







Research Article

Cascading effects of glacier retreat: Hydro-chemical shifts and macroinvertebrate responses in Andean glacier-fed streams

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Abstract

The retreat of tropical glaciers in the Peruvian Andes, particularly in the Cordillera Blanca, has significantly altered hydrogeological and geochemical processes in mountain watersheds. This study investigates the influence of glacier change-driven acid rock drainage (ARD) upon benthic macroinvertebrate communities in 19 glacier-fed streams of the Santa River watershed over two consecutive dry and wet seasons (2019–2020). The findings reveal that ARD driven by glacier melt and sulphide oxidation has led to increased metal concentrations (e.g., Fe, Mn, Al, Pb) and pH reductions (of 2–3 in some sites), creating a “toxic or treat” scenario for aquatic biodiversity. Statistical analyses, including principal component analysis (PCA), principal coordinate analysis (PCoA), and canonical correspondence analysis (CCA), indicate significant correlations between physical and chemical changes and macroinvertebrate assemblages. Collector-gatherers (e.g., Chironomidae, Baetidae) were dominant in sites impacted by ARD, while sensitive functional feeding groups, such as scrapers and shredders, declined under high metal stress. Seasonal variations also affected taxonomic richness, with greater abundance observed during the dry season. These results highlight the cascading effects of climate-induced glacier loss on freshwater ecosystems and provide critical insights into the ecological consequences of ongoing environmental changes in high-altitude Andean rivers.

Key words: Acid rock drainage, functional feeding groups, glacier retreat, macroinvertebrate communities, tropical Andes



Academic editor: Stoyan Nedkov

Received: 27 July 2025

Accepted: 16 January 2026

Published: 05 March 2026

Citation: La Matta Romero F, Arevalo-Seijas V, Valqui-Peña D, Macdonald M, Wadham J, Loayza-Muro R (2026) Cascading effects of glacier retreat: Hydro-chemical shifts and macroinvertebrate responses in Andean glacier-fed streams. *Journal of the Bulgarian Geographical Society* 54: 117–146. <https://doi.org/10.3897/jbgs.e166425>

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1. Introduction

Mountain regions encompass glacial stocks and freshwater reservoirs that play a valuable role providing ecosystem services to large human populations living downstream (e.g. drinking water, food, and electric power, or purifying water). These regions are unique through the heterogeneity of ecosystems and diversity of climates arising from their sharp altitude gradients and thus are considered sensitive sensors of global environmental changes. Approximately 70% of the world's tropical glaciers are located in the Peruvian Andes,

where the Cordillera Blanca covers nearly a quarter of the total area (Vuille et al. 2008a, 2008b). In the last 50 years, these glaciers have lost around 50% of their surface area, and some have entirely disappeared (INAIGEM 2018). Depending on the geological conditions, this process has differently modified the hydrogeology and geochemistry of glacier-fed Andean watersheds, wetlands and rivers (Cuesta et al. 2019). In some areas of the Cordillera Blanca, glacier retreat has accelerated the weathering and oxidation of exposed sulphide-rich rocks, mainly associated with the dominant Chicama Formation, producing acidic conditions (pH 3–4) known as acid rock drainage (ARD), which promotes increased solubility and leaching of toxic metals (e.g. As, Al, Mn, Pb) into lakes, rivers and streams (Magnússon et al. 2020; Bravo-Zevallos et al. 2024; Garcia et al. 2025). However, this process has also leached beneficial essential elements and nutrients, such as phosphates, nitrates, and carbonates from karstic formations (Burns et al. 2011; Frings and Buss 2019). As a result of the patchy distribution of these sulphide-rich geological formations along the Cordillera Blanca, the impacts of glacier retreat on biodiversity and downstream populations may be spatially variable (Vuille et al. 2018; Veettil 2018). In addition, mining environmental liabilities in this region, such as abandoned mine tailings, have also contributed to the acidification of soils and water bodies, and increased potentially toxic metal concentrations in the environment through acid mine drainage (AMD).

Several studies show the effect of ARD and AMD on water chemistry (Abarca et al. 2017; Santofimia et al. 2017), but few document the impacts on aquatic biodiversity (Hogsden and Harding 2012; Talukdar et al. 2016). ARD and AMD have similar toxicity effects in the environment, such as the smothering of streambed substrates by metal oxyhydroxide precipitation, reducing habitat availability for aquatic and benthic fauna, decreasing food quality, and modifying interactions between functional feeding groups (FFG) (Loayza-Muro et al. 2014a, 2014b). Metal oxide precipitates also affect the biodiversity of the exposed area by altering species survival and influencing their distribution by creating migration barriers (Cain et al. 2004; Gerhardt et al. 2004). Despite these conditions, studies on the impact of ARD in freshwater ecosystems are much more limited compared to AMD (Todd et al. 2012; Ilyashuk et al. 2014, 2018; Zarroca et al. 2021). Regarding mountain streams and rivers in temperate regions, such as Canada (Gault et al. 2015), Spain (Sánchez-España et al. 2016), and the Rocky Mountains (Rue and McKnight 2021), examples of ARD include an increase of acidity (pH ~3.3) together with elevated cadmium, zinc, lead, iron and aluminium concentrations, as well as precipitates of metal hydroxy sulphates (Crouch et al. 2013). A similar situation is observed in the Himalayas (Salerno et al. 2016) and the Alps (Ilyashuk et al. 2014), where sulphates and ARD generation have been related to increasing temperatures and glacial retreat.

Benthic macroinvertebrates have been widely used as indicators of water quality in stream assessments because of their diversity, life-history characteristics, and sensitivity to a wide range of environmental changes (He et al. 2014). Compared to lowland regions, macroinvertebrate communities in glacier-fed streams appear to be more structured by local scale variations of discharge, substrate type, water chemistry, oxygen deficiency, and riparian vegetation (Jacobsen 1998; Brittain et al. 2001; Jacobsen et al. 2003; Dunbar et al. 2010;

Jacobsen et al. 2012; Vimos-Lojano et al. 2020; Croijmans et al. 2021), that favour specific habitats for specialised taxa and feeding groups (Tomanova et al. 2007; Espinosa et al. 2020; Muhlfeld et al. 2020). Feeding behaviour in these taxa may have distinct responses to seasonal changes in resource availability (Chará-Serna et al. 2012; Sertić Perić et al. 2021), but also to human influences, such as agriculture and mining (Villada-Bedoya et al. 2017). Warming temperatures and melting glaciers induced by climate change are also leading to cascading impacts on downstream systems that limit the structure of benthic communities (Jacobsen 2008a, 2008b; Jacobsen et al. 2012; Slemmons et al. 2013). In addition, natural stream acidification and metal leaching may create a multiple stress scenario in freshwater ecosystems and benthic macroinvertebrates assemblages, as seen in Andean and Alpine regions (Courtney and Clements 2000; Loayza-Muro et al. 2010; Loayza-Muro 2014).

In the last decades, metal leaching due to glacier loss in high mountain streams has been indicated as a major threat to biodiversity and human populations (Jacobsen et al. 2012; Mark et al. 2017). Several studies show that glacier retreat may drive changes in stream physical and chemical conditions (e.g. nutrient and potentially toxic metal concentrations), frequently associated with differences in water flow and discharge between the rainy and dry seasons (Juen et al. 2007; Mark and McKenzie 2007; Loayza-Muro et al. 2010; Jacobsen et al. 2014). Although this may produce unique “toxic or treat” conditions depending on the complex geology of the Cordillera Blanca, little attention has been devoted to describing their influence on aquatic communities. Therefore, the aim of this study was to assess whether the changes on river water quality associated with glacier retreat influences the composition and functional feeding groups of benthic macroinvertebrate communities in streams in the Cordillera Blanca. To this purpose, streams and macroinvertebrates were sampled in 19 glacierized catchments draining the Santa River along a 200 km transect during the 2019 dry season and 2020 wet season.

2. Materials and methods

2.1. Study area

The Cordillera Blanca is located within the Huascarán National Park, covering a watershed of 12,006 km² and a maximum elevation of 6,768 m a.s.l. It receives an annual average of 1,300 mm of precipitation, much of it falling and accumulating as snow at higher altitudes. Meltwater contributes up to 40% of the total annual discharge to the Santa River and its tributaries during the dry months (May to October) (Mark et al. 2010; Baraer et al. 2009). Water flow ranges between 34.4 m³ s⁻¹ in July and 273.7 m³ s⁻¹ in March, and variations in average annual temperature oscillate between 14°C and 16°C at 3,000 m a.s.l. and decrease to 4°C over 4,500 m a.s.l. (INAIGEM 2018). The Santa River, which is the main river of the department of Ancash, flows North through the Callejón de Huaylas valley from its source in the Lake Conococha to the Cañón del Pato, where it leaves the mountains and turns west towards the Pacific coast (Burns et al. 2011; INAIGEM 2018). In this study, 19 tributaries of the Santa River were sampled along a 200 km transect, between 1,925 and 5,037 m a.s.l. (Fig. 1) during the dry (July 2019) and wet season (February 2020).

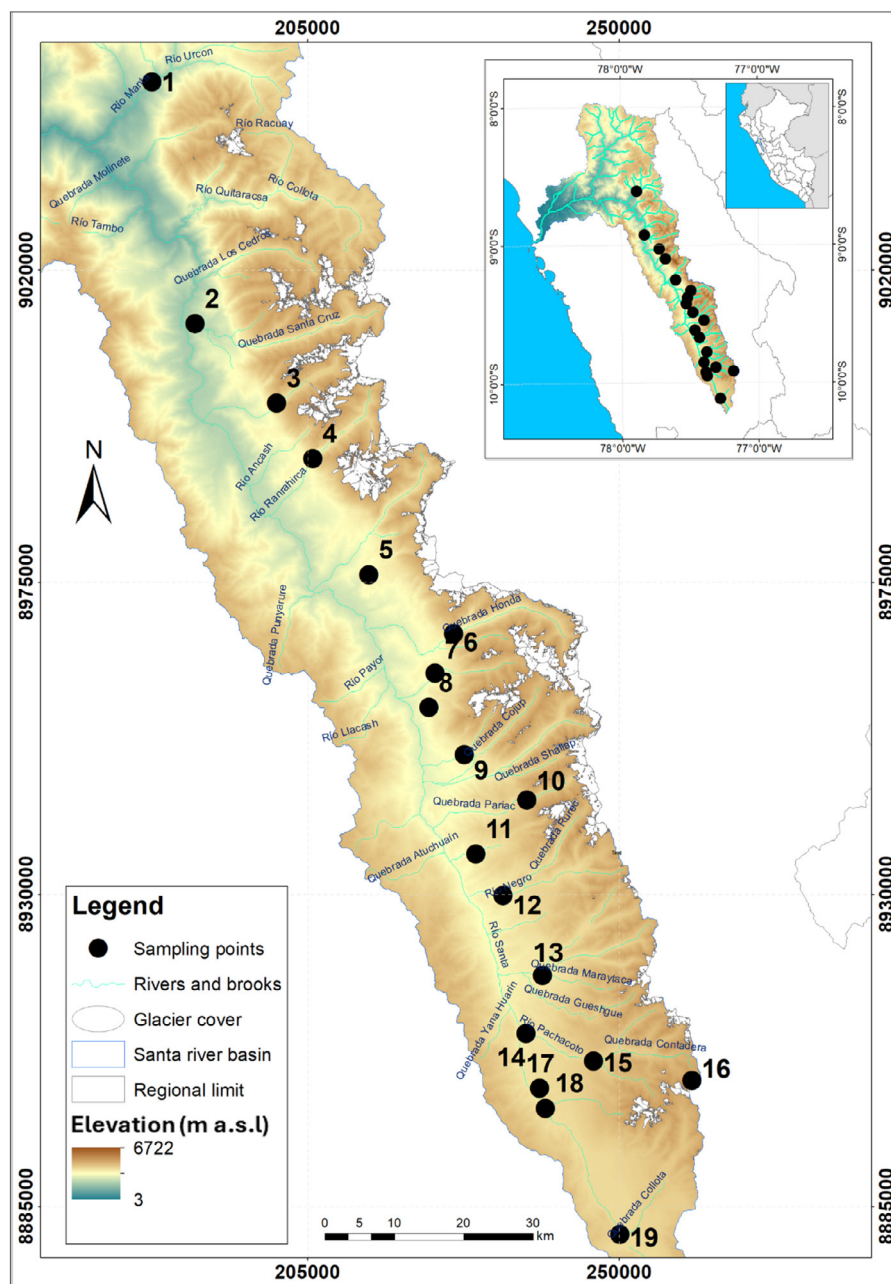


Figure 1. Map of sampling sites (1–19) in the Santa River watershed, Cordillera Blanca, 2019–2020.

2.2. Water chemistry

Water chemistry was characterised during both the dry (July 2019) and wet (February 2020) seasons. The analysis included 17 metals: Mo, Cd, Ba, Pb, U, Li, Al, Ti, V, Cr, Mn, Fe, Co, Ni, Cu, Zn, and Sr; one metalloid: Si; one non-metal: Cl; four alkaline elements: Ca, K, Mg, and Na; and five ions: SO_4^{2-} , N-NH_4^+ , P-PO_4^{3-} , N-NO_3^- , and HCO_3^- .

Environmental variables were recorded in situ. Physical and chemical parameters, such as river pH, temperature ($^{\circ}\text{C}$), electric conductivity (EC, $\mu\text{S}/\text{cm}$), and dissolved oxygen (DO, mg/L), were measured at each sampling site using a Hach HQ40d field multiparameter sonde. Discharge was determined by

salt dilution gauging. For laboratory analyses, water samples were collected in flowing water and filtered in the field using a 0.45 μm polyethylene sulfone syringe filter (Whatman, GD/XP PES) and stored at -20°C until analysis of N-NH_4^+ , N-NO_3^- and P-PO_4^{3-} or at 4°C until analysis of Si. Water samples for trace metal determination were filtered using a 0.45 μm syringe filter (Whatman GD/XP PES) into 15 mL bottles, both previously acid-washed as detailed in Hawkings et al. (2020). Water samples for dissolved organic carbon (DOC, mg/L) were filtered with Whatman Puradisc Aqua 0.45 μm syringe filters into acid-washed bottles and frozen at -20°C until analysis. N-NH_4^+ , N-NO_3^- and P-PO_4^{3-} were analysed by colorimetry using a LaChat QuikChem® 8500 series 2 Flow Injection Analyser. Cl^- and SO_4^{2-} samples were analysed in a Thermo Scientific™ Dionex™ ICS-6000 ion chromatography system, and DOC in a Shimadzu TOC-L CPH/CNP analyser. All analyses were performed in triplicate at the LOWTEX Laboratory, University of Bristol (UK). Trace elements were analysed in a Thermo Scientific™+ Element 2™ HR-ICP-MS (High Resolution Inductively Coupled Mass Spectrometer) with desolvation (apex Q sample inlet system with ACM desolvator; Elemental Scientific®) at Florida State University (USA).

2.3. Benthic macroinvertebrate sampling and identification

Organisms were collected from the sediments using a Surber net (mesh size 500 μm , frame 30x30cm) and by manual collection using forceps and toothbrushes to remove larvae attached to stones and leaves. Sampling was conducted along the riverbanks at depths up to 0.5 m, covering all substrate types (gravel-pebbles, stones, vegetation and sediments). The Surber net was positioned against the current, and the substrate within the quadrat area was carefully disturbed to dislodge the organisms, which then were carried into the net (Samanez Valer et al. 2014). At least three Surber samples were taken per site. The total sampling effort was 20 minutes and covered approximately 50 m of river reach per site. Macroinvertebrates were preserved in 70% alcohol, transported in coolers and identified in the Laboratory of Ecotoxicology, Universidad Peruana Cayetano Heredia, in Lima, Peru. Samples were rinsed using a set of sieves (4.08 mm, 2.18 mm, 0.87 mm and 0.48 mm), sorted and photographed under a Leica Microsystems S9i stereoscope and identified to family level using taxonomic keys (Roldán 1996; Domínguez and Fernández 2009). Adults and pupae were excluded. Abundance and taxa richness were recorded for each sample. FFG classification should ideally be conducted at the genus or species level; however, for this study, functional feeding groups were assigned based on the dominant or primary feeding habit of each family. This approach was adopted because families may include taxa with diverse feeding strategies. Macroinvertebrates were classified into six functional feeding groups (FFG): predators (PR), collector-filterers (CF), scrapers (SC), collector-gatherers (CG), shredders (SH), and piercers (PI) (Ramírez and Gutiérrez-Fonseca 2014; Fierro et al. 2015; Makaka et al. 2018; Min et al. 2019).

2.4. Data analysis

Our statistical analysis had three main components. First, a principal components analysis (PCA) based on a correlation matrix was used to describe the

main variation in physical and chemical variables between sites and seasons, i.e., to determine which variables best explained differences between sites and how these differences could change between seasons. Prior to the analysis, data were standardised to meet normality. We used ANOVAs in the PCA scores to evaluate differences between sites and seasons.

Second, we analysed the macroinvertebrate data by comparing family abundances, looking for seasonal differences. We also assessed differences in the composition of macroinvertebrate communities between sites using a principal coordinate analysis (PCoA) with Bray-Curtis distances. Prior to the ordination, abundances were relativized using $\log(x+1)$ and five sites without individuals were excluded. Seasonal differences were evaluated by using one-way PERMANOVA. A canonical correspondence analysis (CCA) was used to evaluate the effects of the main variation of physical and chemical variables (extracted from a second PCA excluding those sites where no macroinvertebrates were found) on the macroinvertebrate composition of these sites, and a Monte Carlo permutation test ($n = 999$) was used to evaluate the significance of the canonical axis.

Finally, our analysis of FFG abundance involved generalized linear models (GLMs), with physical and chemical parameters and season as explanatory variables. Due to the substantial number of potential predictors ($n = 35$), a forward stepwise regression approach was implemented. Predictor selection for model inclusion adhered to three inclusion criteria: first, we only included predictors that resulted in a decrease greater than 2 in the small sample unbiased Akaike information criterion (AICc). Second, predictors with a p-value below 0.05 were included; however, non-significant predictors that still significantly improved the AICc were also considered. Third, to avoid multicollinearity, only one variable from a set of highly correlated predictors was chosen, preferably one with ecological relevance. For the final models, we prioritized biologically relevant predictors; otherwise, statistically significant predictors were retained even if their biological relevance or linear trend wasn't strongly evident. All analyses were performed with R software version 4.3.1. (R Core Team 2023).

3. Results

3.1. Water chemistry

At all sampling sites, pH ranged from 6 to 9 in both seasons, except for sites 12 and 16, which exhibited significantly lower levels (pH 2–3). The EC differed between seasons, with lower values observed during the wet season. In the dry season, the lowest recorded conductivity was 29.5 $\mu\text{S}/\text{cm}$ (site 9), while the highest reached 628.9 $\mu\text{S}/\text{cm}$ (site 12). DO ranged between 7.82 mg/L (site 1) in the wet season and 5.64 mg/L (site 17) in the dry season, indicating favourable oxygenation conditions for aquatic biota in both seasons, as DO concentrations above 5 mg/L are generally suitable for sustaining macroinvertebrate assemblages in alpine streams (Ward 1994; Milner and Petts 1994). The mean water temperature during the seasons was 12.5°C. In the wet season, temperatures ranged from 6.1°C (site 16) to 18.5°C (site 13), while in the dry season, they varied from 1.4°C (site 16) to 17.7°C (site 2). DOC concentrations showed average values of around 0.54 mg/L. During the dry season, the lowest concen-

high correlation between EC, and most toxic metals, such as Pb, Al, Cr, Mn, Fe, Co, Ni, Cu, and Mg, N-NH₄ and SO₄. These variables were highly negatively correlated with pH, and, to a lesser degree, with temperature and V. PC2 revealed a strong correlation between Ba, Li, Sr, Si, Cl, Ca²⁺, K⁺, Na⁺, HCO₃⁻, P-PO₄³⁻ and N-NO₃⁻. PC3 accounted for variation in DO, Mo, U, Ti, V, N-NO₃⁻, Ca²⁺, and DOC. Finally, PC4 was represented by discharge, Cd, and Zn (Suppl. material 3).

3.2. Composition of benthic macroinvertebrate communities

A total of 14,262 macroinvertebrate specimens were collected, representing 16 orders and 37 taxonomic groups, including two class (Collembola and Oligochaeta), and 35 families (Table 1). Insects accounted for 30 families, with Diptera being the dominant order with 46.3% of the total abundance, followed by Ephemeroptera (27.9%) and Trichoptera (18.8%). Within Diptera, Chironomidae was the most abundant family, representing 33.4% of the total abundance (4773 individuals), followed by Baetidae (22.6%, 3942 individuals) and Hydropsychidae (15.1%, 2163 individuals) (Fig. 3).

An ANOVA was conducted to assess diversity values, revealing significant differences in individual abundance (F=7.93, p<0.01) and richness (F=4.77, p<0.05) between seasons. Specifically, the dry season exhibited higher richness and abundance compared to the wet season. However, no significant variations were observed in the dominance, Shannon, and Berger-Parker indices.

The macroinvertebrate community composition was analyzed based on abundance at each site using a principal coordinate analysis (PCoA). Four axes were generated, explaining 46.5% of the total variation. The PCoA plots revealed notable differences in macroinvertebrate composition during the wet season,

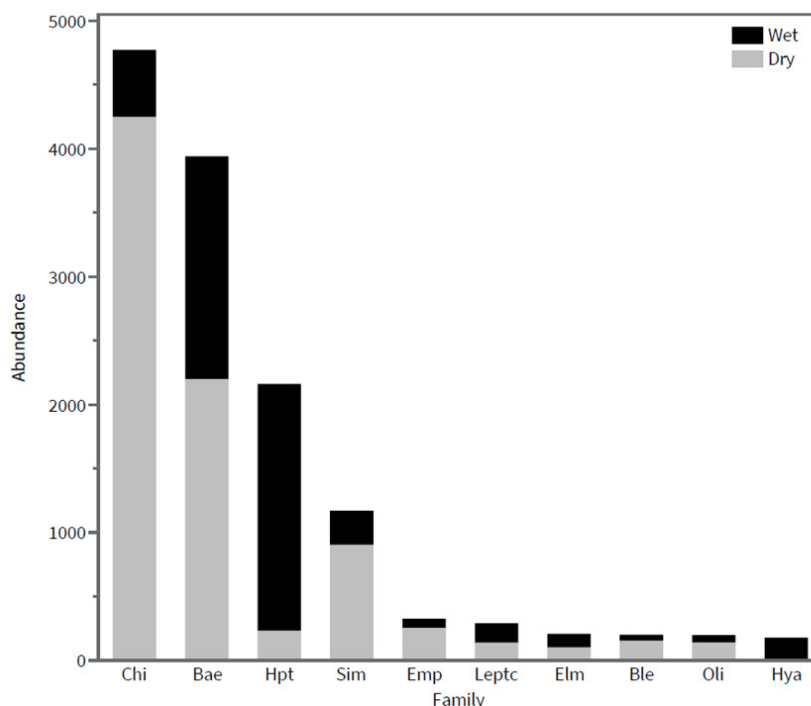


Figure 3. Seasonal variation in the abundance of the ten most abundant macroinvertebrate families recorded at 19 sampling sites.

Table 1. Seasonal taxonomic and functional composition, total abundance of macroinvertebrates and family coding. Legend: CG = Collector/Gatherer, CF=Collector/Filterer, SC = Scraper, SH = Shredder, PR = Predator, PI= Piercer.

Class/Subclass/Order *	Families and codes	Functional Feeding Group	Seasonal abundance	
			Dry	Wet
Tricladida	Dugesiidae (Dug)	PR	27	0
Oligochaeta	Oligochaeta (Oli) (non-Tubificidae)	CG	142	56
Tubificida	Tubificidae (Tub)	CG	33	0
Gastropoda	Physidae (Phy)	SC	6	6
Gastropoda	Hydrobiidae (Hbii)	SC	0	2
Amphipoda	Hyalellidae (Hya)	CG	8	170
Collembola	Collembola (Cole)	CG	3	0
Trombidiformes	Hygrobatidae (Hyg)	PR	25	85
Trombidiformes	Limnesiidae (Limns)	PR	42	4
Ephemeroptera	Baetidae (Bae)	CG	2201	1741
Ephemeroptera	Leptophlebidae (Lep)	CG	6	28
Ephemeroptera	Leptohyphidae (Lept)	CG	2	5
Odonata	Aeshnidae (Aes)	PR	0	1
Plecoptera	Gripopterygidae (Gri)	SC	2	40
Plecoptera	Perlidae (Per)	PR	20	10
Hemiptera	Mesoveliidae (Meso)	PR	5	3
Megaloptera	Corydalidae (Cory)	PR	5	5
Trichoptera	Hydroptilidae (Hpt)	PI	233	1930
Trichoptera	Leptoceridae (Leptc)	CG	140	150
Trichoptera	Limnephilidae (Limn)	SH	38	83
Trichoptera	Hydrobiosidae (Hbi)	PR	54	34
Trichoptera	Hydropsychidae (Hpsy)	CF	17	10
Trichoptera	Glossosomatidae (Glo)	SC	1	0
Coleoptera	Elmidae (Elm)	CG	102	107
Coleoptera	Scirtidae (Sci)	SC	11	49
Coleoptera	Dytiscidae (Dys)	PR	7	0
Coleoptera	Staphylinidae (Sta)	PR	2	0
Diptera	Chironomidae (Chi)	CG	4251	522
Diptera	Simuliidae (Sim)	CF	904	266
Diptera	Empididae (Emp)	PR	257	69
Diptera	Blephariceridae (Ble)	SC	155	46
Diptera	Ceratopogonidae (Cer)	PR	28	42
Diptera	Tipulidae (Tip)	SH	36	8
Diptera	Muscidae (Mus)	PR	9	4
Diptera	Limoniidae (Lim)	SH	9	0
Diptera	Tabanidae (Tab)	PR	2	2
Diptera	Sarcophagidae (Sar)	CG	1	0

*Taxa listed in Column 1 are presented at the highest consistently identifiable taxonomic rank above the family level (class, subclass, or order), depending on the taxonomic group.

with sites 1W, 4W, 6W, 12W, 15W, and 16W exhibiting a higher dispersion and relatively lower abundances (Fig. 4A). The PCoA showed notable season effects and higher abundance for Chironomidae, Leptoceridae, and Baetidae (Fig. 4A; Table 1). The seasonal variation was assessed using a PERMANOVA test, which revealed a significant effect ($F=3.9$; $p \leq 0.001$).

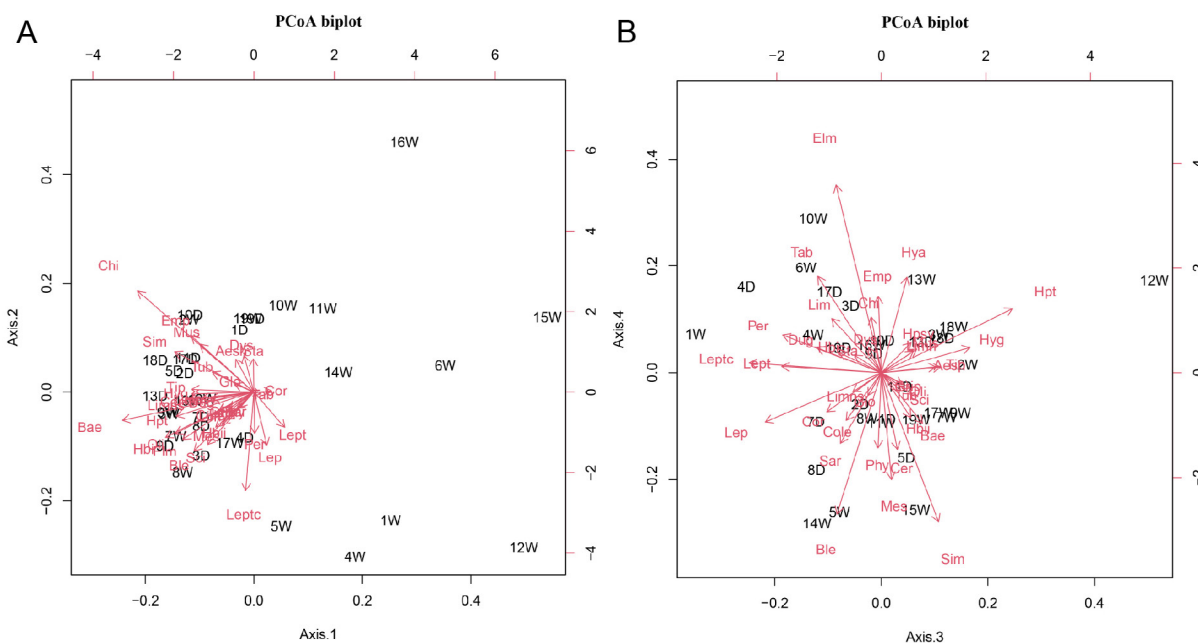


Figure 4. Principal coordinate analysis (PCoA) for macroinvertebrate abundance and sampling sites based on Bray-Curtis dissimilarity. Vectors represent macroinvertebrate family abundances, while the ordination of sites and their corresponding season (wet, W; dry, D) is shown in black labels. **A** PCoA for axis 1 (17.1%) and 2 (10.6%) **B** PCoA for axis 3 (10.1%) and 4 (8.8%). Percent variation explained by each axis is given in brackets.

We performed a second principal component analysis (PCA2) (Suppl. material 1), excluding those sites where no macroinvertebrates were found (Sites 6D, 12D, 14D, 15D, 16D, 12W and 16W), to use the new components as variables for a subsequent canonical correspondence analysis (CCA). PCA2 reduced the 34 physical and chemical variables into four components that explained a total variance of 76.6% (PC1, 30.3%; PC2, 25.1%; PC3, 11.3%; PC4, 9.8%). The loadings along PC1 indicated that the principal variation in physical and chemical variables was based on a positive high correlation between most toxic metals (Pb, Al, V, Cr, Mn, Fe, Co, Ni, and Cu), and EC, $N-NH_4^+$ and SO_4^{2-} , but were highly negatively correlated with pH, and, to a lesser degree, with temperature. In contrast, PC2 was positively associated with non-toxic environmental variables, such as $P-PO_4^{3-}$, $N-NO_3^-$, Si, Cl, Ca^{2+} , K^+ , Mg^{2+} , Na^+ , and HCO_3^- .

A CCA Type-2 explained 72.3% of the variation in macroinvertebrate abundances across sites. However, the second and third CCA axes, which accounted for 29.96% and 22.18% of the variation, respectively, were the only statistically significant ($p < 0.05$) (Table 2).

The families Limnesiidae, Mesovelliidae, Hydrobiosidae, Hydroptilidae, Tubificidae, Oligochaeta, Leptophlebiidae, as well as the dipterans Chironomidae, Limoniidae, Simuliidae and Sarcophagidae, showed association with PC1. PC2 was found to be associated with Muscidae and Empididae, while Tabanidae

Table 3. Seasonal variation of the abundance percentage of FFG.

Functional Feeding Groups	Families	Season				Total abundance percentage
		Dry		Wet		
Collector-Gatherers	Baetidae	31.95	78.42	62.65	50.69	67.8
	Leptophlebitidae	0.09		1.01		
	Leptohyphidae	0.03		0.18		
	Chironomidae	61.71		18.78		
	Sarcophagidae	0.01		0.00		
	Elmidae	1.48		3.85		
	Tubificidae	0.48		0.00		
	Leptoceridae	2.03		5.40		
	Colembola	0.04		0.00		
	Hyalellidae	0.12		6.12		
	Oligochaeta	2.06		2.02		
Predators	Muscidae	1.86	5.50	1.54	4.73	5.2
	Empididae	53.21		26.64		
	Ceratopogenidae	5.80		16.22		
	Tabanidae	0.41		0.77		
	Dytiscidae	1.45		0.00		
	Staphylinidae	0.41		0.00		
	Hydrobiosidae	11.18		13.13		
	Aeschnidae	0.00		0.39		
	Perlidae	4.14		3.86		
	Mesovellidae	1.04		1.16		
	Velidae	0.00		0.00		
	Corydalidae	1.04		1.93		
	Limnesidae	8.70		1.54		
	Hygrobatidae	5.18		32.82		
Dugesiiidae	5.59	0.00				
Shredders	Limonidae	10.84	0.945	0.00	1.66	1.2
	Tipulidae	43.37		8.79		
	Limnephilidae	45.78		91.21		
Collector-Filters	Simuliidae	98.15	10.49	96.38	5.04	8.4
	Hydropsychidae	1.85		3.62		
Scrapers	Blephariceridae	88.57	1.993	32.17	2.61	2.2
	Scirtidae	6.29		34.27		
	Glossomatidae	0.57		0.00		
	Gripopterygidae	1.14		27.97		
	Hydrobiidae	0.00		1.40		
	Physidae	3.43		4.20		
Piercers	Hydroptilidae	100.00	2.653	100.00	35.26	15.2

3.3. Functional feeding groups composition

We categorized the macroinvertebrates into six FFG. Predators exhibited the highest number of taxa (14), followed by collector-gatherers (11), scrapers (6), shredders (3), collector-filterers (2), and piercers (1) (Table 3).

Among these groups, collector-gatherers comprised 67.8% of the total abundance. Within this group, Chironomidae (61.7% in the dry season, and 18.7% in the wet season) and Baetidae (31.9% in the dry season and 62.6% in the wet season) were the most representative. Piercers accounted for 15.1% of the total abundance among the functional feeding groups, mainly due to the increased abundance of Hydroptilidae during the wet season. Collector-filterers contributed 8.4% to the total abundance, followed by predators (5.2%), scrapers (2.6%), and shredders (1.6%) (Table 3). Collector-gatherers, predators and collector-filterers were dominant during the dry season. In contrast, shredders, scrapers and piercers were more abundant during the wet season (Fig. 6).

The relationship between FFG and physical and chemical parameters and the season was examined, and it was found that the abundance of each FFG was associated with a particular group of parameters (Table 4).

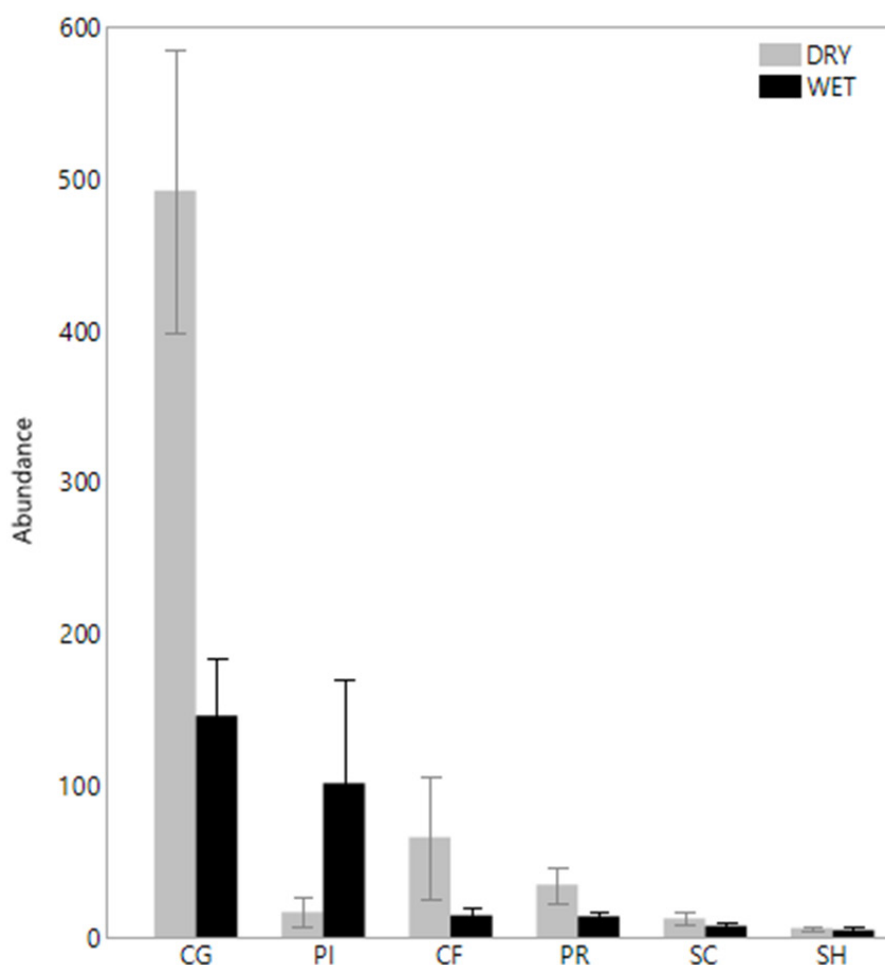


Figure 6. Average seasonal variation of relative abundances of FFG recorded at 19 sampling sites. Legend: CG: collector-gatherers, PI: piercers, CF: collector-filterers, PR: predators, SC: scrapers, SH: shredders.

In the case of the collector-gatherers, the concentrations of Si, Mg²⁺ and DO were significant, but only Si correlated positively with abundance (Fig. 7A). For the collectors-filterers, the abundance was a function of the concentrations of Ti and V, where only the latter showed a positive correlation (Fig. 7B). For predators, the concentrations of Na, Mg, P-PO₄³⁻, temperature and pH were the significant predictors, where only Fe was negatively correlated with the abundance (Fig. 7C). For shredders, the parameters that most influenced their abundance were U and EC, where the latter showed a negative correlation (Fig. 7D). In the case of scrapers, the model showed that the concentrations of N-NO₃⁻, SO₄²⁻ and Fe were significant, but only the N-NO₃⁻ showed a positive correlation (Fig. 7E); while for piercers, their abundance was negatively correlated with DO (Fig. 7F).

Table 4. Selection of models to describe the abundance of each of the six FFG using 34 physical and chemical parameters and the season. The small sample Akaike information criterion (AICc), the determination coefficient (R²), and the estimates of the predictors with their significance according to the model selected for each FFG are shown.

FFG	AICc	R2	term	estimate	p value
Collector-gatherers	511.91	0.687	Intercept	1253.22	0.0095
			Si	149.31	<.0001
			Mg	-33.17	0.0034
			DO	-203.06	0.0049
			Season	62.37	0.0534
Predators	316.75	0.877	Intercept	5.44	0.7817
			Na	7.75	<.0001
			Mg	-5.69	0.0003
			P_PO4	-3343.64	0.0056
			Fe	0.003	0.0086
			T	-1.72	0.0347
			pH	6.06	0.0431
			K	-15.3	0.0762
Shredders	254.93	0.315	Intercept	4.71	0.0162
			U	1.94	0.0048
			EC	-0.02	0.0557
Scrapers	299.06	0.443	Intercept	2.55	0.4924
			N_NO3	120.89	0.0003
			SO4	-0.36	0.0029
			Fe	0.003	0.0140
Piercers	516.42	0.169	Intercept	1191.87	0.0163
			DO	-172.32	0.0180
			Discharge	40.6	0.1100
Collector-filterers	452.09	0.225	Intercept	-8.76	0.6596
			Ti	-15.47	0.0098
			V	464.83	0.0032

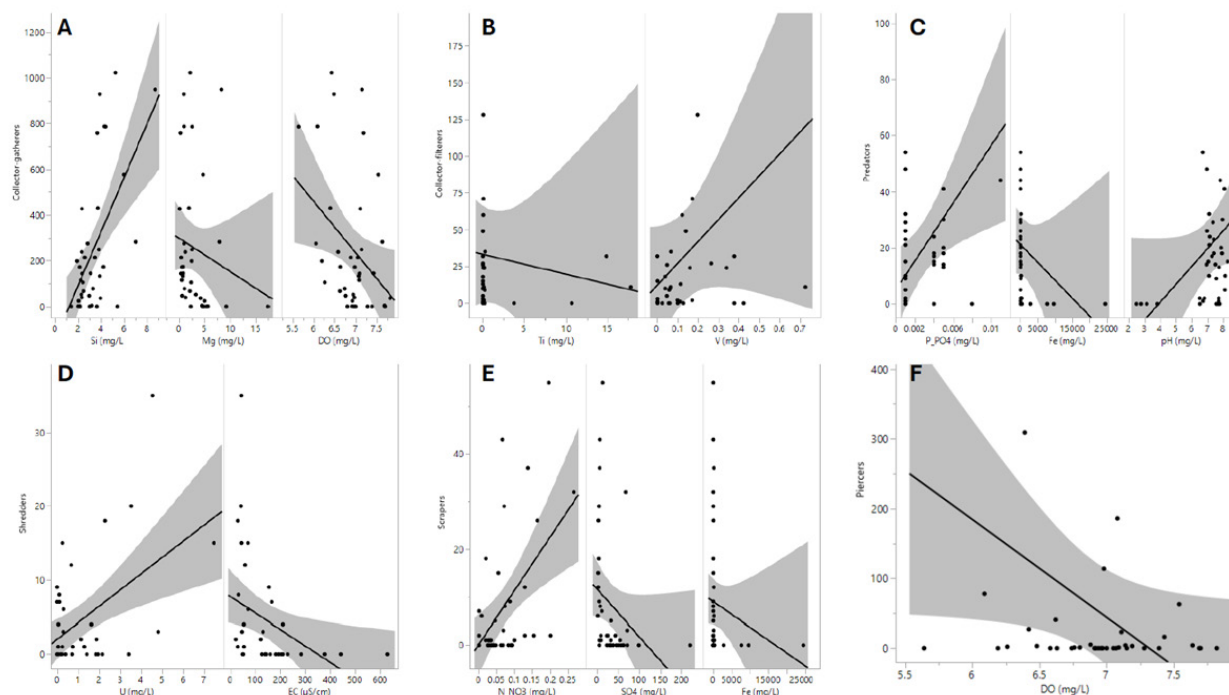


Figure 7. Abundance of six functional feeding groups (FFG) in relation to water quality parameters. **A** collector-gatherers in relation to Si, Mg and DO **B** collector-filterers in relation to Ti and V **C** Predators in relation to PO₄³⁻, Fe and pH **D** shredders in relation to U and EC **E** scrapers in relation to NO₃⁻, SO₄²⁻ and Fe **F** piercers in relation to DO. For each predictor, the regression line is shown, and the shaded areas indicate the 95% confidence intervals.

4. Discussion

4.1. Glacier retreat and the intensification of acid rock drainage in high mountain ecosystems

Bedrock composition significantly influences glacial dynamics, the formation of periglacial landforms, and geochemical processes such as acid rock drainage (ARD). Lithological characteristics affect both the physical landscape and the chemical evolution of high-mountain aquatic ecosystems (Gachev 2021). ARD occurs when sulphide minerals, primarily pyrite (FeS₂), undergo oxidation in oxygen- and water-rich environments. This process produces sulfuric acid and ferrous sulphate, leading to the acidification of water bodies and causing cascading toxic effects on ecosystems, including benthic communities (Nordstrom and Alpers 1997; Loayza-Muro 2013; Ilyashuk et al. 2014). While pyrite is the predominant contributor, other sulphide minerals, such as arsenopyrite, chalcopyrite, sphalerite, and pyrrhotite, also contribute to this phenomenon (Zarroca et al. 2021).

In the Cordillera Blanca, one of the world’s largest metal sulphide-rich regions, glacier retreat accelerates ARD driven by changes in sulphide weathering. This is particularly concerning due to the presence of the Chicama Formation, a major sulphide-rich ore deposit (Fortner et al. 2011; Santofimia et al. 2017). Our findings from Pastoruri and Shallap rivers (sample points 12 and 16) reveal pronounced ARD, with pH values ranging from 2 to 3 and elevated concentrations of Fe, Mn, Al, and SO₄²⁻ (Suppl. material 2). These conditions

significantly degrade water quality and exemplify the severe ecological impacts of ARD (Zarroca et al. 2021).

Similar ARD processes have been documented in other high-mountain environments, including Canada's Sugar Mountains (Gault et al. 2015), the Central Pyrenees spanning Spain and France (Zarroca et al. 2021), and Mt. Evans in the USA (Gammons et al. 2021). In each case, the oxidation of sulphide minerals, particularly pyrite, results in ARD and metal contamination, demonstrating a widespread environmental issue beyond the Cordillera Blanca.

Climate change further intensifies ARD by increasing precipitation, altering hydrological cycles, and accelerating the degradation of glaciers and permafrost. In alpine regions, heavy rainfall following dry periods can sharply elevate acid and metal concentrations in water bodies (Nordstrom 2007). As warming trends continue, changes in the weathering of sulphide-bearing rocks in glacierised regions is likely to amplify ARD processes in areas with abundant metal-sulphide geologies (Ilyashuk et al. 2014; Zarroca et al. 2021). These changes pose an escalating threat to water quality and ecosystem stability in high-altitude environments.

4.2. Benthic macroinvertebrate community composition in relation to physical and chemical characteristics

The variability in the physical and chemical characteristics of water, including parameters such as pH, conductivity, temperature, dissolved oxygen, water hardness, salinity, and phosphate concentrations, plays a pivotal role in shaping the distribution and community composition of benthic macroinvertebrates, mainly due to their sensitivity to these environmental factors (Roldán 1996, 2003; Arocena et al. 2008; Domínguez and Fernández 2009; Loayza-Muro et al. 2014a, 2014b).

Dalu (2017) found that water quality was a better predictor of macroinvertebrate composition than sediment chemical conditions, with factors such as water turbidity, pH, salinity, and phosphate concentration playing a significant role. Similarly, Rezende (2014) identified pebble proportion in the substrate and water electrical conductivity as key local environmental variables affecting macroinvertebrate communities. Other studies at different altitudes in the Andes have demonstrated the effect of 'multiple stressors' caused by the combination of intense solar radiation and natural metal-rich contamination ARD/AMD on the abundance and richness of macroinvertebrate families (Loayza-Muro et al. 2010, 2014b; He et al. 2015). Quinn and Hickey (1990) identified temperature as a determining factor in the distribution of Plecoptera, which were largely restricted to cold rivers (13 to 19°C), while Jacobsen et al. (1997, 2003) and Jacobsen (2008a, 2008b) mentioned that independent of altitude and latitude, the richness and composition of macroinvertebrate communities would be related to maximum temperature and dissolved oxygen.

In our study, similar values of temperature and DO were found at the different sampling sites throughout seasons and were therefore not significant in explaining the variability in community composition between sites. However, the PCoA result showed differences in community structure and composition at sites between seasons, which were significantly associated with the physical and chemical parameters characterizing these sites, with higher abundance of

tolerant families, such as Chironomidae (Chi), Leptoceridae (Leptc), and Baetidae (Bae).

The presence of glaciers at the sampling sites can also have a significant impact on the benthic macroinvertebrate community composition. As mentioned in previous studies (Khamis et al. 2014; Niedrist and Füreder 2017), the meltwater from glaciers can introduce sediment and alter the temperature and nutrient levels of the water, which in turn affects the distribution and abundance of these communities. Furthermore, the seasonal variation in glacier melt can lead to fluctuations in water flow and substrate stability, further influencing the community structure of benthic macroinvertebrates in these ecosystems. During the wet season, intense rainfall and increased flow cause sediment transport and physical disturbance, leading to habitat homogenization and reduced stability (Jacobsen et al. 2008b; Quesada-Alvarado et al. 2020; Sun et al. 2024). In contrast, during the dry season, lower discharge and higher nutrient retention promote more heterogeneous habitats and greater biological diversity (Shen et al. 2024; Sun et al. 2024). These seasonal fluctuations also affect food availability and life cycles, influencing the abundance and composition of aquatic taxa (Chi et al. 2017).

Most of the sites in our study showed higher abundance and richness of macroinvertebrates in the dry season. Contrary to this, some sites with direct influence of glacier melt water (e.g. 3, 6, 13 and 16) showed the opposite trend, presenting in the wet season higher abundance and richness of macroinvertebrates that were also tolerant to contamination, such as Empididae.

The CCA Type-2 results indicated that toxic metals, such as Pb, Al, V, Cr, Mn, Fe, Co, Ni, and Cu, had a significant impact on the composition of benthic macroinvertebrate communities in the tributaries of the Rio Santa. This analysis identified dipterans, hemipterans, trichopteran, and tubificidans as metal- and acid-tolerant groups primarily present at ARD influenced sites, while more sensitive trichopteran and plecopterans were associated with more alkaline sites (pH >6). It is difficult to attribute an isolated impact of a specific variable (e.g. metal and nutrient concentrations, pH, discharge, etc.) on the shift of the community assemblage. Our findings suggest that the broad chemical composition of tributaries influenced by metal leaching from glaciers has an important effect on the community composition of macroinvertebrates, showing a higher abundance of more tolerant taxa (e.g., Chironomidae, Baetidae and Simuliidae), particularly in the dry season, when reduced discharge and dilution capacity may increase the concentration of metals and ions derived from glacial and groundwater sources.

Other studies, such as those by Loayza-Muro et al. (2010, 2014b) and Courtney and Clements (2000), have assessed the effect of increased acidity and potentially toxic trace metal concentrations in high Andean and temperate streams, respectively, showing a resultant reduction in the abundance and species richness of pollution-sensitive macroinvertebrates and a significant increase and change in the composition of more tolerant species (Gerhardt et al. 2004; Loayza-Muro et al. 2014a). These changes in community composition are driven by the influence of highly correlated metals, such as Al, As, Mn, Pb, and Zn, and are further exacerbated by other environmental factors, including geographical, hydrogeomorphological, and physical and chemical factors (Loayza-Muro et al. 2010; Qu et al. 2010; Yanygina 2017).

4.3. Functional feeding groups composition

Seasonal variations in river flow conditions significantly influenced the ecological dynamics of macroinvertebrate abundance and the composition of functional feeding groups (FFGs). During the dry season, characterized by lower water levels and reduced river discharge, the habitat undergoes homogenization, facilitating increased colonization opportunities for macroinvertebrates. Consequently, this period exhibited higher richness and abundance of macroinvertebrates (Fig. 3) and favoured certain FFGs over others. Specifically, collector-gatherers, predators, and collector-filterers showed a higher abundance during the dry season (Fig. 6), indicating a preference for different microhabitats formed due to decreased flow. In alpine streams, the ongoing glacier retreat may influence the variability of habitats with long-term implications on the macroinvertebrates feeding niche (Di Cugno and Robinson 2017).

During the dry season, collector-gatherers (CG) were dominant, followed by collector-filterers (CF). This dominance is likely related to the increased availability of fine particulate organic matter (FPOM) from decomposing periphyton and sediment accumulation, as well as structurally complex habitats that enhance organic matter retention (Gholizadeh and Heydarzadeh 2019). Similar patterns have been reported in other tropical and subtropical freshwater systems experiencing comparable stressors, where collector-gatherers consistently dominate benthic macroinvertebrate assemblages (Masese et al. 2014; Villada-Bedoya et al. 2017; Mangadze et al. 2019; Villamarín et al. 2020; Aguilar Silvano and De Souza Reátegui 2022; Akamagwuna et al. 2022). Likewise, in glacier-fed catchments of the tropical Andes, environmental filtering by altitude and metal contamination has been shown to shape macroinvertebrate communities (Andino et al. 2021). In these systems, altitude and hydrological dynamics directly influence the composition and distribution of macroinvertebrates. In glacier-influenced areas, the combined stress of high solar radiation and the presence of naturally dissolved metals reduce taxa richness (Loayza-Muro 2014; Garcia et al. 2025). In addition, food availability is limited in high Andean zones because primary productivity decreases with altitude (García-Ríos et al. 2020). In higher-altitude sites, increased CG abundance suggests that mountain streams are often dominated by taxa that feed primarily on FPOM, due to the naturally lower availability of periphyton and coarse particulate organic matter (CPOM) in these ecosystems (Tomanova et al. 2007).

During the wet season, piercers exhibited the second highest abundance among FFGs (Fig. 6). This can be attributed to a notable rise in the population of Hydroptilidae, which primarily feed on filamentous algae or periphyton known to grow especially during this season due to an increase in nutrient transport (Springer et al. 2010). However, our findings showed higher nutrient levels (Suppl. material 2), but a smaller abundance of piercers during the dry season, suggesting that this group may be influenced by other factors other than food sources.

Shredders and scrapers, the less abundant FFG, exhibited particularly low abundances during both seasons (Fig. 6). In highland regions, characterized by cold streams and intense UV radiation, alongside less-developed vegetation, the scarcity of these groups can be attributed to several factors, including diminished leaf litter quantity, decreased palatability, and reduced periphyton (Tomanova et al. 2007). However, despite their low abundance, there was an

increase in the population of shredders and scrapers during the wet season. This increase can be attributed to an increasing availability of allochthonous detritus, particularly CPOM (Fierro et al. 2015).

4.4. FFG and environmental variables

The positive correlation between the abundance of collector-gatherers and dissolved silicon highlights the relationship between benthic macroinvertebrates and sediment dynamics (Fig. 7A). Chironomidae, a primary family within the collector-gatherer group, has a significant influence on sediment conditions and metal accumulation, playing a crucial role in shaping the ecological landscape of aquatic environments (Matisoff et al. 1985; Pastorino et al. 2020). Their active burrowing and fluid irrigation activities alter sediment conditions and facilitate nutrient transport across the sediment-water interface. Studies have shown that Chironomidae influence nutrient concentrations, including nitrate, bicarbonate, and silica within sediments, as well as their alkalinity and the distribution of iron and silicon (Matisoff et al. 1985). Environmental factors such as water temperature and chemistry, channel stability, and substrate characteristics play crucial roles in determining the distribution of chironomids. Certain chironomid species, like those of the *Diamesa* genus, demonstrate great adaptation to glacial conditions, characterized by a high channel instability and variable discharge, sheer rock and steep slopes, increased suspended solids and total phosphorus levels, and low conductivity, temperature and dissolved silica content (Lencioni and Rossaro 2005).

Pastorino et al. (2020) indicate that collector-filterers are influenced by concentrations of Cu and Mo. These organisms are exposed to metals through their feeding behavior, which involves filtering water through their gills. Our findings show that collector-filterer abundance was significantly associated with both Ti and V (Fig. 7B), displaying a negative relationship with Ti and a positive one with V. Notably, filter feeder families, such as Hydropsychidae and Simuliidae, have been recognized as significant bioindicators of metal pollution due to their tolerance to heavy metals, such as Zn, Cu, Cd, Tl, and Sb, and their ability to accumulate them (Solà and Prat 2006).

Our results revealed that for predators, Na, Mg, P-PO₄, as well as temperature and pH, emerged as significant predictors, with Fe exhibiting a negative correlation (Fig. 7C). These findings are consistent with prior research, indicating the susceptibility of predators to changes in nitrates concentrations and temperature, particularly in habitats characterized by high flow rates and adequate oxygen levels (El Yaagoubi et al. 2023). Predators have also shown great sensitivity to pollution and the accumulation of Ba, Hg, Li, Se, V, Ti, and Zn, likely acquired through food consumption (Pastorino et al. 2020; Makumbe et al. 2022).

Shredder abundance was primarily influenced by uranium (U) and negatively correlated to EC (Fig. 7D), as described by Masese et al. (2014) together with high turbidity. In Andean rivers, water turbidity tends to increase notably during the rainy season (Suppl. material 2) due to suspended and dissolved particles, which may influence EC levels and limit the development of microalgae and other photosynthetic organisms (Carrasco-Badajoz et al. 2022).

Scrapers were positively influenced by N-NO₃ (Fig. 7E) concentrations, which can be attributed to their role in grazing on periphyton (biofilm) communities that

depend on this nutrient (Ramírez and Gutiérrez-Fonseca 2014; Kilroy et al. 2020). Another study indicates a positive correlation between scrapers and elevated total dissolved solids, which may be linked to fluctuations in algal assemblages (Mangadze et al. 2019). As scrapers graze on this nutrient-enriched periphyton, their abundance increases, leading to the observed positive correlation with nitrate concentrations. However, since periphyton serves as a major sink for metals, scrapers can accumulate them in higher concentrations compared to other functional feeding groups (Landers et al. 2019; Pastorino et al. 2020), which may be significant in Andean streams influenced by a rich geological background.

Our results showed a negative correlation between DO and piercers, which may be related to habitats with low water flow and turbulence. Other studies in Andean areas indicate that pH and radiation can influence their distribution and abundance with Hydroptilidae showing preference for alkaline conditions (Loayza-Muro 2013; Everaert et al. 2014; Aguilar Silvano and De Souza Reátegui 2022). Furthermore, Everaert et al. (2014) reported that this family was negatively influenced by conductivity, although no significant correlations were found with DO levels.

5. Conclusions

This study highlights the cascading effects of climate-induced glacier retreat on the hydro-chemical dynamics and benthic macroinvertebrate communities in high-altitude Andean rivers. The intensification of acid rock drainage (ARD) has led to a pronounced increase in potentially toxic trace metal concentrations and water acidification, creating a “toxic or treat” scenario that differentially impacts aquatic biodiversity. Our findings show that glacier loss promotes shifts in macroinvertebrate community structure by altering flow regimes, reducing habitat heterogeneity, and increasing metal concentrations through enhanced weathering and lower dilution. These changes simplify stream habitats and limit food resources, favouring tolerant taxa (e.g., Chironomidae, Baetidae) over sensitive functional feeding groups such as shredders and scrapers.

The seasonal variability observed in both physical and chemical parameters and macroinvertebrate assemblages underlines the dynamic nature of these ecosystems. The dry season, characterized by reduced discharge and the increased retention of fine organic matter, supported greater macroinvertebrate abundance and diversity. In contrast, the wet season exhibited more fragmented habitats and shifts in functional feeding group composition, particularly with an increase in piercers, likely due to greater availability of periphyton resources. This seasonal influence underscores the need for long-term monitoring to capture the full extent of climate-driven ecological shifts in glacier-fed streams.

The significant relationships between specific water chemistry variables and macroinvertebrate community composition demonstrate the significant role of hydro-chemical changes in shaping aquatic ecosystems. The positive association of collector-gatherers with silicon and predators with phosphates and sodium suggests that glacier-derived sediments and nutrient availability play crucial roles in structuring benthic food webs. Additionally, the negative impact of dissolved oxygen on piercers and the significant influence of sulphates, iron, and nitrates on scrapers highlight the complexity of biogeochemical interactions in these streams.

Our study contributes to the growing body of evidence that climate change-driven deglaciation is fundamentally altering freshwater ecosystems in the tropical Andes. The ongoing exposure of sulphide-rich bedrock, coupled with increasing precipitation variability and warming temperatures, suggests that ARD effects will likely intensify in the coming decades. These changes pose significant challenges for aquatic biodiversity conservation and water quality management, particularly for downstream human populations relying on these water sources.

Future research should focus on understanding the long-term resilience of benthic macroinvertebrate communities to these environmental stressors and exploring potential mitigation strategies, such as watershed restoration and pollution control. Given the unique biogeochemical and ecological conditions of the Cordillera Blanca, site-specific conservation and adaptation strategies will be necessary to mitigate the adverse effects of glacier retreat on freshwater ecosystems.

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Additional information

Conflict of interest

No conflict of interest was declared.

Ethical statement

No ethical statement was reported.

Use of AI

No use of AI was reported.

Funding

This research was funded by Fondo Nacional de Desarrollo Científico, Tecnológico y de Innovación Tecnológica (FONDECYT-Peru), under the financial scheme E031-2018-01-NERC "Glacier Research Circles, Contract N° 006 - 2019-FONDECYT". United Kingdom collaboration was funded by the Newton Paulet Fund, CASCADING impacts of Peruvian glacier Shrinkage on biogeochemical Cycling and Acid Drainage in Aquatic ecosystems (CASCADA) grant NE/S013288/1 awarded to Jemma Wadham..

Author contributions

Conceptualization: JW, RLM. Methodology: FLM, MM, JM, RLM. Formal analysis: FLM, VAS, DVP. Resources: RLM, JW, MM. Data Curation: FLM, VAS, DVP. Writing - Original draft: FLM, VAS. Writing - Review and Editing: FLM, RLM, MM, JW. Visualization: VAS, DVP. Supervision: RLM, JW. Project administration: RLM, JW. Funding Acquisition: RLM, JW..

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

Supplementary material 1

Principal component analysis

Authors: David Valqui-Peña

Data type: pdf

Explanation note: A second Principal component analysis was performed excluding those sites where no macroinvertebrates were found to use the new components as variables for a subsequent canonical correspondence analysis (CCA).

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Link: <https://doi.org/10.3897/jbgs.e166425.suppl1>

Supplementary material 2

Physicochemical characteristics of sampling sites in both seasons (dry and wet)

Authors: Fiorella La Matta Romero

Data type: table

Explanation note: Summary of field and laboratory physicochemical measurements across all sampling sites for dry and wet seasons. Values are reported per site and season and form the basis of the statistical and multivariate analyses conducted in this study.

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Supplementary material 3

Principal component analysis 1 (PCA1) loadings

Authors: David Valqui-Peña

Data type: table

Explanation note: PCA loadings are shown for the first four principal components (PC1–PC4). Values highlighted in red correspond to the highest absolute loading for each variable, indicating the principal component where that variable has its strongest contribution and interpretative relevance.

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