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RESEARCH

Lake Bacterial Communities in North Patagonian Andes: The Effect of the *Nothofagus pumilio* Treeline

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Abstract

One of the most noticeable environmental discontinuities in mountains is the transition that exists in vegetation below and above the treeline. In the North Patagonian Andean lakes (between 900 and 1950 m a.s.l.), we analyzed the bacterial community composition of lakes in relation to surrounding vegetation (erected trees, krummholz belt, and bare rocks), dissolved organic carbon (DOC), and total dissolved nutrients (nitrogen, TDN and phosphorus, TDP). We observed a decrease in DOC, TDP, and TDN concentrations with altitude, reflecting shifts in the source inputs entering the lakes by runoff. Cluster analysis based on bacterial community composition showed a segregation of the lakes below treeline, from those located above. This first cluster was characterized by the cyanobacteria *Cyanobium* PCC-6307, while in the krummholz belt and bare rocks, bacterial communities were dominated by Actinobacteria hgcl-clade and Proteobacteria (*Sandarakinorhabdus* and *Rhodovarius*), with the presence of pigments such as actinorhodopsin, carotenoids, and bacteriochlorophyll *a*. The net relatedness index (NRI), which considers the community phylogenetic dispersion, showed that lakes located on bare rocks were structured by environmental filtering, while communities of lakes below treeline were structured by species interactions such as competition. Beta-diversity was higher among lakes below than among lakes located above the treeline. The contribution of species turnover was more important than nestedness. Our study brings light on how bacterial communities may respond to changes in the surrounding vegetation, highlighting the importance of evaluating different aspects of community structure to understand metacommunity organization.

Keywords Treeline · *Nothofagus pumilio* forest · Krummholz belt · Bacterial community composition · Species turnover · Phylogenetic clustering

Introduction

Mountain ranges are present across the world, and due to their glacial history, lakes are common on these landscapes. These lakes are often remote, with marked fluctuations in temperature, high incidence of ultraviolet radiation, and low nutrient availability [1]. Because of these particular features, high elevation lakes represent sensitive ecosystems to environmental variations related to climate change [2, 3]. The magnitude and direction of lake response to stressors may vary among lakes depending on catchment characteristics. One of the most conspicuous environmental discontinuities in mountains is the abrupt transition from subalpine (below treeline) to alpine (above treeline) vegetation over a few meters. Variations in vegetation, comprising upward shifts of the treeline and krummholz [4], and plant species turnover in high-latitude regions [5], can alter carbon and nutrient availability and therefore bacterial communities' composition [6]. In addition, current climate changes also influence mountain bacterioplankton lake structure and function indirectly through landscape changes, including not only the loss of upstream glaciers and snow packs [7], but also shifts in vegetation type and cover [1]. In this sense, altitude treeline shift has the potential to enrich lake ecosystems with less biodegradable dissolved organic matter, affecting bacterial community function [3].

The study of microbial community patterns across the treeline is important to understand the changes that mountain lakes are experiencing [6, 8]. In lakes located above or below treeline, bacterial communities play a key role

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in processing both nutrients and dissolved organic matter, transferring energy to higher trophic levels [9]. However, the position of the treeline is very sensitive to land use practices and climatic changes including variations in temperature, precipitation, and snowpack duration [10]. Thus, understanding the altitudinal variation of bacterial community composition has a key role in the study of lake ecosystem functioning and shifts under environmental changes.

The β-diversity is the linkage between local alpha diversity and regional gamma diversity and was often used in directional gradients as a measure of the dissimilarity in species composition among sites [11]. In particular, β-diversity may reflect the spatial species turnover (species replacement) and nestedness (species loss) of assemblages along a gradient, based on presence/absence dissimilarities (e.g. Sorensen index) [12]. However, abundance-based dissimilarities (e.g. Bray–Curtis index) can also inform about replacement and loss when comparing different sites [13, 14]. The balanced variation in abundance may be equivalent to species turnover as it considers the substitution of individuals of one species by individuals of another species. In the abundance gradients, individuals of one species are lost and not replaced, and this may be analogous to species nestedness. These two different approximations (presence/absence and abundances) can be applied to the same dataset since they may disentangle different aspects of the community under study [14]. In habitats with high environmental heterogeneity, the contribution of each process to total β-diversity may not be evenly represented in the landscape [12, 15]. In a study of altitudinal variation of vascular plants, butterflies, beetles, spiders, and earthworms, it was observed that turnover increased with increasing elevation distance along the gradient while nestedness decreased [16].

Treeline represents a boundary beyond which trees are no longer capable of establishing; therefore, an increase in lake habitat harshness can be expected. Accordingly, as vegetation changes toward bare rocks, changes in lake bacteria communities can be anticipated [17, 18]. The phylogenetic relatedness among species of the same community may reflect species niche similarity; thus, phylogenetic clustering or overdispersion may result from environmental filtering or competition, respectively [19, 20]. In this sense, closely related taxa with similar niche preferences are expected to dominate microbial communities under harsh habitat conditions.

In the Patagonian Andes of South America, the subalpine forest consists of pure stands of the austral deciduous beech *Nothofagus pumilio* (Poepp. et Endl.) Krasser. This forest dominates high-elevation environments of Argentina and Chile from 35°S down to 55°S on the Andes Mountains, constituting part of the world's most austral forests [21]. Particularly, in the North Patagonian Andes (~41°S), *N. pumilio* grows as erect trees up to ca. 1500 m a.s.l. From ca. 1500 to 1750 m a.s.l., there is a krummholz belt of *N. pumilio*, while above 1700–1750 m, there is bare rock [22]. Below 1300 m, the forest is co-dominated by perennial species such as *Nothofagus dombeyi* (Mirb.) Oerst., *Austrocedrus chilensis* (D.Don) Pic-Serm. & Bizzarri, or other species of the Valdivian rainforest (*Fitzroya cupressoides* (Molina) I. M. Johnst.). Treeline increases in altitude with increasing temperature but it decreases due to warmer and dryer summer conditions [23]. In these landscapes, there are several small lakes formed by the erosive activity of glaciers during the last Pleistocene glaciation. A previous study in different lakes in the area has shown decreasing nutrients and dissolved organic matter concentration towards higher altitudes, which was related to the differential presence of vegetation along the altitudinal gradient [17]. Here, we hypothesized that changes in the surrounding vegetation would drive differences in the structure of bacteria communities of these lakes. For this purpose, we analyzed bacterial community composition comparing seven Andean North Patagonian mountain lakes located below and above the treeline, as well as within the krummholz belt. We combined the analytical framework of ß-diversity and phylogenetic clustering analysis to understand which environmental factors are the primary drivers of the bacterial community composition in these areas with different vegetation.

Methods

Study Area, Sampling, and Data Collection

We sampled seven lakes located at 41° S, 71° W in Nahuel Huapi National Park (Patagonia, Argentina), corresponding to the Glacial Lakes District of the Southern Andes (Fig. 1). Climate is cold temperate and cyclonic precipitations are generated by westerlies that carry humid air masses from the Pacific Ocean and are cooled as they cross the Andes Mountains [24].

The studied lakes are located within a distance of 35 km, and in an altitude between 900 and 1950 m a.s.l. (Table 1). These lakes are included in different catchments with different vegetation landscapes. Two lakes are above 1800 m a.s.l. surrounded by bare rocks, three lakes are within the *Nothofagus pumilio* krummholz belt, and finally, two lakes are located in different forest types. Lake Ilón lies in the *N. pumilio* forest with pure stands of erect trees, while lake Cántaros is in the Valdivian temperate rainforest composed of a diverse mixture of *Nothofagus dombeyi*, *Fitzroya cupressoides*, and broad-leaved evergreen trees (*Eucryphia cordifolia* Cav., *Aextoxicon punctatum* Ruiz et Pav., *Laureliopsis philippiana* (Looser) R. Schodde).

The seven lakes were sampled in February (austral summer) in different consecutive years: four lakes were

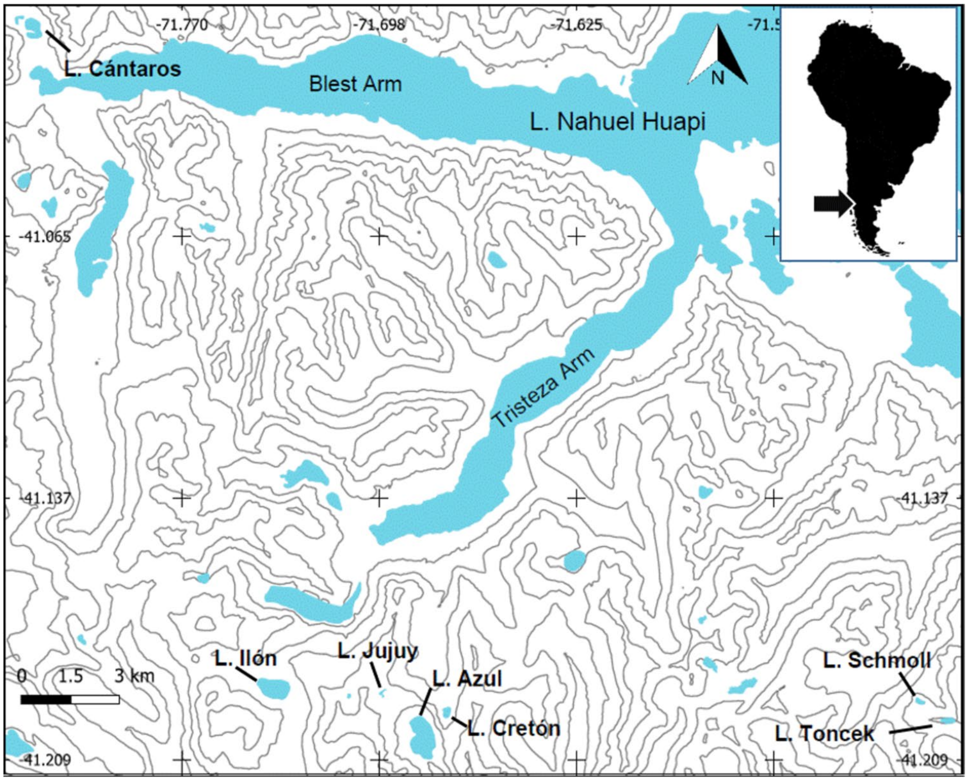


Fig. 1 Map showing the location of the studied lakes in Nahuel Huapi National Park (Patagonia, Argentina)

Table 1 Features of the studied lakes and their location in the vegetation sectors. References: *N. pumilio*=*Nothofagus pumilio*). Z_m maximum depth

Vegetation sectors	Catchment features	Lake	Geographic coordinates	Altitude (m)	Z_m (m)	Area (km^2)	Sampling dates
Below treeline	Valdivian rainforest	Cántaros	41° 00′ 31″ S 71° 49′ 23″ W	900	16	0.25	2015 2016 2017
	N. pumilio erected trees	Ilón	41° 11′ 24″ S 71° 44′ 06″ W	1389	15	0.43	2017 2018
Krummholz	Rocks and *N. pumilio* krummholz	Azul	41° 12′ 17″ S 71° 40′ 54″ W	1509	27	0.71	2017 2018
		Cretón	41° 11′ 45″ S 71° 40′ 20″ W	1649	7	0.06	2018
		Toncek	41° 11′ 55″ S 71° 29′ 21″ W	1754	12	0.05	2017 2018
Above treeline	Bare rocks	Jujuy	41° 11′ 26″ S 71° 41′ 48″ W	1839	3	0.04	2017 2018
		Schmoll	41° 11′ 35″ S 71° 29′ 58″ W	1930	6	0.03	2016 2017 2018

sampled in two consecutive years, two lakes in three consecutive years, and one lake in only one year (Table 1), with a total of 15 samples. On each sampling occasion in the field, we measured altitude with a GPS (Global Positioning System), and temperature with a YSI 85 (Yellow Springs Instruments, Yellow Springs, Ohio). We collected subsurface lake water samples (0.5 m) on a central point of each lake with sterile 2-L Nalgene™ bottles for bacterial community identification. In addition, we collected 2 L water samples in HCl-washed bottles for nutrients, dissolved organic carbon and chlorophyll *a* concentration determination, and dissolved organic matter characterization. Filtration procedures were performed in situ and filters and filtered lake water were transported immediately to the laboratory in thermally insulated containers.

Sample Processing

We quantified total dissolved phosphorus (TDP), total dissolved nitrogen (TDN), and dissolved organic carbon (DOC) in lake water filtered through pre-combusted GF/F filters. TDP was determined by sample digestion with potassium persulphate at 125 °C and 1.5 atm for 1 h, followed by the ascorbate-reduced molybdenum method [25]. TDN was determined using a TN-M1 unit on the Shimadzu TOC V-CSH. DOC concentration was determined with a high-temperature combustion analyzer (Shimadzu TOC V-CSH). To characterize dissolved organic matter (DOM), we constructed excitation-emission matrices (EEMs) with a Perkin-Elmer LS45 fluorescence spectrometer equipped with a xenon discharge lamp. The excitation wavelength intervals were 2 nm, between 240 and 450 nm, and the emission ranged between 300 and 550 nm, with 5-nm increments. The measurements were performed at a constant room temperature of 20 °C in 1-cm quartz fluorescence cell. To characterize DOM, fluorescence data were normalized according to Murphy et al. [26] by dividing the obtained fluorescence values (relative units) by the Raman peak of Milli-Q water at 350 nm excitation on the same day as the measurement. Fluorescence was then expressed as Raman units (RU) [27]. The chlorophyll *a* (Chl *a*) concentration was determined on GF/F filters by extraction with 90% ethanol, according to Nusch [28], using a fluorometer (TurnerDesigns,10-AU).

Samples for bacterial assemblage identification (15 samples) were filtered through 0.22-µm pore-size nucleopore filters (PALL). The nucleopore filters were stored at – 80°C until further processing. DNA was extracted from the filters using a DNeasy PowerSoil Kit MoBio (Qiagen, Hilden, Germany) following the manufacturer's protocol. Purity and quantity of DNA were determined with a Take3 Micro-Volume Plate (BioTek® Instruments, Inc., Winooski, VT, USA) in a Synergy™ HTX Multi-Mode Microplate Reader. The amplicons of the V3–V4 variable region in the 16S rRNA bacterial gene were obtained with the primers 341F (5′-CCT ACG GGNGGC WGC AG-3′) and 805R (5′-GAC TAC HVGGG TAT CTA ATC C-3′). Sequencing was performed with the Illumina MiSeq platform at Macrogen (Seoul, South Korea).

Raw amplicon sequences as FASTQs were bioinformatically analyzed through the DADA2 R package [29]. Sequences were identified as unique amplicon sequence variants (ASV) based on single nucleotide differences. Taxonomic assignment was carried out using the SILVA database (version 138.1) as a reference. A second table was built excluding ASVs with less than 0.001% of total abundance, archaea, chloroplasts, mitochondria, and eukaryotes. This table was normalized to a depth of sampling using the rarefy function from the vegan package [30]. The raw reads have been deposited in the NCBI accession number SRR28714505-SRR28714519 under BioProject PRJNA1098696 (https://dataview.ncbi.nlm.nih.gov/object/PRJNA1098696?reviewer=4691cv6fgt26oul921bplf6eeu).

Statistical Analysis and Calculations

We tested for significant differences in DOC, TDP, and TDN concentrations in the lakes located under different vegetation types with one-way ANOVA. When these tests resulted in significant differences, we performed post hoc multiple comparison Holm-Sidak test. We checked for normality and homoscedasticity before these analyses. These statistical analyses were done with SigmaPlot12.5 (Systat Software Inc., San Jose, CA, USA).

The fluorometric EEMs were analyzed with a parallel factor analysis (PARAFAC) with the DOM-Fluor toolbox in MATLAB R2015a (The MathWorks, Inc., Natick, MA, USA) [31]. The PARAFAC modeling was validated using split-half method analysis [32]. The values of the obtained PARAFAC components were cross-referenced with the OpenFluor database [33].

Environmental characteristics and bacterial community dissimilarities were visualized using dendrograms and non-metric multidimensional scaling (NMDS) analyses based on Bray–Curtis distance. ANOSIM was used to test for significant differences among lakes in the ordinations [34]. We performed a canonical correspondence analysis (CCA), on which environmental variables with a strong correlation were eliminated, and forward selection with Monte Carlo permutation tests ($P < 0.05$) was performed to determine the relationship between bacterioplankton community patterns and environmental variables. These multivariate analyses were performed using '*vegan*' package in R [30].

Total bacterial β-diversity was calculated using the Sørensen dissimilarity index (β_{SOR}) and total Bray–Curtis dissimilarity index (β_{BC}), applied to presence–absence and abundance data, respectively. Then, we applied the Baselga ß diversity partitioning [12, 35] by calculating the contributions of turnover (β_{SIM}, Simpson dissimilarity index) and nestedness (β_{NES}) to the presence/absence dataset. In addition, we analyzed the contributions of balanced-variation ($\beta_{BC.BAL}$) and abundance-gradient ($\beta_{BC.GRA}$) components to the abundance dataset. The dissimilarity indices of bacterial communities were calculated in R, using the function 'beta.pair' and 'beta.pair.abund' in the R package '*betapart*' (v1.5.4). Total bacterial ß-diversity and their partitioning were analyzed by comparing different vegetation sectors: (a) below treeline-Krummholz belt, (b) Krummholz belt-above treeline, and (c) below-above treeline. We generated null models of communities for both presence-absence and abundance data. In the former, we applied the functions 'nullmodel' and 'simulate' of the package '*vegan*', with non-sequential algorithm for binary matrices that preserves the site (row) frequencies (option 'r1'). In the abundance null models, we used the function 'taxo.null' of the package '*NST*', with the abundance option 'region'. In both cases, we generated 1000 null models, we estimated the distance matrices (ß-diversity), and then we calculated the average distance matrix for each kind of index. Then, we compared the ß diversity of the observed dataset comparing the vegetation sectors with those of the corresponding null model with a *t*-test or a Mann–Whitney test when normality was not fulfilled.

To evaluate how bacterial β-diversity was related to environmental variables, we generated pairwise dissimilarity matrices for the six coefficients (β_{SOR}, $\beta_{SIM,}$ β_{NES}, β_{BC}, $\beta_{BC.BAL}$, and $\beta_{BC.GRA}$). Similarly, we generated a matrix for each environmental parameter calculating de difference of the parameter for each pair of samples. We obtained, for each environmental parameter, a matrix with the same dimension of the β-diversity (square, symmetrical matrices with 0 in the diagonal). Then, we performed Pearson correlations among β-diversity parameters and environmental variables using the '*vegan*' package in R [30].The community phylogenetic dispersion of ASVs was analyzed based on the net relatedness index (NRI) [19]. The phylogenetic tree was constructed using MEGAX (v. 10.1.8), with maximum likelihood parameters with 1000 bootstraps. We used 'trialswap' as a null model to calculate NRI, which maintained ASVs richness and ASVs occurrence frequency and abundance across sites. NRI was obtained using '*picante*' R package v. 1.8 [36]. NRI quantifies the structure of a sample phylogeny derived from the mean phylogenetic distance, thus capturing the degree of clustering of the phylogeny from root to terminal leaves. Positive NRI values indicate phylogenetic clustering, with taxa that are more evolutionarily related, suggesting environmental filtering. This implies that habitat characteristics exert selection pressure on the potential community members in a way such that only a non-random subset of related species of the available (global or regional) pool can colonize or invade and persist. On the other hand, negative NRI values indicate an overdispersed phylogeny, with taxa less related than expected by chance, suggesting that interactions such as competition are structuring the community. In this case, phylogenetically closely related species cannot coexist because they share critical traits (and therefore niches) whereas more distantly related species do not [19].

Table 2 Nutrient concentrations (*DOC* dissolved organic carbon, *TDP* total dissolved phosphorus, *TDN* total dissolved nitrogen) in lakes located in the different vegetation sectors. Values are average ± standard error

	DOC (mg L^{-1})	TDP (μg L^{-1})	TDN (μg L^{-1})
Below treeline	1.73 ± 0.20	3.20 ± 052	209.77 ± 68
Krummholz	0.65 ± 0.12	1.95 ± 0.27	60.95 ± 4.30
Above treeline	0.64 ± 0.07	1.68 ± 0.07	56.62 ± 4.80

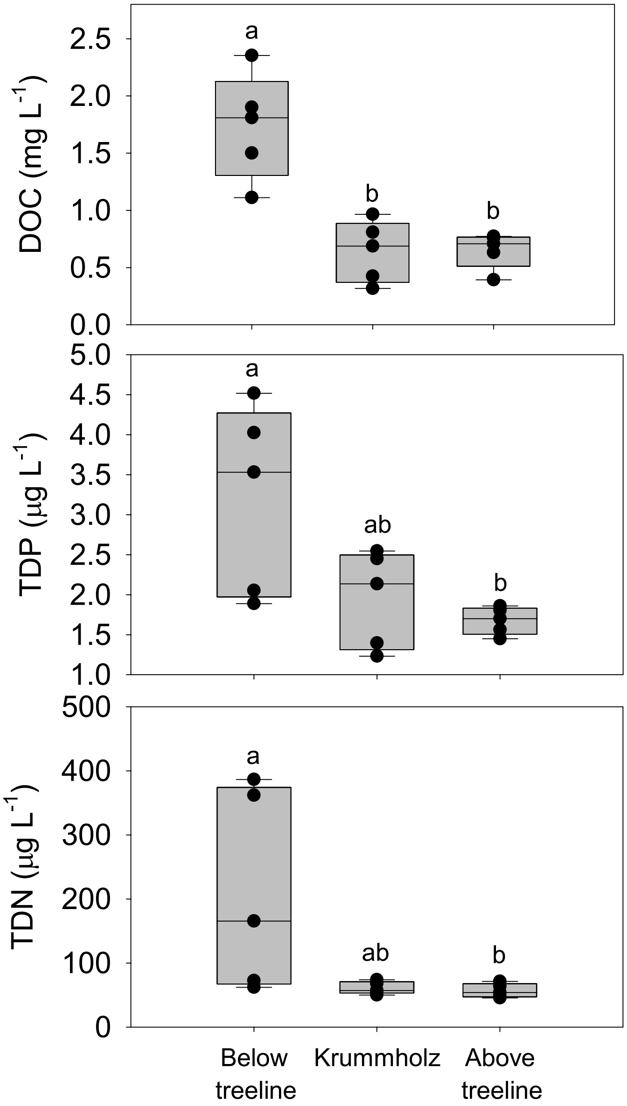


Fig. 2 Box plot of nutrient concentration in lakes located in different vegetation types. DOC, dissolved organic carbon; TDP, total dissolved phosphorus; TDN, total dissolved nitrogen. Different letters above the boxes indicate significant differences (one way ANOVA, $P < 0.05$)

Results

Lakes in the Different Vegetation Sectors

Lakes differed according to the vegetation in the catchment area: (1) below treeline, (2) Krummholz belt, and (3) above treeline. Nutrients concentration (DOC, TDP, and TDN) decreased from lakes below the treeline to lakes above the treeline (Table 2; Fig. 2). For all nutrients, we observed significant differences between lakes below and above the treeline (erected trees and bare rocks) (one-way ANOVA, $P < 0.001$, a posteriori Holm-Sidak test, $P < 0.040$ for below vs. above). DOC was the only variable that showed significant differences between below treeline and krummholz belt (one-way ANOVA, $P < 0.001$, a posteriori Holm-Sidak test, $P < 0.001$). No significant differences were observed between krummholz and above the treeline for any variable (Fig. 2).

The analysis of DOM, based on the fluorometric matrices (PARAFAC analysis), detected three components (Fig. 3a) that could be grouped into two types according to their emission properties. All the components had high similarity scores (> 0.97) with components in the OpenFluor database [33]. The components C1 and C3 had fluorescent properties that are often referred to as humic-like, with emission maxima above 430 nm, typically of terrestrial origin. On the other hand, C2 showed a fluorescence emission at 330 nm, which resembles protein-like fluorescence, similar to that of free dissolved tryptophan. The humic-like component C1 was significantly lower in lakes above the treeline (a posteriori Holm-Sidak test, $P < 0.003$ for both comparisons), whereas the protein-like component C2 showed the highest proportion in these lakes (a posteriori Holm-Sidak test, $P < 0.025$ for both comparisons) (Fig. 3b).

Bacterial Structure and β-Diversity

After the quality control, we obtained a total of 313,362 high-quality sequences, with an average of 20,891 sequences per sample, corresponding to a total of 1670 ASVs. The rarefaction curves of ASVs at each sample indicated that diversity was almost completely sampled in all samples (Fig. S1). Actinobacteria was the dominant phylum in all the datasets, except in Lake Jujuy (bare rocks), with relative abundances up to 85.1% (Fig. 4). Proteobacteria, Cyanobacteria, Patescibacteria, and Bacteroidota were the next phyla in order of importance by their relative abundance, representing a maximum of 46.3%, 33.6%, 12.1%, and 4.1%, respectively (Fig. 4).

Of the total 1670 ASVs recorded in the whole dataset, only 65 (3.9%) were shared by the three lake groups (Fig. 5a), suggesting a clear segregation of bacterial communities in the different vegetation sectors. Indeed, each lake group harbours more than half of their ASVs as unique ones (Fig. 5a). The hierarchical cluster analysis based on Bray–Curtis dissimilarity index confirmed that bacterial community composition was related to the catchment area features. We did not observe differences among different sampling years (Fig. 5b). Lakes below the treeline were included in a single cluster (Fig. 5b), with a community dominated by several ASVs of *Cyanobium* (Cyanobacteria) and Actinobacteriota hgcl-clade. A second cluster, composed of lakes Toncek, Cretón (krummholz belt), and Schmoll (above treeline), showed almost the absence of Cyanobacteria and the dominance of other ASVs of the Actinobacteriota hgcl-clade. Finally, Lakes Jujuy (above treeline) and Azul (krummholz belt) constituted separate clusters. Lake Jujuy exhibited a high abundance of

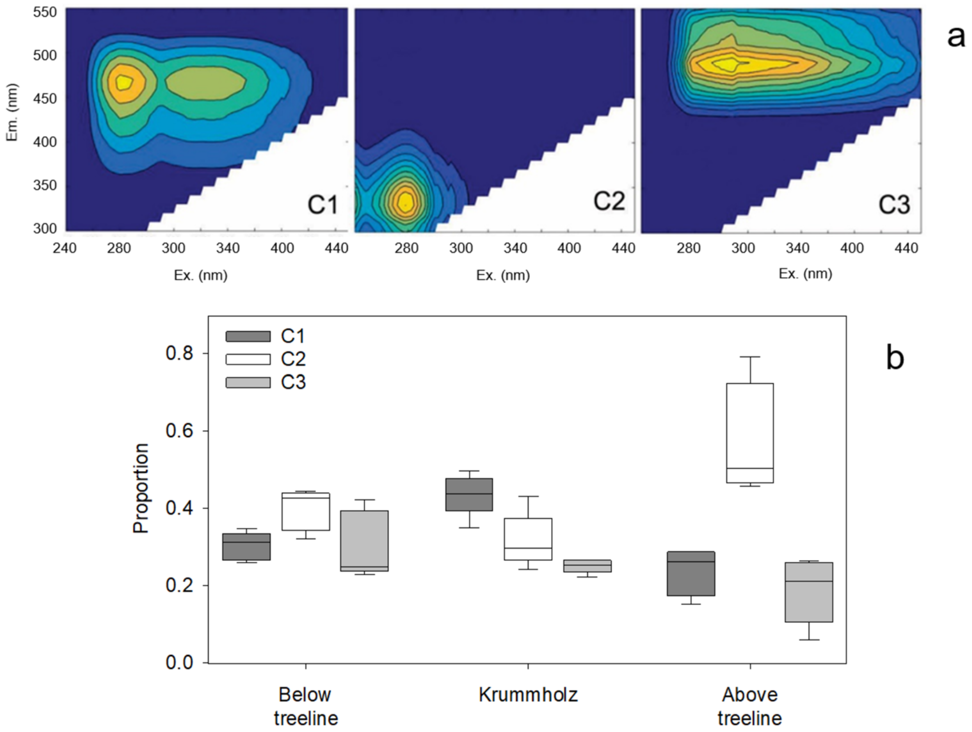
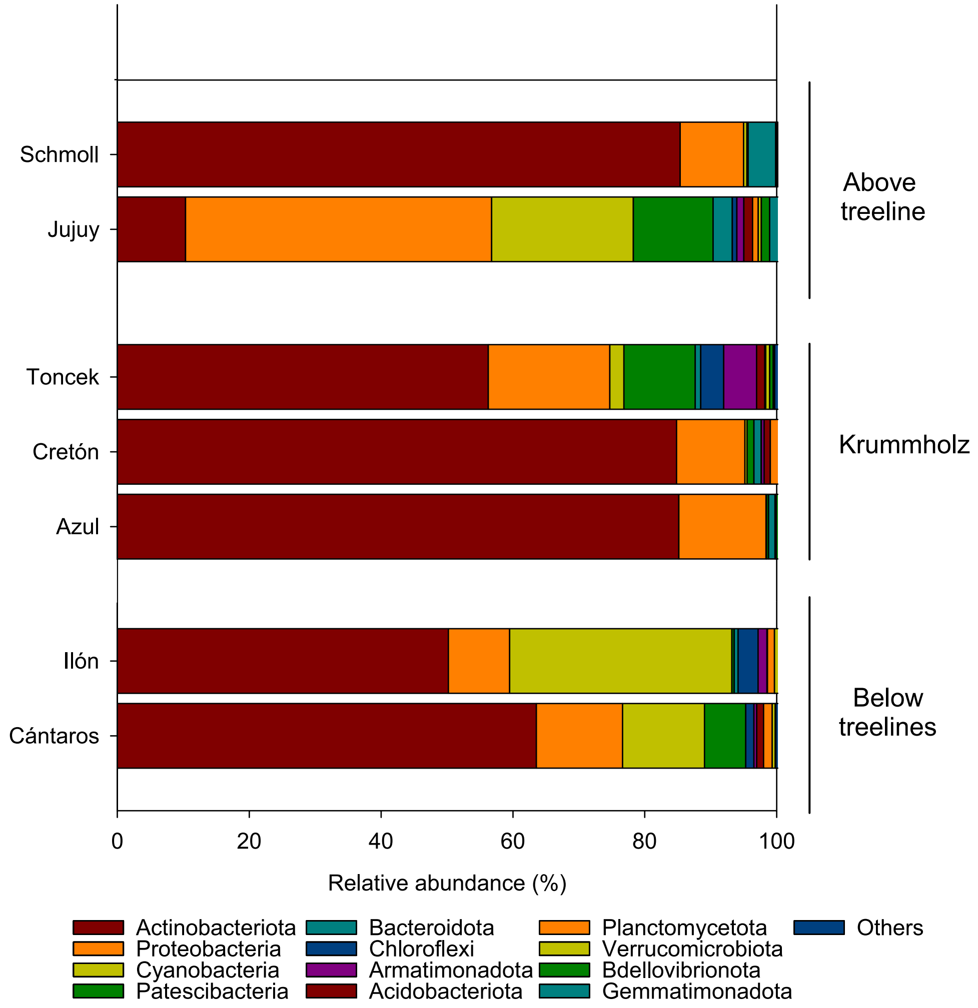


Fig. 3 Dissolved organic matter (DOM) characterization and distribution in lakes located in different vegetation types. **a** Fluorescence signatures of the components identified by the PARAFAC model (excitation–emission matrices, EEM). **b** Proportion of each component in the studied lakes located in different vegetation types

Fig. 4 Average relative abundance of the dominant phyla in the different sampled lakes grouped into below treeline, krummholz belt, and above treeline



Sandarakinorhabdus, *Rhodovarius*, *Polimorphobacter*, and several ASVs of Patescibacteria, while Lake Azul had a high abundance of several ASVs of Actinobacteria hgcl-clade, different from those observed in the second cluster (Fig. 5b).

The NMDS ordination analysis also showed significant differences among the sampled lakes (ANOSIM with Lake as factor, global $R = 0.96$, $P < 0.001$) (Fig. 5c). There were significant differences between lakes below the treeline (Fig. 5c, green dots) and those set on krummholz belt and bare rocks (Fig. 5c, blue and pink dots) (ANOSIM with Catchment vegetation as factor, global $R = 0.37$, $P = 0.002$, *pairwise test* Below vs. krummholz/Above, $P = 0.007$).

The presence/absence dissimilarity analyses of the total ß-diversity ($ß_{SOR}$) and turnover ($ß_{SIM}$) showed high values among sectors (all β_{SOR} and $\beta_{SIM} > 0.75$) (Table 3). Accordingly, nestedness ($ß_{NES}$) values were very low (< 0.1). Similar results were obtained when ß-diversity was based on ASVs abundances. In all cases, maximum values were observed when comparing below and above treeline (Table 3). When we compared the observed ß-diversity values of our presence/absence dataset with those generated by the null models, we observed that only Below-Above treeline showed significant differences with an increase in the turnover component (Table 3). On the contrary, in the comparisons based on the abundance dataset, all pairwise comparisons gave significant results, indicating that although vegetation sectors shared a small proportion of species, the changes in abundances differed even more (Table 3).

Analyses of the phylogenetic relatedness among ASVs in each bacterial community showed two different scenarios. In lakes below the treeline and krummholz belt, most of the NRI values were negative, with taxa less related than expected by chance (Fig. 6). Above the treeline, all the NRI values were positive, indicating that taxa are more closely related than expected by chance (Fig. 6) (one way ANOVA, $P = 0.008$, a posteriori Holm-Sidak test $p = 0.015$ for Above vs. Below/Krummholz).

Influences of Environmental Variables on Community Composition.

The relationship between environmental factors and microbial communities (based on the ASVs abundance) was analyzed by applying a canonical correspondence analysis

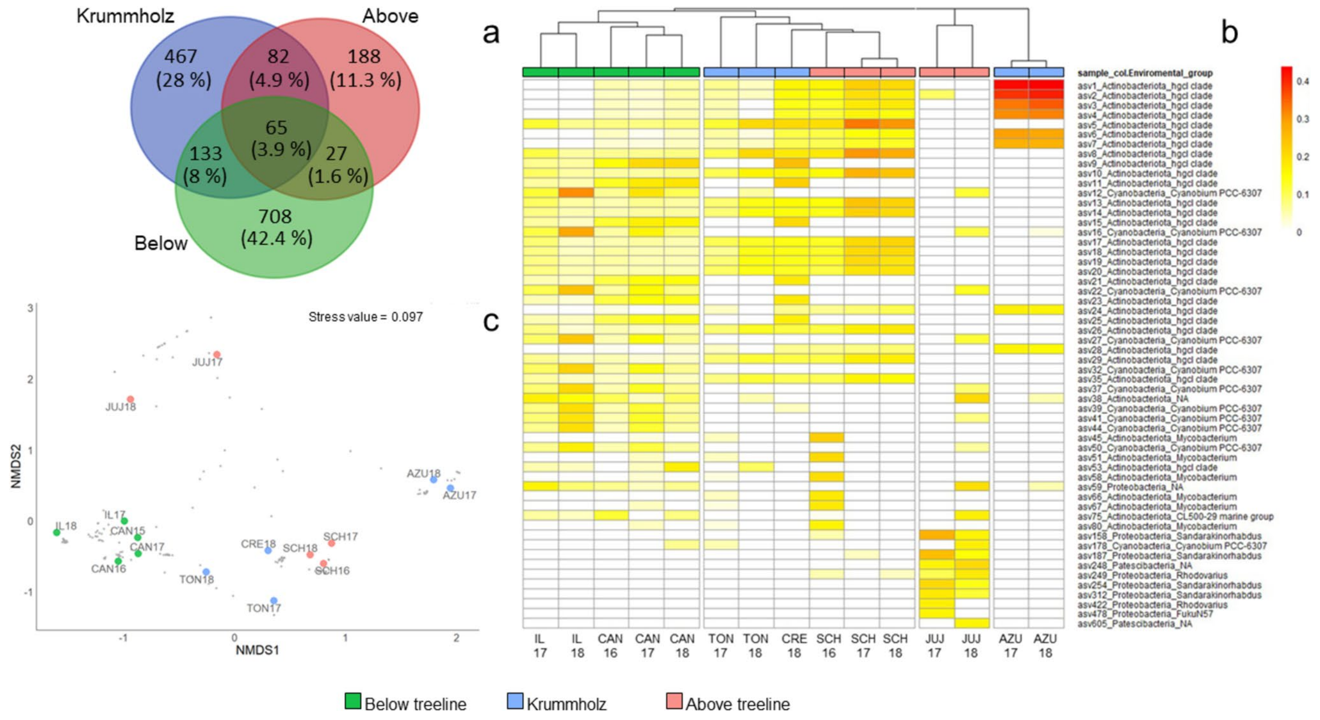


Fig. 5 A **a** Venn diagram showing the number and proportion of shared and unique ASVs among the different vegetation types. Percentage values are calculated relative to the total number of ASVs detected. **b** Hierarchically clustered heatmap showing the relative abundance (proportion) of dominant genera in samples. Clustering of samples is represented by a dendrogram based on Bray–Curtis dissimilarity. **c** Non-metric multidimensional analysis (NMDS) based on Bray–Curtis dissimilarity considering all ASVs are present in all samples. References: CAN, Cántaros; Il, Ilón; TON, Toncek; SCH, Schmoll; CRE, Cretón; AZU, Azul; JUJ, Jujuy. Color references are valid for three graphs

Table 3 Observed values of ß diversity and components among vegetation sectors based on presence-absence data (Sorensen index) and abundance data (Bray Curtis index) and the statistical results of the comparison between observed and null models. For details of null models, see methods. References: values are average ± standard error. β_{SOR} total ß diversity based on Sorensen index, β_{SIM} turnover, β_{NES} nestedness; β_{BC} total ß diversity based on Bray–Curtis dissimilarity index, $\beta_{BC.BAL}$ contributions of balanced-variation, $\beta_{BC.GRA}$ abundance-gradient component. *Significant difference

Index	Below timberline—Krummholz		Krummholz—above timberline		Below–above timberline	
	Observed	Observed-null model	Observed	Observed-null model	Observed	Observed-null model
β_{SOR}	0.843 ± 0.022	$P > 0.05$	0.845 ± 0.022	$P > 0.05$	0.906 ± 0.009	$P < 0.001$*
β_{SIM}	0.769 ± 0.027	$P = 0.009$*	0.785 ± 0.025	$P > 0.05$	0.816 ± 0.020	$P < 0.001$*
β_{NES}	0.074 ± 0.011	$P > 0.05$	0.0605 ± 0.010	$P > 0.05$	0.089 ± 0.014	$P = 0.018$*
β_{BC}	0.902 ± 0.021	$P < 0.001$*	0.868 ± 0.026	$P = 0.001$*	0.951 ± 0.05	$P < 0.001$*
$\beta_{\mathrm{BC.BAL}}$	0.860 ± 0.029	$P < 0.001$*	0.7915 ± 0.037	$P < 0.001$*	0.888 ± 0.20	$P < 0.001$*
$\beta_{\mathrm{BC.GRA}}$	0.042 ± 0.013	$P = 0.016$*	0.073 ± 0. 015	$P < 0.001$*	0.063 ± 0.018	$P < 0.001$*

(CCA). The first axis, which explained 32.5% of the variance, was related to nutrient content, particularly, DOC concentration. The second axis explained 22.1% (cumulative 54.6%) and was associated with the changes in DOM component contribution (Fig. 7). This analysis indicated that community composition in lakes located below treeline was associated with high DOC concentration, whereas in lakes above treeline, it was associated with a high proportion of the protein-like DOM component (pC2) (Fig. 7). The results of a Monte Carlo permutation test demonstrated that DOC concentration was significantly related to the overall changes in the bacterial community composition patterns ($P = 0.001$).

Total β-diversity, both β_{SOR} and β_{BC} showed a positive relationship with DOC concentration differences ($r = 0.22$, $P < 0.001$ for β_{SOR}, and $r = 0.31$, $P = 0.001$ for β_{BC}). DOC concentration difference was also associated positively with $\beta_{\mathrm{BC.BAL}}$ ($r = 0.327$, $P < 0.001$) and negatively to $\beta_{\mathrm{BC.GRA}}$ ($r = -0.21$, $P = 0.031$). Nestedness (β_{NES}) showed a positive

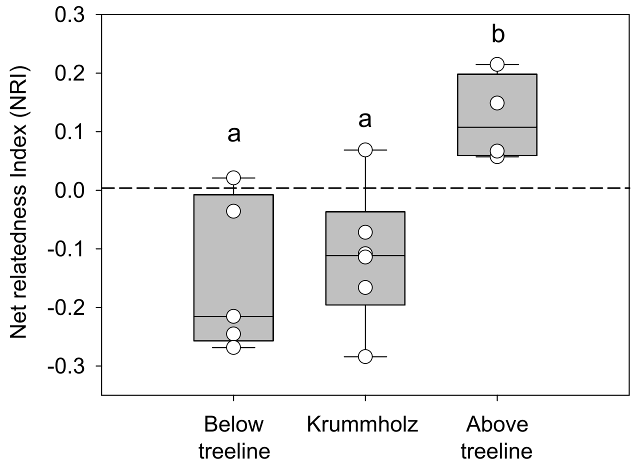


Fig. 6 Net relatedness index (NRI) in lakes below, at, and above the treeline. Different letters above the boxes indicate significant differences and homogeneous groups (one way ANOVA, $P<0.05$, a posteriori Holm-Sidak method)

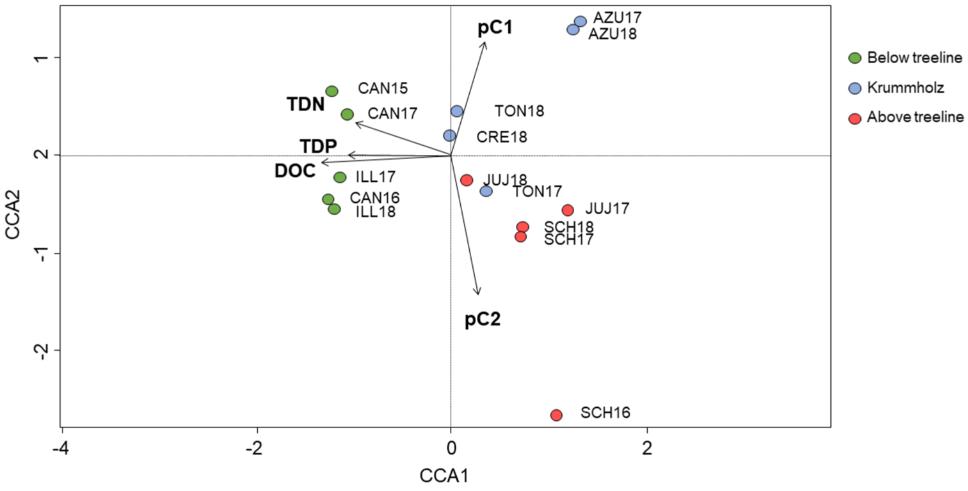
relationship to changes in TDN concentration ($r=0.43$, $P<0.001$) and the proportion of the humic-like component 3 (pC3) ($r=0.24$, $P=0.012$) (Table. S2).

Discussion

One of the most noticeable environmental discontinuities in mountains is the transition that exists in vegetation below and above the treeline. In North Patagonia, treeline is defined by *Nothofagus pumilio* that dominates in the South Andes Mountains forming a monospecific forest, with erect trees up to 1500 m a.s.l. and krummholz from there up to 1700 m a.s.l. [22]. The location of the upper treeline of the *N. pumilio* forest was observed to be sensitive to changes in climate variations, in particular by the interaction of temperature increase and variations in annual precipitation [37]. Our study showed concomitant changes in different environmental variables. Particularly, DOC concentration, humic-like component C1, and nutrients (TDP and TDN) decreased towards bare rock landscapes located at higher altitudes. These changes reflect shifts in the source inputs, coming mainly from soil and vegetation leachates that enter the lakes by runoff [38]. In addition, the presence of the krummholz belt is an important difference from other forests in the world [39] since it may add an intermediate heterogeneity sector buffering the abrupt changes between erected trees and bare rock. Studies performed in the Northern Hemisphere highlighted that changes in the treeline location have the potential to enrich lake ecosystems with less biodegradable DOM, affecting bacterial community function and composition [3]. In this sense, enrichment experimental studies have demonstrated that forest soil additions significantly influenced bacterial communities; however, the direction of change is not always possible to predict [6, 40]. Therefore, the treeline position constitutes a useful framework to analyze the effect of shifts in DOM and nutrients on bacterial communities, due to changes in vegetation types. Hence, the input of material to the lakes will be closely linked to changes in precipitation regimes, associated with climate change. A study in lakes in the Rocky Mountains across a coniferous treeline showed that changes in runoff during the summer resulted in differences between bacterial communities in lakes below and above the treeline [18]. However, the South Andes (> 35°S) are influenced by the westerly circulation from the Pacific, with a cold temperate climate and a winter peak in precipitations [41]. This may explain why we did not observe differences in bacteria communities during different summer samplings and suggest the importance of future studies during autumn and spring when runoff increases.

Clustering analysis based on bacterial community composition showed a segregation of lakes below treeline, included in a unique cluster, from those located at higher altitudes. This first cluster shared ASVs of the picocyanobacteria

Fig. 7 Canonical correspondence analysis (CCA) between bacterial communities (total ASVs) and environmental parameters. References: DOC, dissolved organic carbon; TDP, total dissolved phosphorus; TDN, total dissolved nitrogen; pC1, pC2, and pC3, dissolved organic matter components C1, C2, and C3



Cyanobium PCC-6307, which was dominant in terms of abundance with a maximum value of 56.4% in lake Ilón. *Cyanobium* has been extensively described as a dominant genus in numerous studies [42–44], including deep lakes in North Patagonian Andes [45, 46]. Picocyanobacteria are sensitive to temperature and high light intensities including ultraviolet radiation [47], likely limiting its distribution in lakes at the highest altitude with high irradiances and harsh winters when they are partially or entirely covered by ice and snow.

Lakes located at the krummholz belt and above the treeline were dominated by Actinobacteria and did not conform separate clusters. It is noticeable that variables such as DOC, TDP, and TDN did not show differences between krummholz and bare rocks, so it can be expected that lakes at these catchment areas showed similar community composition. Bacterial communities from these lakes showed differences to those of lakes below treeline, with distinct dominant taxa likely related to the harsher climatic conditions imposed by higher altitudes and the surrounding bare rocks with less carbon and nutrient availability associated with the absence of a forest above the treeline. Indeed, DOC concentration (highly related to surrounding vegetation) is among the variables that better explain community composition in this group of lakes. However, two lakes remained isolated, lakes Azul (krummholz belt) and Jujuy (bare rocks), suggesting that differences observed in community composition among these lakes are probably due to other variables.

Lake Azul, located at the krummholz belt, showed the lowest DOC concentration (0.37 mg L^{-1}) and thus a high water transparency. In this lake, we observed the highest proportion of Actinobacteria (85%), due to the dominance of around 8 ASVs assigned to hgcl-clade, which show several characteristics that can be advantageous in clear oligotrophic mountain lakes. Actinobacteria have polyphosphates storage, strong cell walls, and DNA repair capacity that protect cells against high UV radiation [48]. In particular, the hgcl-clade have actinorhodopsin, which allows using sunlight energy to strengthen heterotrophic growth [49] and they are important bacteria components in deep high mountain lakes with scarce vegetation in the catchment area and long ice-cover duration [50] as lake Azul has. On the other hand, lake Jujuy is located at bare rocks, at the highest altitude of our studied lakes, and also has very low DOC concentration with a concomitant high light penetration. This lake showed a high abundance of aerobic anoxygenic phototrophic bacteria (AAP), whose distribution is linked to light intensity [51], and was observed across an altitudinal gradient to be influenced by DOC concentration [52]. In particular, the genera *Sandarakinorhabdus* and *Rhodovariu*s, dominating in lake Jujuy, have bacteriochlorophyll *a* and light protection pigments such as carotenoids, respectively [53, 54]. Particularly, the AAP *Sandarakinorhabdus* has been observed in other alpine lakes [55] and has been described as a bacteria attached to cyanobacterial phycosphere [56]. Phycosphere constitutes a special microenvironment that supports some unique bacterial communities [57]. In Lake Jujuy, we observed a high abundance of *Pseudoanabaena*, which probably constituted the phycosphere suitable for AAP development. In the same way, Candidatus *Zambryskibacteria* belonging to Patescibacteria, an abundant phylum in this lake, may be also associated with a phycosphere, since it has been previously cited in the core microbiome of *Chlorella vulgaris* [58]. The recorded AAP and Patescibacteria, profiting extracellular substances in the phycospheres, may have a crucial role in nutrient cycling in such ultraoligotrophic environments.

Disentangling the mechanisms driving species distribution patterns is a key issue in ecology and biogeography [59]. β-diversity and its distinct components, turnover, nestedness, balanced variation in abundances, and abundance gradients may reveal the relative importance of different underlying mechanisms in structuring communities [12, 13, 59]. Bacterial communities below-above treeline showed an increase in the ß-diversity and in the turnover component. In addition, we observed significant differences with null models calculated data, suggesting that ecological factors are primary drivers of these communities over probabilistic processes. Indeed, the components of ß-diversity can play different roles in ecological analysis and in particular can be related to ecosystem processes [14]. Turnover implies the replacement of species along environmental gradients due to spatiotemporal constraints and/or environmental sorting [60]; therefore, it is expected to have higher turnover with high environmental heterogeneity [61]. Moreover, NRI values in lakes located on bare rocks were significantly greater than zero, suggesting that the absence of vegetation with increasing altitude (harsher environments) makes bacterial communities phylogenetically clustered. This provides evidence for the dominant role of environmental filtering on community composition [62]. On the contrary, lakes at krummholz belt and below treeline showed, in general, negative NRI values that would suggest an increase in competitive structuring processes.

Among environmental factors, our ordination and β-diversity analysis showed that surrounding vegetation and changes in the associated variables (DOC and nutrient concentrations) are the main drivers of the bacterial community's structure. Lakes below treeline have a higher proportion of humic-like DOM components (this study and [17]). The heterogeneity of the inputs in lakes below treeline, and the diversity of carbon sources from vegetation and organic soil leachates, would be important drivers of the community assembly processes, increasing species interactions such as competition. Other studies, with high-resolution DOM characterization, have revealed that along alpine elevation gradients, the molecular diversity, degree of oxidation, aromaticity, and unsaturation of soil DOM decreased and bacterial diversity decreased too [63]. In addition, our NRI calculations support the hypothesis of increasing species interactions (i.e. competition) in bacteria communities of lakes located below the treeline and also in the krummholz belt.

In summary, our study elucidates the underlying mechanisms structuring bacterial communities in different vegetation landscapes. Here we analyze β-diversity and phylogenetic clustering in mountain lakes, revealing the importance of treeline position and nutrients associated with vegetation and soils as drivers of bacterial community composition. Trees at the upper treeline are particularly sensitive to climate change since the alpine treeline has been recognized as an example of a climate-sensitive species boundary [64]. However, species interactions such as facilitation and competition also play a crucial role in driving treeline shifts [5]. Therefore, predicting the dynamics of the upper treeline can be difficult, since several variables modulate the response of vegetation to climate, including topography, soil properties, and species interactions [65]. In North Patagonia, it was demonstrated that *N. pumilio* establishment and its advance or reduction is related to changes in the interaction of temperature and precipitation due to the Pacific Decadal Oscillation (PDO) [37]. Even if it is difficult to predict the course of change of PDO, any change in the position of the treeline will certainly modify bacterial resources. Thus, our study brings light on the bacterial community's response to future changes caused by variation in the upper treeline, highlighting the importance of evaluating different aspects of community structure.

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Author Contribution M.B.N. conceived the study, sampling, analyzed results, wrote the manuscript; E.B. participated in sampling, analyzed data, analyzed results, contributed to writing the manuscript; B.M. contributed to conceive the study, laboratory analyses, analyzed results, contributed to writing the manuscript.

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Data Availability All sequences are available at https://dataview.ncbi.nlm.nih.gov/object/PRJNA1098696?reviewer=4691cv6fgt26oul921bplf6eeu.

Declarations

Competing Interests The authors declare no competing interests.

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