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Research article

Co-correspondence analysis of fish and macroinvertebrate assemblages in relation to environmental variables in the Bheri and Babai river systems, Nepal

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Abstract

This study investigates the co-occurrence patterns of fish and macroinvertebrate assemblages in the Bheri and Babai rivers of Western Nepal and their relationships with environmental variables. Sampling was conducted at 10 sites encompassing four seasons in 2018 using electrofishing and standardized macroinvertebrate collection protocols. The physico-chemical parameters and substrate composition were recorded at each site. The seasonal abundance data from all sites for both fish and macroinvertebrates were pooled and used in the symmetric Co-correspondence Analysis (CoCA). The CoCA revealed a very strong shared community structure between fish and macroinvertebrates, accounting for more than 99% of the total shared variance in both rivers (Bheri: 99.6%; Babai: 99.7–99.8%). Within this shared structure, the first two CoCA axes captured approximately 57% of the shared variation, reflecting clear ecological gradients in each system. The Envfit analysis identified sulphate, electric conductivity (EC), and temperature as significant drivers in the Bheri River system, while EC and substrate heterogeneity particularly boulder and gravel, were most influential in the Babai River system. These findings suggest that the Bheri River system assemblages are primarily structured by water chemistry, whereas the Babai River system is shaped by physical habitat complexity. The strong biotic congruence between fish and macroinvertebrates highlights their potential as complementary bioindicators, offering an integrated framework for biodiversity assessment and management in Nepalese river ecosystems.

Keywords: Bioindicators; Environmental variables; Fish assemblage; Macroinvertebrates; River systems

1 | Introduction

Rivers are dynamic and complex natural systems shaped by precipitation and gravity. They play vital roles in sculpting landscapes, providing essential ecosystem services and supporting fish, aquatic insects, amphibians, and riparian vegetation uniquely adapted to riverine environments (Khosrovyan 2024). Through the continuous processes of erosion and deposition, rivers form diverse physical features such as floodplains, wetlands, and braided channels that serve as critical habitats for a wide range of organisms (Lane et al. 2018). Physical habitat, including riffles, pools, and submerged vegetation are crucial to support species across different life stages of aquatic species (Calderon & An 2016).

The ecological integrity of river system depends on the interplay of physical, chemical, and biological factors. The water quality parameters such as temperature, pH, dissolved oxygen, and nutrient concentrations directly influence the composition and functioning of aquatic communities (Jaffar et al. 2020). Deviations from these optimal conditions caused by altered flow regimes, habitat degradation, or climate-induced temperature rise can disrupt nutrient cycling, energy flow, and species interactions (Rose et al. 2023) and result in reduced biodiversity and shift in community structure, as certain species are favored while others decline (Nimma et al. 2025). Additionally, habitat fragmentation and degradation may isolate populations, reduce genetic diversity, and elevate the risk of local extinctions (Yang et al. 2025).

Among the physical drivers, substrate composition plays a foundational role in structuring riverine habitats. The texture and composition of the riverbed ranging from organic matter like leaf litter to mineral substrates such as sand, gravel, and cobble create a mosaic of microhabitats within the river ecosystems (Bastian et al. 2007; Zhu et al. 2023). A coarse substrate offers stable surfaces for algal growth, spawning grounds for fish, and refuges for macroinvertebrates whereas fine sediments support different communities adapted to softer substrates (Jones et al. 2012). This variability not only shapes species distribution patterns but also influences oxygen availability, sediment transport, and overall habitat quality (Greig et al. 2005; Levin & Gage 1998).

Fish and macroinvertebrates are integral components of freshwater ecosystems and respond sensitively to environmental changes, such as fluctuations in temperature, oxygen availability, and habitat complexity (Khaliq et al. 2024; López-López & Sedeño-Díaz 2014). These organisms are not only indicators of ecological health but also perform essential ecological functions (Herman & Nejadhashemi 2015). The temperature fluctuations, for example, can impair growth, reproduction, and survival of fish, while also altering development rates and emergence timing in macroinvertebrates (Volkoff & Rønnestad 2020; Bonacina et al. 2023). Similarly, low dissolved oxygen (DO) levels in water, frequently caused by pollution and warming, negatively impact sensitive aquatic species like trout and salmonids, as well as pollution-intolerant macroinvertebrates such as mayflies, stoneflies, and caddisflies (Connolly et al. 2004; Friberg et al. 2010). These organisms are particularly vulnerable to low DO because they require sufficient oxygen for respiration (Chapman et al. 2004).

The habitat structure is also equally critical. Fish require diverse habitat types for shelter, spawning, and foraging; which are often disrupted by sedimentation, flow alteration, and barriers like dams (ADB 2018; Chen et al. 2023). Macroinvertebrates, too, show strong preferences for specific substrate types, with different species adapted to gravel, cobble, or fine sediments (Bylak & Kukuła 2022; McManamay et al. 2013). The lower habitat heterogeneity, or decrease in the diversity of habitat types, is typically associated with a reduction in species richness and functional diversity within both fish and macroinvertebrate communities (de Sá Ferreira Lima et al. 2025).

Ecologically, fish and macroinvertebrates occupy distinct yet interconnected roles. Macroinvertebrates contribute to organic matter decomposition and nutrient cycling, serving as key links in the aquatic food web and as primary prey for many fish species (Macadam & Stockan 2015). Fish, particularly predatory fish, play a vital role in regulating prey populations and maintaining the stability of aquatic ecosystems through a process called trophic cascade. By consuming smaller fish and other organisms, they can significantly influence the abundance of their prey, which in turn affects populations further down the food chain (Whitfield et al. 2024). Because of their ecological complementarity and differing sensitivity, both groups are widely used as bioindicators. The fish typically reflect long-term and catchment scale changes, while macroinvertebrates respond to more immediate, localized stressors (De Carvalho et al. 2025). Together, they provide a robust and integrated view of freshwater ecosystem health.

Previous studies have reported variable concordance between fish and macroinvertebrate assemblages, reflecting shared responses to environmental gradients (e.g., water quality, habitat structure, flow regime) alongside context dependent differences linked to life-history traits and habitat use (Larsen et al. 2012; Paavola et al. 2006). In Nepal, river ecosystems are increasingly affected by hydropower development, urban and agricultural pollution as well as climate variability with consequent alteration of flow regimes, water chemistry, and substrate conditions (ADB 2018; Suwal et al. 2020). Yet, considering the rich network of rivers and water-based infrastructural developments in pipeline, ecological assessments remain limited, particularly those using integrated, multi taxa approaches. Fish and macro-invertebrates are established bioindicators due to their ecological interdependence and differing sensitivities, but few Himalayan studies quantify their co-variation using multivariate methods. This study applies Co-correspondence analysis (CoCA) to evaluate shared community responses across different sites, identify key environmental drivers (water quality and substrate), and assess whether these drivers differ between glacial and rain-fed river systems. By linking biotic congruence with environmental controls, the study provides an integrated basis for river bioassessment, conservation, and management in Nepal.

2 | Materials and methods

2.1| Study area

This study was conducted in the Bheri and Babai rivers and their tributaries in western Nepal. A total of 10 sites were sampled covering upstream and downstream sections relative to the Bheri water diversion and release to the Babai River (Fig. 1). Specifically, three upstream tributaries were sampled above the Bheri water-diversion site, and three upstream sites (two tributaries and one mainstem) were sampled above the water release site at the Babai. In addition, two downstream sites were selected from each river system.

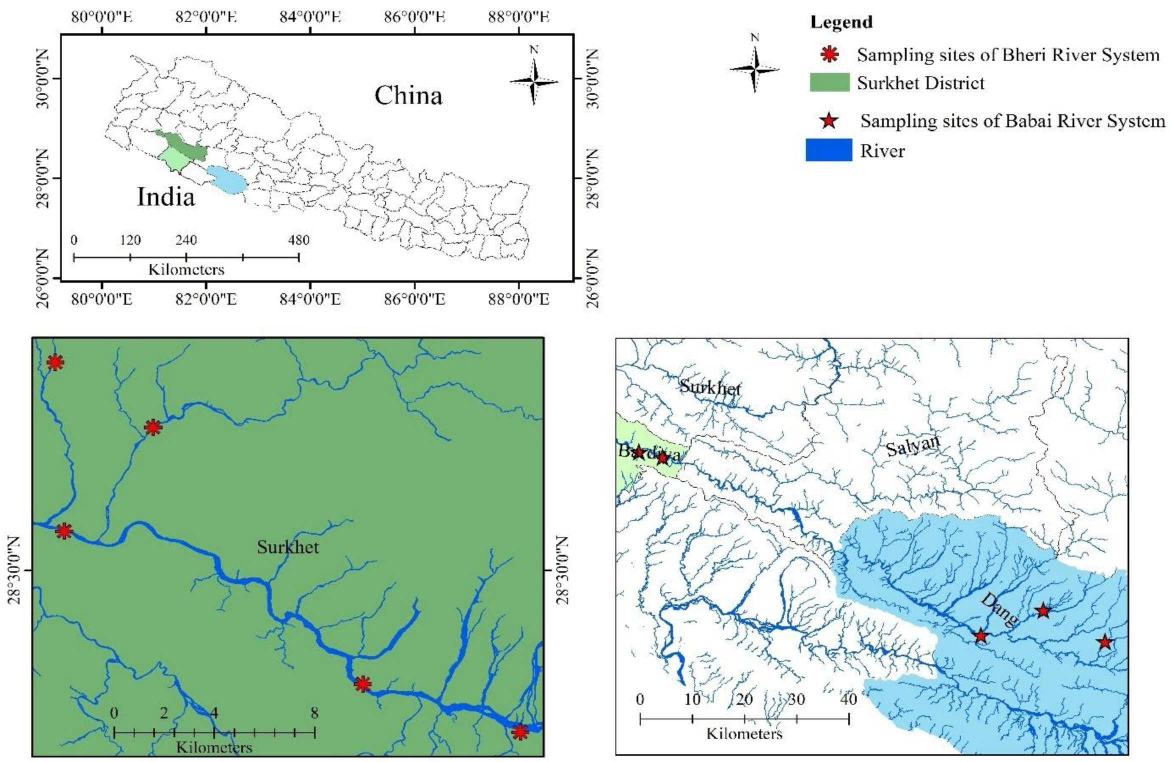

Figure 1. Location map of the study area inside Nepal (upper); and sampling points at the Bheri and Babai River systems (lower).

2.2| Field methods

2.2.1| Fish sampling

Fish sampling was conducted in 2018 across four seasons. Electrofishing was performed using the wading method (Jha, 2006), with two times 20-minute runs along approximately 100 m reaches at each site, under permission from the Department of National Parks and Wildlife Conservation (DNPWC) (Ref. No. 1376-074/075). Fish were identified in the field using standard references (Shrestha 1981, 1994; Shrestha 2019), photographed, and released. The representative specimens were preserved in 70% ethanol and brought to Kathmandu University for further confirmative analysis following standard literatures (Froese & Pauly 2019; Jayaram 2012; Talwar & Jhingran 1991) and have been deposited as voucher specimens at the Central Department of Zoology, Tribhuvan University for record.

2.2.2| Macroinvertebrates sampling

Macroinvertebrates were sampled using a multihabitat approach (Barbour et al. 1999), targeting riffles, pools, and runs. A 250 µm mesh net was used to collect organisms by disturbing the substrate. At each site, 50–100 m stretch was sampled with 10 jabs forming a composite sample. All samples were preserved in 70% ethanol for laboratory analysis and brought to the laboratory at Kathmandu University for further analysis. Macroinvertebrates were sorted and identified to family level using standard references (Dudgeon 1999; Merritt & Cummins 1996).

2.2.3| Physico-chemical parameters

The on-site measurements of pH, dissolved oxygen (DO), electrical conductivity (EC), total dissolved solids (TDS), and temperature were taken in triplicate using a Hanna HI98193 multi-parameter probe. At each site, one liter water samples were collected in high density polyethylene (HDPE) bottles, stored at 4°C, and brought to the laboratory at Kathmandu University for further analysis. Water samples were analyzed for major cations and anions following APHA (2005). The findings of major ions analyses is described in Khatri et al. (2023).

2.2.4| Substrate sampling

Substrate composition in each selected sites of both river systems was estimated using the Transect Method (Fig. 2). A 100-meter stretch of the riverbed was selected, and sampling was conducted at 20-meter intervals along rivers, and five points were selected across the river width, resulting in a total of 25 sampling points per site (Fig 2). At each point, the dominant substrate type was recorded following Wentworth (1922) and Cummins (1962). In large or fast flowing river sections where transect sampling was not feasible, visual estimates of substrate composition were made. To ensure consistency and reduce observer's bias, all visual assessments were performed by the same individual throughout the sampling. Habitats were classified into six categories based on the dominant substrate type observed at each site viz Cobble, Boulder, Gravel, Pebble, Pebble–Gravel, and Cobble–Pebble.

2.3| Data analysis

Seasonal abundance data of all seasons from all sites for fish and macroinvertebrate taxa were prepared for each river system using datasets reported in Khatri et al. (2022) and Khatri et al. (2024). Co-correspondence analysis (CoCA) was applied to explore shared community structures by maximizing the covariance between site scores of both groups. This method is particularly ideal for datasets involving two biological communities sampled at the same locations. Biplots were generated using contribution scaling to visualize taxa with strong influence on the ordination axes (ter Braak & Schaffers 2004). Furthermore, to aid ecological interpretation of the ordination results, selected environmental variables were passively fitted onto the CoCA ordination using the envfit() function.

All statistical analyses were conducted in R (version 4.3.3; R Core Team) using RStudio (version 2024.12.1 Build 563). The vegan package (version 2.6-6.1) was used for ordination analyses, VIF calculation, environmental fitting (envfit), permutation tests, and the cocorresp package (version 0.4-2) was used for Co-correspondence Analysis. Symmetric CoCA was used to assess

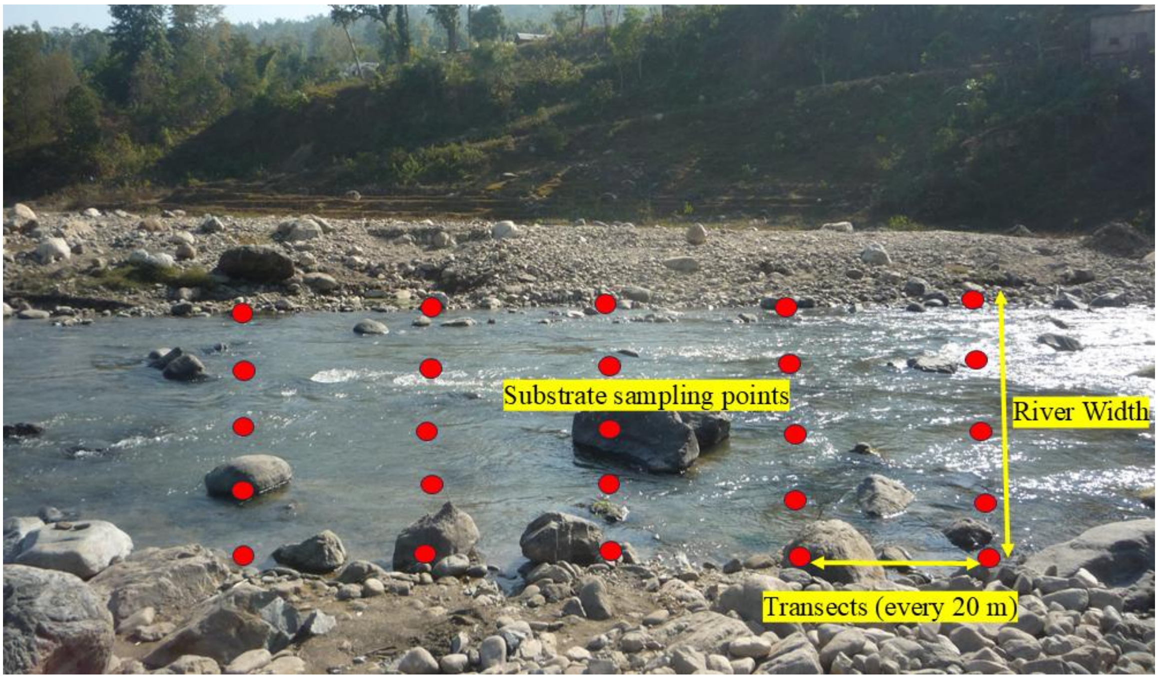

Figure 2. Schematic diagram illustrating substrate estimation using the transect method

shared community structure between fish and macroinvertebrates in the Bheri and Babai river systems. CoCA maximized covariance between fish and macroinvertebrate site scores, and taxa with higher contributions were visualized in ordination biplots.

3 | Results

In the Bheri River system, 32 fish taxa and 42 macroinvertebrate taxa were included, while 42 fish and 49 macroinvertebrate taxa were included for the Babai River system. Ordination diagrams for the two river systems are presented in Figures 3 and 4, showing site and species scores for both fish and macroinvertebrate assemblages. CoCA in the Bheri system accounted for 99.6% of the total shared variance between datasets. The first two axes explained 38.94% and 17.97% of this variation, with remaining variation distributed among higher axes. Fish and macroinvertebrate site scores showed high correlations on the first two axes (Axis 1: r = 0.887; Axis 2: r = 0.922). The Predicted Residual Error Sum of Squares (PRESS) statistic was 2.33, indicating moderate predictive performance in cross-validation. A permutation test indicated that neither the first axis nor all axes combined were statistically significant (first axis: p = 0.176; all axes: p = 0.158).

Fish species scores showed separation along both axes. On Axis 1, *Schizothorax progastus*, *Schistura savona*, and *Glyptothorax trilineatus* were positioned toward the positive end, whereas *Cabdio jaya* and *Tariqilabeo macmahoni* were positioned toward the negative end. On Axis 2, *Channa punctata* and *Amblyceps mangois* occurred toward the positive side, and *Opsarius bendelisis* and *Pseudecheneis sulcata* toward the negative side. Macroinvertebrate scores showed similar separation patterns. On Axis 1, Potamanthidae and Macromiidae were positioned toward the positive side, whereas Arthropleidae, Psephenidae, and Euphaeidae were positioned toward the negative side. On Axis 2, Hydropsychidae and Chironomidae positioned toward positive values, and Ephemerellidae and Elmidae toward negative values.

Table 1. Envfit results showing correlations of environmental and substrate variables with CoCA axes, including r^2 and *p*-values of the Bheri River system

Environmental Variables	COCA 1	COCA 2	r^2	p
Magnesium (mg/L)	-0.159	0.987	0.272	0.113
Chloride (mg/L)	-0.992	-0.124	0.179	0.221
Sulphate (mg/L)	0.761	-0.648	0.435	0.009
Nitrate (mg/L)	-0.991	0.130	0.083	0.527
Total alkalinity (mg/L)	-0.699	0.715	0.139	0.309
pH	-0.564	-0.826	0.166	0.260
DO (mg/L)	0.680	0.733	0.199	0.215
EC (µS/cm)	-0.261	0.965	0.423	0.020
TDS (mg/L)	-0.136	0.991	0.333	0.062
Temperature (°C)	0.153	0.988	0.344	0.027
Boulder	-0.212	-0.977	0.151	0.339
Cobble	0.782	-0.623	0.004	0.973
Cobble-Pebble	0.797	0.604	0.117	0.285
Gravel	0.383	-0.924	0.008	0.898
Pebble- Gravel	-0.244	0.970	0.269	0.153

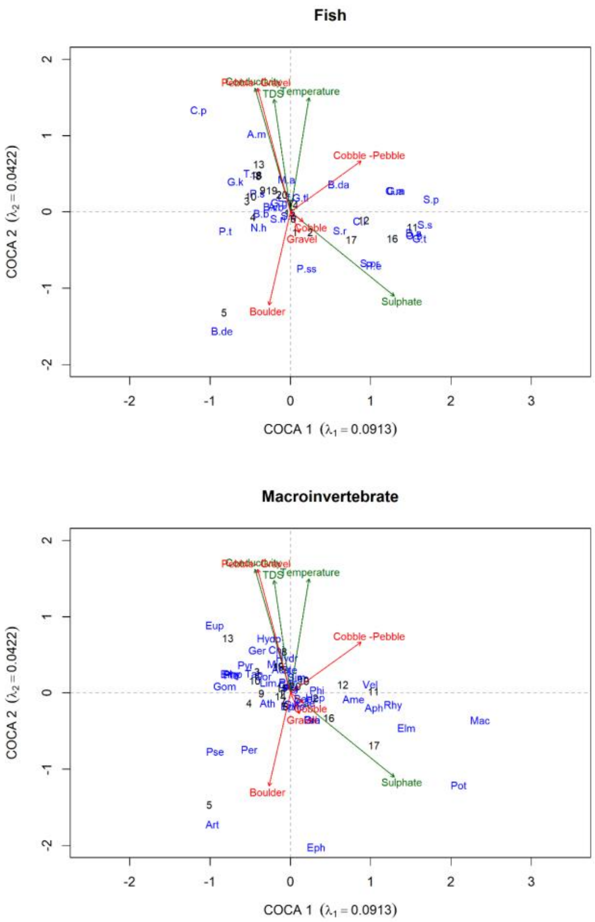

Figure 3. Corresponding biplots for fish and macroinvertebrates in the co-correspondence analysis of the Bheri River system

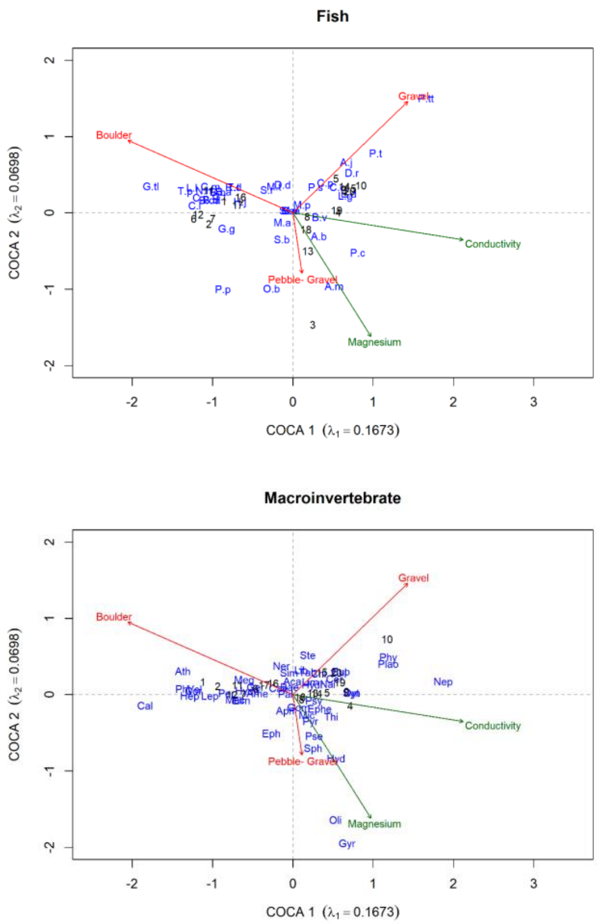

Figure 4. Corresponding biplots for fish and macroinvertebrates in the co-correspondence analysis of the Babai River system

Envfit analysis identified sulphate, conductivity, and temperature as the variables most strongly aligned with the ordination (Table 1). No substrate variable was statistically significant; pebble–gravel produced the highest non-significant fit, whereas boulder, cobble–pebble, cobble, and gravel showed lower fits.

In the Babai system, 99.7% of variation in the fish dataset and 99.8% in the macroinvertebrate dataset were shared under the CoCA model. The first two axes explained 40.35% and 16.84% of this shared variation, with remaining variation distributed among higher axes.

Fish and macroinvertebrate site scores again showed high correlations on the first two axes (Axis 1: r = 0.92; Axis 2: r = 0.86). The PRESS statistic was 2.71, indicating moderate predictive performance. Permutation testing indicated statistical significance for the first axis only (p = 0.0001), while cumulative axes showed non-significant values.

Fish scores showed marked separation. On Axis 1, *Pethia ticto* and *Puntius terio* were positioned toward the positive side, while *Tor putitora* and *Glyptothorax telchitta* were located toward the negative side. On Axis 2, *Cabdio jaya* and *Danio rerio* were positioned toward the positive side, whereas *Xenentodon cancila* and *Opsarius bendelisis* plotted toward the negative side.

Macroinvertebrates exhibited analogous separation. On Axis 1, Physidae and Planorbidae were positioned toward positive values, whereas Calopterygidae and Nepidae were positioned toward negative values. On Axis 2, Stenopsychidae and Nereididae were positioned on the positive side, and Gyrinidae and Brachycentridae on the negative side.

Envfit analysis for the Babai River system identified conductivity as the only statistically significant water chemistry variable associated with the ordination (r^2 = 0.342, p = 0.033). TDS showed a moderate but non-significant fit (r^2 = 0.225, p = 0.113) (Table 2). Among substrate variables, boulder and gravel displayed strong and statistically significant fits, while pebble–gravel showed a weak, non-significant association.

Table 2. Envfit results showing correlations of environmental and substrate variables with CoCA axes, including r^2 and *p*-values of the Babai River system

Environmental Variables	COCA 1	COCA 2	r²	p
Magnesium (mg/L)	0.515	-0.857	0.264	0.076
Potassium (mg/L)	0.292	0.956	0.010	0.908
Sulphate (mg/L)	-0.128	-0.992	0.003	0.974
Nitrate (mg/L)	0.644	0.765	0.046	0.714
pH	-0.331	-0.944	0.155	0.237
DO (mg/L)	-0.134	-0.991	0.039	0.707
EC (μS/cm)	0.987	-0.163	0.342	0.033
TDS (mg/L)	0.972	0.234	0.225	0.113
Temperature (°C)	-0.034	0.999	0.040	0.710
Boulder	-0.908	0.419	0.941	0.001
Gravel	0.700	0.714	0.766	0.001
Pebble- gravel	0.141	-0.990	0.117	0.236

4 | Discussion

The symmetric CoCA demonstrated a very strong shared community structure between fish and macroinvertebrate assemblages in both river systems, indicating clear ecological gradients and a high degree of biotic concordance. This suggests that the two groups respond similarly to environmental variation and shift in parallel as environmental conditions change (Rubio-Gracia et al. 2022). For example, substrate types that support particular fish species also tend to favor specific macroinvertebrate taxa (Munyai et al. 2025). The close correspondence between site scores further indicates that one assemblage could potentially serve as a proxy for the other in biomonitoring, improving efficiency in ecosystem health assessment (Infante et al. 2009; Kaushal et al. 2018).

The cross validation indicated that the ordination models had moderate predictive strength, suggesting that major environmental variables accounted for a meaningful proportion of the observed community patterns. The predictability was slightly stronger in the Bheri River system, implying that its community structure is more consistently shaped by the measured variables than in the Babai River system. However, in both cases some variation remained unexplained, likely reflecting unmeasured influences or stochastic ecological processes. Permutation outcomes pointed to clearer environmental structuring in Babai River system, while patterns in the Bheri River system appeared to involve more complex gradients and potential influences not captured in the current dataset (Legendre & Legendre 2012).

The taxa scores showed clear contrasts along the main community gradient in the Bheri River system, separating small cyprinids and lentic tolerant gastropods from rheophilic fish and current dependent macroinvertebrates. The former group typically favors slower currents, finer substrates and elevated nutrient levels (Merritt et al. 2019; Shrestha 2019), while rheophilic taxa such as *Tor* and *Glyptothorax*, together with flow dependent insect families, are associated with well oxygenated reaches, coarse substrates and lower nutrient loads (Allan & Castillo 2007; Dudgeon 1999; Poff & Allan 1995). These patterns reinforce the interpretation that flow, substrate composition and water quality are major determinants of community structure (Legendre & Legendre 2012; ter Braak & Šmilauer 2012).

In the Babai River system, fish taxa associated with muddy, shallow or slow flowing habitats formed a clear contrast against taxa characteristic of clearer and faster waters. Macroinvertebrate assemblages also showed comparable divisions, with families typical of moderately to fast flowing, oxygen rich channels separating from those favouring stable coarse substrates or lower disturbance conditions (Dudgeon 1999; Rosenberg & Resh 1993). Additional contrasts reflected to respiratory adaptations; air breathing groups tolerant of reduced oxygen diverged from gill breathing taxa sensitive to depletion and associated with cooler, well oxygenated flows. Together, these patterns highlight the combined influence of hydrological regimes, substrate composition and oxygen availability as dominant ecological drivers in the Babai River system.

Sulphate as a major correlate of community structure in the present study suggests a strong role for ionic composition and nutrient loading. Elevated sulphate may be derived from natural weathering or human inputs such as agricultural runoff and wastewater (Chapman 1996; Wetzel 2001) and can influence osmoregulation and habitat suitability (Camargo & Alonso 2006). Conductivity showed a comparable influence, consistent with its role as an integrative indicator of dissolved ions linked to mineral weathering, groundwater contributions and anthropogenic disturbance (Allan & Castillo 2007), and its importance has been documented in other Himalayan rivers as well (Dass et al. 2025; Rai et al. 2025). Temperature emerged as another influential factor, shaping metabolic processes, growth and life cycle timing (Bonacina et al. 2023). In snow fed Himalayan systems, sharp longitudinal temperature gradients from cold headwaters to warmer downstream sections create predictable transitions in aquatic assemblages, reflecting reduced glacier influence and increased thermal inputs downstream (Waldock et al. 2019).

In the Bheri River system, substrate categories showed weaker associations with community structure, suggesting that water chemistry plays a more dominant role in shaping assemblages than habitat heterogeneity. This reflects patterns seen in other large

Himalayan rivers, where high flows and sediment transport reduce the influence of substrate mosaics (Sørensen & Pedersen 2021). In contrast, the Babai River system exhibited stronger association with substrate complexity, particularly where coarse materials provide refuge, feeding surfaces and hydraulic variability (Allan & Castillo 2007; Beatty et al. 2020). These river specific differences likely stem from contrasts in geomorphology, origin, hydrology and disturbance regimes. Accordingly, management priorities diverge, maintaining water quality integrity is especially critical in the Bheri River system, whereas conserving substrate diversity and habitat complexity is key in the Babai River system.

5 | Conclusions

A strong fish and macroinvertebrates association was observed in both the rivers, consistent with their roles in river food webs, with fish functioning as top predators and macroinvertebrates linking primary producers to higher trophic levels. The taxa driving patterns differ between systems: the Bheri River assemblages reflect adaptations to high dissolved oxygen and cooler water, whereas the Babai River assemblages are suited to low flow, warmer, and higher TDS conditions reflecting river types in terms of environmental regimes.

In the Bheri River system, community structure is shaped primarily by water chemistry, especially ionic composition, nutrient loading, and temperature while in the Babai River system, substrate heterogeneity dominates, reflecting geomorphological, hydrological, and disturbance differences. These results show that both chemical and physical habitat parameters are essential for biomonitoring and conservation planning. The strong CoCA correlations indicate that fish and macroinvertebrates function as complementary bioindicators, supporting ecosystem health assessment. The potential impacts from damming, land use change, pollution and climate variability may alter water chemistry and substrate structure. So, integrated ecological evaluation and long-term monitoring will further improve understanding of ecological resilience in these river systems.

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Authors' contributions

All authors contributed to the study, conception, and design. Material preparation, data collection and analysis were performed by B.R.J., S.G., U.R.K., S.S., and K.K. The first draft of the manuscript was written by K.K., and S.S. All authors rigorously worked, revised the manuscript, read, and approved the final manuscript.

Conflicts of interest

The authors declare no conflict of interest.

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