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Capturing the spatial structure of the benthic microbiome under an intensive aquaculture scenario in Chilean Patagonia

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Abstract

Background Identifying the microbial taxa that structure assemblages in response to local disturbances along the Chilean Patagonian coast is critical for understanding community reorganization and ecological risk in this vulnerable marine environment. Here, we examined benthic microbial interactions across sixteen sites spanning 42–44°S in the Inner Sea of Chiloé and adjacent fjord systems. Using co-occurrence network analysis, we characterized spatial interaction patterns and identified keystone taxa whose relationships with environmental variables may serve as ecological indicators. The presence of keystone taxa supports the concept of microbial "seed banks," which sustain community stability and ecosystem functionality under stress. Networks revealed structured communities dominated by niche-specialist taxa, consistent with ecological processes of niche differentiation and environmental filtering.

Results The benthic environment was found to harbor niche-specialist taxa, including *Flavobacteriaceae*, *Gemmataceae*, *Humimicrobiaceae*, *Clostridiaceae*, and *Sulfurovaceae*, typically associated with organic enrichment and anthropogenic influence. These microbial families showed strong correlations with environmental gradients such as nitrate, phosphate, silicate, pH, salinity, and phaeopigments. Alpha-diversity analyses revealed greater microbial richness in FZ compared to the ISC, likely reflecting higher environmental heterogeneity and long-term adaptation to dynamic and fluctuating conditions. Beta-diversity analyses further supported the presence of distinct microbial assemblages between the two zones. Multivariate statistics and co-occurrence network analyses demonstrated that FZ communities display enhanced taxonomic interactions and greater network complexity, suggesting increased ecological stability. In contrast, microbial networks in the ISC exhibited reduced connectivity, potentially indicative of environmental stressors disrupting microbial spatial organization and network resilience. Moreover, the identification of indigenous bacterial isolates provided evidence for the presence of opportunistic host-associated pathogens, highlighting the utility of microbial biomarkers in detecting early ecological responses to human impacts.

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Conclusion Microbial co-occurrence patterns in northern Patagonian sediments reveal shifts in community assembly and increased network complexity that may enhance resilience to perturbations. The detection of strains harboring opportunistic pathogen biomarkers highlights risks under intense anthropogenic pressures. Monitoring keystone taxa thus offers early warning of functional decline. Broader spatio-temporal assessments remain essential to clarify microbial dynamics and their implications for ecosystem health and antimicrobial resistance.

Keywords Microbial interactions, Coastal sediment, Host-pathogen, Southern pacific coast

Background

Coastal zones represent hotspots of microbial activity that mediate fundamental ecological functions involved in benthic–pelagic coupling, particularly nutrient recycling and pollutant degradation [1, 2]. The ecological significance of microbial communities arises not only from the presence and diversity of individual taxa but also from their organization into interaction networks, where generalists and specialists engage in both cooperative and competitive dynamics [3, 4]. These interactions underpin ecosystem resilience [5] and the provision of essential services, including the regulation of nutrient fluxes in highly dynamic environments [6, 7].

Consequently, microbial communities act both as regulators of benthic ecosystem health and as sensitive indicators of anthropogenic disturbance [8, 9]. In southern Chile, aquaculture activities contribute to the deposition of large quantities of organic matter, heavy metals, antibiotics, and pharmaceutical residues into sediments [10–12]. These inputs reduce ecosystem resilience and trigger cascading ecological effects [13], including the development of hypoxic or anoxic conditions [14, 15] and the selection of metabolically versatile opportunistic taxa [1, 16, 17]. Such changes constrain the capacity of benthic ecosystems to buffer disturbances [1] and reconfigure both microbial interaction patterns and food web dynamics [7, 18].

Beyond their local pollution signature, contaminants from marine anthropogenic activities can disperse into surrounding waters, intensifying the risks of eutrophication, harmful algal blooms [19, 20], and the spread of antimicrobial resistance [12, 21, 22]. In this regard, numerous studies have reported that micropollutants such as pharmaceuticals, pesticides, and personal care products impact aquatic ecosystems across multiple trophic levels, from microbial communities [23–25] to macroinvertebrates [26], driving both structural and functional alterations in natural ecosystems.

Recent evidence shows that anthropogenic activities do not merely alter microbial diversity [27–29] but also fundamentally reshape interaction networks. For instance, Frühe et al. [30] demonstrated that salmon farming generates consistent global patterns of microbial change, characterized by reduced bacterial diversity and networks increasingly dominated by opportunistic taxa.

Despite global evidence of disturbance-induced restructuring of microbial communities [25, 28, 31, 32], there remains limited understanding of how these processes unfold in Patagonian ecosystems. Most existing research has concentrated on shifts in microbial diversity or taxonomic composition [2, 33, 34], leaving the interaction patterns of benthic microbial assemblages largely underexplored. Moreover, evidence regarding the influence of pollutants on microbial co-occurrence patterns within the coastal system is still scarce. Identifying the key microbial taxa around which assemblages organize in response to local pollution fingerprints is therefore essential for elucidating the drivers of community restructuring and the potential ecological risks affecting this vulnerable marine environment [35].

In the absence of standardized methodologies for evaluating the effects of micropollutants, including pharmaceuticals, pesticides, and personal care products, on microbial communities, and considering the limited availability of baseline data for northern Patagonia, it is essential to integrate existing datasets from key sites that overlap with the focal study area. This study aims to address these gaps by analyzing benthic microbial networks in northern Patagonian coastal ecosystems, with the objective of elucidating the spatial interaction patterns of microbial assemblages and their relationships with environmental variables and micropollutant signatures (see Inostroza et al. [36] for a detailed review). In addition, we propose to employ a cultivation-dependent approach to characterize indigenous bacterial strains, as this may provide valuable insights into the opportunistic potential of specific taxa across different study zones.

The integration of microbial network analysis with broader ecological assessments of the marine benthic environment offers a robust framework for detecting subtle but ecologically significant alterations in ecosystem functioning [6, 37, 38]. Furthermore, this approach can inform the development of adaptive management strategies in marine ecosystems where aquaculture expansion overlaps with high ecological vulnerability.

Methods

Fieldwork and sediment sample collection

The northern Patagonian coast (42–44°S) is characterized by a large inland sea and an extensive system of fjords and channels, which result in distinctive hydrographic

and hydrodynamic conditions [39]. These conditions are influenced by Pacific Ocean waters, river discharge, continental runoff, and glacial meltwater [15, 40]. In addition, this region has been subject to significant and ongoing economic pressure from high-density salmon aquaculture since 1973 [10, 41, 42].

Sample collection was designed to account for the contrasting geographical features of the Inner Sea of Chiloé (ISC) and adjacent fjord zones (FZ; Fig. 1). Specifically, sampling campaigns were carried out between October 2022 and March 2023, encompassing both Austral spring and summer seasons. Surface sediment samples were collected using a 0.1 m^2 Ekman grab sampler at ten sites located within the ISC (brown box in the map) and six sites within the FZ (black box).

A total of 80 samples were collected, with a minimum of five replicates per sampling point across 16 sites. From these, only one triplicate per site was analyzed ($n = 51$; see Table S3), except at the buoy site, where five replicates were included. The buoy operates as an oceanographic monitoring platform managed by the i~mar Research Center (Universidad de Los Lagos), facilitating the continuous acquisition of oceanographic and meteorological data to advance the understanding of climate dynamics in Patagonia and their associated processes. All surface sediment samples collected (~50 g each) were transferred into labeled 50 mL Falcon tubes, stored in a cooler with gel packs (– 4 °C), and transported to the laboratory (Centro i~mar in Puerto Montt), where they were stored at – 80 °C until further processing.

In addition, at each site, water samples were collected using 10 L Niskin bottles for nutrient concentration measurements and subsequent laboratory analyses. Specifically, concentrations of nitrate (NO_3^-), nitrite (NO_2^-), phosphate (PO_4^{3-}), silicate ($Si(OH)_4$), active chlorophyll, chlorophyll-a (Chl-a), and phaeopigments were determined in the laboratory following previously described methods [40]. Water column parameters, including pH, dissolved oxygen (DO; mg/L), salinity, and temperature (°C) were measured in-situ using a CTD AML Model Metrec-XL instrument (Table S1). No specific permits were required for the fieldwork described, and the study sites are not located on privately owned land. Detailed procedures for sample pre-treatment and analytical methods are provided in the supplementary materials.

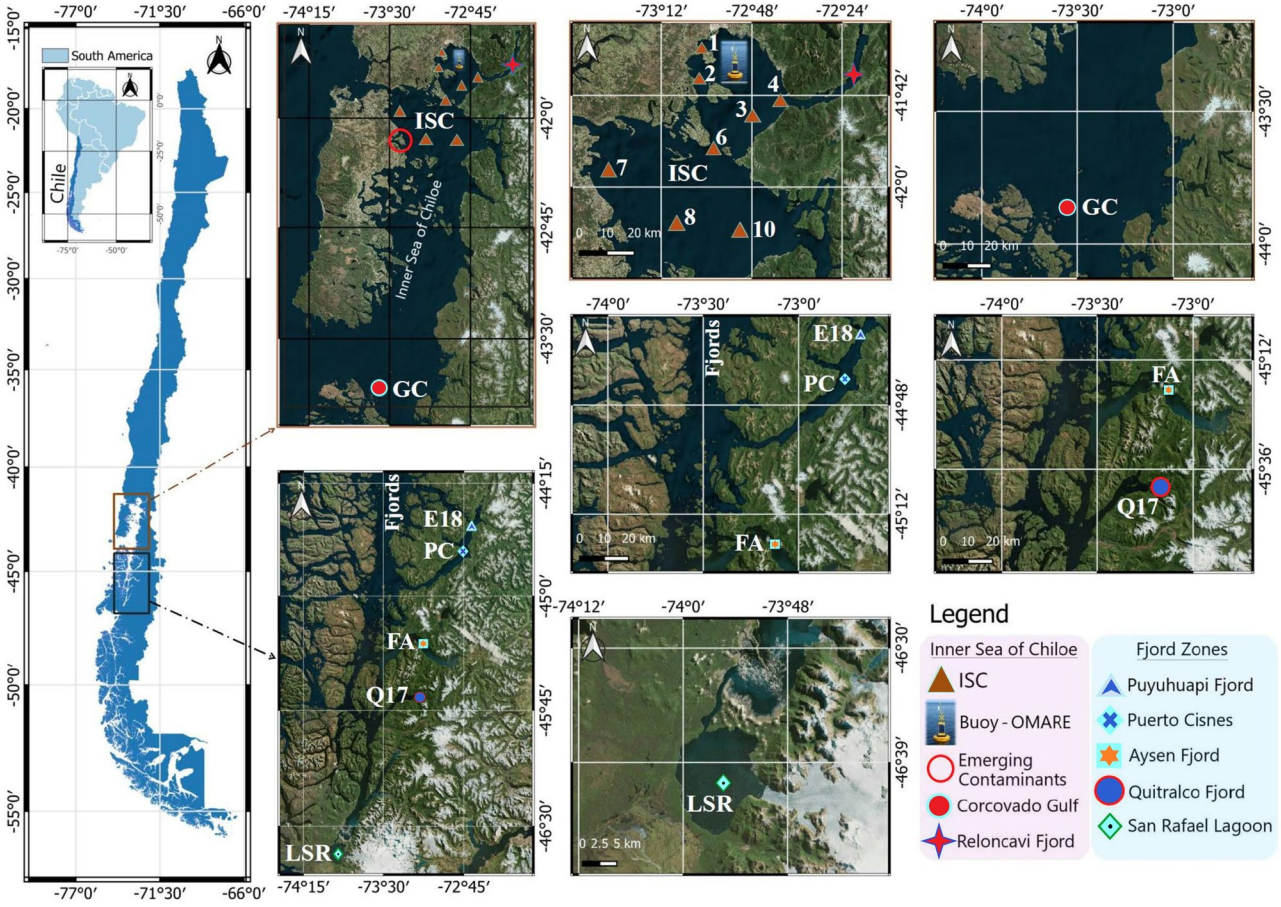

Fig. 1 Map showing sediment sampling sites across the coastal Patagonian ecosystem. Legend colors correspond to distinct sampling locations

Assessing sediment toxicity to aquatic microbiota remains particularly challenging due to the limited availability of baseline data for northern Patagonia. It is also important to consider the complex interactions between chemical contaminants and sediment matrices, which strongly modulate contaminant bioavailability.

To address this gap, we analyzed the datasets provided by Inostroza et al. [36]. These datasets encompassed a broad spectrum of micropollutants, including pesticides, pharmaceuticals, industrial chemicals, polycyclic aromatic hydrocarbons (PAHs), per- and polyfluoroalkyl substances (PFAS), and persistent organic pollutants (POPs), measured in interstitial water, benthic boundary layer samples, and sediments from the ISC area (Fig. 1). Detailed methodologies for sampling, analytical extractions, and quantifications are available in Inostroza et al. [36].

Focusing on micropollutants, we combined concentration ranges and chemical fingerprints of emerging contaminants with the toxic unit (TU) approach [23, 43]. TU is a dimensionless measure that quantifies the individual toxicity contribution of each chemical within a sample and integrates these contributions to describe the total micropollutant stress. Finally, the calculated TU values were used as environmental vectors to explore correlations with the observed microbial responses to micropollutant exposure.

Phylogenetic diversity of culturable bacteria

Sediment bacteria were isolated by mixing 10 g of sediment with 10–15 mL sterile PBS buffer, vortexing for 5 min, and allowing the mixture to stand to enable sedimentation of large solid particles. Subsequently, 1 mL of the supernatant was transferred to a clean tube and centrifuged at 2000 ×g for 1 min. Then, 100 µL of the supernatant was plated onto nutritive agar plates. Different culture media were used to assess growth preferences and enhance the recovery of bacterial diversity. Four types of agar media were used for bacterial isolation: Luria-Bertani (LB) agar, Tryptic Soy agar (TSA), Reasoner's 2 A medium (R2A), and International Streptomyces Project-2 agar (ISP-2), composed of yeast extract (4 g/L), malt extract (10 g/L), glucose (4 g/L), and agar (20 g/L) at pH 7.2. All media were prepared according to the manufacturers' instructions.

Following inoculation, plates were incubated at 15–18 °C for five days, or until distinct colonies became visible. Bacterial isolates were then selected based on discernible morphological characteristics, including colony color, texture, elevation, margin, and overall shape, to maximize phenotypic diversity and reduce redundancy in the culturable collection. Representative colonies were subcultured onto the corresponding growth media to ensure purity, and each isolate was subsequently labeled and catalogued according to sampling site, Gram-staining results, and colony and cell morphology. This approach facilitated the preliminary differentiation of strains prior to molecular or functional characterization. For long-term preservation, well-grown cultures were prepared in LB broth, mixed 1:1 with sterile 50% glycerol, and stored at − 80 °C, following standard cryopreservation procedures for bacterial isolates [44].

Genomic DNA from fresh bacterial cultures was extracted using the DNeasy® PowerSoil® Pro Kit (Qiagen, Inc.). The 16 S rRNA gene was amplified by PCR using the universal primers 27 F (5′-AGA GTT TGA TCC TGG CTC AG-3′) and 1492R (5′-TAC GGY TAC CTT GTT ACG ACT T-3′). The PCR products were enzymatically purified using ExoSAP-IT™ Express, and Sanger sequencing was performed using the BigDye Terminator v3.1 Cycle Sequencing kit (Thermo Scientific, USA) on an Applied Biosystems 3500 Genetic Analyzer (Applied Biosystems, USA), provided by the Scientific and Technological Bioresources Nucleus at Universidad de La Frontera (BIOREN-UFRO). Raw sequences were trimmed and quality-filtered using Geneious Prime® 2023.1.1 software. Consensus sequences longer than 800 bp were used for species-level taxonomic affiliation (≥ 90% identity) by comparing them against 16 S rRNA gene sequences available in the GenBank database (https://www.ncbi.nlm.nih.gov/genbank/) using the NCBI BLAST tool, and in the EZBioClound database (https://www.ezbiocloud.net/) using its integrated taxonomic assignment platform.

DNA extraction and 16 S rRNA amplicon sequencing of sediment samples

Total DNA was extracted from 0.50 g of sediment (wet weight) using the DNeasy PowerSoil Pro kit (Qiagen®, Germany), following the manufacturer's instructions. DNA quality and concentration were assessed using a Qubit 2.0 Fluorometer (Life Technologies), and amplicon specificity was confirmed via gel electrophoresis. The extracted DNA was stored at − 80 °C until further processing at Novogene Bioinformatics Technology Co. (Beijing, China), where it was sequenced on the Illumina NovaSeq 6000 platform (300 bp paired-end).

The primer set of 341 F (5′-CCT AYG GGR BGC ASC AG-3′) and 806R (5′-GGA CTA CNN GGG TAT CTA AT-3′) were used to amplify the V3–V4 hypervariable region of the 16 S rRNA gene from both bacteria and archaea [45, 46]. PCR conditions provided by Novogene Bioinformatics Technology Co. were as follows: initial denaturation at 98 °C for 1 min, followed by 30 cycles of denaturation at 98 °C for 10 s, annealing at 50 °C for 30 s, and extension at 72 °C for 30 s, with a final extension at 72 °C for 5 min. PCR products were purified using the GeneJET Gel Extraction kit (Thermo Scientific). Sequencing libraries were prepared with the NEB

Next® Ultra™ DNA Library Prep kit for Illumina (NEB, USA), following the manufacturer's recommendations, and index codes were added. The sequence data generated in this study are publicly available in the NCBI Short Reads Archive (SRA) database under accession number *PRJNA1249584*.

Bioinformatics and statistical analyses

For bioinformatic processing, raw 16 S rRNA gene amplicon sequencing data from sediment samples were trimmed (retaining at least 75% of reads; forward reads at 244 bp and reverse reads at 197 bp), denoised, merged, and filtered for chimeras using the nf-core/ampliseq pipeline (https://nf-co.re/ampliseq/2.12.0) with default workflow settings [47, 48]. Reproducible software environments were used through the Bioconda [49] and BioContainers [50] platforms. Sequences assigned to chloroplasts, mitochondria, eukaryotes, as well as singletons, were filtered out prior to downstream analyses. ASVs abundances were rarefied to an equal number of sequences per sample (n = 15,000 reads) to ensure consistent sampling depth across all samples. On average, 71.6% of the sequences per sample passed the quality filtering steps, with less than 36.9% of sequences discarded in any given sample.

Taxonomic classification was performed using DADA2 [51] and the SBDI-GTDB - Sativa curated database [52], which includes 56,171 sequences, covering 96.4% of the dataset. Amplicon sequence variants (ASVs), along with their abundance data and taxonomic assignments, were imported into QIIME2 [53] for further processing. All data handling, statistical analyses and graphics were conducted in the R environment (v.4.4.1), using the phyloseq, microbiomeSeq, and ggplot2 packages in combination with the tidyverse framework (v. 2.0.0) [54, 55].

Alpha diversity (α-diversity) metrics, including the Shannon index and the Chao1 richness estimator, were calculated and compared among sample groups (Buoy, ISC, and FZ) using Kruskal–Wallis tests. When significant differences were detected, pairwise post hoc comparisons were performed using the Wilcoxon rank-sum test. Beta diversity (β-diversity) was assessed using the Bray-Curtis dissimilarity index and visualized via non-metric multidimensional scaling (nMDS). Principal component analysis (PCA) was also employed as an exploratory method for dimensionality reduction based on Bray-Curtis dissimilarities [56]. Additionally, we performed a permutational multivariate analysis of variance (PERMANOVA) to assess whether microbial community structures (ASVs profiles) differed significantly between the study zones (ISC and fjords), using the *adonis2* function in the R package vegan with 9999 permutations.

Partial least squares discriminant analysis (PLS-DA) and Variable Importance in Projection-PLS-DA (VIP-PLS-DA) were performed using the ggplot2 and mixOmics packages in R [54, 57]. For VIP-PLS-DA, only variables with a VIP score greater than 1 were retained. The relative importance of each variable was calculated by dividing its VIP score by the sum of all VIP scores.

Linear discriminant analysis (LDA) of microbial abundance data was performed using the online platform MicrobiomeAnalyst [58]. Taxa were considered significant if they exhibited an LDA score greater than 4.0 and a p-value less than 0.01, thereby retaining only those with very strong discriminatory effects. Moreover, the logarithmic LDA score threshold was set to 2.0 as the minimum criterion for biological relevance [59]. This ensures that taxa with at least moderate effect sizes are included, while those exceeding 4.0 are emphasized as the most robust discriminants.

The influence of environmental and contaminant variables on bacterial community structure was evaluated through distance-based redundancy analysis (db-RDA) using Bray-Curtis dissimilarities. Prior to analysis, community abundance data were log-transformed, and environmental/contaminant variables were standardized, with collinearity reduced by retaining only predictors with variance inflation factors (VIF) < 4. Both global models, incorporating *Site* and the environmental/contaminant variables, and partial models, isolating the pure effect of environmental variables while accounting for *Site*, were constructed. Model significance was assessed using PERMANOVA, and forward selection was applied to identify the most parsimonious set of predictors.

Co-occurrence networks for ISC and FZ groups were constructed to assess the complexity of microbial interactions and ecological association within each sampling zone. Spearman's rank correlations were calculated between ASVs, with correlations considered significant when the coefficient was $r \geq 0.7$ and the p-value < 0.01. In the resulting networks, nodes represent individual ASVs, and edges indicate statistically significant correlations between them. Network graphs were based on a set of topological features, including the number of nodes and edges, node degree, clustering coefficient, modularity, average path length, network diameter, betweenness centrality, closeness centrality, and density. Keystone taxa comprising module hubs, connectors, and network hubs were identified, as their removal is predicted to disrupt overall network stability [60, 61]. Network visualization and the calculation of topological properties were performed using the interactive platform Gephi (v0.9.5) [62], using the Fruchterman-Reingold algorithm with 10,000 permutations.

Results

Hydrographic variables and emerging contaminants

Oceanographic profiles across the study area in the Patagonian fjord region are presented in Figure S1. In both the ISC and FZ, notable variations in physico-chemical parameters were observed. Oxygen concentrations were higher in the upper 20 m of the water column compared to deeper layers (Fig. S1A), coinciding with a warming trend exceeding 15 °C within the same depth range (Fig. S1C). In contrast, the upper 50 m in other areas showed colder surface waters (< 10 °C). Notably, the Reloncaví (98.9 μmol L^{-1}; 35.3% saturation), Puyuhuapi (62.3 μmol L^{-1}; 21.3% saturation), and Quitralco (1.5 μmol L^{-1}; 2.1% saturation) fjords exhibited the lowest recorded oxygen concentrations in the study area.

Average water temperatures in the ISC ranged from 11.3 °C to 17.3 °C, whereas in the FZ, mean values varied between 7.7 °C and 13.8 °C during the study period (October 2022 to March 2023), encompassing the Austral spring and summer seasons. The analysis of water masses using the salinity diagram (Fig. S1D) revealed variable contributions from Sub-Antarctic Water (SAAW, > 33 psu), Modified Sub-Antarctic Water (MSAAW, 31–33 psu), and Estuarine-Salty Water (EW, 11–21 psu) throughout the water column. These patterns indicate a strong influence of ice melt and river discharge on the hydrographic structure of Patagonian fjords.

Chlorophyll concentrations were high in the surface layer of the water column (Fig. S1B, F, H), coinciding with elevated levels of inorganic nutrients. In particular, silicate ($Si(OH)_4$) and phaeopigment concentrations showed increasing trends toward the Reloncaví and Aysén fjords. Nitrate (NO_3^-) consistently exceeded nitrite (NO_2^-) concentrations, indicating that NO_3^- was the predominant form of dissolved inorganic nitrogen in the FZ. The mean concentration of NO_3^- was 17.70 μM, compared to a mean of 0.18 μM for NO_2^-. Phosphate ($PO4^{3-}$) concentrations were especially low in the Puyuhuapi Fjord and San Rafael Lagoon, with maximum values of 0.75 μM and 1.18 μM, respectively.

The TU analysis suggests that veterinary pharmaceuticals, biocides, pesticides, and other pharmaceutical compounds are likely the main contributors to micropollutant stress within the ISC area (Fig. S4, S5). Although extrapolating these data to other sampling sites within the study area involves inherent limitations, this approach was considered both conservative and scientifically robust for capturing the legacy of four decades of farming activity in the region. Notably, the sampling for the present study was conducted six months after the survey by Inostroza et al.

Diversity of culturable bacteria and presence of genera associated with opportunistic taxa

Given the intense anthropogenic disturbances affecting northern Chilean Patagonia, we investigated the potential threats posed by opportunistic pathogenic bacteria isolated from marine sediments in the study area. A total of 64 bacterial isolates, belonging to 30 species, were identified through amplification and sequencing of the 16 S rRNA gene. The resulting sequences were compared against the NCBI database for taxonomic assignment. Strain codes and percentage sequence identities for all isolates are provided in Table S2.

The 16 S rRNA analysis allowed for a comprehensive assessment of culturable bacteria diversity (Table S2). Sequence identities exceeding 96.0% were observed between the isolates and corresponding type strains. The identified taxa included representatives from the genera *Pseudomonas* (*P. guineae*, *P. peli*, *P. brenneri*), *Bacillus* (*B. mycoides*, *B. aerius*), *Shewanella* (*S. vesiculosa*, *S. kaireitica*), *Psychrobacter* (*P. nivimaris*, *P. adeliensis*, *P. cibarius*, *P. fjordensis*), *Dietzia* (*D. psychralcaliphila*, *D. maris*), *Rhodococcus* (*R. globerulus*, *R. cerastii*, *R. yunnanensis*, *R. cercidiphylli*, *R. fascians*), *Sporosarcina* (*S. psychrophila*, *S. aquimarina*), *Pseudoalteromonas* (*P. nigrifaciens*, *P. carrageenovora*, *P. guineae*, *P. peli*, *P. brenneri*), as well as *Salinibacterium amurskyense*, *Marinomonas foliarum*, *Azoarcus olearius*, *Parasphingorhabdus flavimaris*, *Vibrio atlanticus*, *Nocardia coeliaca*, *Photobacterium frigidiphilum*, and *Microbacterium maritypicum*.

Benthic microbial community and diversity in Northern coastal Patagonia

The 16 S rRNA gene sequencing yielded a total of 58,260 reads, comprising 87,962,715 bp, of which 56,171 sequences (96.4%) passed quality control After quality filtering, between 21.04% and 39.58% of reads per sample were retained, with an average retention rate of 29.2%. Rarefaction curve analysis of individual samples indicated that sufficient sequencing depth was achieved to accurately capture microbial diversity, as evidenced by the plateauing of species richness curves (Figure S2).

Taxonomic classification using DADA2, along with the SBDI-GTDB Sativa curated 16 S GTDB database, assigned 99.99% of ASVs at the domain and kingdom levels, 97.43% at the phylum level, 94.09% at class level, 83.1% at order level, 73.42% at family level, 54.04% at genus level, and 46.17% at species level. The ASVs count table contained in total 1,883,778 counts, ranging from 15,312 to 63,564 ASVs per sample (average 36,937; Fig. S3). In total, 17,372 ASVs were identified across all samples.

Pseudomonadota (33.09%) was the most abundant microbial phylum across all sediment samples, followed by Chloroflexota (14.05%), Bacteroidota (11.11%),

Actinomycetota (7.64%), Myxococcota (7.30%), Acidobacteriota (6.10%), and Planctomycetota (5.81%). Together, these phyla accounted for >85% of the total microbial community. A small fraction of sequences (0.37%) was affiliated with the domain Archaea, with contributions from Nanoarchaeota (0.165%), Thermoproteota (0.119%), Thermoplasmatota (0.026%), and Asgardarchaeota (0.023%). The relative abundance of Nanoarchaeota and Asgardarchaeota was higher in the FZ (0.03%) than in the ISC (0.01%).

The dominant benthic microbial families included *Hyphomicrobiaceae*, *Sulfurovaceae*, *Woeseiaceae*, *Flavobacteriaceae*, *and Gemmataceae* (Fig. 2A). Most of these families showed higher relative abundance in the ISC. In contrast, several taxa were more prevalent in the FZ, including *SG8-38* (2.90%), UBA4823 (2.19%), UBA5704 (1.43%), *Methyloligellaceae* (0.58%), E44_bin32 (0.65%), *Aminicenantaceae* (0.63%), *Desulfatiglandaceae* (0.63%), *Halieaceae* (0.49%), *Sphingomonadaceae* (0.48%), and *Miltoncostaeaceae* (0.26).

An UpSet plot was generated to illustrate the ASVs shared among the different sampling zones (Fig. 2B). The FZ contained 297 unique ASVs, representing 38.17% of the total. In contrast, the ISC region exhibited 104 unique ASVs (13.37%), while 377 ASVs (48.45%) were shared across all sampling zones. In total, 640 genera were detected in the FZ, with 235 genera exclusive to the ISC and 506 genera shared across the entire dataset.

Significant differences in Shannon diversity were detected among zones (χ^2 = 9.49, $p = 0.009$), with higher diversity in the Fjord compared to the Buoy ($p = 0.0025$) and the Inner Sea of Chiloé (ISC) ($p = 0.019$). For Chao1 richness, overall differences were also significant (χ^2 = 6.47, $p = 0.039$), with greater richness in the Fjord than in the Buoy ($p = 0.037$), whereas the remaining pairwise comparisons were not significant. A decline in α-diversity indices was also observed at ISC sites 2, 3, and 4, as well as at Buoy sites and in the Corcovado Gulf, Reloncaví Fjord, and Puerto Cisnes (Fig. 2C).

Spatial partitioning pattern of microbial community assemblage

The nMDS plot based on Bray-Curtis dissimilarity revealed two distinct clusters (Fig. 3A), corresponding to microbial communities from the ISC (green) and FZ (blue). Notably, microbial communities in sediments from San Rafael Lagoon (LSR) were completely separated from those of the other sampling sites (Fig. 3A, B).

This zone-dependent clustering pattern was confirmed by PERMANOVA ($p < 0.001$), indicating significant structural and compositional differences (based on presence/absence data) between microbial communities in the ISC and FZ (Fig. 3B). These findings were further supported by statistical analyses and VIP scores from the PLS-DA analysis (Fig. 4).

In the PLS-DA plots, 10% and 6% of the total variation were explained by PLS1 and PLS2, respectively, showing clear separation among the three groups (Fig. 4A). Significant differences in microbial community profiles among the ISC, buoy and FZ groups (PERMANOVA: $R^2 = 0.267$, $p = 0.001^{***}$) are presented in a heat map of the top 15 families (Fig. 4B, C), suggesting that community composition was largely structured at a local scale, with site-specific effects accounting for 16% of the total variation. Importantly, in PLS-DA, low variance explained per component does not imply poor model performance. The method seeks latent variables that maximize group separation rather than capture the total variance. Consequently, robust discrimination between groups can be achieved even when individual components account for only a modest proportion of the variance.

Among the VIP scores from the PLS-DA analysis, *Flavobacteriaceae*, *Gemmataceae*, *Humimicrobiaceae*, *Methyloligellaceae*, and *Nitrosomonadaceae* emerged as predominant biomarker families contributing to component 1 (comp1). In contrast, *Clostridiaceae*, *Methyloligellaceae*, and *Miltoncostaeaceae* were the main contributors to component 2 (comp2) (Fig. 4B).

Linear discriminant analysis effect size (LEfSe), with a logarithmic LDA score cutoff > 2.0, was used to identify the bacterial families contributing most to the observed differences (Fig. 4D). In the ISC zone, *Sulfurovaceae* and *Desulfocapsaceae* were the most distinctive families. In the FZ, families such as *Sphingomonadaceae*, *SG8-38* (*Polyangiales*), *Woeseiaceae*, *Hyphomicrobiaceae*, *Methyloligellaceae*, and *Desulfurivibrionaceae* were enriched in San Rafael Lagoon, Reloncaví, Quitralco, and Puyuhuapi fjords (Fig. 4E), suggesting that spatial variation at local scales is primarily driven by differences in closely related environmental factors.

The physicochemical variables that best explained the observed microbial patterns differed between the ISC and FZ. pH, redox potential, $Si(OH)_4$, and NO_3^- were identified as key drivers of benthic microbial assemblage distribution in fjord zones, whereas phaeopigments, salinity, and active chlorophyll were most influential in the ISC area. The first dbRDA axis had the highest eigenvalue, explaining 41.4% of the constrained variation, while the second axis accounted for 24.0% of this variance (Fig. 5A). With respect to micropollutants, veterinary pharmaceuticals, biocides, pesticides, and other pharmaceutical compounds played a predominant role, together accounting for 82.1% of the variance in the ISC area (Fig. S5A, B).

Correlation analyses between microbial biomarker families and environmental variables revealed that pH, NO_3^-, PO_4^{3-}, $Si(OH)_4$, salinity, and phaeopigments

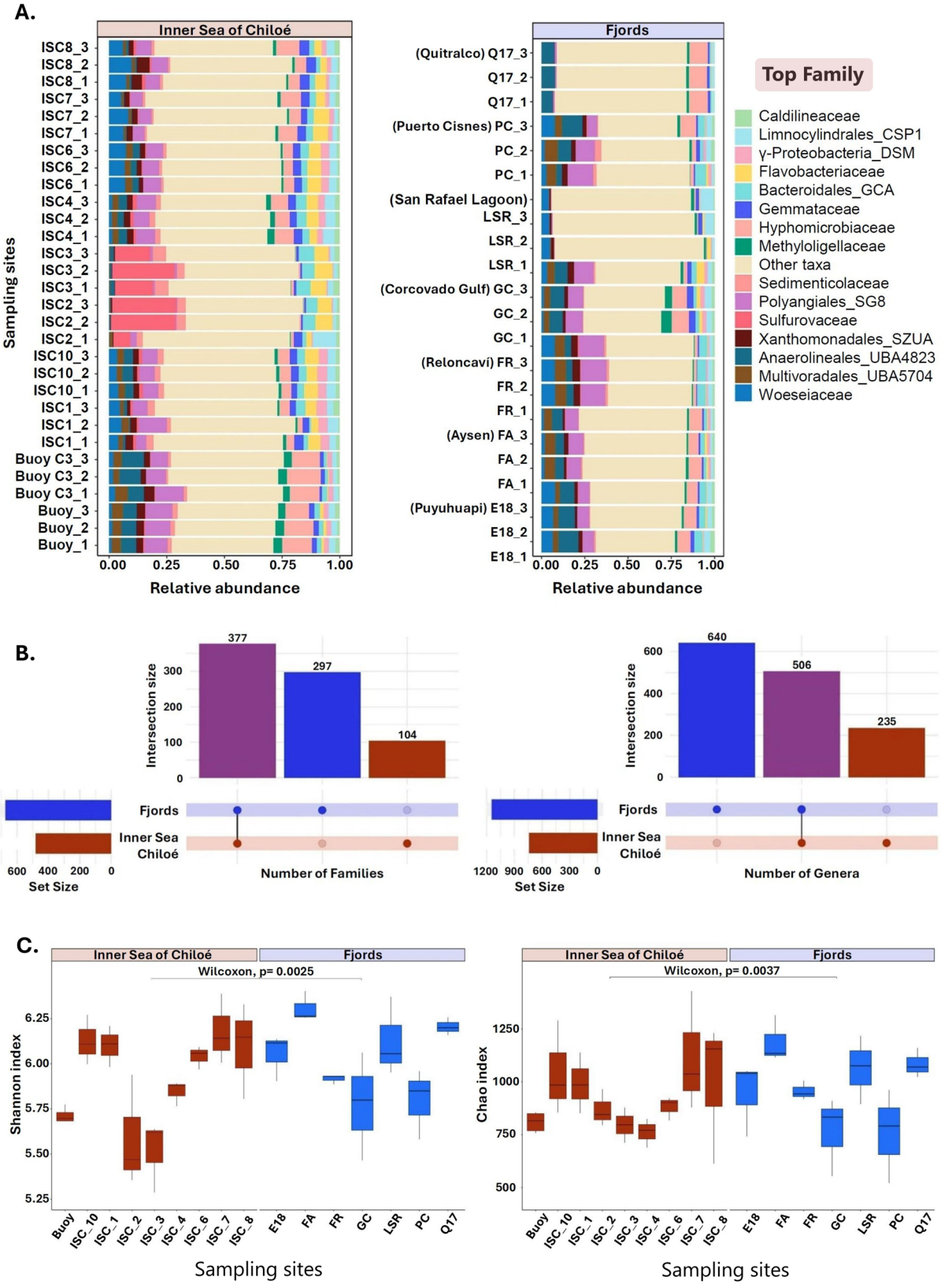

Fig. 2 Microbial community composition. (A) Top dominant families observed across sampling zones; (B) UpSet plot showing the presence/absence of ASVs at the family and genus levels in each sampling zone (ISC: wine; FZ: blue; shared: purple). Dots represent unique taxonomy presence per set, while vertical bars indicate the size of each intersection; (C) Alpha-diversity indices of the benthic microbial community across sampling zones. Box plots display the medians (central horizontal lines), inter-quartile ranges (boxes), and 95% confidence intervals (whiskers).

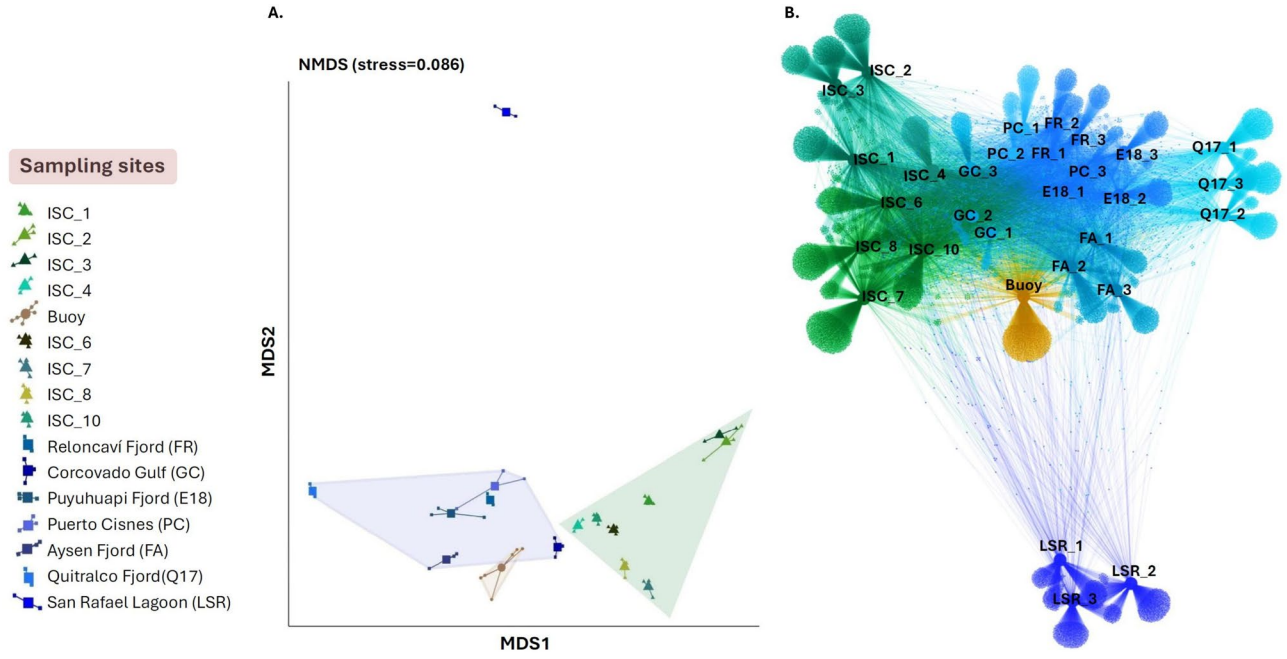

Fig. 3 Non-metric multidimensional scaling (nMDS) plot based on (A) Bray-Curtis dissimilarity calculated from ASVs composition; (B) Presence-absence network showing microbial community structure, with nodes colored according to sampling zones: Buoy (mustard), ISC (green), and FZ (blue).

exhibited the strongest and most significant associations with distinct microbial communities (Fig. 5B). A total of 18 microbial taxa showed positive correlations with at least one environmental factor, while 30 families displayed negative associations with multiple variables. No significant correlations were detected between the major biomarker taxa and dissolved oxygen (DO) concentrations, except for positive relationships observed for *Anaerolineaceae*, *Desulfatiglandaceae*, and *Spirochaetaceae*. Likewise, temperature, and nitrite (NO_2^-) did not exhibit significant associations with most benthic microbial communities.

Benthic microbial co-occurrence networks

Co-occurrence network analysis was used to investigate the complexity of interactions among bacterial families within each sampling zone (Fig. 6). Significant topological properties were calculated for each network to describe the patterns of interrelationships among nodes (Table S4). The network constructed for the ISC (Fig. 6A) consisted of 302 nodes (family) and 3,381 edges, with an average degree of 11.19, average path length of 2.96, a diameter of 10, a clustering coefficient of 0.283, and a modularity index of 0.58 (values > 0.4 suggest modular structure). In comparison, the FZ exhibited increased network complexity, with 333 nodes, 3,322 edges, an average degree of 9.97, an average path length of 3.03, a diameter of 11, a clustering coefficient of 0.297, and a modularity index of 0.60.

Based on betweenness centrality scores, five module hubs structuring the networks (indicated by color) were identified. In the ISC region, these hubs were primarily composed of taxa such as γ-Proteobacteria (Incertae Sedis, AT-s2-59), *Ilumatobacteraceae*, *Kiloniellaceae*, *Rhodobacteraceae*, *Methyloligellaceae*, *Sulfurovaceae*, *Sedimenticolaceae*, *Flavobacteriaceae*, *Caldilineaceae*, *and Anaerolineaceae*, among others (Fig. 6A). In contrast, the keystone taxa in the FZ were affiliated with *Thermoanaerobaculaceae*, *Microtrichaceae*, *Cyclobacteriaceae*, the UBA20353 marine group, *Ectothiorhodospiraceae*, *Hyphomicrobiaceae*, *Geopsychrobacteraceae*, *Nitrospiraceae*, *Solirubrobacteraceae*, *Nitrosococcaceae*, *Sandaracinaceae*, and members of the *Woeseiaceae* family (Fig. 6B).

Overall, the microbial networks were composed of highly connected families and displayed topological features characteristic of complex systems, including small-world properties and modularity (Table S4). These patterns indicate a non-random network structure, consistent with real-world ecological networks, which tend to be significantly more clustered than Erdös-Rényi random graphs.

Discussion

The distinctive hydrographic and hydrodynamic conditions of northern Patagonia [15, 40], together with its long history of intensive aquaculture [13, 42], create an ideal setting for identifying key attributes of benthic microbial assemblages and examining how they interact

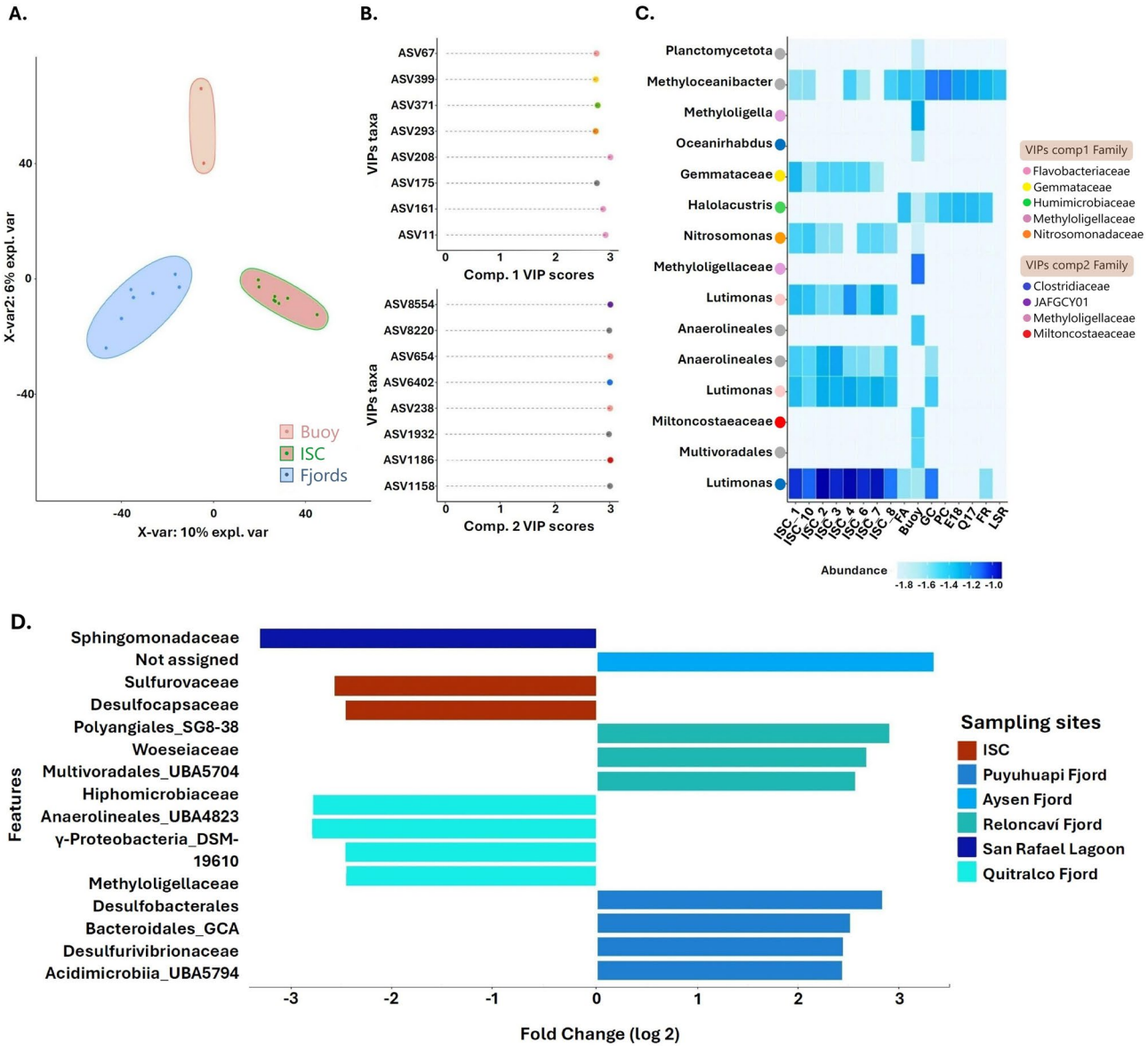

Fig. 4 Partial least-squares discriminant analysis (PLS-DA) of sediment microbial community composition. (A) Separation of microbial profiles among buoy, ISC, and FZ sampling. (B) Variable importance in projection (VIP) scores highlighting the bacterial families that contribute most to group differentiation. (C) Heatmap showing the relative abundances of the top contributing families across sampling zones. (D) Bacterial taxa showing significant differences among sampling sites, identified by linear discriminant analysis (LDA).

spatially and respond to characteristic environmental drivers.

Distinct environmental drivers characterize the Northern Patagonian Coast

The hydrographic behavior of the water column observed during the study period was consistent with the distribution of SAAW, MSAAW, and EW water masses, which have been previously described as representative of Patagonian fjords [15, 40].

The variability in the physicochemical conditions of the observed water masses in this extreme environment (Fig. S1) is largely shaped by riverine inputs, which transport substantial loads of fine suspended sediments primarily derived from glacial meltwater [15, 63]. These inputs, together with nutrient enrichment from intensive salmon aquaculture and the accumulation of autochthonous organic matter, contribute to reduced DO concentrations in both the water column and the underlying sediments [20, 41, 64]. The Reloncaví, Puyuhuapi, and Quitralco fjords were the sites with the lowest oxygen concentrations recorded in the study area. Previous studies have also reported that these fjords exhibit a high risk of

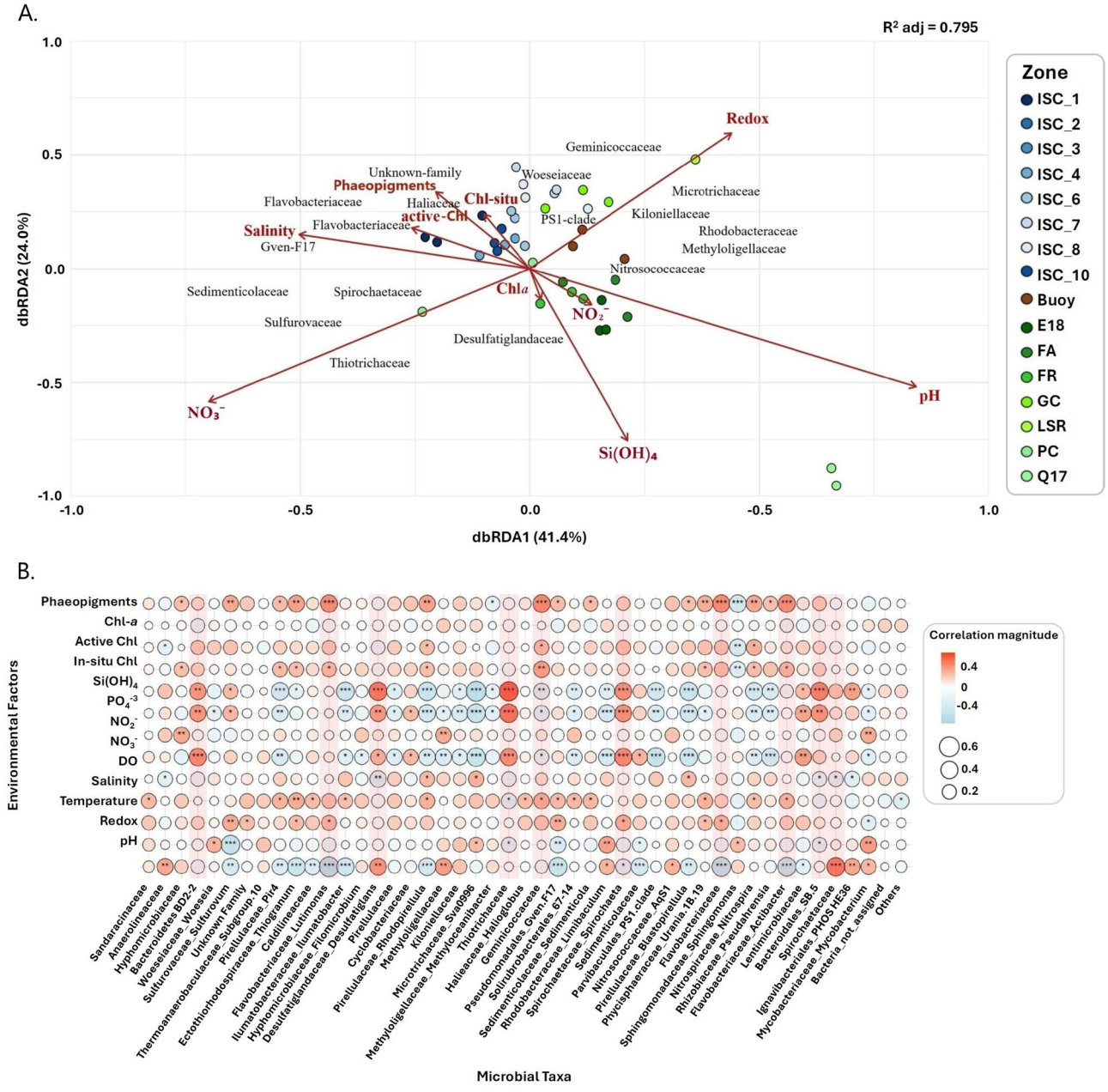

Fig. 5 Variation patterns of benthic microbial assemblages and measured environmental variables. (A) Distance-based redundancy analysis (db-RDA), using Bray Curtis dissimilarities) including only the most relevant variables after stepwise model selection using permutation tests. Each axis (i.e., dbRDA1 and dbRDA2) indicates the amount of variance it explains according to the associated eigenvalues (both dbRDA1 and dbRDA2 are significant [$p < 0.01$]). The color of the samples (circles) indicates the study zone to which they belong. Arrows indicate the direction of the gradient, and their length represents the strength of the correlation between ASVs and a particular environmental variable. (B) Spearman correlation heatmap showing the correlations between benthic microbial taxa and environmental variables. Red represents a positive correlation coefficient, while blue indicates negative correlations (*$p \leq 0.05$, **$p \leq 0.01$, ***$p \leq 0.001$)

eutrophication events, largely associated with the high density of salmon farming operations in these areas [20, 64, 65].

Consistent with findings from previous studies, our results indicate that NO_3^-, PO_4^{3-}, $Si(OH)_4$, pH, salinity, and phaeopigments were significant drivers influencing the structure of microbial communities [66, 67]. These environmental variables are commonly regarded as modulators rather than direct controllers of microbial diversity, influencing community composition through indirect effects and ecological filtering processes [2, 68, 69].

Similarly, the findings suggest that some micropollutants may be responsible for the structural dissimilarities

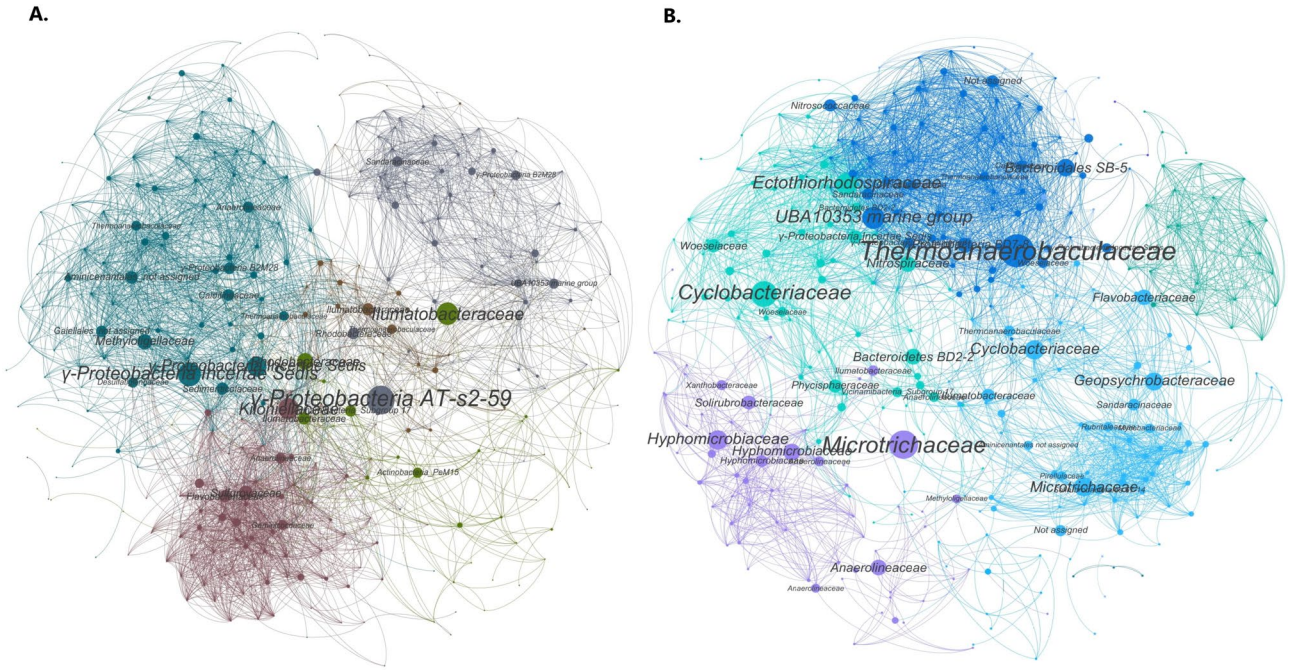

Fig. 6 Southern Pacific coastal sediment microbial community co-occurrence networks based on differences in keystone taxa between (**A**) ISC and (**B**) FZ area. Each node represents an ASV, with node size proportional to its betweenness centrality score. Nodes are colored according to their respective module hub affiliations, highlighting significantly correlated clusters within the network

[25] observed within the ISC microbial assemblages. It is emphasized that the use of the micropollutant dataset represents a pragmatic approach to utilizing the available information for a preliminary assessment of micropollutant influence, pending the implementation of more comprehensive and spatially resolved investigations in the future.

In this context, comparative α-diversity and correlation analyses suggest that the observed differences in microbial diversity between the ISC and FZ are likely driven by variations in habitat heterogeneity [33, 34, 70]. Classical niche theory posits that environmental heterogeneity promotes higher species richness by enabling the coexistence of multiple taxa, each of which may become dominant under distinct environmental conditions or disturbances [71]. A plausible explanation for the elevated microbial diversity in benthic Patagonia may therefore lie in the legacy of persistent environmental stressors, including pollution-related disturbances, which could have fostered adaptive responses to a heterogeneous and dynamic habitat [2, 72]. Such adaptive responses may, in turn, promote the emergence of more complex community structures [73, 74], as will be further discussed below.

Moreover, given the intrinsic variability of microbial communities, a detailed spatio-temporal investigation across larger sample sets is required to properly characterize general trends in bacterial diversity and community composition shifts along aquaculture impact gradients. Such patterns often remain obscured in smaller datasets restricted to individual farms, seasons, or geographic regions [34].

Differential core microbial taxa in coastal Patagonian sediments

Shifts in microbial community structure were assessed using various multivariate approaches. β-diversity analyses revealed that microbial communities in the ISC exhibited a distinct assembly pattern compared to those in the FZ sediment. This differentiation suggests the presence of structured communities composed of niche-specialist taxa that are well adapted to local environmental conditions [33]. Consequently, changes in the spatial distribution of microbial taxa may facilitate localized interactions that are regulated by feedback mechanisms linking physicochemical conditions [75, 76] with the ecological functionality of the Patagonian coastal ecosystem [65, 77].

According to the core microbiome (i.e., those common members of microbial assemblages associated with the benthic habitat; [78]), most microbial families identified were specific to FZ (38.17%) with only a small proportion of unique ASVs in the ISC (13.37%), highlighting the heterogeneity among sites.

Site-specific differences, investigated using VIP-PLS-DA, revealed that *Flavobacteriaceae*, *Gemmataceae*, *Humimicrobiaceae*, *Methyloligellaceae*, *Nitrosomonadaceae*, *Clostridiaceae*, and *Miltoncostaeaceae* were the

primary contributors to the observed variation. These microbial groups, previously identified through discriminant analysis, are well known for their roles in the degradation of particulate organic matter under hypoxic conditions, where anaerobic processes such as sulfurization of organic material are favored. For example, members of the *Flavobacteriaceae* and *Gemmataceae* are frequently enriched in nutrient-enriched marine habitats [2, 72, 79], as well as in environments impacted by hydrocarbon contamination [80].

Previous studies have also shown that *Sulfurovaceae* (discriminant in the ISC zone) and *Woeseiaceae* (enriched in FR) are favored in surface sediments experiencing anoxic-to-oxic transitions (i.e., episodic variations in oxygen concentration), where they contribute to enhanced hydrogen sulfide removal [81–83].

Interestingly, the bacterial family *Sphingomonadaceae* is a distinguishing component of the microbial community in San Rafael Lagoon. This lagoon is technically a brackish water body located at the head of a fjord, where extremely harsh environmental conditions. As a consequence, the microbial community is dominated by opportunistic species that are well adapted to environmental stress and display a high degree of physiological tolerance [84]. Members of this family have also been implicated in hydrocarbon degradation processes [85], which in turn, constitute a significant fraction of anthropogenic dissolved organic carbon in the marine environment [86].

Further groups identified through discriminant analysis, including *Desulfobulbaceae*, *Desulfobacteraceae*, *Desulfocapsaceae*, *Desulfatiglandaceae*, *and Desulfosarcinaceae*, have been reported in the Black Sea and other upwelling systems [87–89], where they play a key role in the degradation of particulate organic matter under hypoxic conditions and contribute to anaerobic processes such as the sulfurization of organic material [74, 90].

Despite their low relative abundance, sequences assigned to the phyla *Nanoarchaeota*, *Thermoproteota*, *Thermoplasmatota*, and *Asgardarchaeota* were detected at most sampling sites, consistent with their widespread distribution in marine sediments across diverse geographic regions [91, 92]. The low abundance of sequences affiliated with the domain Archaea (< 0.5%) may, however, be partly explained by methodological biases, particularly those associated with the primers commonly used for archaeal 16 S rRNA gene amplification [93]. Diversity surveys in anoxic marine sediments have shown that *Thermoproteota*, *Nanoarchaeota*, and *Asgardarchaeota* are globally distributed. Importantly, although the ecology and metabolic functions of archaea remain poorly understood [94, 95], recent studies employing rapidly advancing technologies have shed light on their diversity, metabolism, evolution, and interactions, highlighting archaea as key players in coastal carbon biogeochemical cycling [72].

On the other hand, the culture-dependent approach allowed the identification of several bacterial families recognized as reservoirs of opportunistic bacteria, including *Arcobacteraceae*, *Bacteroidaceae*, *Caldibacillaceae*, *Clostridiaceae*, *Coriobacteriaceae*, *Cyclobacteriaceae*, *Micrococcaceae*, *Moraxellaceae*, *Mycobacteriaceae*, *Neisseriaceae*, *Pseudomonadaceae*, *Rhodobacteraceae*, *Shewanellaceae*, *Sphingomonadaceae*, and *Vibrionaceae* [96, 97].

The high abundance of these groups is consistent with previous studies and indicates that some of these taxa are among the most successful in marine environments. Importantly, the microbiota can exert both beneficial and detrimental effects; however, an imbalance (dysbiosis) may shift their composition toward pathogenic species and thereby facilitate disease outbreaks [27].

In this context, many of these bacterial families have previously been associated with opportunistic pathogens [17]. Jurelevicius et al. [98] and Verhoeven et al. [1] developed a list of bacterial surveillance related to disease in marine environment. Further detailed investigations of opportunistic, host-associated pathogens inhabiting these environments are required [17, 99], particularly through shotgun metagenomic sequencing approaches capable of linking antibiotic resistance genes (ARGs) to specific bacterial phylogenetic markers.

Keystone microbial taxa organize local-related modules in coastal Patagonian sediments

The module hubs identified in this study corroborate that benthic habitat structure differs between sampling zones. Network topological features varied accordingly, with distinct patterns emerging and the highest complexity observed in the FZ compared to the ISC (see Fig. 6). This suggest more frequent interconnections and a more cohesive network structure in the FZ sediments. Greater network complexity, as indicated by a modularity index greater than 0.4, reflects the presence of functionally diverse keystone taxa. These taxa may enhance the efficiency of information flow within the network and enable rapid feedback responses to environmental perturbations [100, 101], thereby contributing to microbial community stability.

The observed patterns may reflect the adaptation of specific bacterial lineages to distinct geochemical conditions, enabling them to dominate within particular environmental niches [102, 103]. For example, the environmental heterogeneity of the fjord habitat, associated with varying physical and chemical conditions, may have fostered taxonomic interactions, thereby increasing the complexity of co-occurrence networks [104].

Moreover, selection driven by fitness differences among taxa within the network is likely the predominant mechanism governing community assembly in the benthic environments of northern coastal Patagonia [69, 72]. Indeed, previous studies have identified selection as a major driver of microbial community assembly in marine sediments [105, 106]. Nevertheless, several factors may have contributed to these patterns, including local disturbances. Consequently, cumulative regional impacts likely disrupted microbial interactions, leading to reduced network complexity in the ISC (see Fig. 6A), which in turn, poses a significant threat to the ecosystem's ecological functioning [6].

Overall, microbial networks offer valuable insights into the complex interactions that drive community shifts in fragile coastal ecosystems of Patagonia. The ecological influence of the identified keystone taxa extends beyond local habitat conditions, as these taxa shape niches that sustain broader microbial diversity and potentially facilitate trophic interactions with higher organisms [6, 107].

Preserving a broad spectrum of these interactions may enhance community resilience, which is closely associated with microbial ecosystem functioning [72, 73]. Consistently, closely related microbial taxa identified across the study zones may serve as reliable indicators of ecosystem quality [33, 108], given their ecological preferences across a broad range of environmental gradients and their ability to tolerate fluctuating conditions and pollutant stressors [20, 33]. Furthermore, intensive aquaculture activities in the Northern Patagonia ecosystem may serve as hotspots for the selection of prokaryotic communities harboring antimicrobial resistance genes [21, 34, 109]. This highlights the urgent need to better understand the ecological risks associated with emerging pollutants and to generate robust scientific evidence concerning the spread of antimicrobial resistance.

To address these knowledge gaps, future research should incorporate more comprehensive and high-resolution environmental metadata, including quantitative data on the presence and concentrations of heavy metals, pharmaceutical residues, and other relevant contaminants. Such information is crucial for deepening our understanding of the ecological roles played by sensitive microbial taxa, particularly those involved in biogeochemical processes and community-level responses to anthropogenic stressors. Moreover, it is essential for accurately characterizing the composition, distribution, and functional potential of the benthic microbial resistome in aquaculture-influenced environments. These ecosystems, often subject to chronic pollutant exposure, may act as long-term reservoirs and sources of antimicrobial-resistant pathogens, posing significant ecological and public health concerns [90, 108, 110]. A more integrated approach that combines environmental chemistry, microbial ecology, and resistance profiling will be critical to assess the full extent of aquaculture-related impacts and to inform future monitoring and mitigation strategies.

Conclusion

Local microbial co-occurrence patterns observed in the benthic environment of northern coastal Patagonia reflect shifts in spatial community assembly driven by the environmental gradients sampled. Notably, the resulting networks resembled structured communities composed of niche-specialist taxa, well-adapted to specific local conditions and exhibiting properties consistent with ecological processes such as niche differentiation and environmental filtering. Multivariate analyses, combined with co-occurrence network approaches, further revealed that the fragile coastal ecosystems of Patagonia support tightly interconnected microbial communities. These interconnections contribute to increased network complexity, potentially enabling rapid functional responses and enhanced resilience to environmental perturbations. The identification of keystone taxa supports the concept of microbial "seed banks" that may sustain community stability and maintain ecosystem functionality under stress. In addition, bacterial strains harboring biomarkers of opportunistic pathogens were detected using a culture-dependent approach. This is particularly relevant in coastal and shelf sediments subjected to intensive anthropogenic pressures, where monitoring shifts in keystone taxa may provide early warning signals of functional decline. Nonetheless, drawing more definitive conclusions will require high-resolution spatiotemporal monitoring across larger sample sets to properly characterize general trends in bacterial assemblages. Future research should also evaluate the ecological risks posed by these taxa, particularly in relation to the dissemination of antimicrobial resistance across broader spatial and temporal scales. We hope this study will provide a roadmap for advancing functional investigations of microbial metabolic networks and their role in supporting more sustainable management of coastal ecosystems, with the broader aim of elucidating how the instability of microbial communities can cascade upward to affect ecologically and environmentally important processes.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s12866-025-04460-z.

Supplementary Material 1.

Supplementary Material 2.

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Authors' contributions
AZ, LB and AHB conceptualized the research idea. JZF, PB, BL, AZ and MA analyzed data and drafted the manuscript. CV and AZ conducted laboratory work. JLB, CMB, DL and MVC designed, and gave feedback on data analysis. IPS, PAI, JLB analyzed data, and helped draft the manuscript. IPS contributed with oceanographic data. All authors read, gave feedback, and approved the final manuscript.

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Data availability
All data analyzed in this study are available in the Supplementary Data and the raw sequences were deposited in the National Center for Biotechnology Information (NCBI) Sequence Read Archive under BioProject number PRJNA1249584.

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
Not applicable.

Competing interests
The authors declare no competing interests.

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