

Article

Macroinvertebrate Biodiversity Trends and Habitat Relationships within Headwater Rivers of the Qinghai-Tibet Plateau

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Abstract: Highland running-water biodiversity has gained growing interest around the world, because of the more pristine conditions and higher sensitivity to environmental changes of highland rivers compared to the lowland rivers. This study presents the findings of systematic investigations and analyses on running-water biodiversity of macroinvertebrate assemblages in the most important headwater streams in the Yalutsangpo and Sanjiangyuan River basins in the Qinghai-Tibet Plateau and the lowland headwaters of the Songhua River, Juma River, and East River during the non-flood seasons of 2012 to 2016. The results indicated that the headwaters on the plateau had a higher regional biodiversity compared to the lowland rivers with the similar flow and substrate conditions. Even though the local diversity of the highland rivers was not significantly different at each single site, the taxonomic composition was significantly different with several rarely seen species scattering among the different sites, resulting in a high regional biodiversity. The biodiversity and composition of macroinvertebrates were strongly affected by the altitude gradient and the environmental variables associated with altitude. To be specific, for the Yalutsangpo River, canonical correspondence analyses of the macroinvertebrate assemblages and their environmental variables indicated that altitude, stream condition (represented by river pattern, riverbed structures, substrate composition), and water temperature influence macroinvertebrate taxa composition. Because of the restrictive plateau conditions including low water temperature, poor aquatic and riparian vegetation, and low runoff, the macroinvertebrate assemblages showed low biodiversity and were vulnerable to potential human disturbance/climate change. Therefore, it is essential to conserve suitable conditions of the determinative environmental variables to protect the unique and high regional biodiversity of the headwaters on the Qinghai-Tibet Plateau.

Keywords: highland headwater; macroinvertebrate; biodiversity; altitude gradient

1. Introduction

Studying and protecting highland (i.e., high altitude) running-water biodiversity has gained growing interest over the world, because of more pristine conditions and higher sensitivity to environmental changes in highland rivers than in lowland rivers [1]. The Qinghai-Tibet Plateau

is usually called “the water tower of Asia” due to its active water cycle and because it serves as the headwaters for most of the largest Asian rivers. The plateau representing an ecologically interesting transition between the Palaearctic and Oriental regions, covers an area of about 2.3 million km² with an average altitude of over 4000 m a.s.l., and includes the topographically highest and least studied lotic ecosystems [2]. Its environmental and ecological conditions have been the focus of attention for decades owing to its unique geographical location and ecological functions including water resource conservation and biodiversity protection [3]. It has been expected to have novel relationships of macroinvertebrate communities with stream habitat variables since highly diverse and unique assemblages of aquatic Protozoa, Insecta, Hirudinea, Rotatoria, and Crustacea have been reported [4,5].

However, climate change and anthropogenic activities have significantly influenced the physical and ecological conditions of the headwaters on the plateau [6]. Temperature and precipitation variations were regarded as the main driving forces for such changes [7]. The plateau river ecosystems appeared to be suffering decreasing surface runoff, shrinking lakes and wetlands, and conflicts between ecological protection and social economic development under the increasing influences of global warming and human disturbance [8]. Understanding the aquatic biodiversity, especially the relationships of biodiversity with major geographical and other environmental variables of the plateau is important for protecting the highland ecology and the headwater ecosystem functions of large Asian rivers.

Macroinvertebrates are among the most important components of the aquatic ecosystem and have been considered as useful indicators for analyses of relationships of biotic communities with stream habitat variables because of their confinement to the river bed, limited movement abilities, long life cycles, and sensitivity to environmental changes [9]. Xu et al. [5] reported the major features of the macroinvertebrate communities in several sections of the main stem and tributaries of the Yalutsangpo River. Jiang et al. [2] analyzed the longitudinal patterns of macroinvertebrates in relation to environmental factors in the Niyang River, the largest first-order tributary of the Yalutsangpo. Pan et al. [10] investigated the macroinvertebrates in the Sanjiangyuan river basin at the center of the plateau. These studies consistently indicated that the compositions of macroinvertebrate assemblages in the plateau were significantly associated with the high altitudes and the variation trends of biodiversity might be different from that of the lowland rivers. However, how the macroinvertebrate communities responded to altitude gradient and the other environmental variables associated with altitude was not clear from these three studies [2,5,10].

According to the River Continuum Concept (RCC) theory, as a river changes along the altitude gradient from headwaters to the lower reaches, the physical geomorphological features change and thus structural and functional characteristics of stream communities are adapted to the most probable position or mean state of the physical habitat; and therefore, there will be a change in the relationship between the production and consumption (respiration) of the material [11]. The hypothesis of this study was that the macroinvertebrate communities and their environmental variables varied with altitude, and a greater altitude gradient could attribute larger variations of macroinvertebrate community structure. The objectives were (1) to illuminate the differences in the macroinvertebrate communities and their environmental variables between the rivers with larger altitude gradients (highland rivers) and the rivers with smaller altitude gradients (lowland rivers); and (2) to document the influence of altitude gradient on macroinvertebrate assemblages and their environment variables.

We investigated the highland headwater rivers, including the Yalutsangpo River and the source region of the Yellow, Yangtze, and Mekong Rivers (called Sanjiangyuan in Figure 1a) on the Qinghai-Tibet Plateau, and the lowland rivers: Songhua River, Juma River, and East River (Figure 1a). Comparison based on statistical analyses was carried out to explore the variations in macroinvertebrate communities and stream habitat variables along the altitude gradient. With the intent to analyze in detail the missing difference in altitude, in particular between 3500–<1000 m a.s.l., more detailed sampling were carried out in the Yalutsangpo River basin (Figure 1b), in which the altitude gradient

was among the largest on earth. Further, based on the detailed samplings, the determinative physical variables affecting the macroinvertebrate assemblage composition were identified along the large altitude gradient.

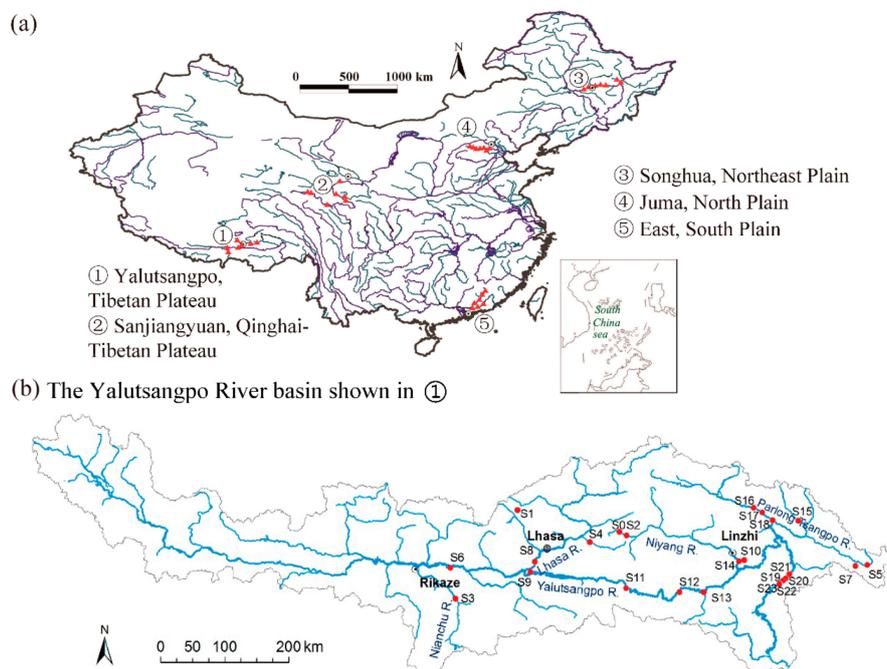


Figure 1. Study area and sampling sites: (a) sampling sites in the five selected rivers in different altitude regions; (b) sampling sites in the Yalutsangpo River basin.

2. Study Areas and Methods

2.1. Study Areas

The sampling sites in the five selected rivers were shown in Figure 1a. The Yalutsangpo River basin is located along the southwest boundary of the plateau, and the Sanjiangyuan river basin is located in center of the plateau. These two headwater river basins are among the most remote and undisturbed aquatic environments in the world. The Songhua River is located on the Northeast Plain, the Juma River is located on the North Plain, and the East River is located on the South Plain, representing rivers in the major lowland regions in China. The sites in the three lowland river basins were generally located on the 1st to 3rd order streams with little human disturbance. The altitudes of the sites in the Yalutsangpo, Sanjiangyuan, Songhua, Juma, and East rivers were in 3500–4500, 3500–4900, <500, <300, and <300 m a.s.l., respectively.

The systematic sampling sites (with average length of 50–100 m) were generally located on the 1st to 5th order streams in the Yalutsangpo River Basin, which is 1200 km long and flows from the west with an altitude of 4500 m a.s.l. to the east with an altitude <1000 m a.s.l., providing headwaters for the Brahmaputra River (Figure 1b). In East Tibet, the Yalutsangpo passes through the world's largest and deepest river canyon (i.e., Yalutsangpo Grand Canyon) and then flows to India as Brahmaputra River. Annual precipitation varies from less than 300 mm in the upstream to over 4000 mm in the downstream as the altitude descending from over 4000 m to below 700 m. Average annual air temperature of the downstream is at least 10 °C higher than the upstream. The sites S6, S9, S11, S12, S13, and S19–23 were located in the stem of Yalutsangpo; to be specific, S21–S23 were in the Grand Canyon segment. The other sites were in the tributaries of Yalutsangpo: S3 in the Nianchu River; S1, S4, and S8 in the Lhasa River; S0, S2, S10, S14 in the Niyang River; S5, S7, and S15–S18 in the Parlung Tsangpo River. S0–S3 were located in the altitude region of 4000–5000 m, followed by S4–S11 in 3000–4000 m, S12–S17 in 2000–3000 m, S18–S20 in 1000–2000 m, and S21–S23 in <1000 m.

2.2. Environmental Variable Measurement

The field investigations were carried out in the early summers of 2012 to 2016, before the summer floods occurred, guaranteeing that at the time of sampling, macroinvertebrate communities had not been disturbed by flood events [12]. Specifically, the investigations were carried out in April 2012 in East River, May 2013 in Juma River, June 2012 in Songhua River, July 2013 in Sanjiangyuan, and May 2012 and May 2014 in Yalutsangpo River. Geographical locations and altitudes (H) of the sampling sites were obtained using an iHand differential GPS (GPS 72H, Huaxing, Zhengzhou, China). On each sampling occasion, multiple measurements of physical and chemical parameters were made along multiple transects within each site and the averages of the multiple measurements were recorded (Tables 1 and 7). River width (W) was measured with a laser rangefinder. Water depth (h) was measured with a sounding lead or a steel ruler. Flow velocity (v) was measured at 60% of the water depth from the river bed with a propeller-type current meter (Model LS 1206B; Nanjing Automation Institute of Water Conservancy and Hydrology, Nanjing, China).

Water samples were taken (500 mL each, mixed with 250 mL water near the surface and 250 mL water near the bottom) and sediment samples (200 g each) were taken from the substrate for laboratory analyses. Dominant substrates were visually estimated and assigned into different types: silt and clay, sand, pebbles and fine gravel, cobbles, and boulders according to the classification of Subcommittee on Sediment Terminology [13]. Median grain size (D_{50}) was measured by combining measurement of coarse grains by sieving and fine particles using an instrument of laser diffraction particle sizing—Malvern Mastersizer 2000 (Malvern, Worcestershire, UK). The general features of land use, river patterns, and riparian vegetation were recorded and photographed. Scores for stream condition were assigned to the sites according to the statues of their river patterns, substrate compositions, and riparian vegetation, etc. [14]. The better the condition's suitability for macroinvertebrates, the higher the score was (Appendix A Table A1, e.g., the sites with scores over 10 generally had better suitability compared to the sites with scores lower than 5). For the detailed sampling in the Yalutsangpo River basin, an EXO Sondes and EXO Handheld System were used to obtain in situ measurements of water temperature (T), dissolved oxygen (DO).

2.3. Macroinvertebrate Sampling

For all the sampling sites, the kick net (1 m \times 1 m area, 420 μ m mesh) was used to take samples from the bed surface to a depth of 15 cm in the substrate along the riverbanks with water depth less than 1 m as well as the central of the rivers if the water depth was less than 1 m. For the river center with water depth over 1 m, a Peterson dredge sampler with a sampling area of 1/16 m² was also applied for taking supplementary samples in addition to the samples along the riverbanks. For each site, at least three samples were sampled from a quadrat of 10 m \times 10 m, and the sampled area of all the samples were added up to 1 m². The samples were sieved with a 500 μ m sieve. Then they were manually picked out using a white porcelain plate and stored in 75% ethanol.

Macroinvertebrates were brought back to the lab after the sampling and identified following standard taxonomic literature [15–18] under a stereoscopic microscope and an optical microscope. Jacobsen [19] indicated that family-level identification of macroinvertebrates was suitable for evaluating the biodiversity trends along geographic gradients. We identified aquatic insects mostly to genus level and crustaceans and annelids mostly to family level (Tables 2 and 8). Photographs of the specimens were captured in a SmartV Camera image acquisition system, and then the body length of each individual specimen was measured (to the nearest 0.01 mm). Individuals were counted for density estimations (ind./m²).

Considering the different regions of the five rivers, the family/genus level taxa richness would be more reasonable in order to have a homogeneous scale for the biodiversity of the among river comparison. While for the specific case of the Yalutsangpo River, to reveal the detailed differences in the macroinvertebrate assemblages due to the variation in altitude, some taxa were identified to genus or species level. Only in these conditions were comparisons possible.

2.4. Data Analyses

Taxa richness S , Shannon-Wiener index H' , and Improved Shannon-Wiener index B were calculated to evaluate alpha (local) diversity of macroinvertebrates for each site. Taxa richness S , the number of taxa (family for the five river comparison; the lowest identified taxon level for the detailed investigation of the Yalutsangpo River), provides a measure of both ecological diversity and habitat conditions of streams. Shannon-Wiener index H' defined by Krebs [20], integrates taxa richness and the contribution of each taxon in the assemblage. Considering difference attributed to the assemblage abundance, an Improved Shannon-Wiener index B was defined by Wang et al. [21] by coupling the abundance with the Shannon-Wiener index H' as

$$B = -(\ln N) \sum_{i=1}^S (n_i/N) \ln(n_i/N) \quad (1)$$

in which N is the density (abundance) of macroinvertebrate assemblage at a sampling site, and n_i is the density of the i th taxon.

A one way analysis of variance (ANOVA) and Kruskal Wallis test were conducted to determine if the alpha diversity indices differed among each of the investigated river basins. For the data tested to normally distributed using Shapiro-Wilk test, the ANOVA was adopted, otherwise the Kruskal Wallis test would be used. Post-hoc analysis on alpha biodiversity indices was carried out using the Tukey HSD method to detect the pairs of the rivers attributing to the overall difference. Moreover, multi-response permutation procedure (MRPP) was performed to determine if taxa composition (based on Bray-Curtis distance measure) differed among the river basins, and the pairwise comparison was conducted using the Bonferroni corrected p . All of the mentioned statistical analyses were conducted using the packages in R (R Foundation, Austria). In addition to analyses of variance and multi-response permutation procedure, K-dominant curves were plotted in this study for comparison of biodiversity among the different river basins and the different altitude regions. K-dominant curve, conveniently combining the taxa richness and the evenness of each taxa in the community, is usually used to illustrate the difference among different assemblages [10]. In this method, dominance patterns are represented by plotting accumulative abundance of each taxa (%) ranked in decreasing order of dominance. If curve 1 is under curve 2, the biodiversity of assemblage 1 is higher than that of assemblage 2.

Ordination analyses were applied to the data matrix of taxa on the lowest taxonomic level as in Table 8 with environmental variables using CANOCO 4.5 (Microcomputer Power, New York, NY, USA) to obtain responses of macroinvertebrates to environmental gradients from the perspective of assemblage composition. Average or score values of the environmental variables, including altitude, substrate median diameter, water depth and flow velocity at the sampling site, dissolved oxygen, water temperature, stream condition (Appendix A Table A1) were analyzed pairwise using SPSS 22.0 (IBM SPSS, Armonk, New York, NY, USA) to examine the Spearman correlations. Only uncorrelated (correlation $|r| < 0.4$) environmental variables were used in the ordination analysis to reduce arch effects [22]. The detrended correspondence analysis (DCA) was conducted first using only macroinvertebrate data to ascertain correspondence patterns between macroinvertebrates and environmental gradients. As Lepš and Šmilauer [22] suggested, a canonical correspondence analysis (CCA, based on unimodal response models) was conducted if the longest gradient in the DCA results exceeded a threshold value ($L_{th} = 4.0$, the index to determine the heterogeneity and deviation of taxa). Macroinvertebrate density data were $\log(x + 1)$ transformed, and the downweighting option was checked to reduce the influence of rare taxa. Forward selection with Monte Carlo permutation tests (499 permutations) was used to select a parsimonious set of explanatory variables under the cutoff point of $p < 0.10$.

3. Results

3.1. Comparison of Macroinvertebrate Biodiversity in Highland and Lowland Rivers

For the five rivers (Figure 1a), the physical conditions (altitude H , substrate composition, water depth h , and flow velocity v) and alpha-diversity indices (S , H' , B) are listed in Table 1; and compositions of macroinvertebrate assemblages were listed in Table 2. The sites in the Yalutsangpo (YA) and Juma (JU) were characterized by relatively coarser substrates (e.g., boulder, pebble, cobble, etc.) compared to the sites in the Sanjiangyuan (SA), Songhua (SO), and East (EA), which mainly consist of finer particles (e.g., gravel, sand, silt, fluid mud, etc.). Water depth and flow velocity were non-significantly different among all the sampled sites. For the coarse substrate Yalutsangpo and Juma River, the average values of their alpha-diversity indices taxa richness, and Shannon-Wiener index as well as improved Shannon-Wiener index were all in similar ranges. Similarly, no visible difference was seen in each of the alpha-diversity indices among the three fine substrate rivers.

Table 1. Comparison of physical variables and alpha diversity indices among the two highland rivers and the three lowland rivers.

SR	H	Substrate Composition	D_{50} (mm)	W (m)	H (m)	V (m/s)	Alpha-Diversity Indices		
							S	H'	B
YA	3500–4500	five sites with boulder, pebble, cobble, sand, and aquatic macrophytes; two with sand, gravel	20–200	5–40	0–0.5	0.3–0.8	17–33	1.7–2.7	9.8–19.2
SA	3500–4900	five sites with gravel, sand, and aquatic macrophytes; two with silt and gravel	0.5–5.0	5–60	0–0.6	0–0.5	6–21	0.5–2.1	3.0–10.0
SO	<500	five sites with gravel, sand, and aquatic macrophytes; two with silt, fluid mud	0.01–5.0	5–30	0.3–1.5	0–0.8	6–13	1.2–1.8	3.7–8.9
JU	<300	five sites with boulder, pebble, gravel, sand, and aquatic macrophytes; two with sand, silt	20–100	5–30	0.2–0.7	0.1–0.6	16–38	1.2–2.6	7.5–17.3
EA	<100	three sites with gravel, sand, aquatic macrophytes; two with gravel and sand; two with fine sand, silt and clay	0.1–2.0	5–40	0.3–1.3	0.3–1.0	6–15	1.1–1.9	4.1–10.1

Note: SR: Study Rivers; YA: Yalutsangpo; SA: Sanjiangyuan; SO: Songhua; JU: Juma; EA: East; H: altitude, m a.s.l.; D_{50} : median diameter of substrate, W: river width, H: water depth, V: flow velocity (m/s) were averages for multiple measurements of each sampling site.

Table 2. Taxa composition of macroinvertebrate assemblages in the five river basins (“+” indicates occurrence of the corresponding taxon).

Phylum	Class	Family	YA	SA	SO	JU	EA
Platyhelminthes	Turbellaria	n.d.	+			+	
Nematoda	Nematoda	n.d.	+	+			
Annelida	Hirudinea	Glossiphoniidae	+				

Table 2. Cont.

Phylum	Class	Family	YA	SA	SO	JU	EA	
Mollusca	Oligochaeta	Glossiphoniidae			+	+		
		Piscicolidae	+					
		Branchiobdellidae	+					
		Erpobdellidae			+			
		Hirudinidae			+	+	+	
		Tubificidae	+	+	+	+	+	
		Lumbriculidae	+				+	
		Naididae	+	+				
		Lymnaeidae	+	+		+	+	
		Planorbidae	+	+	+	+		
		Physidae	+					
		Hydrobiidae			+	+		
		Pleuroceridae				+	+	
		Stenothyridae				+	+	
		Arthropoda	Bivalvia	Turbinidae				
Viviparidae							+	
Corbiculidae					+	+	+	
Crustacea	Unionidae					+		
	Gammaridae		+	+		+		
	Palaemonidae				+		+	
	Atyidae						+	
	Arachnida		Hydrachnidae	+	+	+	+	
			Insecta	Baetidae	+	+	+	+
	Heptageniidae			+	+	+	+	
	Ephemerellidae			+	+	+	+	
	Ephemeridae						+	
	Leptophlebiidae			+		+	+	+
Siphonuridae	+						+	
Caenidae				+		+	+	
Potamanthidae						+		
Isonychiidae						+		
Neoephemeridae						+		
Coenagrionidae						+	+	
Gomphidae						+	+	
Corduliidae						+	+	
Macromiidae						+		
Platycnemididae					+	+		
Agriidae						+		
Perlidae	+				+	+		
Chloroperlidae	+							
Nemouridae	+					+		
Capniidae	+							
Pteronarcidae	+							
Perlodidae	+							
Naucoridae				+	+	+	+	
Corixidae				+	+			
Sisyridae	+							
Corydalidae					+	+		
Hydropsychidae	+		+		+	+		
Hydroptilidae				+				
Rhyacophilidae	+		+					
Limnephilidae	+			+				
Polycentropodidae					+			
Stenopsychidae				+				
Leptoceridae		+		+				
Psychomyiidae	+							

Table 2. Cont.

Phylum	Class	Family	YA	SA	SO	JU	EA
		Molannidae	+				
		Brachycentridae	+	+			
		Hydrobiosidae	+			+	
		Arctopsychidae				+	
		Glossosomatidae	+				
		Philopotamidae	+				
		Pyralidae		+			
		Dytiscidae		+		+	+
		Elmidae	+	+	+	+	+
		Hydrophilidae				+	
		Chrysomelidae			+		
		Entomobryomorpha	+				
		Tipulidae	+	+	+	+	+
		Simuliidae	+	+	+	+	
		Ephydriidae		+			
		Culicidae		+	+	+	
		Ceratopogonidae	+			+	+
		Psychodidae	+			+	
		Dolichopodidae				+	
		Empididae	+			+	
		Stratiomyiidae			+		
		Tabanidae			+	+	
		Blephariceridae	+				
		Muscidae				+	
		Chironomidae	+	+	+	+	+

Note: n.d.—did not identified to family.

The results of the ANOVA test suggested that global variations in taxa richness, density, Shannon-Wiener index, and Improved Shannon-Wiener index were significant among the five rivers (Table 3). Pairwise comparisons of alpha diversity indices among the five rivers (Table 4) indicated that the local biodiversity was generally not significantly different within the fine substrate rivers Songhua, East, Sanjiangyuan, nor were they within the coarse substrate rivers Juma and Yalutsangpo. Significant differences were mainly found between the fine and coarse substrates rivers. In other words, the local biodiversity was not significantly affected by altitude gradients as it was almost the same for the highland rivers and the lowland rivers if their substrates were comparable.

Table 3. Global variation of the alpha diversity indices among all of the sampling sites in the five rivers.

Variable	HVT	Method	Statistical Value	Sig.
Taxa richness	0.140	ANOVA	14.410	0.000 *
Density (ind./m ²)	0.000	KW	15.230	0.004 *
Shannon-Wiener index	0.165	ANOVA	4.377	0.005 *
Improved Shannon-Wiener index	0.905	ANOVA	11.766	0.000 *

Note: HVT: homogeneous variance test; KW: Kruskal-Wallis; Statistical value: KW.chi or ANOVA.F; *: Significant difference with confidential level of 95%.

Table 4. Pair comparison among each of the alpha diversity indices of the five rivers based on post-hoc test.

Pairwise Comparison	Taxa Richness. <i>p</i> -Value	Density. <i>p</i> -Value	Shannon-Wiener Index. <i>p</i> -Value	Improved Shannon-Wiener Index. <i>p</i> -Value
SO-EA	0.655	0.559	0.942	0.496
SO-SA	0.999	1.000	0.938	0.996
SO-JU	0.000 ***	1.000	0.100	0.007 **
SO-YA	0.261	0.588	0.662	0.024 *
EA-SA	0.825	0.750	1.000	0.774
EA-JU	0.000 ***	0.012 *	0.009 **	0.000 ***
EA-YA	0.006 **	0.002 **	0.177	0.000 ***
SA-JU	0.000 ***	1.000	0.020 *	0.003 **
SA-YA	0.197	0.602	0.244	0.012 *
JU-YA	0.016 *	1.000	0.708	0.976

Note: “*”—Significant difference with confidential level of 95%; “**”—Significant difference with confidential level of 99%; “***”—Significant difference with confidential level of 99.9%.

The MRPP results and pair-comparison both indicated that the taxa compositions of macroinvertebrate assemblages of the five rivers were generally significantly different (Tables 5 and 6). It was indicated that even though the local biodiversity had a non-significant difference, the assemblage composition varied significantly among sites, attributing to the difference between the different rivers.

Table 5. MRPP test of the compositions of macroinvertebrate assemblages of the five rivers.

MRPP Statistics	SO	EA	SA	JM	YA
delta	0.8978	0.9200	0.8557	0.8005	0.8989
n	8	12	7	8	9

Chance corrected within-group agreement A: 0.0721; Based on observed delta 0.8797 and expected delta 0.948.

Note: Significance of delta: 0.001; Permutation: free; Number of permutations: 999.

Table 6. Pair comparison of macroinvertebrate assemblages of the five rivers based on Tukey’s post-hoc test.

Pairs	F Model	R ²	<i>p</i> -Value	Adjusted <i>p</i>
SO-EA	1.640	0.084	0.037	0.37
SO-SA	2.144	0.142	0.002	0.02 *
SO-JU	2.999	0.176	0.002	0.02 *
SO-YA	1.801	0.107	0.009	0.09
EA-SA	2.264	0.118	0.002	0.02 *
EA-JU	2.949	0.141	0.001	0.01 *
EA-YA	2.292	0.108	0.001	0.01 *
SA-JU	3.490	0.212	0.001	0.01 *
SA-YA	2.193	0.135	0.001	0.01 *
JU-YA	2.780	0.156	0.001	0.01 *

Note: “*”—Significant difference with confidential level of 95%.

The K-dominant curves of macroinvertebrate assemblages of the five rivers clearly show that the regional taxa richness was the highest and regional taxa distribution was the most even in the Yalutsangpo, followed by the Juma, Sanjiangyuan, East, and the least in the Songhua (Figure 2). Considering the influence of substrates, consistent with the MRPP test, the highland Yalutsangpo had a higher regional biodiversity than the lowland Juma, and the highland Sanjiangyuan had a higher regional biodiversity than the lowland Songhua and East.

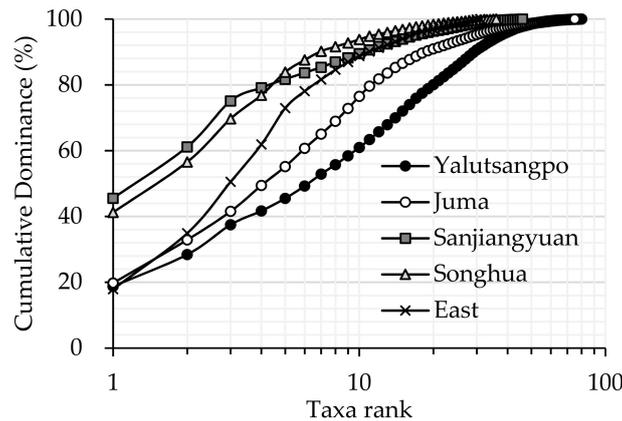


Figure 2. K-dominant curves of macroinvertebrates in the different rivers.

3.2. Relationships of Macroinvertebrate Communities with Stream Habitat Variables of the Yalutsangpo River

Environmental parameters and density of macroinvertebrates captured from 24 sites in the Yalutsangpo basin are listed in Tables 7 and 8, respectively. DO in all sites was within optimal limits for macroinvertebrates (6.2–10.0 mg/L). Water depth and flow velocity of the sites were seldom different. While generally, the medium grain size of substrates, water temperature, stream condition, and riparian condition varied as the altitude decreased.

Altogether, 125 taxa of macroinvertebrates belonging to 65 families and 118 genera were identified (Table 8). Among them were 1 Turbellaria, 1 Nematoda, 3 Hirudinea, 17 Oligochaeta, 7 mollusks, 1 Arachnida, 2 Crustacea, and 93 Insecta. Aquatic insects contributed 74.4% of the total richness, with Chironomidae (31.2%, 39 taxa), Oligochaeta (13.6%, 17 taxa), Trichoptera (9.6%, 12 taxa), Ephemeroptera (7.2%, 9 taxa), and Plecoptera (6.4%, 8 taxa) as the dominant groups. As indicated by the present rate (the number of the sites where the taxon present divided by the number of all sites) being lower than 5%, there were 24 rare taxa, such as Piscicolidae (only present at S6), Blephariceridae (S2), Enchytraeidae (S5), Muscidae (S4), etc. These rare taxa were scattered in the different altitude regions and were essential for sustaining the high regional biodiversity. Taxa richness and evenness of distribution were the highest in the altitude range of 3000–4000 m, followed by 4000–5000 m, 2000–3000 m, and 1000–2000 m, successively (Figure 3). No specimen has been found in the sites with altitudes below 1000 m. It should be noted that these low altitude sites ($H < 1000$ m) were located in the Grand Canyon reach, where the velocity of the main flow was extremely high (>8 m/s), which restrained macroinvertebrate inhabitation. It could also be due to sampling difficulties of such a high velocity condition, but at least it is indicated that the abundance of macroinvertebrate assemblages were low and could not be caught by regular sampling methods.

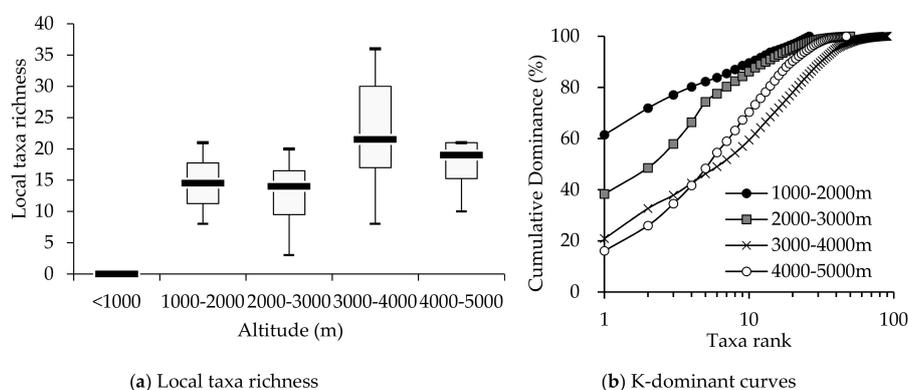


Figure 3. (a) Local taxa richness and (b) K-dominant curves of macroinvertebrate assemblages for the different altitude regions in the Yalutsangpo basin.

The CCA biplots of sampling sites-environments of the Yalutsangpo River (Figure 4) indicated that the dominant environmental parameters (incorporated values were listed in Appendix A Table A1) influencing the abundance and distribution of macroinvertebrates in the Yalutsangpo were altitude (H), water temperature (T), and stream condition (SC) scores including river patterns, bed structures, bed material compositions, etc. Axes 1 and 2 accounted for 78.4% of the taxa-environment relations, and both axes were significant at $p < 0.05$. Axis 1 indicated predominantly gradients of stream condition scores and water temperature. Axis 2 indicated predominantly gradients of altitude and water temperature. The sites characterized by stable substrates (e.g., step-pool systems and gravel beds) were mainly arranged at the left side of Axis 2. The sites characterized by less stable substrates, were mainly arranged at the right side of Axis 2. Additionally, the arrangement of the fine substrate sites also revealed the influence of river patterns: Along Axis 1 there were barrier lakes, wetland, and braided rivers, successively. For each type of substrate (connected by the thin dotted lines), the sites were generally arranged along Axis 2 according to their altitudes.

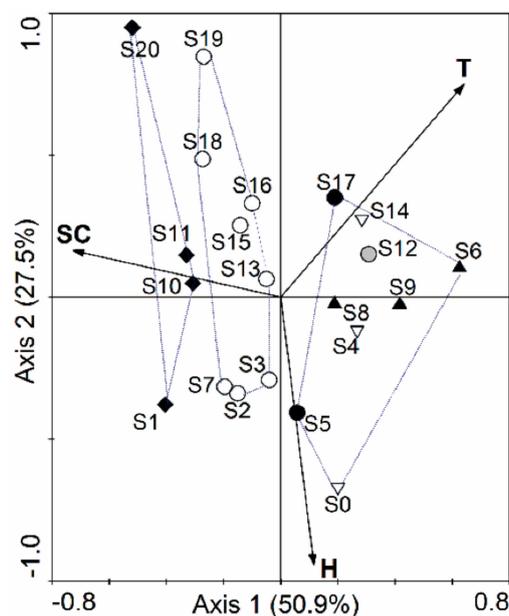


Figure 4. Canonical correspondence analysis (CCA) ordination plots of the Yalutsangpo. H: altitude, T: water temperature, SC: stream condition, S0–S20: the sampling sites. ◆: mountain streams with step-pool systems developed, ○: rivers with stable gravel bed, ●: barrier lakes (river dammed by landslides), ▽: wetland, ▲: braided rivers.

Table 7. Means (\pm SE) and ranges of environmental parameters of the sites in the Yalutsangpo basin.

S	H	D_{50}	h	v	DO	T	Stream Pattern & Bed Structure	Riparian Condition (VC and VH)
0	4873 \pm 2	5	0.2–0.8	0–0.1	6.4 \pm 0.2	2.4 \pm 0.1	wetland, mud pool	Alpine meadow, VC = 80%, VH = 1–5 cm
1	4484 \pm 3	40	0–0.2	0.3–0.5	8.4 \pm 0.2	1.3 \pm 0.1	Step-pool developed	Alpine meadow, VC = 100%, VH = 1–5 cm
2	4228 \pm 2	100	0.1–0.4	0.83	8.1 \pm 0.1	3.5 \pm 0.2	stable bed	Alpine meadow, VC = 100%, VH = 1–5 cm
3	4014 \pm 3	50	0–0.25	0.3–0.5	7.9 \pm 0.3	4.7 \pm 0.1	braided stream, macro-algae covered bed	Channelized bank, VC < 5%
4	3916 \pm 4	5	0–0.15	0.1–0.3	6.2 \pm 0.2	10.5 \pm 0.2	wetland linked with channel, rich humus	Alpine meadow, VC = 100%, VH = 5–20 cm
5	3901 \pm 2	5	0.2–0.4	0.1	7.9 \pm 0.3	3.1 \pm 0.2	barrier lake, sand bed	No vegetation
6	3768 \pm 2	10	0–0.3	0.3	9.6 \pm 0.2	17.4 \pm 0.3	braided, gravel bed	No vegetation
7	3752 \pm 4	300	0.1–0.3	0.3–0.5	8.5 \pm 0.1	2.2 \pm 0.2	glacial stream, gravel bed	Shrub, VC = 10%
8	3598 \pm 5	150	0–0.5	0.3–0.8	10.0 \pm 0.3	10.5 \pm 0.2	braided river, wide valley, gravel bed	Herbaceous vegetation and trees, VC = 100%
9	3566 \pm 3	200	0–0.5	0.3	7.7 \pm 0.2	12.4 \pm 0.3	braided river, wide valley, gravel-clay bed	No vegetation
10	3514 \pm 4	500	0–0.4	0.3–0.5	8.1 \pm 0.4	7.2 \pm 0.2	step-pool developed	Channelized bank, VC < 2%
11	3237 \pm 3	1000	0.5–1.5	0.5–1.5	8.0 \pm 0.3	8.0 \pm 0.1	step-pool developed	No vegetation
12	2993 \pm 4	800	0.1–0.5	0	6.7 \pm 0.1	13.0 \pm 0.2	river bend, lentic	No vegetation
13	2959 \pm 3	300	0.2–0.4	1.5–2	7.8 \pm 0.4	8.0 \pm 0.3	gravel bed, lotic	Alpine meadow, VC = 50%, VH = 5–200 cm
14	2948 \pm 4	30	0.3–1.0	0.3–2.0	7.5 \pm 0.2	15.0 \pm 0.2	wetland, gravel bed	Alpine meadow, VC = 80%, VH = 1–10 cm
15	2744 \pm 4	150	0.1–0.5	0.5–1.0	8.5 \pm 0.3	10.1 \pm 0.1	stable bed	Herbaceous vegetation, VC < 10%
16	2228 \pm 5	150	0–0.2	0.3	9.6 \pm 0.1	10.3 \pm 0.2	gravel bed, river bend	Herbaceous vegetation and shrubs, VC > 80%, VH = 20–500 cm
17	2208 \pm 6	5	0.2–0.4	0.1	7.9 \pm 0.2	13.2 \pm 0.2	barrier lake, sand bed	No vegetation
18	1998 \pm 5	180	0–0.4	0.3–0.5	9.6 \pm 0.2	11.0 \pm 0.2	gravel and sand bed	Herbaceous vegetation and shrubs, VC > 60%, VH = 10–200 cm
19	1100 \pm 6	50	0.1–0.3	0.3–0.8	9.5 \pm 0.3	15.0 \pm 0.1	stable bed	Herbaceous vegetation and shrubs, VC > 70%, VH = 20–300 cm
20	1001 \pm 5	120	0–0.3	0–0.3	9.3 \pm 0.4	14.4 \pm 0.2	Step-pool developed	Herbaceous vegetation and shrubs, VC > 70%, VH = 20–200 cm
21	718 \pm 7	300	0–0.5	0.3–0.5	9.2 \pm 0.1	13.5 \pm 0.3	river bend, lentic	No vegetation
22	705 \pm 6	200	0–0.4	0.3–0.5	9.5 \pm 0.3	14.6 \pm 0.1	gravel bed, lotic	No vegetation
23	688 \pm 8	200	0–0.4	0.4–0.5	9.4 \pm 0.2	14.1 \pm 0.2	river bend, lentic	No vegetation

Note: S: sites; H: altitude, m; D_{50} : median particle diameter of substrate, mm; h : water depth of the zone where macroinvertebrate samples were taken, m; v : flow velocity of the zone where macroinvertebrate samples were taken, m/s; DO: dissolved oxygen, mg/L; T: water temperature, °C; VC and VH: riparian vegetation coverage rate and height, respectively.

Table 8. Taxa and density compositions of macroinvertebrates in the sampling sites of Yalutsangpo basin (numbers indicate density, ind./m²).

Family	Genus	S0	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	S11	S12	S13	S14	S15	S16	S17	S18	S19	S20	S21	S22	S23
Planariidae	n.d.	0	0	12	0	0	0	0	16	0	0	17	0	0	0	0	0	0	0	0	0	0	0	0	0
Pratylenchidae	n.d.	0	0	0	0	0	0	1	0	0	2	1	0	0	0	0	0	0	0	0	1	0	0	0	0
Glossiphoniidae	n.d.	0	0	0	1	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Glossiphoniidae	<i>Helobdella</i>	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Piscicolidae	<i>Piscicola geometra</i>	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Branchiobdellidae	n.d.	0	0	0	0	0	0	3	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0
	<i>Limnodrilus</i> sp.	0	0	0	0	5	0	2	2	10	24	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>Limnodrilus claparedeianus</i>	0	0	0	0	0	0	0	2	0	0	0	0	0	0	256	0	0	0	0	0	0	0	0	0
Tubificidae	<i>Limnodrilus hoffmeisteri</i>	0	0	0	0	0	8	0	2	0	0	0	0	14	0	0	0	0	0	0	0	0	0	0	0
	<i>Rhyacodrilus stephesoni</i>	0	0	0	0	0	0	0	1	0	0	148	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>Tubifex tubifex</i>	15	0	0	0	0	6	1	2	120	38	0	0	2	1	27	0	0	0	0	0	0	0	0	0
Lumbriculidae	<i>Lumbriculus variegatus</i>	0	0	0	0	21	0	0	0	102	0	0	0	0	0	65	0	0	0	0	0	0	0	0	0
Enchytraeidae	n.d.	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>Chaetogaster diaphanus</i>	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>Nais barbata</i>	0	0	0	0	0	0	0	2	2	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
	<i>Nais bretscheri</i>	0	0	0	0	0	0	4	1	54	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>Nais communis</i>	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>Nais elinguis</i>	0	0	0	0	0	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>Nais pardalis</i>	0	0	0	0	0	0	4	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>Paranais frici</i>	0	0	0	0	0	0	2	1	9	274	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>Stylaria lacustris</i>	0	0	0	0	0	0	0	1	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>Uncinaiis uncinata</i>	0	0	0	0	0	0	5	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lymnaeidae	<i>Radix</i> sp1	0	0	0	0	3	0	16	0	53	2	0	20	10	0	0	0	0	0	0	1	0	0	0	0
	<i>Radix</i> sp2	0	0	0	0	0	0	0	0	41	2	0	19	10	0	0	0	0	0	0	0	0	0	0	0
Planorbidae	<i>Gyraulus</i> sp.	0	0	0	0	36	0	3	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
	<i>Hipppeutis</i> sp.	0	0	0	0	0	0	3	0	80	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Physidae	<i>Physa</i> sp.	0	0	0	0	0	0	0	0	133	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Ampullariidae	n.d.	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0
Sphaeriidae	n.d.	46	0	0	0	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gammaridae	n.d.	0	1	0	0	0	0	55	0	22	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Clausidiidae	n.d.	57	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hydrachnidae	n.d.	0	253	0	47	0	0	7	0	78	10	220	4	22	0	47	8	5	0	0	0	0	0	0	0
Entomobryomorpha	n.d.	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Elmidae	n.d.	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0
Chrysomelidae	n.d.	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Ptilodactylidae	<i>Stenocolus</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0

Table 8. Cont.

Family	Genus	S0	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	S11	S12	S13	S14	S15	S16	S17	S18	S19	S20	S21	S22	S23	
Dryopidae	<i>Elmoparnus</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	
Ceratopogonidae	n.d.	0	0	0	0	29	1	0	2	0	0	13	4	0	0	2	0	0	0	0	0	0	0	0	0	
Chironomidae	<i>Alotanypus</i> sp.	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>Brillia</i> sp.	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>Cardiocladius</i> sp.	0	0	0	18	0	0	0	0	15	0	0	69	0	0	54	0	3	0	0	0	0	0	0	0	0
	<i>Chaetodadius</i> sp.	0	0	0	133	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>Conclvapelopia</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	1	17	0	0	0	0	0	0	0	0	0	0
	<i>Cricotopus</i> sp.	0	0	0	0	0	0	9	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>Diamesa</i> sp.	0	45	0	0	0	168	0	2	1	0	0	0	0	0	16	0	0	0	0	0	0	0	0	0	0
	<i>Dicrotendipes</i> sp.	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>Eukiefferiella</i> sp.	0	4	0	3	0	0	0	3	0	0	0	52	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>Heleniella</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
	<i>Heterotrissodadius</i> sp.	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>Kiefferulus</i> sp.	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>Larsia</i> sp.	0	5	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>Limnphyes</i> sp.	0	0	0	0	0	0	0	1	0	0	0	8	0	0	0	0	3	0	0	0	0	0	0	0	0
	<i>Metriocnemus</i> sp.	35	0	0	12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>Micropsectra</i> sp.	0	11	0	0	0	0	15	0	3	136	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>Monodiamesa</i> sp.	0	0	0	0	0	0	0	0	0	4	0	0	42	1	0	5	0	0	0	0	0	0	0	0	0
	<i>Orthocladius</i> sp.	0	36	2	0	0	0	12	0	20	110	4	7	0	1	7	18	3	0	0	2	1	0	0	0	0
	<i>Pagastia</i> sp.	0	19	1	0	0	0	0	1	0	0	3	0	0	0	1	5	0	0	0	0	0	0	0	0	0
	<i>Paracladopelma</i> sp.	0	0	0	0	0	0	0	0	3	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>Paradadapelma</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	24	0	0	0	0	0	0	0
	<i>Parakiefferiella</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	19	0	0	0	0	0	0	0
	<i>Parametriocnemus</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
	<i>Paratanytarsus</i> sp.	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>Paratendipes</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1156	0	0	0	0	0	0	0	0	0	0
	<i>Paratrichodadius</i> sp.	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>Polypedilum</i> sp.	0	0	0	0	0	0	4	0	21	54	0	0	236	0	0	39	0	7	0	0	0	0	0	0	0
	<i>Porilla</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
	<i>Psectrodadius</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	308	0	0	0	0	0	0	0	0	0	0	0	0
	<i>Pseudodiamesa</i> sp.	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>Pseudorthocladius</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
	<i>Radotanypus</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0
<i>Rheocricotopus</i> sp.	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Stictochironomus</i> sp.	0	0	0	0	62	0	58	0	22	578	0	0	0	0	0	0	0	30	0	0	0	0	0	0	0	
<i>Symphothastia</i> sp.	0	0	0	0	0	0	0	0	0	0	0	45	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Tanypus</i> sp.	0	0	0	0	0	0	0	0	0	18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Tanytarsus</i> sp.	3	0	0	0	0	0	11	19	0	0	0	9	5	4	10	18	0	0	0	0	0	0	0	0	0	
<i>Tendipus</i> sp.	32	0	0	0	0	0	102	0	3	1170	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	

Table 8. Cont.

Family	Genus	S0	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	S11	S12	S13	S14	S15	S16	S17	S18	S19	S20	S21	S22	S23
Gomphus	n.d.	0	0	0	0	0	0	0	0	0	0	0	0	14	0	0	0	0	0	0	0	2	0	0	0
Aeshnidae	n.d.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0
Sisyridae	n.d.	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	4	0	0	0
Perlidae	n.d.	0	37	0	1	0	0	1	10	0	0	0	0	0	1	0	1	5	0	0	0	1	0	0	0
Chloroperlidae	n.d.	0	47	30	0	0	0	0	37	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nemouridae	n.d.	0	0	13	0	0	0	0	40	0	0	70	0	0	2	0	0	3	0	1	0	0	0	0	0
Capniidae	n.d.	0	0	0	0	0	0	0	37	0	0	69	0	0	0	0	0	0	0	0	0	0	0	0	0
Pteronarcidae	n.d.	0	0	23	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Perlodidae	n.d.	0	0	0	0	0	0	0	36	0	0	2	0	0	2	0	3	1	0	0	0	2	0	0	0
Styloperlidae	<i>Cerconychia</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0
Leuctridae	n.d.	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Note: n.d.—did not identified to genus.

4. Discussion

Altitude has been considered as the most important variable determining the living conditions of macroinvertebrates in plateau areas [23]. Xu et al. [5] showed that assemblage structures and functional feeding compositions of macroinvertebrates were closely related to altitude. This study indicated that the local biodiversity may not be significantly affected by altitude, while the high regional biodiversity of highland rivers was obviously associated with the high altitudes, and especially the high altitude gradients, which created the high habitat heterogeneity. Füreder et al. [24] showed similar findings, that in high altitude regions great altitude gradients and the physical variables associated with the altitude, such as climate, riparian vegetation, and water temperature affected macroinvertebrate assemblages in terms of the functional feeding groups and biodiversity. Especially, water temperature and channel stability were regarded as the principle parameters determining the macroinvertebrate community [25].

In this study, it was found that the environmental parameters of aquatic habitat, including dissolved oxygen; water temperature; and medium grain size, which essentially determined the channel stability, changed significantly as altitude decreased. Following the Yalutsangpo, as the altitude descended from 4000–5000 m to 3000–4000 m and then to 2000 m, the riparian vegetation changed from cold desert to arid steppe and then to deciduous scrub, which resulted in changes in taxa composition and the formation of a high regionally diverse macroinvertebrate community. For the central plateau headwaters, the Sanjiangyuan possessed a less diverse macroinvertebrate community compared with the Yalutsangpo, owing to its smaller altitude gradients and less variations in the altitude-associated environmental conditions [26].

Milner and Petts's conceptual model [25] indicated that turbidity, discharge, sediment transport, and channel form all affected the channel stability and consequently influenced the biotic communities by influencing primary productivity, habitat suitability, attachment, and production of macroinvertebrates and fish. The CCA analyses of the Yalutsangpo (this study) and the Yellow River Source Region [26] both confirmed that the diversity of the macroinvertebrate assemblage was positively correlated with the heterogeneity and stability of substrates. It was believed that coarse substrates provide a wide range of refuges and principal habitats for macroinvertebrates [27]. In addition, our CCA analyses also indicated that water temperature was another determinative parameter influencing the assemblage composition, which was also consistent with the findings of Milner and Petts [25]. As most of the source water in the Yalutsangpo was glacial in origin, the aquatic biota was adapted to persistent low temperature [28]. Many psychrophilic taxa, such as Rhyacophilidae, Enchytraeidae, Ecdyuridae, etc. were indeed sampled in our investigation. Similarly, psychrophilic taxa were also commonly seen in the Sanjiangyuan basin with the average altitude higher than 3000 m [26]. In general, as altitude decreased to less than 2000 m, water temperature increased because of less glacial origin water input, as a result, less psychrophilic taxa were present.

In addition to the variables influencing macroinvertebrates that were revealed in the CCA analyses, flow velocity was also suggested as a significant predictor of the community variance by Jiang et al. [2] in their study of the Niyang River, the tributary of Yalutsangpo. Flow influences many important structural attributes of stream ecosystems such as substrate stability, habitat volume and channel morphology [29]. Extremely high velocity (>3 m/s) can cause bedload movement, which destroys aquatic habitat [14,30]. Zhou et al. [31] indicated that in the Yalutsangpo River the flow velocity and stream power increased as the altitude descended and consequently most of the taxa that preferred low or medium stream power conditions disappeared, while only the taxa that either have strong attachment or swimming abilities could survive. No macroinvertebrate was captured from the Yalutsangpo Grand Canyon during our study, confirming that the high current velocity restrained the aquatic biota.

Therefore, according to the macroinvertebrate biodiversity trends and the relationships of macroinvertebrates with stream habitat variables explored in this study, the following strategies for conservation of such highland headwater systems are proposed: (1) Conserving the high regional

heterogeneity of aquatic habitat in different altitude regions, especially in 3000–4000 m, because the taxa composition varied among the different altitude regions and the high habitat heterogeneity supported high regional diversity of aquatic biota; (2) protecting suitable habitat conditions, including natural stream conditions, suitable flow velocity, and riparian vegetation conditions from anthropological disturbance to sustain suitable habitat conditions for diverse macroinvertebrate assemblages. Step-pool systems, stable gravel beds, and riparian wetland zones were suggested to be preserved or restored for suitable stream condition. Channelization, gravel mining, and riparian vegetation deterioration should be avoided, especially in the altitudes of 3000–4000 m. For the Yalutsangpo Grand Canyon, reasonable adjustments like increasing river bed roughness structures or knickpoints to reduce the extremely high flow velocity could be beneficial for aquatic biota.

Moreover, as in the remote areas, the plateau headwaters were nearly-pristine and well-preserved, and are supposed to have good water quality and little pollution. Owing to the harsh natural conditions of the high plateau, a gentle disturbance could result in a great deterioration in the eco-environment. For instance, as detected by Liu et al. [26], the macroinvertebrate assemblages varied significantly from the headwaters to the tributaries and the main stem of the Yellow River source: fewer EPT taxa, more Chironomidae and more Oligochaeta were found in the headwater streams suffering livestock grazing and nitrogen enrichment owing to the low flow discharge of the headwater and low denitrification rate under the low temperature plateau condition. In summary, sustainable expansion of anthropological activities should pay more attention to conservation of the plateau aquatic ecosystem. Nevertheless, considering the ongoing climate change and the plateau being especially sensitive to climate change, the water temperature may change and cause disturbance to the aquatic ecosystem due to changes of water sources, e.g., may include more melting water. Such changes may cause a significant impact on the aquatic communities and should be studied further for better conservation.

5. Conclusions

This study indicated that the Tibetan highland rivers have much higher regional diversity of macroinvertebrates compared to the lowland rivers with similar flow and substrate conditions. The high regional biodiversity was obviously associated with high altitudes, which created high habitat heterogeneity among different altitude regions. The plateau boundary river Yalutsangpo was characterized by high regional biodiversity and more rarely present taxa scattering in the large range of altitudes. Along with the great altitude gradient, the stream bed condition and water temperature were among the important environmental variables influencing the abundance and distribution of macroinvertebrates. The highest taxa richness and evenness of distribution of macroinvertebrates in the altitude region 3000–4000 m, was attributed to the optimal conditions of substrate composition and river pattern, water temperature, and riparian condition. Owing to the harsh natural conditions of the high plateau, a gentle disturbance could result in a great deterioration of the eco-environment. Therefore, conserving the high regional heterogeneity of aquatic habitat in the different altitude regions, especially the high altitude gradient regions, is crucial for sustaining rare taxa and high heterogeneity of aquatic biota.

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Appendix A

Table A1. Values assigned for the environmental parameters of the sites in the Yalutsangpo basin for CCA.

Site	H (m)	D ₅₀ (mm)	h (cm)	v (m/s)	DO (mg/L)	T (°C)	Bed Structure Score	Riparian Condition Score	Stream Condition Score = Bed Structure Score × Riparian Condition Score
S0	4873	5	50	0.05	6.4	2.4	4	8	32
S1	4484	40	15	0.4	8.4	1.3	9	10	90
S2	4228	100	30	0.83	8.1	3.5	6	10	60
S3	4014	50	20	0.4	7.9	4.7	3	2	6
S4	3916	5	15	0.3	6.15	10.5	4.5	10	45
S5	3901	5	30	0.1	7.9	3	2	1	2
S6	3768	10	20	0.3	9.6	17.4	4.5	1	4.5
S7	3752	300	25	0.4	8.5	2	3.5	4	14
S8	3598	150	35	0.6	10.3	10.5	4.5	6	27
S9	3566	200	35	0.3	7.7	12.4	2.5	1	2.5
S10	3514	500	30	0.4	8.1	7.2	9	2	18
S11	3237	1000	100	1	8	8	9	1	9
S12	2993	800	35	0	6.7	13	2.5	1	2.5
S13	2959	300	30	2	7.8	8	3.5	6	21
S14	2948	30	70	0.9	7.5	15	4.5	7	31.5
S15	2744	150	30	0.75	8.5	10.1	6	4	24
S16	2228	150	15	0.3	9.6	10.3	3.5	8	28
S17	2208	5	30	0.1	7.9	13.2	1.5	1	1.5
S18	2008	180	20	0.4	9.6	11	6	6	36
S19	1100	50	15	0.55	9.5	15	6	7	42
S20	1001	120	15	0.15	9.3	14.4	9	7	63
S21	718	300	25	0.4	9.2	13.5	2.5	1	2.5
S22	705	200	20	0.4	9.5	14.6	3.5	1	3.5
S23	688	200	20	0.45	9.4	14.1	2.5	1	2.5

Note: Scores for bed structure and riparian condition were based on the suitability of them for macroinvertebrate assemblages [14].

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