on local and regional scales. On a local scale, ASVs were classified considering those from each lake separately, whereas regional classification considered ASVs from all the lakes encompassed in the study. Following the Sabio y García et al. (2024) classification of BCC in lakes from the STR Plateau, locally abundant ASVs were defined as those which represented 1% or more of all the ASVs in a particular lake, whereas locally rare ASVs were those with a relative abundance of less than 1% in a lake. On a regional scale, the criteria of Pearman et al. (2022)

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were adapted as follows: regionally abundant ASVs were those representing more than 0.1% of total ASVs across all 37 lakes analysed, and regionally, rare ASVs were those with a relative abundance of 0.1% or less across lakes.

Table S1 provides all ASVs for each lake. The raw sequence data are available in the European Nucleotide Archive (See accession numbers in Table S1).

2.5 | Data Analysis

Principal component analysis (PCA) was performed to detect patterns in environmental variables indicating relationships between samples and/or between variables (pH, DO, conductivity, P-PO_4, DIN, and Chl*a*). All variables were standardised prior to analysis. In addition, a scatter plot of PCA scores for components 1 and 2 was created and partitioned by the 'plateau' variable, to assess whether the lakes were separated by plateau on the basis of the environmental variables analysed.

To compare the taxonomic structure of bacterial communities between plateaus, we carried out a non-metric multidimensional scaling (NMDS) ordination based on the Bray–Curtis similarity index with the total community, as well as local and regional classifications of abundant and rare ASVs, followed by an analysis of dissimilarities (ANOSIM). To further explore associations between individual environmental variables on BCC, we used the function *envfit* (Oksanen et al. 2007) to check for correlations between the main ordination axes and significant environmental variables.

Shannon diversity ($H' = -\Sigma pi \ln(pi)$) and Evenness ($EH' = H'/\ln S$) and ASV richness (total bacteria) were calculated with Past4.07b software (Hammer et al. 2001) to study patterns in α diversity. Kruskal–Wallis non-parametric variance was used to evaluate differences among lakes, whereas Spearman correlation analyses were performed to evaluate relationships/associations between variables. Venn diagrams were created using Venny's on-line reference (Oliveros 2015) for visualisation of shared and exclusive ASVs between plateaus for total bacteria, as well as regionally rare and abundant classifications.

Diversity was partitioned into local species richness (number of species) at each lake studied (α), diversity among lakes within each plateau (β1), and diversity among lakes in different plateaus (β2) using the 'adipart' function in the *vegan* package (Oksanen et al. 2019). Regional diversity (γ) for total bacteria was estimated as the sum of the categories mentioned above ($\gamma = \alpha + \beta1 + \beta2$) following MacArthur et al. (1966) and Levins (1968). The additive partitioning of diversity has the advantage of yielding both total diversity and its components in the same unit, which allows for direct comparison (Lande 1996). The diversity values observed were compared to expected random values obtained from null models (r2dtable method, with 999 simulations) (Crist et al. 2003), which provide a basis for inferences on drivers of species diversity across scales. The r2dtable function generates random contingency tables that preserve the observed row and column sums, effectively maintaining species frequencies and sample totals. By comparing the observed diversity metrics (α, β, γ) to those obtained from these randomised tables, this approach helps in identifying underlying ecological processes structuring the community. For example, β values lower than expected were considered indicative of efficient dispersal, as variation among communities was smaller than expected. In contrast, β values higher than random expectations were regarded as indicative of limited dispersal.

Simple and partial Mantel tests (Mantel and Valand 1970), using Spearman correlation and Bray–Curtis similarity, were used to disentangle relationships between environmental variables (pH, DOC, Chl*a*, DIN, PO_4, lake altitude and area, and the dummy variables depth, macrophyte, and fish), spatial factors (latitude and longitude), and community similarity (total community, local, and regionally abundant and rare communities), while controlling for the effect of one of the matrices mentioned above (partial Mantel test). Both simple and partial Mantel tests were assessed using the *vegan* package in R.

Multivariate analyses (NMDS and Mantel test) were performed on the Hellinger-transformed ASV relative abundance matrix (total, abundant, and rare) (Legendre and Gallagher 2001; Ramette 2007).

Packages were run in R (4.0 and 3.4.4 versions; R Core Team 2020 R: A language and environment for statistical computing. Vienna: R Foundation for Statistical Computing, 2018) using the RStudio environment (1.2.5042 version; RStudio Team 2020).

3 | Results

3.1 | Limnological Characterisation

A wide range of environmental conditions were documented in lakes from both plateaus (Table 1). Altitudes ranged between 749 and 1472 m a.s.l. with most lakes located above 1000 m a.s.l., and lake areas varied between 0.01 and 17.24 km^2. All lakes were alkaline, with pH ranging between 7.9 and 9.5. DOC concentration and conductivity values showed high variability, ranging between 0.87 and 1400 $mg\,L^{-1}$ and between 44 and 14,740 $\mu S\,cm^{-1}$, respectively. Chl*a* concentrations also displayed a wide variation, ranging between 1.02 and 56.61 $\mu g\,L^{-1}$, with the highest value measured in samples from a shallow inorganic turbid lake (PondX, STR Plateau). Regarding dissolved nutrients, DIN showed low values in general, ranging from 0.00 to 0.71 $mg\,L^{-1}$. The highest value corresponded to Nieve (STR Plateau). P-PO_4 values varied between 0.001 and 5.76 $mg\,L^{-1}$, with the highest value recorded in PondX.

The first two axes of the PCA based on limnological variables explained 55.11% of the variance, showing lakes arranged along a gradient matching the first axis (PC1 = 35.29%) (Figure 2). This axis positively correlated with P-PO_4 ($r = 0.79$), Chl*a* ($r = 0.63$), and conductivity ($r = 0.55$) and was negatively correlated with DO ($r = -0.55$). In general, P-PO_4, conductivity, and Chl*a* values were lower in BA lakes than in STR lakes. Axis 2 (PC2 = 19.82%) was positively associated with pH ($r = 0.52$) and negatively associated with DIN ($r = -0.73$), with the latter showing a gradient from the lowest values in BA lakes to the highest values in STR lakes, including fishless and stocked lakes (Figure 2). The scatter plot of the PCA components 1 and 2 partitioned by the

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TABLE 1 | Values of physical and chemical variables for the 37 lakes from the Buenos Aires and Strobel plateaus.

Plateau	Lake id	Year	Alt (m a.s.l)	Area (km^2)	Depth	Fish	Macrophyte	Temp (C°)	pH	Conductivity ($\mu S\ cm^{-1}$)	DO ($mg\ L^{-1}$)	Chl*a* ($\mu g\ L^{-1}$)	DIN ($mg\ L^{-1}$)	P-PO_4 ($mg\ L^{-1}$)	DOC ($mg\ L^{-1}$)	Kd (m^{-1})
Buenos Aires	Cervecero	2015	1037	0.12	Shallow	NO	YES	6.4	8.0	92	8.15	5.43	0.05	0.07	13.98	2.72
	Chapu		1193	0.18	Shallow		YES	8.0	8.4	320	11.11	39.73	0.00	0.06	28.78	4.20
	Sello		1472	17.24	Deep		YES	4.6	8.9	126	10.48	1.53	0.04	0.001	9.53	0.65
	Honda		1146	0.40	Deep		NO	10.7	8.8	14,740	9.86	2.85	0.02	0.02	1400	0.92
	9dejulio		1258	0.37	Shallow		INT	7.3	7.9	103	10.30	1.02	0.02	0.03	12.37	1.54
	E25	2016	1178	0.87	Shallow		INT	14.2	8.5	79	10.88	7.41	0.00	0.05	2.99	1.04
	Gaviotero		1172	0.64	Shallow		INT	14.3	8.9	116	10.52	9.59	0.01	0.02	4.66	1.55
	Huevo		1258	0.03	Shallow		NO	16.2	8.4	74	11.54	1.49	0.02	0.08	0.87	0.48
	Soñada		1213	0.19	Shallow		INT	13.0	8.5	65	9.73	2.44	0.01	0.13	2.14	1.51
	Bax37	2017	1401	0.48	Shallow		YES	4.2	9.5	89	9.09	2.70	0.01	0.14	7.42	—
	Bax39		1418	0.04	Shallow		NO	11.3	9.4	64	9.32	31.49	0.02	0.24	6.83	—
	Bax40		1427	0.26	Shallow		NO	14.1	8.5	82	10.25	21.45	0.01	0.14	5.85	—
	LA4		1424	0.07	Shallow		INT	9.2	8.9	44	9.47	1.42	0.01	0.05	9.46	2.35
	LA5		1425	0.07	Shallow		YES	7.0	9.1	61	10.08	19.79	0.02	0.16	9.19	6.25
Strobel	S44	2011	824	0.15	Shallow	NO	NO	16.3	9.2	5680	10.90	30.48	0.10	0.36	62.00	1.00
	Justita		916	0.07	Shallow		YES	19.9	8.6	172	10.67	2.18	0.07	0.14	26.20	2.03
	S64		886	0.03	Shallow		YES	18.3	8.4	96	9.50	7.26	0.08	0.23	13.90	1.42
	PondX		925	0.69	Shallow		NO	15.6	9.4	5660	8.94	56.61	0.11	5.76	211.60	20.98
	Colorad		749	2.35	Shallow		YES	15.3	8.7	420	11.20	5.81	0.08	1.17	26.90	1.23
	Nieve		930	0.02	Shallow		YES	21.0	8.5	79	9.71	11.61	0.71	0.16	26.20	2.38
	Pifie	2015	1034	0.01	Shallow		NO	8.7	8.6	513	10.31	28.52	0.00	0.01	40.63	5.72
	Rod9		996	0.04	Deep		YES	11.4	8.7	240	14.32	6.79	0.00	0.03	26.00	2.35
	Rod18		1035	0.06	Shallow		NO	7.0	8.4	390	10.16	16.30	0.10	0.10	20.19	2.95
	S94		965	0.10	Deep		INT	8.5	8.6	1061	10.36	8.96	0.01	0.32	34.47	1.44
	Rod19	2017	1036	0.14	Shallow		YES	10.5	8.1	1560	10.52	2.44	0.03	0.20	15.79	1.45
	Rod22		1061	0.28	Deep		NO	10.0	8.0	67	10.18	9.05	0.02	0.17	5.64	2.94
	Rod26		1056	0.31	Deep		NO	10.9	8.3	77	10.20	10.97	0.02	0.29	5.55	2.08

(Continues)

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TABLE 1 | (Continued)

Plateau	Lake id	Year	Alt (m a.s.l)	Area (km^2)	Depth	Fish	Macrophyte	Temp (C°)	pH	Conductivity ($\mu S\ cm^{-1}$)	DO ($mg\ L^{-1}$)	Chl*a* ($\mu g\ L^{-1}$)	DIN ($mg\ L^{-1}$)	P-PO_4 ($mg\ L^{-1}$)	DOC ($mg\ L^{-1}$)	Kd (m^{-1})
	La8	2011	895	0.15	Shallow	YES	YES	17.7	8.9	921	8.90	55.16	0.04	0.21	98.60	3.45
	La9		892	0.09	Shallow		YES	16.9	8.6	326	10.21	15.37	0.07	0.17	37.90	6.77
	Temp		885	0.08	Shallow		YES	15.2	8.2	570	9.74	9.25	0.07	0.90	66.50	3.73
	Camp	2015	924	0.40	Deep		NO	13.8	8.1	215	11.37	12.22	0.02	0.16	9.92	2.89
	Herrad		1036	0.14	Deep		INT	8.1	8.1	330	12.02	9.51	0.03	0.02	16.57	1.09
	Potre		881	0.67	Deep		NO	10.7	8.1	710	12.64	3.06	0.06	0.20	31.55	2.57
	Rod2	2017	933	0.16	Shallow		NO	10.7	8.2	1210	9.61	5.26	0.05	0.31	10.23	2.67
	Rod3		984	0.10	Shallow		NO	11.7	8.3	789	9.97	7.19	0.03	0.36	19.24	6.90
	Rod8		1011	0.06	Shallow		NO	10.5	8.0	899	9.83	16.30	0.02	0.33	30.98	—
	Rod24		1053	0.12	Shallow		NO	10.2	8.6	222	9.97	8.15	0.09	0.28	17.78	6.71

Abbreviations: Alt, Altitude; Chl*a*, chlorophyll *a*; DIN, dissolved inorganic nitrogen; DO, dissolved oxygen; DOC, dissolved organic carbon; INT Macrophyte, intermediate vegetation cover; Kd, vertical attenuation coefficient of PAR; P-PO_4, soluble reactive phosphorus; Temp, temperature.

'plateau' (based on the factors analysed) revealed a slight separation of lakes by plateau (Figure S2).

3.2 | BCC and Diversity Analysis

A total of 3106 ASVs were obtained from 2,385,153 reads after all filtering steps and normalisation of samples to 19,659 (Table S1). The rarefaction curve of each sample reached a plateau, indicating that sampling depth and sequencing coverage were adequate (Figure S1). The ASVs affiliated taxonomically to 30 phyla in both plateaus, with the higher relative abundances distributed across *Bacteroidota* (28% in BA, 24% in STR), *Proteobacteria* (27% in BA, 22% in STR), *Actinobacteriota* (19% BA, 23% in STR), *Verrucomicrobiota* (16% in BA, 11% in STR), and *Cyanobacteria* (3% in BA, 10% in STR) (Figure 3a,b). The most abundant classes in both plateaus were *Bacteroidia* (28% in BA, 22% in STR), *Actinobacteria* (18% in BA, 20% in STR), *Gammaproteobacteria* (20% in BA, 13% in STR), *Verrucomicrobiae* (16% in BA, 11% in STR), *Alphaproteobacteria* (7% in BA, 9% in STR), and *Cyanobacteriia* (3% in BA, 10% in STR) (Figure 3c,d).

The mean richness of ASVs was similar among lakes from both plateaus, with results showing 316 and 311 for BA and STR, respectively. The Evenness and Shannon indexes were similar between lakes in both groups ($p > 0.05$; Table 2). Lakes from the STR Plateau presented 2371 ASVs, while lakes from the BA Plateau presented 2001 ASVs. Out of all 3106 ASVs, 1266 (41%) were shared among lakes between both plateaus. The analysis of regionally abundant taxa, which rendered 170 ASVs, revealed an increase (81%) in the percentage of shared ASVs between plateaus. At variance, regionally rare taxa accounted for the majority of ASVs and rendered 38% similarities between plateaus, in line with total ASV values. Lakes from the STR plateau presented the highest percentage of exclusive (total, regionally abundant and rare) ASVs (Figure 4).

The additive partitioning of bacterioplankton diversity showed that β1 diversity was a major contributor to regional bacteria diversity, followed by β2. Null model analyses showed that β2 was higher than expected at random (Figure 5), which indicates that the communities are rather heterogeneous at this scale. In contrast, β1 was lower than expected at random, which suggests great similarity among bacterioplankton communities within each plateau. Finally, α was higher than expected at random for total bacteria (Figure 5).

3.3 | Influence of Environmental and Spatial Variables

The ordination of total ASVs in an NMDS showed separation of lakes by plateau, revealing a weak overlap between plateaus (Figure 6a). Further similarity analysis showed significant differences in the composition of total ASVs among lakes from the BA and STR plateaus (ANOSIM $R = 0.2407$, $p = 0.002$). The *envfit* analysis also confirmed the ASV ordination patterns by plateau ($r^2 = 0.4051$, $p = 0.001$). In the NMDS plot, lakes from the STR plateau were ordered in the upper quadrants, while those from the BA plateau were in the lower ones. The correlated scores derived from lake ordination (NMDS1 and NMDS2)

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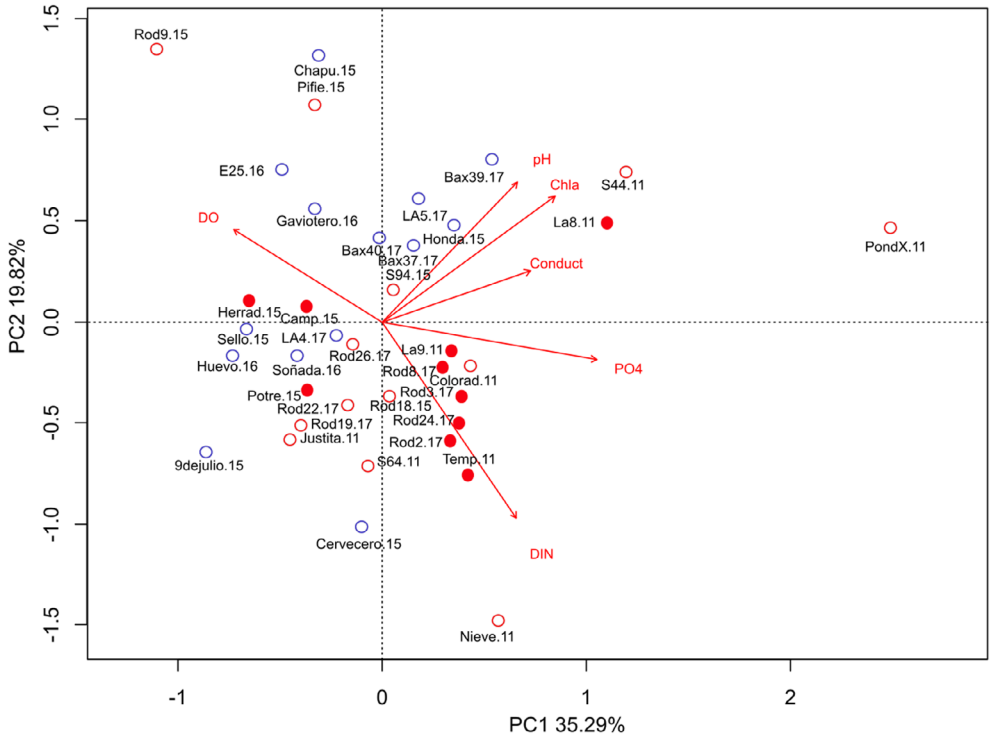


FIGURE 2 | Principal component analysis based on limnological data from 23 lakes in the Strobel (red dots) and 14 in the Buenos Aires (blue dots) plateaus. Arrows indicate the loading of each variable on the two first axes. The filled red dots represent fish-stocked lakes, while the empty dots denote fishless lakes.

with environmental variables showed that the BCC of BA lakes was related to high pH values, macrophytes (more than 50% of cover), high altitude, and shallow depth, while STR lakes ordinated toward higher values of conductivity, DOC, P-PO_4, and the presence of fish (Figure 6a).

NMDS analyses of rare and abundant bacteria, both locally (Figure S3) and regionally (Figure 6b,c), produced ordination patterns similar to those of the total ASV matrix. For rare bacteria, lakes were clearly separated by plateau, showing greater heterogeneity between plateaus based on rare rather than abundant ASVs (regional: *envfit* $r^2 = 0.4501$, $p = 0.001$; ANOSIM $R = 0.282$, $p = 0.001$, Figure 6b; locally: *envfit* $r^2 = 0.3647$, $p = 0.001$; ANOSIM $R = 0.2353$, $p = 0.003$, Figure S3a). In contrast, both regionally and locally abundant ASVs were still separated by plateau but showed clearer lake clustering, with less heterogeneity between plateaus than rare ASVs (regional: *envfit* $r^2 = 0.1796$, $p = 0.030$; ANOSIM $R = 0.2171$, $p = 0.001$, Figure 6c; locally: *envfit* $r^2 = 0.3519$, $p = 0.002$; ANOSIM $R = 0.2346$, $p = 0.003$, Figure S3b). The correlated scores from lake ordination with environmental variables showed results similar to those obtained for total bacteria, except for depth—which was not a significant factor for regionally rare bacteria—and altitude and P-PO_4—which were not significant for abundant bacteria. Additionally, *envfit* analyses indicated that lake ordination was influenced by the presence/absence of fish for both rare and abundant bacteria (Figure 6b–c and Figure S3).

The simple Mantel test revealed greater BCC similarity with environmental proximity ($r = 0.37$, $p < 0.0001$) and less similarity at greater distances between lakes ($r = -0.22$, $p = 0.002$). The simple Mantel test also showed that environmental factors were spatially structured ($r = -0.41$, $p < 0.0001$), as the similarities in the environmental matrix decreased with increasing distance (Table 3). These results were consistent for both rare and abundant BCC, regardless of their regional or local classifications. However, when the effect of environmental factors was removed (partial Mantel test, Table 3), total BCC and locally abundant BCC similarities decreased non-significantly with increasing distance ($r = -0.084$, $p = 0.076$; $r = -0.085$, $p = 0.092$, respectively). In addition, when the effect of space was removed, BCC similarities increased significantly with environmental proximity, with the highest correlation observed for regionally abundant bacteria ($r = 0.43$, $p < 0.0001$). Regionally rare and abundant bacteria exhibited stronger and more significant correlations with environmental and spatial factors, whereas total and locally rare and abundant bacteria showed lower and more similar correlation values (Table 3).

Regarding environmental variables, lakes differing in fish presence, macrophyte cover, DOC, and conductivity exhibited significant differences in BCC. Fish-stocked lakes showed significantly greater abundance of *Alphaproteobacteria* (Clade_III, ASV 2) and lower abundance of *Bacteroidia* and *Gammaproteobacteria* compared to fishless lakes (Figure 7). Similarly, water bodies lacking submerged macrophytes displayed greater abundance of *Cyanobacteria* (*Cyanobium*_PCC-6307, ASV 7, Figure 8a) and *Planctomycetota* (*Pirellulaceae*, ASV 93, Figure 8b) than lakes with high and moderate cover of *M. quitense*. Fishless lakes and habitats with high macrophyte cover exhibited significantly higher values of *Bacteroidota* (*Flavobacterium*, ASV 10) than stocked lakes and those without vegetation (Figures 7a,b and 8c, respectively). As for bacterial composition at the phylum level and DOC values, *Firmicutes*

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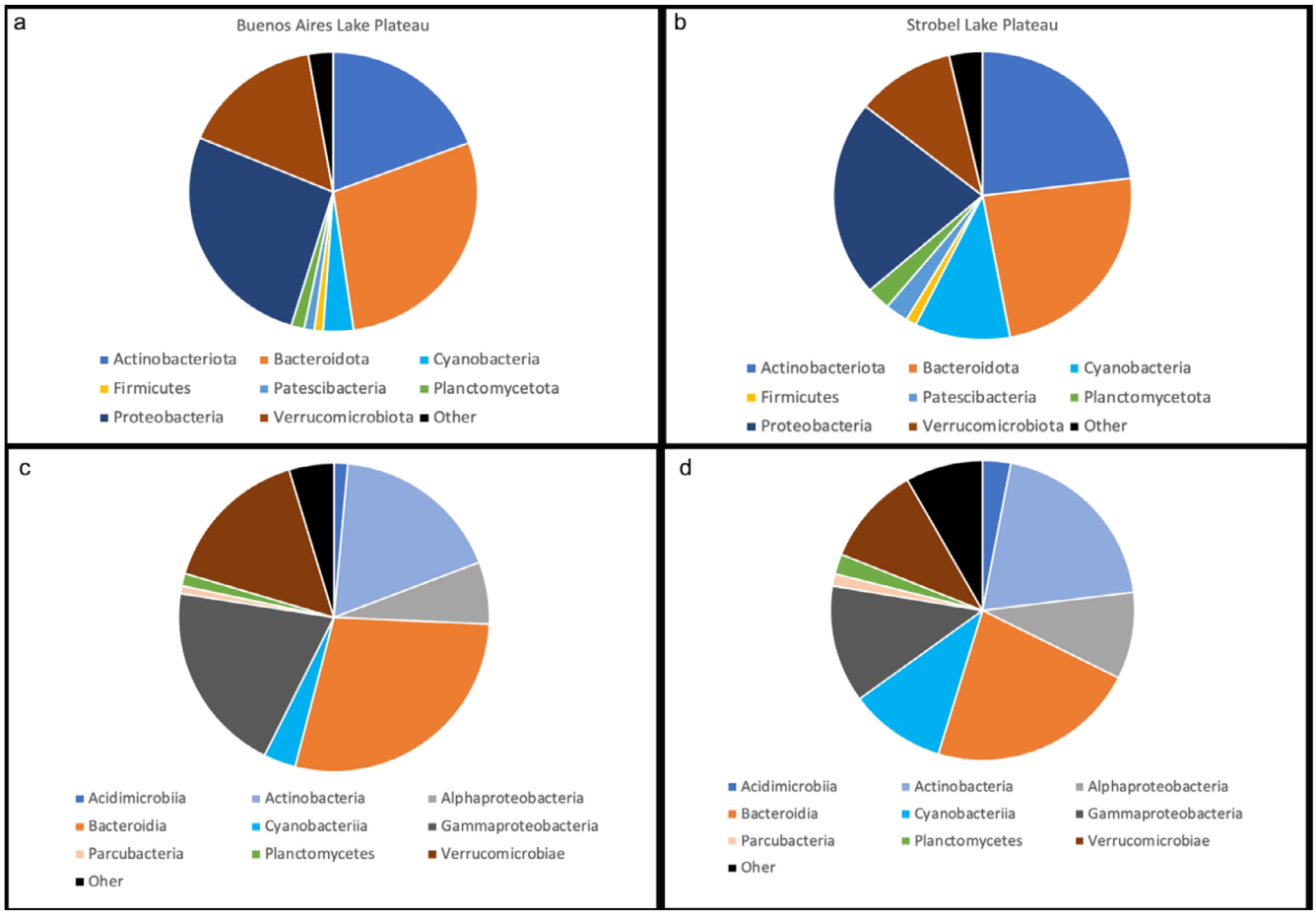


FIGURE 3 | Relative abundances of phyla (at the top) and classes (at the bottom) of bacteria in lakes from the Buenos Aires (a, c) and Strobel (b, d) plateaus.

TABLE 2 | Median (± standard deviation) of diversity indexes.

Index	Buenos aires plateau	Strobel plateau	*p*
Richness_s	316 (±97)	311 (±58)	0.79
Shannon_H	4.09 (±0.61)	3.92 (±0.37)	0.55
Evenness_E^H/s	0.21 (±0.07)	0.19 (±0.06)	0.45

was the only taxon showing a significantly positive correlation with this factor (rho Spearman = 0.46, $p = 0.004$).

No ASV was present in all the lakes studied. Additionally, 12 ASVs were recorded only in the lakes PondX, S44, and Honda from both STR and BA Plateaus, which are environments with the highest conductivity values, ranging from 5680 to 14,740 μS cm^{-1}. These 12 ASVs shared by the three lakes belong to the following taxonomic classes: *Bacteroidia*, *Alphaproteobacteria*, *Gammaproteobacteria*, *Actinobacteria*, BD2-11 terrestrial group, and *Planctomycetes*. Some of them were identified down to the genus level, including *Planktosalinus* (ASV 261), GKS98 freshwater group (ASV 274), *Seohaeicola* (ASV 364), *Lunatimonas* (ASV 392), *Salinarimonas* (ASV 395), *Paracoccus* (ASV 411), and *Pirullela* (ASV 1007) (Table S1).

4 | Discussion

Our results reveal that aquatic habitat diversity promotes bacterial diversity, mainly attributed to the high environmental variability among lakes, as previously observed in other planktonic communities in these high-altitude lakes (Porcel et al. 2020). The bacterial communities in the lakes on both Patagonian plateaus were characterised by the dominance of *Bacteroidota*, *Proteobacteria*, *Actinobacteriota*, *Verrucomicrobiota*, and *Cyanobacteria* phyla, in keeping with reports on other freshwater systems throughout the globe (Newton et al. 2011; Tessler et al. 2017).

β diversity within each plateau was the most important contributor to regional bacterioplankton diversity. Despite being a major component, β1 values were lower than random, which suggests a bacterial homogenisation process and limited dispersal limitation within each plateau. We can infer that the high dispersal capacity of these small individuals within plateaus tends to homogenise these communities. In this context, the intense west winds in this region combined with abundant waterbird movements facilitate the transport of propagules across lakes, a phenomenon commonly observed in other habitats (Hervàs et al. 2009; Figuerola et al. 2003, 2005). This homogenisation trend in lakes on the same plateau could also be related to past hydrological connections. Indeed, the structure of

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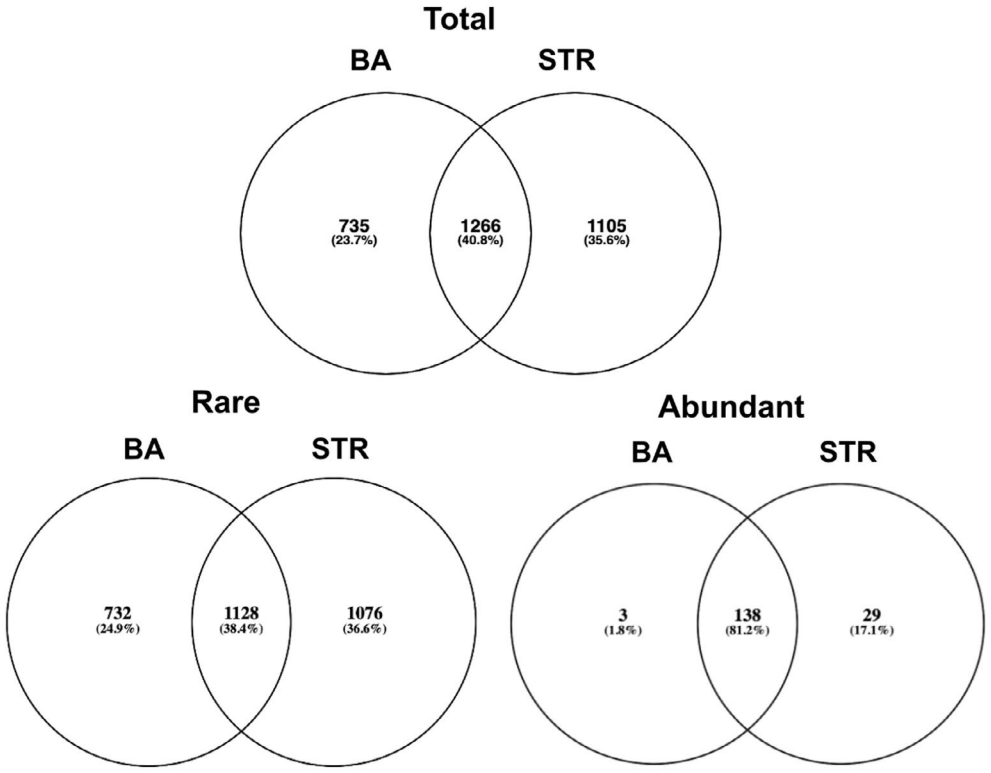


FIGURE 4 | Venn diagrams show the distribution of shared and exclusive ASVs from the whole set (up) and discriminated between regionally rare (bottom left) and abundant (bottom right), from lakes of the Buenos Aires (BA) and Strobel (STR) plateaus, expressed as absolute numbers and percentages in brackets.

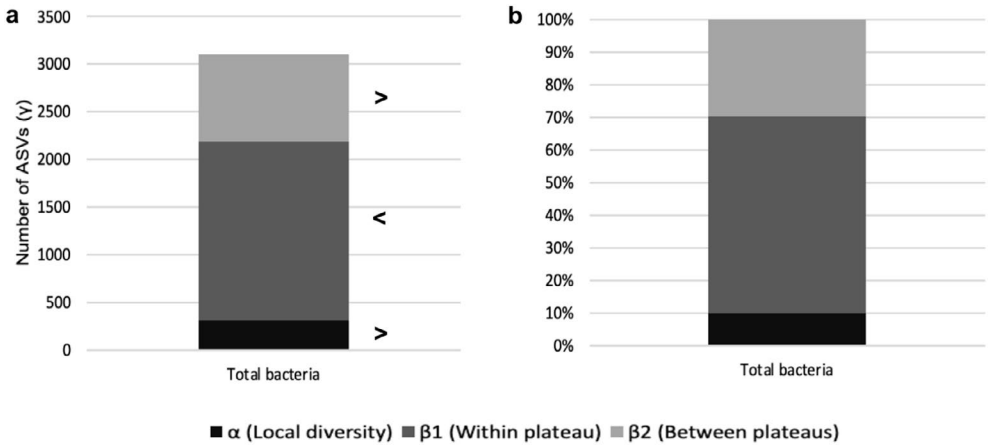


FIGURE 5 | Plots of the (a) additive partition of regional diversity (richness) and (b) its relative contribution in 37 lakes from the Buenos Aires and Strobel plateaus for total bacteria. The symbols "<, less than" and ">, greater than" show significant differences compared to random values ($p < 0.05$).

aquatic microbial communities may be shaped by hydrological networks, which balance bacterial migration from adjacent ecosystems (Ruiz-González et al. 2015). Most of the lake basins in this study were isolated (arheic basins) due to extreme droughts over the last decade (Lancelotti et al. 2020; Izaguirre et al. 2018). Inter-lake connections, however, may have existed in the past and could have favoured bacterial interchange between lakes, although more specific studies are needed to explore this factor. The geographic isolation of these plateaus could also promote relatively homogeneous BCC among lakes within each plateau. In this regard, lakes from the same plateau were more similar in total bacterial composition and locally abundant bacteria, as spatial factors had a weaker influence according to the partial Mantel test and NMDS results. At the regional level, lake-to-lake distance had greater influence on the similarities in rare bacterial composition, which indicates that more distant lakes (i.e., those from different plateaus) show greater differences in the composition of rare ASVs. This is supported by Mantel test results as well as NMDS analyses.

It should be noted that lakes on the same plateau were physically and chemically more similar to one another than lakes

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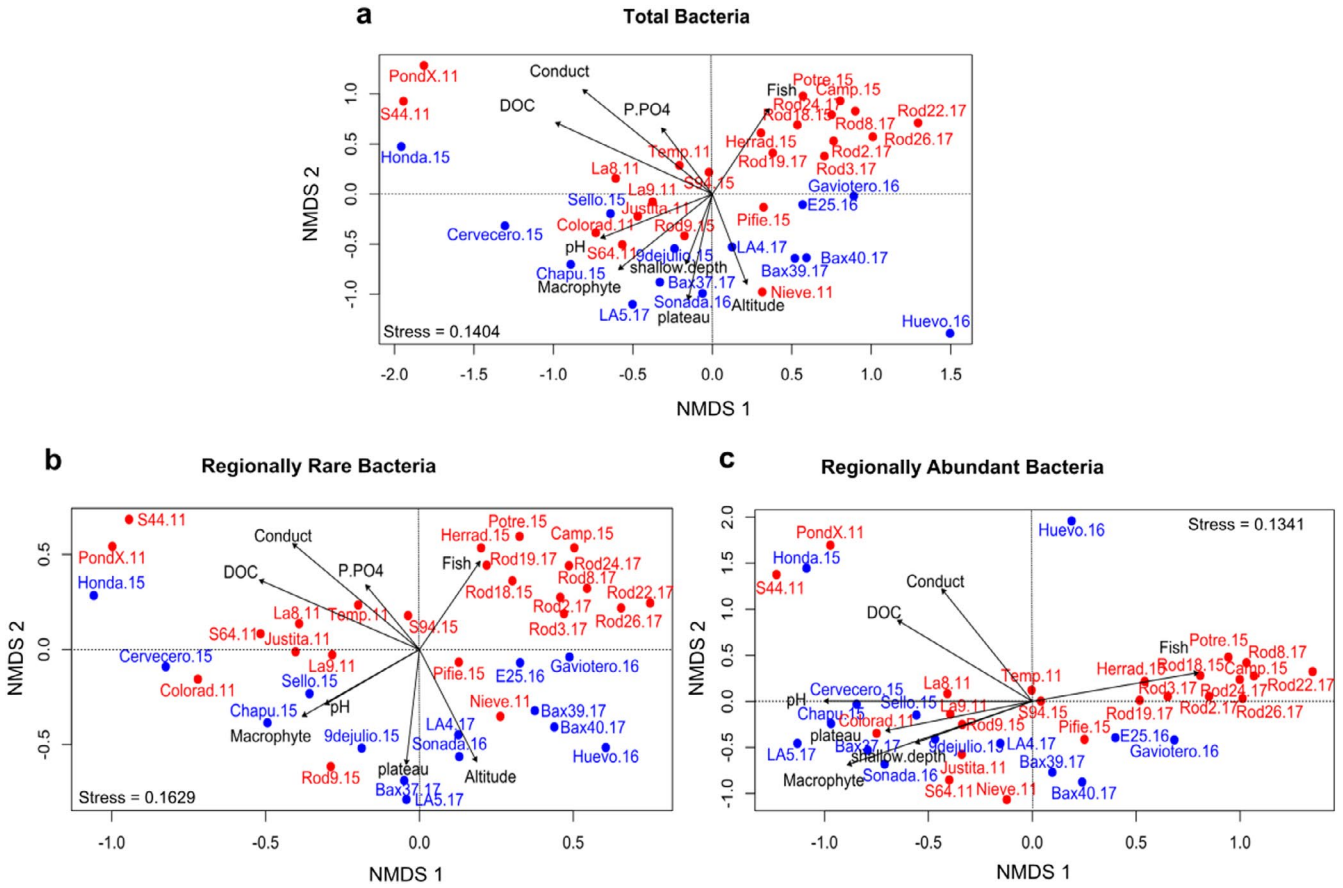


FIGURE 6 | Non-metric multidimensional scaling (NMDS) performed on Hellinger-transformed bacterioplankton community composition using Bray–Curtis similarity index for 37 lakes: (a) total and regionally (b) rare and (c) abundant bacteria. Arrows indicate the significant correlations ($p < 0.05$) between environmental variables and the ordination axes and were calculated passively after NMDS by the *envfit* function. The red colour corresponds to the Strobel Plateau, and the blue colour to the Buenos Aires Plateau.

on different plateaus, as demonstrated by the PCA and Mantel test. Our analyses showed that differences in local environmental conditions were well reflected by differences in BCC among lakes from both plateaus. More than 50% of all ASVs were exclusive to each plateau, with 35.6% found only in STR and 23.7% only in BA Plateau. The results of the additive partition of regional diversity indicate significant heterogeneity in BCC between BA and STR plateaus (β2 values were higher than expected at random). This pattern likely arises from the distance (ca. 120 km) and local environmental differences between plateaus, including macrophyte cover, presence of fish, conductivity, DOC, pH, and altitude, as indicated by NMDS. The Mantel test further supports this result, indicating that environmental factors were spatially structured. This can be indirectly masked by some environmental features, such as the presence or absence of fish. Fish were introduced only at the STR Plateau, mainly in large permanent lakes, both vegetated and unvegetated ones, which potentially contributed to autocorrelation between variables. This trend has also been observed in phytoplankton and microzooplankton communities in lakes from the same plateaus (Porcel et al. 2020).

Our results are similar to those reported in other studies of bacterial communities from isolated aquatic systems. For example, Pearman et al. (2022) found that environmental processes had a stronger relationship with total BCC than geographic distance in lakes in New Zealand. The authors found that environmental processes played a major role in shaping the structure of regionally abundant bacteria, whereas spatial factors had a greater influence on regionally rare bacteria. In the same line, Bai et al. (2020) found that both types of variables were significant for BCC, with spatial variables explaining most rare community variations and environmental variables showing a stronger explanatory power in abundant community variations. In our study, environmental variables were the primary contributors to the composition of total, rare, and abundant bacteria. However, both regionally and locally rare bacteria showed a stronger correlation with spatial factors than total or abundant bacteria, in agreement with Bai et al.'s conclusions and partly with our third hypothesis. Other studies suggest that abundant and rare bacterial taxa are mostly influenced by environmental variables in isolated coastal Antarctic lakes (Logares et al. 2013). Similarly, Li et al. (2017) found that environmental filtering played an important role in shaping both abundant and rare bacterial assemblages in lakes along various elevation gradients.

Furthermore, our study showed that regionally abundant ASVs were mostly shared by the plateaus, whereas rare ASVs were mostly exclusive to each plateau. Shared ASVs may be explained

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TABLE 3 | Simple and partial Mantel test of the total bacterial community, locally and regionally abundant and rare similarity matrices with the spatial matrix and the environmental matrix for the 37 lakes from both plateaus.

	Mantel test			
	Simple		Partial	
	r	*p*	*r*	*p*
Total BCC vs. Environment	**0.37**	**< 0.0001**		
Total BCC vs. Space	**−0.22**	**0.002**		
Space vs. Environment	**−0.41**	**< 0.0001**		
Total BCC vs. Environment (Space)			**0.35**	**0.001**
Total BCC vs. Space (Environment)			−0.084	0.076
Regionally				
Rare BCC vs. Environment	**0.50**	**< 0.0001**		
Rare BCC vs. Space	**−0.30**	**< 0.0001**		
Space vs. Environment	**−0.54**	**< 0.0001**		
Rare BCC vs. Environment (Space)			**0.35**	**< 0.0001**
Rare BCC vs. Space (Environment)			**−0.17**	**0.0001**
Abundant BCC vs. Environment	**0.46**	**< 0.0001**		
Abundant BCC vs. Space	**−0.18**	**< 0.0001**		
Space vs. Environment	**−0.19**	**< 0.0001**		
Abundant BCC vs. Environment (Space)			**0.43**	**< 0.0001**
Abundant BCC vs. Space (Environment)			**−0.14**	**0.0001**
Locally				
Rare BCC vs. Environment	**0.35**	**< 0.0001**		
Rare BCC vs. Space	**−0.28**	**0.005**		
Space vs. Environment	**−0.41**	**< 0.0001**		
Rare BCC vs. Environment (Space)			**0.30**	**< 0.0001**
Rare BCC vs. Space (Environment)			**−0.17**	**0.001**
Abundant BCC vs. Environment	**0.37**	**< 0.0001**		
Abundant BCC vs. Space	**−0.22**	**0.005**		
Space vs. Environment	**−0.47**	**< 0.0001**		
Abundant BCC vs. Environment (Space)			**0.35**	**0.001**
Abundant BCC vs. Space (Environment)			−0.085	0.092

Note: Significance of bold values indicate significant effects ($p < 0.05$).

by the high probability of dispersal by abundant bacteria among lakes from different plateaus, with abundances within a lake subsequently shaped by local environmental processes. In contrast, the exclusivity of ASVs to each plateau may result from the very low abundances of rare taxa, which likely reduce the influence of dispersal between lakes. This assumption is in agreement with other studies showing more restricted distribution for regionally rare bacteria (Bai et al. 2020; Pearman et al. 2022).

Abiotic factors act as filters for the microbial composition in these lakes of the Patagonian plateaus, as previously found in other aquatic systems (Hengy et al. 2017; Sadeghi et al. 2021; Mateus-Barros et al. 2021). A notable example is the occurrence of halophile bacteria, which were exclusively recorded in lakes with the highest conductivity (i.e., PondX, S44 in STR Plateau and Honda in BA Plateau). This result is consistent with previous findings. For instance, *Planktosalinus* (*Bacteroidetes*) was identified in a

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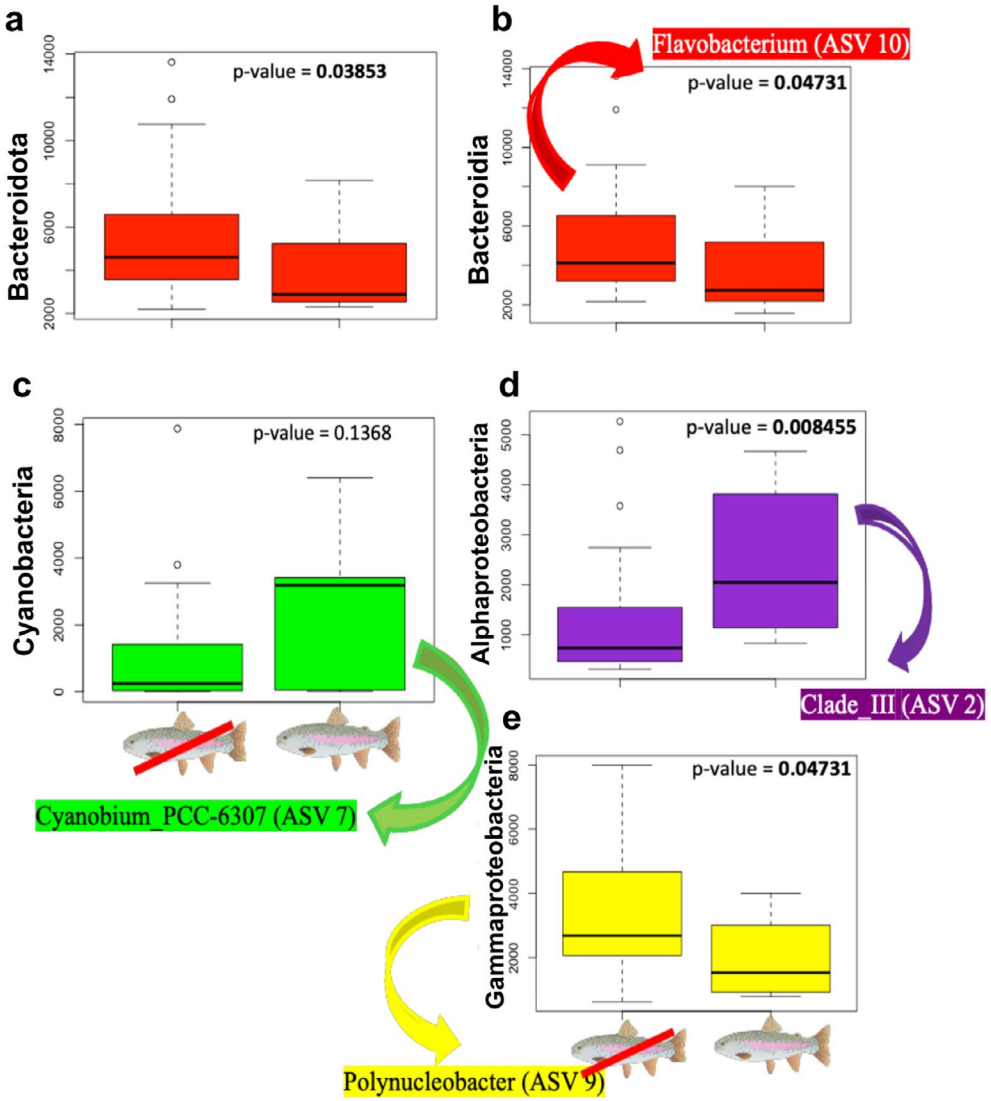


FIGURE 7 | Comparison between fishless and stocked lakes from both plateaus regarding the relative abundance of (a) phylum *Bacteroidota*, (b) class *Bacteroidia*, (c) phylum *Cyanobacteria*, (d) class *Alphaproteobacteria*, and (e) class *Gammaproteobacteria*. Arrows indicate the dominant ASVs within the taxa mentioned.

salt lake in China (Zhong et al. 2016), and the cluster GKS98 has been found in both freshwater and hypersaline lakes (Wu et al. 2006). Similarly, *Paracoccus*, slightly halophilic bacteria, were isolated from saline lake sediments (Meng et al. 2019; Gao et al. 2022). Additionally, *Seohaeicola* and *Pirellula* exhibited the highest identity with sequences recovered from marine habitats (Rabus et al. 2002; Pizzetti et al. 2011; Wang et al. 2017).

Submerged macrophytes also affect the bacterioplankton community structure (Jürgens and Jeppesen 1998; Huss and Wehr 2004; Wu et al. 2007). Aquatic vegetation could have a dual influence on planktonic bacteria: an indirect effect by suppressing algal growth—which results in lower algal extracellular release—and a direct effect by supplying microbes with carbon and nutrients (Sigee 2005). Mentes et al. (2017) observed that the type of macrophyte also controls bacterial composition. For example, some aquatic plant species produce compounds that may act as antimicrobial agents, such as anthocyanin-producing waterlily (Fossen et al. 1998), and their selective action (Cisowska et al. 2011) could have a structuring effect on the bacterial community.

On the other hand, certain *Cyanobacteria* dominate in eutrophic water bodies and produce cyanotoxins that exert allelopathic effects, which may contribute to a reduction in macrophytes (Mohamed 2017). Lakes from the basaltic Patagonian plateaus in this study showed differences in this regard; water bodies without macrophytes showed significantly higher relative abundance of *Cyanobacteria* than environments with intermediate vegetation cover. In addition, lakes without macrophytes showed greater abundances of *Planctomycetota* (*Pirellulaceae*) than lakes with vegetation. In general, *Pirellulaceae* are heterotrophic and aerobic, with few exceptions capable of microaerobic or anaerobic growth (Vitorino and Lage 2022). Conversely, lakes with macrophytes in the plateaus studied exhibited the highest relative abundance of *Bacteroidota* (*Flavobacterium*). This observation aligns with Mentes et al. (2017), who sampled various water bodies with distinct aquatic vegetation. The

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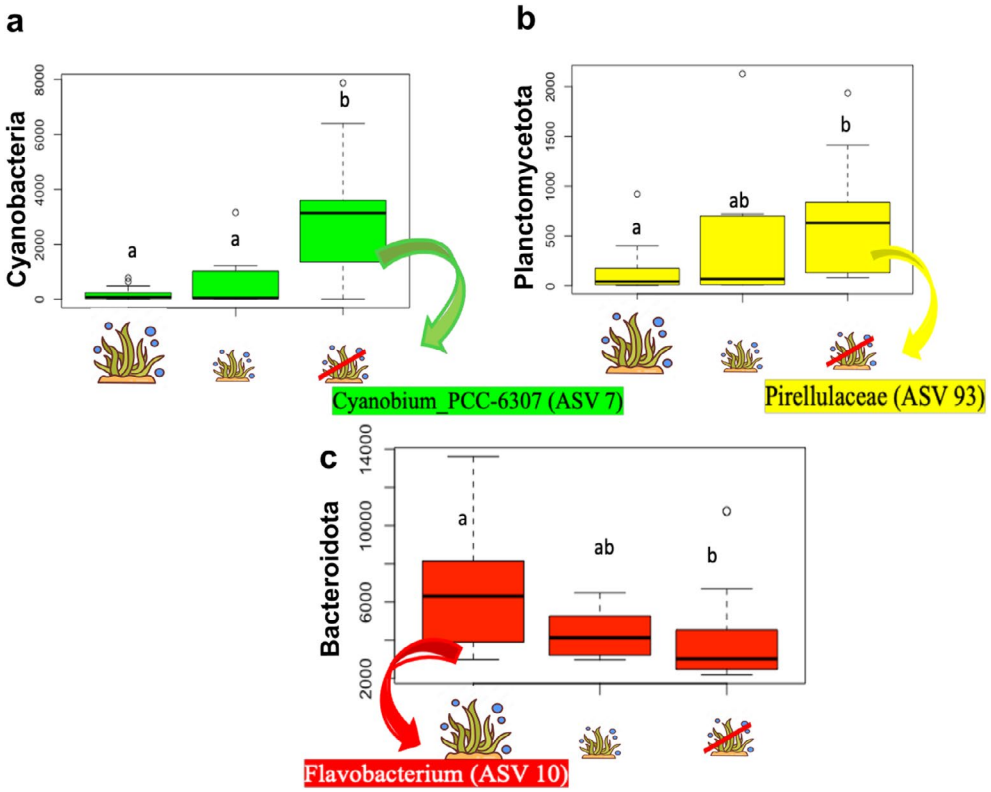


FIGURE 8 | Comparison between lakes with vegetation (more than 50% of cover), intermediate vegetation cover (~50%) and without vegetation (< 15% of cover) regarding the relative abundance of (a) phylum *Cyanobacteria*, (b) class *Planctomycetota*, and (c) phylum *Bacteroidota*. Different letters indicate significant differences ($p < 0.05$) among lake types. Arrows indicate the dominant ASVs within the taxa mentioned.

authors highlighted the prevalence of bacterial taxa capable of using plant degradation products or humic substances, which constitute 12%–33% of *Bacteroidetes*. The representatives of this phylum are primarily chemoorganotrophic bacteria that consume various forms of organic matter. Notably, *Flavobacterium* is a typical genus within this phylum known for its capability to degrade macromolecules (Krieg et al. 2010).

In line with our previous studies, the introduction of rainbow trout was identified as an influential factor in plankton communities in these freshwater systems (Porcel et al. 2022 and cites therein). Fish-stocked lakes are known for having smaller average zooplankton sizes (Lancelotti et al. 2017) and larger phytoplankton biomass (Izaguirre and Saad 2014; Izaguirre et al. 2018). Consequently, lakes with and without fish in the STR Plateau exhibited differences in BCC influenced by a combination of top-down and bottom-up effects (Sabio y García et al. 2024). The present results revealed differences at the phylum and class levels, as fish-stocked lakes showed greater abundance of *Alphaproteobacteria* (*Proteobacteria*) and *Cyanobacteria* than fishless lakes, consistent with previous studies in Patagonian lakes (Reissig et al. 2006; Izaguirre and Saad 2014; Sabio y García et al. 2024). Furthermore, we observed significantly greater abundance of *Bacteroidia* (*Bacteroidota*) and *Gammaproteobacteria* (*Proteobacteria*) in fishless than in trout-stocked lakes.

Our study revealed that, in lakes of the Patagonian basaltic plateaus, local environmental variables have more influence on the structure of BCC than spatial variables, regardless of bacterial abundance or rarity at local or regional scales, which is not completely consistent with our second hypothesis. However, numerous studies have emphasised the importance of geographical factors in influencing microbial communities, suggesting a combined impact of environmental and spatial factors on community structure (Cottenie 2005; Lovejoy and Potvin 2011; Sadeghi et al. 2021). Soininen et al. (2011) proposed a scale-dependent balance between dispersal-driven assembly and local ecological determinism in freshwater planktonic communities. Some discrepancy between our findings and those of other studies may be attributed to differences in environmental gradients. Our study covered a broad environmental gradient within a relatively short altitudinal (749–1472 m a.s.l) and geographical distance (46° S, 71° W—48° S, 70° W), which could influence the assembly of both regionally abundant and rare bacterial communities. On the other hand, we cannot discard the influence of temporal variability since our study involved a 6-year period, which might introduce interannual differences in BCC, but this source of variation was not considered in the present study.

While environmental variables were strongly associated with BCC, microbial interactions are undoubtedly also involved (Lima-Mendez et al. 2015; Zhou et al. 2018; Ji et al. 2019). The next step is to explore the extent to which these interactions contribute to the patterns observed in each plateau and in each type of lake (e.g., turbid organic/inorganic, vegetated/unvegetated, fishless/stocked and mesohaline lakes). Moreover, expanding our regional scope by sampling additional remote lakes from neighbouring plateaus in the Patagonian steppe and collecting a more extensive dataset for cross-environment and area

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comparisons could provide stronger evidence of correlations between spatial factors and microbial diversity. Including airborne studies and adding bird migrations as a contributing factor may further help elucidate the complex dynamics of bacterial sorting within these extreme and remote aquatic habitats. Additionally, repeating samplings of the same lakes over years would offer insights into the role of interannual hydrological fluctuations and connectivity in shaping microbial communities.

These lake ecosystems serve as the primary habitat for a diverse and plentiful waterbird community (Lancelotti et al. 2009) and are the sole reproductive habitat for the threatened Hooded grebe (*Podiceps gallardoi*) (Roesler et al. 2012). Our analyses show how bacterial communities reflect environmental conditions, including differentiation driven by natural factors and anthropogenic impact such as fish introduction. Our results also reveal that each plateau harbours different seed banks of rare bacteria, which could play a key role in specific ecological processes. By providing valuable ecological insights, this research work supports informed management decisions aimed at preserving these vital habitats and the species that depend on them.

Author Contributions

Conceptualization: I.I., J.L., I.R., and S.P. Developing methods: S.P., C.A.S.G., M.R.S., G.C., and M.d.C.D. Data analysis: S.P., C.A.S.G., M.R.S., and G.C. Preparation of figures and tables: S.P., C.A.S.G., M.R.S., G.C., and J.L. Conducting research, data interpretation, and writing: S.P., C.A.S.G., M.R.S., G.C., I.I., M.d.C.D., J.L., and I.R.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The raw sequence data are available in the European Nucleotide Archive (See Accession Numbers in Table S1).

References

Acinas, S. G., V. Klepac-Ceraj, D. E. Hunt, et al. 2004. "Fine-Scale Phylogenetic Architecture of a Complex Bacterial Community." *Nature* 430: 551–554.

APHA. 2005. *Standard Methods for the Examination of Water and Wastewater*. American Public Health Association.

Bai, C., J. Cai, L. Zhou, et al. 2020. "Geographic Patterns of Bacterioplankton Among Lakes of the Middle and Lower Reaches of the Yangtze River Basin, China." *Applied and Environmental Microbiology* 86, no. 6: e02423-19.

Barberán, A., and E. O. Casamayor. 2010. "Global Phylogenetic Community Structure and β-Diversity Patterns in Surface Bacterioplankton Metacommunities." *Aquatic Microbial Ecology* 59: 1–10. https://doi.org/10.3354/ame01389.

Beisner, B. E., P. R. Peres-Neto, E. S. Lindström, A. Barnett, and M. L. Longhi. 2006. "The Role of Environmental and Spatial Processes in Structuring Lake Communities From Bacteria to Fish." *Ecology* 87: 2985–2991.

Beule, L., and P. Karlovsky. 2020. "Improved Normalization of Species Count Data in Ecology by Scaling With Ranked Subsampling (SRS): Application to Microbial Communities." *PeerJ* 8: e9593.

Borcard, D., P. Legendre, C. Avois-Jacquet, and H. Tuomisto. 2004. "Dissecting the Spatial Structure of Ecological Data at Multiple Scales." *Ecology* 85: 1826–1832.

Cabrera, A. L. 1976. "Regiones Fitogeográficas Argentinas." In *Enciclopedia Argentina de Agricultura y Jardinería*, 1–85. ACME, Tomo II. Fascículo 1.

Callahan, B. J., P. J. McMurdie, M. J. Rosen, A. W. Han, A. J. A. Johnson, and S. P. Holmes. 2016. "DADA2: High-Resolution Sample Inference From Illumina Amplicon Data." *Naure Methods* 13: 581–583.

Casamayor, E. O., H. Schäfer, L. Bañeras, C. Pedrós-Alió, and G. Muyzer. 2000. "Identification of and Spatio-Temporal Differences Between Microbial Assemblages From Two Neighboring Sulfurous Lakes: Comparison by Microscopy and Denaturing Gradient Gel Electrophoresis." *Applied and Environmental Microbiology* 66: 499–508.

Cisowska, A., D. Wojnicz, and A. B. Hendrich. 2011. "Anthocyanins as Antimicrobial Agents of Natural Plant Origin." *Natural Product Communications* 6: 149–156.

Cotner, J. B., and B. A. Biddanda. 2002. "Small Players, Large Role: Microbial Influence on Biogeochemical Processes in Pelagic Aquatic Ecosystems." *Ecosystems* 5: 105–121.

Cottenie, K. 2005. "Integrating Environmental and Spatial Processes in Ecological Community Dynamics." *Ecology Letters* 8: 1175–1182.

Crist, T. O., J. A. Veech, J. C. Gering, and K. S. Summerville. 2003. "Partitioning Species Diversity Across Landscapes and Regions: A Hierarchical Analysis of α, β, and γ -Diversity." *American Naturalist* 162: 734–743.

Declerck, S. A. J., J. S. Coronel, P. Legendre, and L. Brendonck. 2011. "Scale Dependency of Processes Structuring Metacommunities of Cladocerans in Temporary Pools of High-Andes Wetlands." *Ecography* 34: 296–305.

Fernández Zenoff, V. F., F. Sineriz, and M. E. Farias. 2006. "Diverse Responses to UV-B Radiation and Repair Mechanisms of Bacteria Isolated From High-Altitude Aquatic Environments." *Applied and Environmental Microbiology* 72: 7857–7863.

Figuerola, J., A. J. Green, and T. C. Michot. 2005. "Invertebrate Eggs Can Fly: Evidence of Waterfowl Mediated Gene Flow in Aquatic Invertebrates." *American Naturalist* 165: 274–280.

Figuerola, J., A. J. Green, and L. Santamaría. 2003. "Passive Internal Transport of Aquatic Organisms by Waterfowl in Doñana, Southwest Spain." *Global Ecology and Biogeography* 12: 427–436.

Fillinger, L., K. Hug, and C. Griebler. 2019. "Selection Imposed by Local Environmental Conditions Drives Differences in Microbial Community Composition Across Geographically Distinct Groundwater Aquifers." *FEMS Microbiology Ecology* 95, no. 11: fiz160.

Finlay, B. J. 2002. "Global Dispersal of Free-Living Microbial Eukaryote Species." *Science* 296: 1061–1063.

Fossen, T., A. Larsen, and Ø. M. Andersen. 1998. "Anthocyanins From Flowers and Leaves of Nymphaéa × Marliacea Cultivars." *Phytochemistry* 48: 823–827.

13652427, 2025, 5, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/1wb.70047 by UNNOBA Uni Nacional del Noroeste de la Provincia de Buenos A, Wiley Online Library on [19/05/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Gao, L., B. Z. Fang, Y. H. Liu, et al. 2022. "*Paracoccus salsus* sp. Nov., A Novel Slightly Halophilic Bacterium Isolated From Saline Lake Sediment." *International Journal of Systematic and Evolutionary Microbiology* 72, no. 8: 005473.

Hammer, Ø., D. A. T. Harper, and P. D. Ryan. 2001. "PAST: Paleontological Statistics Software Package for Education and Data Analysis."

Hengy, M. H., D. J. Horton, D. G. Uzarski, and D. R. Learman. 2017. "Microbial Community Diversity Patterns Are Related to Physical and Chemical Differences Among Temperate Lakes Near Beaver Island, MI." *PeerJ* 5: e3937. https://doi.org/10.7717/peerj.3937.

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.

Hervàs, A., L. Camarero, I. Reche, and E. O. Casamayor. 2009. "Viability and Potential for Immigration of Airborne Bacteria From Africa That Reach High Mountain Lakes in Europe." *Environmental Microbiology* 11, no. 6: 1612–1623.

Hubbell, S. P. 2001. *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press.

Huss, A. A., and J. D. Wehr. 2004. "Strong Indirect Effects of a Submersed Aquatic Macrophyte, *Vallisneria americana*, on Bacterioplankton Densities in a Mesotrophic Lake." *Microbial Ecology* 47: 305–315.

Hutchinson, G. E. 1959. "Homage to Santa Rosalia, or Why Are There So Many Kinds of Animals?" *American Naturalist* 93: 145–159.

Izaguirre, I., J. Lancelotti, J. F. Saad, et al. 2018. "Influence of Fish Introduction and Water Level Decrease on Lakes of the Arid Patagonian Plateaus With Importance for Biodiversity Conservation." *Global Ecology and Conservation* 14: e00391.

Izaguirre, I., and J. F. Saad. 2014. "Phytoplankton From Natural Water Bodies of the Patagonian Plateau." *Advances in Limnology* 65: 309–319.

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, no. 12: fiz190.

Jones, S. E., and J. T. Lennon. 2010. "Dormancy Contributes to the Maintenance of Microbial Diversity." *Proceedings of the National Academy of Sciences of the United States of America* 107: 5881–5886.

Jürgens, K., and E. Jeppesen. 1998. "Cascading Effects on Microbial Food Web Structure in a Dense Macrophyte Bed." In *The Structuring Role of Submerged Macrophytes in Lakes. Ecological Studies, Book*, edited by E. Jeppesen, M. A. Søndergaard, M. O. Søndergaard, et al., vol. 131. Springer-Verlag.

Kirk, J. T. O. 1994. *Light and Photosynthesis in Aquatic Ecosystems*. Cambridge University Press.

Krieg, N. R., W. Ludwig, J. Euzéby, and W. B. Whitman. 2010. "Phylum XIV. Bacteroidetes Phyl Nov." In *Bergey's Manual of Systematic Bacteriology*, 25–469. Springer.

Lancelotti, J. L. 2009. "Caracterización limnológica de lagunas de la Provincia de Santa Cruz y efectos de la introducción de Trucha Arco iris (*Oncorhynchus mykiss*) sobre las comunidades receptoras." PhD Thesis, Universidad Nacional del Comahue.

Lancelotti, J. L., M. C. Marinone, and I. Roesler. 2017. "Rainbow Trout Effects on Zooplankton in the Reproductive Area of the Critically Endangered Hooded Grebe." *Aquatic Conservation: Marine and Freshwater Ecosystems* 27, no. 1: 128–136. https://doi.org/10.1002/aqc.2629.

Lancelotti, J. L., M. A. Pascual, and A. Gagliardini. 2010. "A Dynamic Perspective of Shallow Lakes of Arid Patagonia as Habitat for Waterbirds." In *Ponds: Formation Characteristics and Uses*, edited by P. L. Meyer, 208–231. Nova Science Publishers Incorporated.

Lancelotti, J. L., N. L. Pessacg, I. C. Roesler, and M. A. Pascual. 2020. "Climate Variability and Trends in the Reproductive Habitat of the Critically Endangered Hooded Grebe." *Aquatic Conservation: Marine and Freshwater Ecosystems* 30, no. 3: 554–564. https://doi.org/10.1002/aqc.3240.

Lancelotti, J. L., L. M. Pozzi, F. Márquez, P. Yorio, and M. A. Pascual. 2009. "Waterbird Occurrence and Abundance in the Strobel Plateau, Patagonia, Argentina." *El Hornero* 24: 13–20.

Lande, R. 1996. "Statistics and Partitioning of Species Diversity, and Similarity Among Multiple Communities." *Oikos* 76, no. 1: 5–13.

Legendre, P., and E. D. Gallagher. 2001. "Ecologically Meaningful Transformations for Ordination of Species Data." *Oecologia* 129: 271–280.

Leibold, M. A., M. Holyoak, N. Mouquet, et al. 2004. "The Metacommunity Concept: A Framework for Multi-Scale Community Ecology." *Ecology Letters* 7, no. 7: 601–613.

Levins, R. 1968. *Evolution in Changing Environments: Some Theoretical Explorations*. Princeton University Press.

Li, H., J. Zeng, L. Ren, J. Wang, P. Xing, and Q. L. Wu. 2017. "Contrasting Patterns of Diversity of Abundant and Rare Bacterioplankton in Freshwater Lakes Along an Elevation Gradient." *Limnology and Oceanography* 62: 1570–1585. https://doi.org/10.1002/lno.10518.

Lima-Mendez, G., K. Faust, N. Henry, et al. 2015. "Determinants of Community Structure in the Global Plankton Interactome." *Science* 348: 9.

Lindström, E. S., M. Forslund, G. Algesten, and A. K. Bergström. 2006. "External Control of Bacterial Community Structure in Lakes." *Limnology and Oceanography* 51, no. 1: 339–342.

Lindström, E. S., and S. Langenheder. 2012. "Local and Regional Factors Influencing Bacterial Community Assembly." *Environmental Microbiology Reports* 4, no. 1: 1–9.

Liu, J., Z. Meng, X. Liu, and X.-H. Zhang. 2019. "Microbial Assembly, Interaction, Functioning, Activity and Diversification: A Review Derived From Community Compositional Data." *Marine Life Science & Technology* 1: 112–128. https://doi.org/10.1007/s42995-019-00004-3.

Liu, Y., T. J. Vick-Majors, J. C. Priscu, et al. 2017. "Biogeography of Cryoconite Bacterial Communities on Glaciers of the Tibetan Plateau." *FEMS Microbiology Ecology* 93, no. 6: 1–10. https://doi.org/10.1093/femsec/fix072.

Logares, R., E. S. Lindstrom, S. Langenheder, et al. 2013. "Biogeography of Bacterial Communities Exposed to Progressive Long-Term Environmental Change." *ISME Journal* 7: 937–948. https://doi.org/10.1038/ismej.2012.168.

Lovejoy, C., and M. Potvin. 2011. "Microbial Eukaryotic Distribution in a Dynamic Beaufort Sea and the Arctic Ocean." *Journal of Plankton Research* 33: 431–444.

MacArthur, R., H. Recher, and M. Cody. 1966. "On the Relation Between Habitat Selection and Species Diversity." *American Naturalist* 100: 319–332.

Mantel, N., and R. S. Valand. 1970. "A Technique of Nonparametric Multivariate Analysis." *Biometrics* 26: 547–558.

Marker, A. F. H., A. Nusch, H. Rai, and B. Riemann. 1980. "The Measurement of Photosynthetic Pigments in Freshwater and Standardization of Methods: Conclusions and Recommendations." *Archiv für Hydrobiologie. Beihefte, Ergebnisse Der Limnologie* 14: 91–106.

Mateus-Barros, E., M. L. de Melo, I. L. Bagatini, A. Caliman, and H. Sarmento. 2021. "Local and Geographic Factors Shape the Occupancy-Frequency Distribution of Freshwater Bacteria." *Microbial Ecology* 81: 26–35. https://doi.org/10.1007/s00248-020-01560-3.

McMurdie, P. J., and S. Holmes. 2013. "Phyloseq: An R Package for Reproducible Interactive Analysis and Graphics of Microbiome Census

13652427, 2025, 5, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/fwb.70047 by UNNOBA Uni Nacional del Noroeste de la Provincia de Buenos A, Wiley Online Library on [19/05/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Data." *PLoS One* 8: e61217. https://doi.org/10.1371/journal.pone.0061217.

Meng, X. L., H. Ming, J. R. Huang, et al. 2019. "*Paracoccus halotolerans* sp. Nov., Isolated From a Salt Lake." *International Journal of Systematic and Evolutionary Microbiology* 69, no. 2: 523–528.

Mentes, A., A. Szabo, B. Somogyi, et al. 2017. "Differences in Planktonic Microbial Communities Associated With Three Types of Macrophyte Stands in a Shallow Lake." *FEMS Microbiology Ecology* 94, no. 2: fix164.

Metz, S., P. Huber, E. Mateus-Barros, et al. 2022. "A Georeferenced rRNA Amplicon Database of Aquatic Microbiomes From South America." *Scientific Data* 9, no. 1: 565.

Mohamed, Z. A. 2017. "Macrophytes-*Cyanobacteria* Allelopathic Interactions and Their Implications for 999 Water Resources Management—A Review." *Limnologica* 63: 122–132.

Morin, P. 1999. *Community Ecology*. Blackwell Science.

Newton, R. J., S. E. Jones, A. Eiler, K. D. McMahon, and S. Bertilsson. 2011. "A Guide to the Natural History of Freshwater Lake Bacteria." *Microbiology and Molecular Biology Reviews* 75: 14–49. https://doi.org/10.1128/MMBR.00028-10.

Oksanen, J., F. G. Blanchet, M. Friendly, et al. 2019. "Vegan: Community Ecology Package." R Package Version 2.5-6. Community Ecology Package. https://CRAN.R-project.org/package=vegan.

Oksanen, J., P. Legendre, B. O'Hara, M. H. H. Stevens, M. J. Oksanen, and M. Suggests. 2007. "Vegan." Community Ecology Package. 631–637. http://cc.oulu.fi/~jarioksa.

Oliveros, J. C. 2015. "Venny an Interactive Tool for Comparing Lists With Venn's Diagrams." https://bioinfogp.cnb.csic.es/tools/venny/index.html.

Panza, J. L., and M. R. Franchi. 2002. "Extra-Andean Cenozoic Basaltic Magmatism." In *Geología y Recursos Naturales de Santa Cruz*, edited by M. J. Haller, 201–236. Relatorio del XV congreso Geológico Argentino, El Calafate.

Pearman, J. K., G. Thomson-Laing, J. Thomson-Laing, L. Thompson, L. Reyes, and S. A. Wood. 2022. "The Role of Environmental Processes and Geographic Distance in Regulating Local and Regionally Abundant and Rare Bacterioplankton in Lakes." *Frontiers in Microbiology* 12: 793441.

Pedrós-Alió, C. 2012. "The Rare Bacterial Biosphere." *Annual Review of Marine Science* 4: 449–466. https://doi.org/10.1146/annurev-marine-120710-100948.

Pizzetti, I., A. Gobet, B. M. Fuchs, R. Amann, and S. Fazi. 2011. "Abundance and Diversity of Planctomycetes in a Tyrrhenian Coastal System of Central Italy." *Aquatic Microbial Ecology* 65, no. 2: 129–141.

Porcel, S., G. Chaparro, M. C. Marinone, J. F. Saad, J. Lancelotti, and I. Izaguirre. 2020. "The Role of Environmental, Geographical, Morphometric and Spatial Variables on Plankton Communities in Lakes of the Arid Patagonian Plateaus." *Journal of Plankton Research* 42: 173–187.

Porcel, S., M. L. Fogel, I. Izaguirre, I. C. Roesler, and J. L. Lancelotti. 2022. "Effect of Rainbow Trout Introductions on Food Webs in Lakes of the Arid Patagonia." *Hydrobiologia* 849. https://doi.org/10.1007/s10750-022-04848-2.

Porcel, S., J. F. Saad, C. A. Sabio Y García, and I. Izaguirre. 2019. "Microbial Planktonic Communities in Lakes From a Patagonian Basaltic Plateau: Influence of the Water Level Decrease." *Aquatic Sciences* 81: 51.

R Core Team. 2020. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. https://www.Rproject.org/.

RStudio Team. 2020. "RStudio: Integrated Development Environment for R." RStudio Team, Boston.

Rabus, R., D. Gade, R. Helbig, et al. 2002. "Analysis of N-Acetylglucosamine Metabolism in the Marine Bacterium Pirellula sp Strain 1 by a Proteomic Approach." *Proteomics* 2, no. 6: 649–655.

Ramette, A. 2007. "Multivariate Analyses in Microbial Ecology." *FEMS Microbiology Ecology* 62: 142–160. https://doi.org/10.1111/j.1574-6941.2007.00375.x.

Reissig, M., C. Trochine, C. Queimaliños, E. Balseiro, and B. Modenutti. 2006. "Impacts of Fish Introduction on Planktonic Food Webs in Lakes of the Patagonian Plateau." *Biological Conservation* 132: e447.

Roesler, I. 2016. "Conservación del Macá Tobiano (*Podiceps gallardoi*): Factores que Afectan la Viabilidad de sus Poblaciones." Universidad de Buenos Aires, Argentina (PhD thesis).

Roesler, I., S. Imberti, H. Casañas, B. Mahler, and J. C. Reboreda. 2012. "Hooded Grebe *Podiceps gallardoi* Population Decreased by Eighty Per Cent in the Last Twenty-Five Years." *Bird Conservation International* 22: 371–382.

Ruiz-González, C., J. P. Niño-García, and P. A. Del Giorgio. 2015. "Terrestrial Origin of Bacterial Communities in Complex Boreal Freshwater Networks." *Ecology Letters* 18, no. 11: 1198–1206.

Saad, J. F., S. Porcel, J. Lancelotti, I. O'Farrell, and I. Izaguirre. 2018. "Both Lake Regime and Fish Introduction Shape Autotrophic Planktonic Communities of Lakes From the Patagonian Plateau (Argentina)." *Hydrobiologia* 831: 133–145.

Sabio y García, C. A., S. Porcel, M. R. Schiaffino, et al. 2024. "Differences in Bacterial Community Composition Between Fish Stocked and Fishless Lakes From an Arid Patagonia Plateau." *Hydrobiologia* 851: 4709–4726. https://doi.org/10.1007/s10750-024-05622-2.

Sadeghi, J., S. R. Chaganti, A. H. Shahraki, and D. D. Heath. 2021. "Microbial Community and Abiotic Effects on Aquatic Bacterial Communities in North Temperate Lakes." *Science of the Total Environment* 781: 146771. https://doi.org/10.1016/j.scitotenv.2021.146771.

Sharp, J. H., E. T. Peltzer, M. J. Alperin, et al. 1993. "Procedures Subgroup Report." *Marine Chemistry* 41, no. 1–3: 37–49.

Sigee, D. C. 2005. *Freshwater Microbiology: Biodiversity and Dynamic Interactions of Microorganisms in the Aquatic Environment*. John Wiley and Sons Ltd.

Soininen, J., J. J. Korhonen, J. Karhu, and A. Vetterli. 2011. "Disentangling the Spatial Patterns in Community Composition of Prokaryotic and Eukaryotic Lake Plankton." *Limnology and Oceanography* 56: 508–520.

Tessler, M., M. R. Brugler, R. DeSalle, et al. 2017. "A Global eDNA Comparison of Freshwater Bacterioplankton Assemblages Focusing on Large-River Floodplain Lakes of Brazil." *Microbial Ecology* 73, no. 1: 1–14.

Veech, J. A., K. S. Summerville, T. O. Crist, and J. C. Gering. 2002. "The Additive Partitioning of Species Diversity: Recent Revival of an Old Idea." *Oikos* 99: 3–9.

Vitorino, I. R., and O. M. Lage. 2022. "The Planctomycetia: An Overview of the Currently Largest Class Within the Phylum Planctomycetes." *Antonie Van Leeuwenhoek* 115, no. 2: 169–201.

Wang, L., X. Liu, S. Yu, X. Shi, X. Wang, and X. H. Zhang. 2017. "Bacterial Community Structure in Intertidal Sediments of Fildes Peninsula, Maritime Antarctica." *Polar Biology* 40: 339–349.

Whittaker, R. H. 1972. "Evolution and Measurement of Species Diversity." *Taxon* 21: 213–251.

Wu, Q. L., G. Zwart, M. Schauer, M. P. Kamst-van Agterveld, and M. W. Hahn. 2006. "Bacterioplankton Community Composition Along a Salinity Gradient of Sixteen High-Mountain Lakes Located on the Tibetan Plateau, China." *Applied and Environmental Microbiology* 72: 5478–5485.

13652427, 2025, 5, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/1462.70047 by UNNOBA Uni Nacional del Noroeste de la Provincia de Buenos A, Wiley Online Library on [19/05/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Wu, Q. L., G. Zwart, J. Wu, M. P. Kamst-van Agterveld, S. Liu, and M. W. Hahn. 2007. "Submersed Macrophytes Play a Key Role in Structuring Bacterioplankton Community Composition in the Large, Shallow, Subtropical Taihu Lake, China." *Environmental Microbiology* 9: 2765–2774.

Yang, Y., R. Hu, Q. Lin, et al. 2018. "Spatial Structure and β-Diversity of Phytoplankton in Tibetan Plateau Lakes: Nestedness or Replacement?" *Hydrobiologia* 808, no. 1: 301–314.

Zhang, L., T. T. Zhao, Q. Wang, L. Li, T. T. Shen, and G. Gao. 2019. "Bacterial Community Composition in Aquatic and Sediment Samples With Spatiotemporal Dynamics in Large, Shallow, Eutrophic Lake Chaohu, China." *Journal of Freshwater Ecology* 34, no. 1: 575–589.

Zhong, Z. P., Y. Liu, F. Wang, et al. 2016. "*Planktosalinus lacus* Gen. Nov., sp. Nov., a Member of the Family Flavobacteriaceae Isolated From a Salt Lake." *International Journal of Systematic and Evolutionary Microbiology* 66, no. 5: 2084–2089.

Zhou, J., and D. Ning. 2017. "Stochastic Community Assembly: Does It Matter in Microbial Ecology?" *Microbiology and Molecular Biology Reviews* 81: e00002-17. https://doi.org/10.1128/MMBR.00002-17.

Zhou, J., X. Song, C. Y. Zhang, et al. 2018. "Distribution Patterns of Microbial Community Structure Along a 7000-Mile Latitudinal Transect From the Mediterranean Sea Across the Atlantic Ocean to the Brazilian Coastal Sea." *Microbial Ecology* 76: 592–609.

Supporting Information

Additional supporting information can be found online in the Supporting Information section.

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