Postprint: Species Diversity and Functional Diversity of Benthic Macroinvertebrates in the Xin Xue River

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Abstract

Investigating the relationship between functional diversity and species diversity and their variation patterns along environmental gradients helps to understand the coexistence mechanisms of organisms in communities; however, studies on the relationship between the two are still rarely reported in freshwater ecology. Through seasonal surveys of benthic animals in typical reaches of the Xin Xue River (A: slow-flow reach, B: intermittent-flow reach, C: organic pollution reach, D: control reach, E: human-disturbance reach), we studied the spatiotemporal dynamics and relationship between species diversity and functional diversity. The results showed that: along the spatial sequence, species diversity indices were all lowest in reach B, indicating that intermittent flow interruption has a significant impact on species diversity. Functional richness was highest in reach D and lowest in reach A; functional evenness was higher in reach A than in other reaches; functional divergence was highest in reaches A and B, and lowest in reach D. Along the temporal sequence, the mean values of species richness and Shannon index were lowest in October and highest in April; the evenness index was lowest in December and highest in October. The three functional diversity indices differed significantly among seasons and were independent of each other, mainly influenced by hydrological conditions and the life history of benthic animals. Correlation analysis showed that there was no significant correlation among functional diversity indices; functional richness was significantly correlated with species richness and Shannon index, and functional evenness was significantly correlated with species evenness. Stepwise regression analysis found that functional richness was significantly affected by species richness and Shannon index, and functional evenness was significantly affected by species evenness; the overall goodness-of-fit between functional diversity and species diversity indices was not high. The research results further indicated that: compared with species diversity, functional diversity responds more comprehensively

to habitat gradient changes.

Full Text

Preamble

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Study of Macroinvertebrate Species and Functional Diversity in the New Xue River, Shandong Province, China

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Abstract

Understanding the relationship between functional and species diversity and their variation along environmental gradients is crucial for elucidating species coexistence mechanisms in ecological communities. However, such research remains scarce in freshwater ecology. This study investigated the spatiotemporal dynamics of species diversity and functional diversity indices and their relationships in typical reaches of the New Xue River, including an organically polluted reach.

In the spatial sequence, functional evenness was lowest in reach B, indicating that intermittent disconnection significantly impacted species diversity. Functional richness was highest in reach D and lowest in reach A, while functional evenness was highest in reach A and functional divergence was highest in reaches A and B but lowest in reach D.

In the temporal sequence, mean values of species richness and Shannon index were lowest in October and highest in April, whereas the evenness index was lowest in December and highest in October. The three functional diversity indices differed significantly among seasons and were primarily influenced by hydrological conditions and benthic animal life history traits.

Correlation analysis revealed no significant correlations among the functional diversity indices themselves. Functional richness was significantly correlated with species richness and Shannon index, while functional evenness was significantly correlated with species evenness. Stepwise regression analysis showed that functional richness was significantly affected by species richness and Shannon index, and functional evenness was significantly affected by species evenness. The overall fitting degree between functional diversity and species diversity indices was not high.

These results demonstrate that functional diversity provides a more comprehensive response to habitat gradient changes compared to species diversity alone.

Keywords: macroinvertebrate; functional diversity; species diversity; the New Xue River

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Introduction

Species diversity has been widely used to characterize biodiversity in stream macroinvertebrate ecology research [1-4]. An increasing number of studies confirm that trait-based approaches provide more information for understanding important ecological processes such as ecosystem functioning and community composition than simple species diversity metrics [5-6]. Biodiversity research has expanded to the functional level, with functional diversity becoming a central focus in current macroinvertebrate ecology [7].

Investigating the relationship between species diversity and functional diversity helps illuminate interspecific coexistence mechanisms [8-9] and niche complementarity [10], representing a key component in studying biodiversity effects on ecosystem functioning [11]. Compared to plant functional diversity research, animal functional diversity studies in China started relatively recently, with only sporadic reports emerging in recent years [7,12]. Research on the relationship between macroinvertebrate functional diversity and species diversity remains limited.

The relationship between functional and species diversity depends on the ecosystem type and context [13]. Some studies have found significant positive correlations between functional diversity and species diversity [14], while others suggest they are independent [15-16]. Many studies have not considered the multifaceted nature of functional diversity, which includes three independent components: functional richness, functional evenness, and functional divergence [11]. The precise relationships among these components and with species diversity warrant further investigation [17].

Community responses to environmental change depend primarily on species functional trait composition [18], and studying biodiversity patterns along environmental gradients aids in understanding the direct effects of habitat heterogeneity on diversity [9]. This study selected representative reaches in the New Xue River, Shandong Province, to investigate seasonal dynamics of stream macroinvertebrate diversity along environmental gradients, aiming to clarify how species diversity and functional diversity change with environmental conditions and to provide baseline data and theoretical foundations for future research.

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1. Regional Overview and Sampling Site Selection

The New Xue River is located in southwestern Shandong Province and belongs to the Nansi Lake water system. The study area is situated below the Shizui Reservoir dam, covering a length of 89.6 km with a catchment area of 686 km^2. Based on habitat characteristics, we established five sampling reaches:

- **Reach A**: Located immediately below the Shizui Reservoir dam. Flow is limited by upstream reservoir discharge, and the channel frequently experiences drying.
- **Reach B**: Downstream, adjacent to Shanting District of Zaozhuang City. Receives urban sewage after sedimentation treatment. Population is relatively dense.
- **Reach C**: Downstream of Shanting District. Intermittently affected by human disturbance.
- **Reach D**: Farther from urban areas, with relatively good habitat quality. Dominated by slow flow and still water with abundant sediments.
- **Reach E**: Additional reference reach with minimal disturbance.

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2. Macroinvertebrate Collection and Identification

From April 2012 to April 2013 (with the exception of January and February 2013), benthic macroinvertebrates were collected monthly at mid-month. A Surber sampler (0.09 m^2) was used to collect three replicate samples at each reach along the flow direction. Macroinvertebrates were picked from the net, placed in specimen bottles, and fixed with 10% formalin solution. In the laboratory, specimens were identified to the lowest possible taxonomic level and counted [19-21]. A total of 180 samples were collected across all reaches and sampling dates.

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3. Functional Traits and Biodiversity Calculations

Functional traits were primarily determined based on relevant literature [22-24], with trait assignments for specific taxa based on specimen characteristics or taxonomic descriptions. Nine traits were included in the analysis: voltinism, size at maturity, occurrence in drift, swimming ability, attachment morphology, body shape, rheophily, thermal preference, and trophic habit. Trait categories and levels follow previous studies [7,22].

Species diversity indices included species richness, Shannon index, and species evenness index. Functional diversity indices comprised functional richness (FRic), functional evenness (FEve), and functional divergence (FDiv), calculated following established methods [3,26]. The formulas are as follows:

- **Functional richness (FRic)**: Measures the amount of niche space occupied by species in community i, where Rc is the absolute range of trait c and $SFci$ is the niche space occupied by community i.
- **Functional evenness (FEve)**: Calculated as the sum of minimum values of local weighted evenness ($PEWi$) for each species i across all traits, where S is species richness.
- **Functional divergence (FDiv)**: Calculated using the formula involving the weighted mean of natural logarithms of species trait values.

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4. Data Analysis

All statistical analyses were performed using R version 3.1.3 with the FDiversity package [27] and IBM SPSS Statistics 19.0. One-way ANOVA was used to compare spatiotemporal differences in diversity indices. Pearson correlation analysis examined relationships among biodiversity indices, while partial correlation analysis assessed relationships between functional evenness and functional divergence controlling for species evenness. Stepwise regression analysis evaluated the effects of species diversity on functional diversity. Figures were prepared using OriginPro and Excel 2007.

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1. Spatiotemporal Patterns of Species Diversity

Statistical analysis of spatial patterns revealed that species diversity indices varied significantly among reaches ($p < 0.05$). Mean species richness ranged from 12.5 to 17.7 across reaches A, C, D, and E, while Shannon index values ranged from 1.3 to 2.0. Evenness index means ranged from 0.53 to 0.75, with reach B showing significantly lower values than other reaches ($p < 0.05$).

Seasonal dynamics analysis showed that species richness and Shannon index were lowest in October (9.8 and 1.6, respectively) and highest in April (18.6 and 2.0, respectively; $p < 0.05$). The evenness index was lowest in December (0.53) and highest in October (0.73; $p < 0.05$) [Figure 2: see original paper].

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2. Spatiotemporal Patterns of Functional Diversity

Spatial analysis of functional diversity indices indicated that functional richness was highest in reach D (40.4) and lowest in reach A (23.5; $p < 0.05$). Functional evenness was highest in reach A (0.90) and lowest in reach D (0.40; p

< 0.05). Functional divergence was highest in reaches A and B (0.74 and 0.75, respectively) and lowest in reach D (0.56; $p < 0.05$) [Figure 3: see original paper].

Seasonal dynamics of functional diversity showed that functional richness was highest in April (41.0) and lowest in December (24.7; $p < 0.05$). Functional evenness was highest in October (0.62) and lowest in April (0.42; $p < 0.05$). Functional divergence was highest in December (0.88) and significantly lower in April and October ($p < 0.05$) [Figure 4: see original paper]. The three functional diversity indices showed independent variation patterns across seasons.

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3. Relationships Between Species Diversity and Functional Diversity

Pearson correlation analysis revealed that functional richness was significantly correlated with species richness ($r = 0.603$, $p < 0.01$) and Shannon index ($r = 0.487$, $p < 0.05$). Functional evenness was significantly correlated with species evenness ($r = 0.364$, $p < 0.05$). The correlation between functional divergence and species evenness approached significance ($r = 0.345$, $p = 0.052$). No significant correlations were detected among the three functional diversity indices ($p > 0.05$) .

Given the significant correlation between functional evenness and functional divergence with species evenness, we conducted partial correlation analysis controlling for species evenness. The results confirmed that functional evenness and functional divergence were not significantly correlated ($p > 0.05$), further supporting their independence.

Stepwise regression analysis demonstrated that species richness and Shannon index significantly influenced functional richness ($p < 0.05$), while species evenness significantly affected functional evenness ($p < 0.05$). The overall fitting degree between functional diversity and species diversity indices was relatively low ($R^2 < 0.364$), indicating complex non-linear relationships [Figure 5: see original paper].

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3. Discussion

Analysis of species diversity patterns revealed that reach B, which experiences intermittent disturbance, showed higher species richness than reach A, consistent with the intermediate disturbance hypothesis [28]. Reach A, characterized by frequent channel drying, exhibited the lowest values for all species diversity metrics (species richness, Shannon index, and evenness index), indicating that flow intermittency had the greatest impact on benthic community structure within the watershed.

In the temporal sequence, species richness in October was significantly lower than in other months, while the Shannon index showed similar trends to the evenness index, suggesting that species evenness exerted greater influence than species richness on the Shannon index. The higher species richness and Shannon index in April primarily resulted from abundant water flow during this period, which expanded bottom habitats and facilitated aggregation of various benthic taxa [29]. Benthic densities in April, October, and December were 896, 5259, and 13352 individuals/m^2, respectively, indicating that species richness had greater influence on the Shannon index than species evenness across the temporal gradient.

Functional richness, which measures the niche space occupied by species, was lower in slow-flowing reach D compared to other reaches, including reach A with the lowest species richness, suggesting that flow regime significantly influences functional richness. Conversely, functional richness was higher in reach A than in other reaches despite its low species richness, indicating that functional richness responds more comprehensively to environmental pressure than species richness alone. Low functional richness implies substantial unutilized resources in the community [17].

Functional evenness measures whether species traits are regularly distributed within the occupied trait space. Low functional evenness indicates underutilized or overutilized resources and can serve as an indicator of productivity and invasion resistance [11]. Reach A exhibited the highest functional evenness, primarily due to its low benthic density and relatively uniform functional trait composition. In contrast, reach D showed the lowest functional evenness because urban sewage discharge promoted benthic algal growth, allowing algivorous chironomid larvae (e.g., *Orthocladius vaillanti*, *Neozarelia* sp., and *Chaetocladius* sp.) to dominate absolutely, with three taxa comprising 39.6% of relative abundance.

Functional divergence reflects the degree of niche complementarity among species, with high values indicating minimal niche overlap and efficient resource utilization [11,25]. High functional divergence in reaches A and B resulted from low species richness and consequently reduced trait overlap. According to the calculation method [26], the high functional divergence in reach A was mainly attributed to *Paratanytarsus* sp. E, which occupied marginal positions in the trait niche space, accounting for 63% of relative abundance.

In the temporal sequence, the three functional diversity indices showed independent variation patterns. Functional richness was lowest in October primarily because spring represents an important emergence period for aquatic insects, during which some traits disappear or decrease as insects leave the community. Functional evenness was higher in October than in April because stable hydrological conditions in October allowed competitively dominant species to proliferate, leading to more uneven distribution of biological traits. Functional divergence was highest in December because emergence of chironomids and other aquatic insects, especially dominant groups, reduced overall trait overlap.

The independence among functional diversity indices and between functional and species diversity indices suggests that significant associations, when present, result from ecological processes rather than mathematical artifacts [11]. The lack of significant correlations among functional diversity indices in the New Xue River macroinvertebrate community confirms their independence. The Shannon index, influenced by both species richness and evenness [30], showed significant correlations with both, as expected.

While changes in species diversity are widely recognized to cause corresponding changes in functional diversity, the specific relationship remains unknown in many ecosystems [31]. Our finding that functional richness is significantly affected by species richness and Shannon index aligns with niche partitioning theory, where increased species number leads to finer niche differentiation [32-33]. However, we note that functional diversity-species diversity relationships vary across ecosystems. For instance, Devictor et al. [35] found functional diversity decreased with increasing species richness. Functional evenness and divergence are primarily influenced by functional trait distribution rather than species richness, though species evenness can affect trait distribution to varying degrees, consistent with Xue et al. [17].

The generally low fitting degree between functional diversity and species diversity indices suggests complex non-linear relationships [36]. Zhang et al. [36] proposed that such non-linear relationships indicate functional diversity provides unique information complementary to species diversity. Our results support this conclusion, demonstrating that functional diversity offers a more comprehensive perspective on habitat gradient responses than species diversity alone.

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Note: Figure translations are in progress. See original paper for figures.