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Article

# Spatial Patterns of Benthic Macroinvertebrate Diversity and Their Environmental Drivers in the Middle and Lower Yangtze River

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## Abstract

Benthic macroinvertebrates are widely used as bioindicators for assessing freshwater ecosystem health. This study investigated the diversity patterns and community structure of benthic macroinvertebrates across 21 sampling sites along the middle and lower reaches of the Yangtze River. A total of 74 species belonging to 3 phyla, 7 classes, 17 orders, 37 families, and 58 genera were identified, with aquatic insects dominating the assemblages. Alpha diversity indices showed no significant differences among river sections, whereas multivariate analyses (NMDS and PERMANOVA) revealed significant spatial variation in community composition, indicating that beta diversity plays a key role in structuring assemblages at the basin scale. Canonical correspondence analysis (CCA) identified nutrient variables (TN and NH<sub>4</sub><sup>+</sup>-N), as well as pH and conductivity, as the main environmental drivers influencing community distribution. The results suggest that benthic macroinvertebrate diversity patterns in large river systems are jointly shaped by regional environmental gradients and local habitat conditions. These findings provide insights into biodiversity conservation and ecological management of large river ecosystems.

**Keywords:** benthic macroinvertebrates; NMDS; CCA; nutrient gradients; middle and lower Yangtze River

## 1. Introduction

The Yangtze River, the largest river in China, is among the most biodiverse inland river systems globally and plays a critical role in maintaining national ecological security and regional ecological balance [1]. The middle and lower reaches, characterized by a subtropical monsoon climate, complex hydrological regimes, and numerous tributaries, support diverse ecosystem types and high habitat heterogeneity, thereby sustaining a large number of endemic and threatened aquatic species [2]. However, rapid economic development and intensified human activities have imposed multiple pressures on the river system. Shipping, land reclamation, shoreline hardening, pollutant discharge, and hydraulic engineering have collectively led to water quality deterioration, habitat fragmentation, and reduced hydrological connectivity, resulting in significant declines in aquatic biodiversity and ecosystem stability [3–8].

Benthic macroinvertebrates occupy a central position in freshwater ecosystems, contributing to organic matter decomposition, primary production transfer, and energy flow across trophic levels [9–14]. Owing to their relatively long life cycles, limited mobility, and sensitivity to environmental changes, they are widely recognized as reliable indicators of ecological status and environmental stress [15–21]. Previous studies have demonstrated that benthic community structure responds significantly to water pollution and habitat degradation [22,23]. However, most existing research has

been conducted at local or single-reach scales, often constrained by administrative boundaries, resulting in a lack of integrative understanding of community patterns along large river continua [24–26]. Moreover, the relative importance of environmental gradients versus spatial heterogeneity in shaping benthic communities at the mainstem scale remains insufficiently resolved.

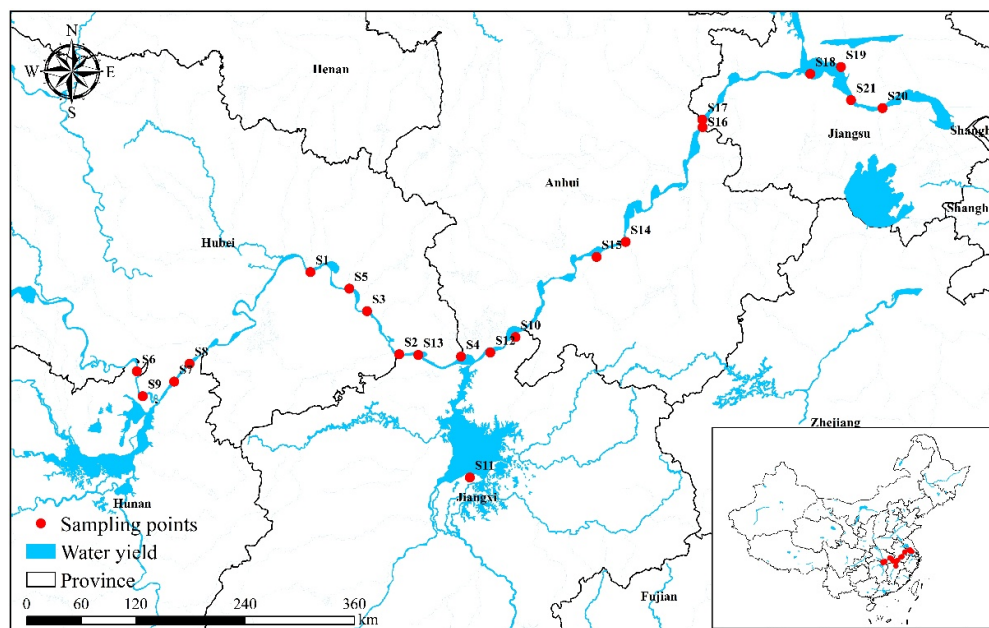
In this context, the present study investigated benthic macroinvertebrate communities along the Yangtze River mainstem from Hubei to Jiangsu. Specifically, we (i) characterized community composition and diversity patterns across river sections, (ii) evaluated spatial variation in community structure, and (iii) identified key environmental drivers using multivariate statistical approaches. The results provide new insights into the mechanisms underlying large-scale biodiversity patterns in the Yangtze River and offer a scientific basis for ecological restoration and refined management of the mainstem.

## 2. Materials and Methods

### 2.1. Study Area and Sampling Design

The study was conducted along the middle and lower reaches of the Yangtze River mainstem, spanning five provinces from Hubei to Jiangsu. This region is characterized by a subtropical monsoon climate, complex hydrological regimes, numerous tributaries, and diverse land-use patterns and channel morphologies along the river continuum.

Based on the distribution of national surface water quality monitoring sections and considering shoreline utilization and habitat characteristics, a total of 21 sampling sites were established along the mainstem (Figure 1), including 5 sites in Hubei, 4 in Hunan, 4 in Jiangxi, 4 in Anhui, and 4 in Jiangsu. Field investigations were conducted in April 2025, during which habitat conditions, anthropogenic disturbances, and physicochemical parameters were recorded at each site.



**Figure 1.** Distribution of sampling sites along the middle and lower Yangtze River mainstem.

### 2.2. Sample Collection and Identification

#### 2.2.1. Physicochemical Parameters

Water temperature (WT), pH, dissolved oxygen (DO), and electrical conductivity (EC) were measured in situ using a portable water quality analyzer (LH-T600). Water samples were collected

from surface, middle, and bottom layers using a 2 L water sampler, mixed thoroughly, and subsampled (2 L) for laboratory analysis. The samples were stored at low temperature and transported to the laboratory for further analysis. Total nitrogen (TN), total phosphorus (TP), ammonium nitrogen ( $\text{NH}_4^+\text{-N}$ ), and permanganate index ( $\text{COD}_{\text{Mn}}$ ) were determined following standard methods described in Standard Methods for the Examination of Water and Wastewater (4th edition).

### 2.2.2. Benthic Macroinvertebrates

Benthic macroinvertebrates were collected in the littoral zone using a D-frame net (30 cm diameter, 60 mesh). A multi-habitat sampling approach [27] was applied, with sampling effort allocated proportionally to habitat types within each site. Kick sampling, sweeping, and hand netting were combined to collect organisms. At each site, 20 subsamples were collected, covering a total sampling area of approximately 1.8 m<sup>2</sup>. In non-wadeable areas, a Peterson grab sampler (1/16 m<sup>2</sup>) was used, with three replicate samples collected per site. All samples were washed through a 60-mesh sieve, pooled into a composite sample, and preserved in 95% ethanol. In the laboratory, all individuals were sorted, identified, and counted, with identification performed to the lowest possible taxonomic level, typically genus or species [28-32].

## 2.3. Data Analysis

### 2.3.1. Diversity Indices

Dominant species were identified using the McNaughton dominance index ( $Y$ ), with species having  $Y > 0.02$  considered dominant. Community diversity was evaluated using the Shannon–Wiener diversity index ( $H'$ ) and Simpson index ( $D$ ), calculated as follows:

$$Y = (n_i/N) \times f_i \quad (1)$$

$$H' = - \sum_{i=1}^S (n_i/N) \ln(n_i/N) \quad (2)$$

$$D = 1 - \sum_{i=1}^S (n_i/N)^2 \quad (3)$$

where  $n_i$  is the abundance of the  $i$ -th taxon,  $N$  is the total abundance of all taxa, and  $f_i$  is the frequency of occurrence of the  $i$ -th taxon across sampling sites.

### 2.3.2. Statistical Analysis

One-way analysis of variance (ANOVA) was used to test differences in physicochemical parameters and community characteristics among river sections. A Bray–Curtis dissimilarity matrix was constructed based on species abundance data, and non-metric multidimensional scaling (NMDS) was applied to visualize differences in community composition. Permutational multivariate analysis of variance (PERMANOVA) was performed to test for differences in community composition among river sections, based on 999 permutations. To evaluate whether differences detected by PERMANOVA were influenced by heterogeneity of dispersion, a multivariate dispersion analysis (betadisper) was conducted.

Canonical correspondence analysis (CCA) was performed to identify the main environmental factors driving variation in community composition. The significance of the overall CCA model and

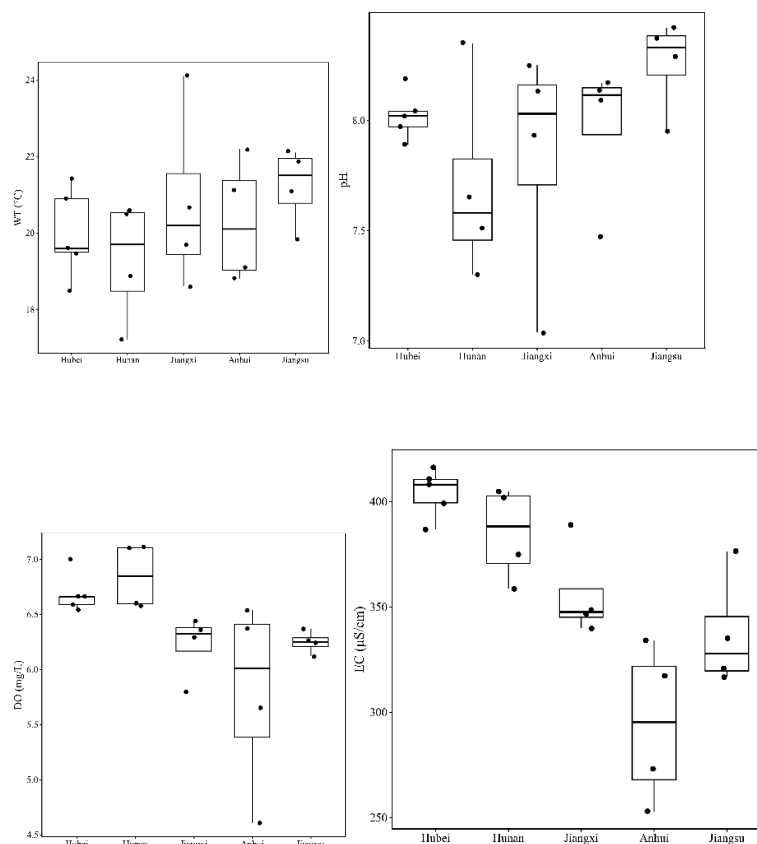
individual environmental variables was tested using Monte Carlo permutation tests. Environmental fitting (envfit) was further applied to quantify the correlations between environmental variables and ordination axes and to assess their statistical significance. Basic statistical analyses were conducted in Excel 2021, and all multivariate analyses were performed in R (version 4.5.2).

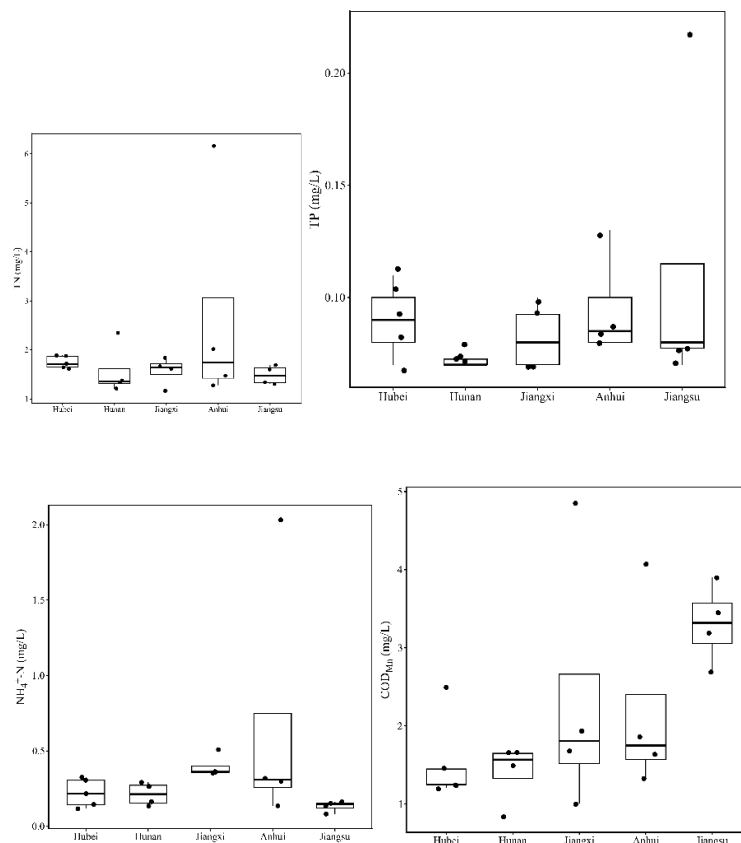
### 3. Results

#### 3.1. Spatial Variation in Physicochemical Parameters

Physicochemical parameters exhibited spatial variation among river sections along the middle and lower Yangtze River. Dissolved oxygen (DO) and electrical conductivity (EC) exhibited overall declining trends from upstream to downstream, with local fluctuations among river sections, whereas total nitrogen (TN), total phosphorus (TP), ammonium ( $\text{NH}_4^+\text{-N}$ ), and permanganate index ( $\text{COD}_{\text{Mn}}$ ) showed increasing trends. Lower DO and EC values were mainly observed in the Anhui section (**Figure 2**), while higher TN, TP, and  $\text{NH}_4^+\text{-N}$  concentrations were also concentrated in this section.  $\text{COD}_{\text{Mn}}$  reached its highest values in the Jiangsu section.

Among river sections, the highest mean EC was recorded in Hubei (404.24  $\mu\text{S}/\text{cm}$ ), while the highest mean DO occurred in Hunan (6.85 mg/L). The Anhui section exhibited the highest mean TN (2.74 mg/L) and  $\text{NH}_4^+\text{-N}$  (0.70 mg/L), whereas the Jiangsu section had the highest mean TP (0.11 mg/L) and  $\text{COD}_{\text{Mn}}$  (3.31 mg/L) (**Table 1**). One-way ANOVA indicated that DO and EC differed significantly among river sections ( $P < 0.05$ ), whereas WT, pH, TN, TP,  $\text{NH}_4^+\text{-N}$ , and  $\text{COD}_{\text{Mn}}$  showed no significant differences ( $P > 0.05$ ).





**Figure 2.** Spatial variation of physical and chemical parameters along the middle and lower Yangtze River mainstem.

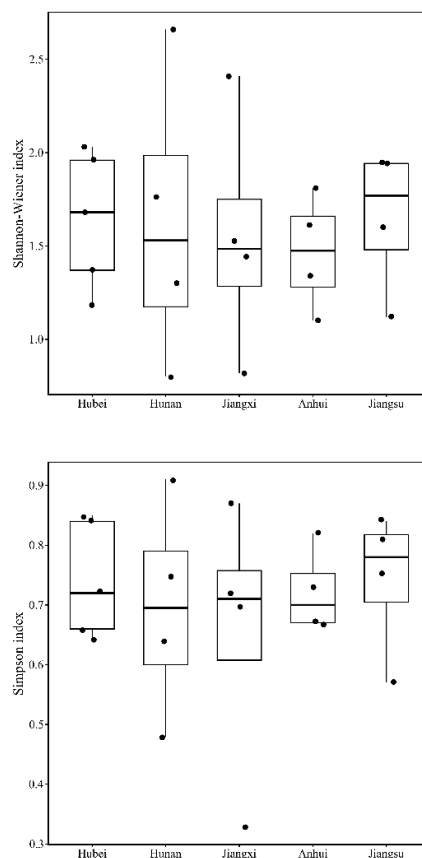
**Table 1.** Physical and chemical parameters along the middle and lower Yangtze River mainstem.

Physicochemical parameters		Hubei	Hunan	Jiangxi	Anhui	Jiangsu	<i>P</i>
WT (°C)	Mean ± SD	19.98 ± 1.16	19.30 ± 1.60	20.78 ± 2.38	20.33 ± 1.64	21.23 ± 1.04	0.51
	Min – Max	18.50 - 21.40	17.20 - 20.60	18.60 - 24.10	18.80 - 22.20	19.80 - 22.10	
pH	Mean ± SD	8.02 ± 0.11	7.70 ± 0.46	7.84 ± 0.55	7.97 ± 0.33	8.26 ± 0.21	0.29
	Min – Max	7.89 - 8.19	7.30 - 8.35	7.04 - 8.25	7.47 - 8.17	7.95 - 8.42	
DO (mg/L)	Mean ± SD	6.69 ± 0.18	6.85 ± 0.30	6.22 ± 0.29	5.79 ± 0.88	6.25 ± 0.10	0.02
	Min – Max	6.54 - 7.0	6.58 - 7.11	5.80 - 6.44	4.61 - 6.54	6.12 - 6.37	
EC (μS/cm)	Mean ± SD	404.24 ± 11.56	385.00 ± 22.22	356.11 ± 22.35	294.41 ± 37.92	337.22 ± 27.21	< 0.001
	Min – Max	386.72 - 416.52	358.59 - 404.87	339.99 - 389.19	252.73 - 334.24	316.87 - 376.28	
TN (mg/L)	Mean ± SD	1.74 ± 0.13	1.57 ± 0.52	1.57 ± 0.29	2.74 ± 2.31	1.49 ± 0.19	0.43
	Min – Max	1.61 - 1.89	1.21 - 2.34	1.17 - 1.84	1.28 - 6.17	1.30 - 1.69	
TP (mg/L)	Mean ± SD	0.09 ± 0.02	0.08 ± 0.01	0.08 ± 0.02	0.09 ± 0.02	0.11 ± 0.07	0.59
	Min – Max	0.07 - 0.11	0.07 - 0.08	0.07 - 0.10	0.08 - 0.13	0.07 - 0.22	
NH <sub>4</sub> <sup>+</sup> -N (mg/L)	Mean ± SD	0.22 ± 0.09	0.21 ± 0.08	0.40 ± 0.08	0.70 ± 0.89	0.13 ± 0.04	0.30
	Min – Max	0.12 - 0.32	0.13 - 0.29	0.35 - 0.51	0.14 - 2.03	0.08 - 0.16	
COD <sub>Mn</sub> (mg/L)	Mean ± SD	1.53 ± 0.55	1.41 ± 0.38	2.37 ± 1.71	2.22 ± 1.24	3.31 ± 0.51	0.09
	Min – Max	1.21 - 2.49	0.84 - 1.65	1.01 - 4.86	1.33 - 4.06	2.69 - 3.90	

### 3.2. Community Composition and Structure of Benthic Macroinvertebrates

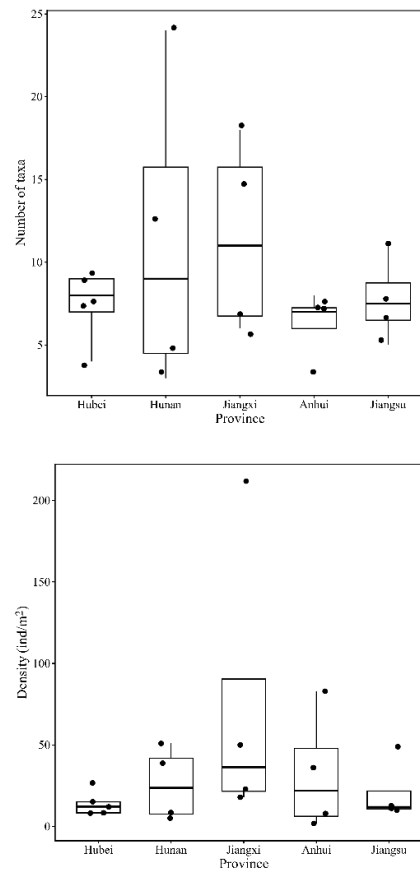
A total of 74 taxa were identified, belonging to 3 phyla, 7 classes, 17 orders, and 37 families. Insecta was the most diverse group, comprising 46 species from 17 families, followed by Malacostraca (9 species, 8 families). Mollusca included Gastropoda (8 species, 6 families) and Bivalvia (5 species, 3 families), while Annelida was represented by Oligochaeta (4 species) and one species each of Polychaeta and Hirudinea.

The dominant species across the study area were *Cricotopus trifasciatus* ( $Y = 0.08$ ) and *Limnoperna fortunei* ( $Y = 0.04$ ). The Shannon–Wiener diversity index ranged from 1.47 to 1.65, and the Simpson index ranged from 0.66 to 0.74 among river sections (Figure 3), with no significant differences detected ( $P > 0.05$ ).



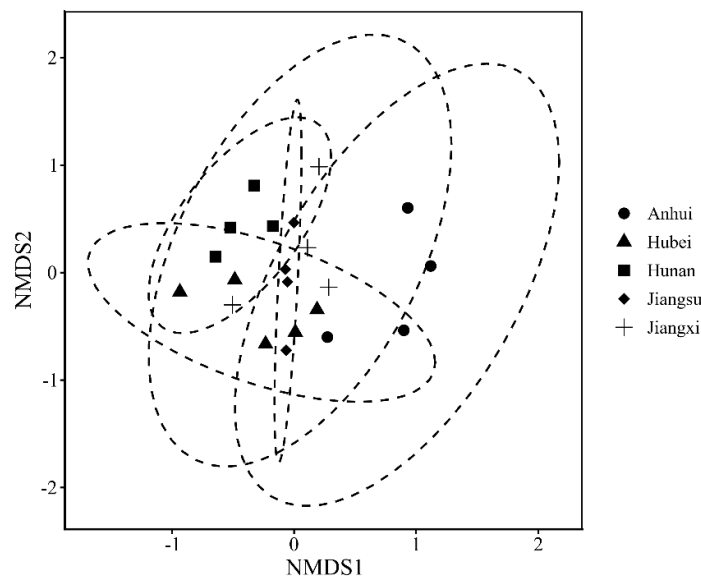
**Figure 3.** Biodiversity indices along the middle and lower Yangtze River mainstem.

Among river sections, the highest species richness was observed in the Jiangxi section (35 taxa), with a density of 75.56 ind/m<sup>2</sup> (Figure 4). Dominant species included *Cricotopus trifasciatus*, *Glyptotendipes cauliginellus*, and *Limnoperna fortunei*. The Hunan section followed, with 34 taxa and a density of 25.83 ind/m<sup>2</sup>, where *Lithoglyphopsis* sp., Ephydridae sp., and *Psychoda alternata* were dominant. The Hubei section recorded 22 taxa with a density of 14.11 ind/m<sup>2</sup>, dominated by *Limnoperna fortunei*, *Macrobrachium nipponense*, and *Psychoda alternata*. The Jiangsu section contained 21 taxa with a density of 20.70 ind/m<sup>2</sup>, and dominant species included *Cricotopus trifasciatus*, *Limnoperna fortunei*, and *Rhagio* sp. The Anhui section had the lowest richness (18 taxa) with a density of 32.09 ind/m<sup>2</sup>, dominated by *Stictochironomus akizukii*, *Chironomus flaviplumus*, and *Microchironomus tener*.



**Figure 4.** Taxa richness and density along the middle and lower Yangtze River mainstem.

NMDS ordination based on Bray–Curtis distances showed a moderate separation of samples among river sections (**Figure 5**), with a stress value of 0.184, indicating a moderate representation of community patterns. PERMANOVA further confirmed significant differences in community composition among river sections ( $R^2 = 0.27$ ,  $F = 1.51$ ,  $P = 0.001$ ). The betadisper analysis showed no significant differences in dispersion among groups ( $P = 0.152$ ), suggesting that the observed differences were primarily due to shifts in community centroid positions rather than dispersion.



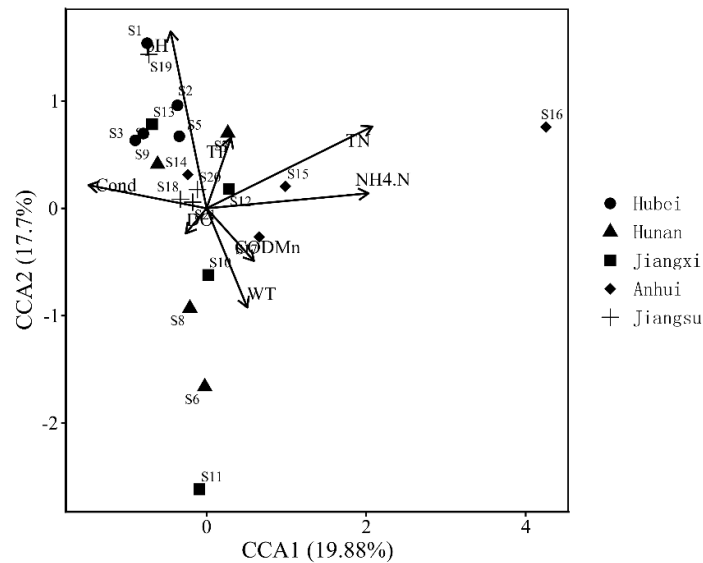
**Figure 5.** NMDS ordination of benthic macroinvertebrate community composition along the middle and lower Yangtze River mainstem.

### 3.3. Relationships between Benthic Communities and Environmental Factors

The CCA results showed that the first two canonical axes explained 20.00% and 16.71% of the variation in the species–environment relationship, respectively, with a cumulative explanation of 36.71% (**Figure 6**), indicating that additional unmeasured factors (e.g., hydrodynamics or substrate heterogeneity) may also contribute to community variation. The overall CCA model was significant ( $F = 1.27$ ,  $P = 0.013$ ), supporting the role of environmental variables in structuring community composition.

The envfit analysis revealed that TN ( $R^2 = 0.94$ ,  $P = 0.001$ ),  $\text{NH}_4^+\text{-N}$  ( $R^2 = 0.83$ ,  $P = 0.023$ ), pH ( $R^2 = 0.46$ ,  $P = 0.006$ ), and EC ( $R^2 = 0.35$ ,  $P = 0.020$ ) were significantly correlated with community variation. In the ordination space, TN and  $\text{NH}_4^+\text{-N}$  were primarily aligned along the positive direction of CCA1, whereas pH and EC were associated with CCA2, indicating that nutrient gradients and physicochemical conditions jointly structured community distribution patterns.

Sampling sites exhibited spatial differentiation in the ordination space. Site S16 (Anhui section) was located at the positive end of CCA1 and showed strong associations with TN and  $\text{NH}_4^+\text{-N}$ . Several sites in the Hunan section (e.g., S6 and S8) were distributed along the negative direction of CCA2 and were related to water temperature. In contrast, most sites in the Hubei, Jiangxi, and Jiangsu sections were clustered near the center of the ordination, reflecting combined influences of multiple environmental factors.



**Figure 6.** CCA ordination of benthic macroinvertebrate community composition along the middle and lower Yangtze River mainstem.

#### 4. Discussion

A total of 74 species belonging to 3 phyla, 7 classes, 17 orders, 37 families, and 58 genera were recorded, with aquatic insects dominating the assemblages. This pattern is consistent with previous studies [22,33–36] and reflects a typical characteristic of benthic communities in large river systems. Such dominance is likely associated with strong hydrodynamic conditions and relatively homogeneous substrates, which favor taxa with short life cycles, high reproductive capacity, and strong environmental tolerance, such as Chironomidae [37,38].

The prevalence of tolerant taxa, including *Prosilocerus akamusi* and bivalves, may indicate that the current community structure has been influenced by long-term anthropogenic disturbances. These taxa are well adapted to environments with elevated organic matter and hydrodynamic disturbance [39,40], and their dominance may reflect a moderately impacted ecological condition in the middle and lower reaches of the Yangtze River. This interpretation is consistent with previous findings that human activities can promote the proliferation of opportunistic and pollution-tolerant species, thereby altering community composition and ecosystem functioning.

In terms of alpha diversity, no significant differences were observed among river sections based on the Shannon–Wiener and Simpson indices, which is consistent with earlier studies [41]. This pattern may be attributed to the strong hydrological connectivity and water exchange in the Yangtze River mainstem, which facilitate species dispersal and promote community homogenization across large spatial scales. However, multivariate analyses (NMDS and PERMANOVA) revealed significant differences in community composition among river sections, indicating that spatial variation is primarily driven by species turnover rather than differences in overall diversity levels [42]. This decoupling between alpha and beta diversity highlights the importance of considering compositional heterogeneity in large river systems.

The betadisper results showed no significant differences in dispersion among groups, suggesting that the observed differences were mainly due to shifts in community centroids rather than differences in within-group variability [43].

Spatial heterogeneity in benthic assemblages is likely driven by a combination of longitudinal environmental gradients, hydrological conditions, and land-use patterns along the river [44–46]. For example, the Jiangxi section exhibited relatively higher species richness and density, which may be associated with more complex habitat structures or greater resource availability. In contrast, the Anhui section showed lower species richness but higher dominance of certain chironomid taxa, which may be related to elevated nutrient concentrations and organic enrichment. Previous studies have demonstrated that eutrophication can promote the expansion of tolerant or opportunistic species, leading to shifts in community composition [47,48].

Environmental driver analysis based on CCA indicated that nutrient variables (TN and  $\text{NH}_4^+\text{-N}$ ), as well as pH and conductivity, are important factors associated with variation in benthic community structure. TN and  $\text{NH}_4^+\text{-N}$  showed significant correlations with ordination axes, suggesting that nutrient gradients play an important role in shaping spatial patterns of benthic assemblages. Increased nutrient levels can enhance primary productivity and organic matter accumulation [49,50], thereby altering sediment characteristics [51] and influencing benthic habitats. Meanwhile, pH and conductivity reflect broader hydrochemical conditions, which may be affected by geological background, tributary inputs, and anthropogenic activities [52–54]. The clustering of sites in the Anhui section along nutrient gradients further supports the potential influence of eutrophication on local communities.

It should be noted that the explanatory power of the CCA model was moderate, indicating that additional unmeasured factors may also contribute to community variation. These may include hydrodynamic conditions, substrate heterogeneity, and biotic interactions, which were not explicitly quantified in the present study. Incorporating such variables in future studies would help to improve the understanding of mechanisms underlying benthic community dynamics.

From a biodiversity perspective, the observed spatial variation highlights the importance of beta diversity in large river ecosystems. Although alpha diversity remained relatively stable, species turnover contributed substantially to regional diversity patterns, emphasizing the need to incorporate multiple diversity metrics in ecological assessments.

Overall, the results suggest that benthic macroinvertebrate assemblages in large river systems are jointly regulated by regional-scale environmental gradients and local habitat conditions. These findings have important implications for river management, emphasizing the need for nutrient control, habitat restoration, and maintenance of hydrological connectivity. Future research should incorporate multi-temporal data and hydrodynamic processes to further elucidate the mechanisms driving community dynamics.

## 5. Conclusions

This study investigated benthic macroinvertebrate diversity and its environmental drivers along the middle and lower reaches of the Yangtze River. Aquatic insects dominated the assemblages, and although alpha diversity remained relatively stable among river sections, significant spatial variation in community composition was observed, primarily driven by species turnover.

Nutrient variables (TN and  $\text{NH}_4^+\text{-N}$ ), along with pH and conductivity, were identified as key factors influencing community structure, highlighting the importance of water quality and hydrochemical conditions.

This study emphasizes the role of beta diversity in shaping biodiversity patterns in large river systems and provides insights for biodiversity conservation and ecological management.

**Author Contributions:** Methodology, Ying W.; software, Y.C. and H.S.; validation, J.W., H.S. and G.N.; formal analysis, Y.C. and P.C.; investigation, Y.C., P.C. and J.W.; resources, L.G.; data curation, X.W. and Yu W.; writing—original draft preparation, Y.C.; writing—review and editing, P.C., H.S. and G.N.; visualization, J.W.; supervision, Q.H.; project administration, X.J.; funding acquisition, L.G. All authors have read and agreed to the published version of the manuscript.

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**Conflicts of Interest:** The authors declare no conflicts of interest.

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