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Keywords: fish diversity; environmental DNA; economic development



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Article

Positive Correlation Between Economic Activities and Fish Diversity in Small River Basins of Less Developed Regions

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Simple Summary

Economic activities exert extensive impacts on fish. In this study, we employed environmental DNA (eDNA) technology to conduct surveys in the Lixian River basin, where economic development exhibits a gradient pattern. The results indicated that fish communities showed an obvious gradient variation from the upstream to the downstream. Surprisingly, we found significant positive correlations between agricultural population, total grain production, total population, and the diversity index. This suggests that in less economically developed regions, the development of local economic activities may enhance fish diversity, revealing a potential synergistic relationship between economic activities and fish diversity in small-scale river basins and providing a new perspective for understanding economic-ecological interactions.

Abstract

(1) Background: Affected by multiple factors, the decline of fish species diversity in some aquatic ecosystems has become increasingly pronounced. At a broad spatial scale, economic development has been widely recognized as one of the key factors influencing the fish distribution pattern. However, at a small scale, within a single river basin, effects of economic development on the freshwater fish distribution and communities remain largely uninvestigated. **(2) Methods:** environmental DNA (eDNA) samples were collected from 26 sampling sites of the Lixian River in both the summer (June) and winter (November). Economic data from the Lixian River basin were collected, and analyses including multivariate regression tree analysis and generalized linear model fitting were performed using R software. **(3) Results:** A total of 65 fish species was characterized, and the Chao 1 diversity indices in the upstream (13.42) and downstream (13.00) were significantly higher than that in the middle reaches (8.55, $P < 0.01$) of this river. The species communities exhibited a obvious gradient changing pattern from the up- to the downstream, with parameters of water quality including transparency, pH, dissolved oxygen and temperature and climatic factors functioning as the key variables. Furthermore, the analysis of generalized linear model revealed significant positive correlations between agricultural population ($P = 0.00106$), total grain production ($P = 0.00476$), total population ($P = 0.00192$) and Chao 1 index. **(4) Conclusion:** Climatic factors are the key factors affecting the fish diversity in the Lixian River. In less economically developed areas, the development of local economic activities may enhance fish diversity.

Keywords: fish diversity; environmental DNA; economic development

1. Introduction

Over 10,000 fish species inhabit freshwater environments around the world [1], they account for about 40% of global fish and one-quarter of all vertebrate species [2]. Over the past half century, freshwater ecosystems have experienced a significant decline in fish species diversity due to habitat destruction, climate change, introduction of non-native species, and so on [3,4]. Changes in fish species composition and distribution always serve as effective indicators of aquatic ecosystems health; thus, monitoring fish diversity has long been proposed as a critical first step in developing and implementing effective conservation and management strategies [5].

Currently, there is no consensus on the main drivers shaping fish diversity and community composition [6]. Natural biogeographic factors such as climate and geographic features are widely recognized as interactively affecting key factors in large-scale fish diversity and distribution [7–9]. However, in recent years, human-induced disturbances have significantly altered environmental conditions and profoundly impact on biodiversity patterns [10]. Besides, socio-economic factors, including population growth, economic development, urbanization, and fishery-related activities such as overfishing and the introduction of non-native species, have increasingly emerged as significant drives of fish diversity [4,11,12]. Therefore, quantifying the effects of anthropogenic factors on biodiversity is crucial for ensuring the health and sustainable development of ecosystems [13]. Existing researches on large-scale freshwater systems have consistently shown that, socio-economic development is a key factor contributing to the decline of fish diversity. Specifically, the population and economic growth in North America has been reported to be the primary drivers of freshwater fish diversity loss [14]. Similarly, deleterious effects of increases in national economic level on threatened fish species have been pointed out more earlier [15]. In addition, a study found that the species richness of freshwater fish is not only related to physical geography and climate factors such as rainfall, air temperature, and the area of surface water bodies, but also positively correlated with the inland fishery production in China [16]. However, at a small scale, within a single river basin, effects of economic development on the freshwater communities remain largely uninvestigated.

The environmental DNA (eDNA) technique has emerged as an innovative and effective technology in fish diversity monitoring in recent years [17]. Compared to traditional fishing methods, the eDNA technique offers several advantages including high sensitivity and efficiency, cost-effectiveness, and environmental friendliness [18]. Besides fish diversity, it has also been extensively applied in the monitoring of invasive aquatic species [19,20], tracking endangered species [21,22], as well as the assessment of species abundance and biomass across various aquatic organisms [23,24]. Notably, this technique can successfully detect target species at density as low as 1 - 2 individuals per square kilometer [25]. Additionally, by integrating environmental factor data, the eDNA technique can effectively address challenges that traditional methods cannot. For example, by employing an eDNA-based multitrophic-level biological monitoring dataset, interactive effects of dams and nutrient enrichment on aquatic communities at the levels of α -diversity, β -diversity, and food webs have been successfully developed [26].

The Lixian River, a first-order tributary of the Honghe River, stretches for 427 km within Yunnan Province, featuring a natural drop of 1,980 m, a drainage area of 20,140 km², and an average annual flow rate of 470 m³/s. As a typical mountainous river, it is characterized by fast water flow and rich fish resources [27,28]. Originating in Dali, this river flows through several counties with different levels of socio-economic development, including Jingdong Yi Autonomous County, Zhenyuan Yi, Hani and Lahu Autonomous County, Mojiang Hani Autonomous County, Ning'er Hani and Yi Autonomous County, and Jiangcheng Hani and Yi Autonomous County. Jingdong and Zhenyuan counties, located in the upper reaches of the Lixian River basin, are important production areas for grains, sugarcane, walnuts, and tropical fruits in Yunnan Province. Mojiang County in the middle reaches mainly cultivates food crops such as rice and corn, and it also focus on three key agricultural industries, namely tea, pig farming, and purple rice production. As the origin of the Ancient Tea-Horse Road, Ning'er County is predominantly renowned for its agricultural specialties, including tea, coffee, and Chinese herbal medicines. Jiangcheng County and Lüchun County in the lower reaches

mainly engage in characteristic industries such as cultivation of rubber, tea, star anise, and pepper. Moreover, this area has the only soluble potash deposit in China.

To investigate the influence of economic development on the diversity and distribution patterns of freshwater fish within a relatively small-scale area, and to provide new insights into the ecological conservation of mountainous river ecosystems, eDNA samples were collected at 26 sampling sites across the Lixian River basin in Yunnan Province in both summer and winter. Fish species were identified, and the diversity and distribution patterns in the up-, mid- and down-stream reaches of this river were comparatively analyzed. Furthermore, the environmental and economic factors that drive these patterns within this river were also investigated.

2. Materials and Methods

2.1. Sample Collection

A total of 26 sampling sites were set up within the Lixian River basin (Figure 1), L1 -L9, L10-L19, and L20-L26 were located in the upstream, midstream, and downstream of this river, respectively. eDNA samples were collected in both summer (June) and winter (November) of 2023, based on a protocol of a previous study [29]. In brief, three replicates and one negative control were collected at each site in each season, and all samples were filtered using a 0.45 μm mixed cellulose ester membrane under vacuum within 24 hours. After the filtration, all membranes were stored at -20 °C until use.

During the sample collection at each site, indicators of water quality including dissolved oxygen (DO), water temperature (Temp), pH, electrical conductivity (EC), salinity (SAL) and water transparency (WT) were simultaneously measured by a portable dissolved oxygen tester (HACH, USA), a pH meter, a conductivity meter, a salinity meter (all SMART SENSOR, China), and a Secchi disk (Table S1).

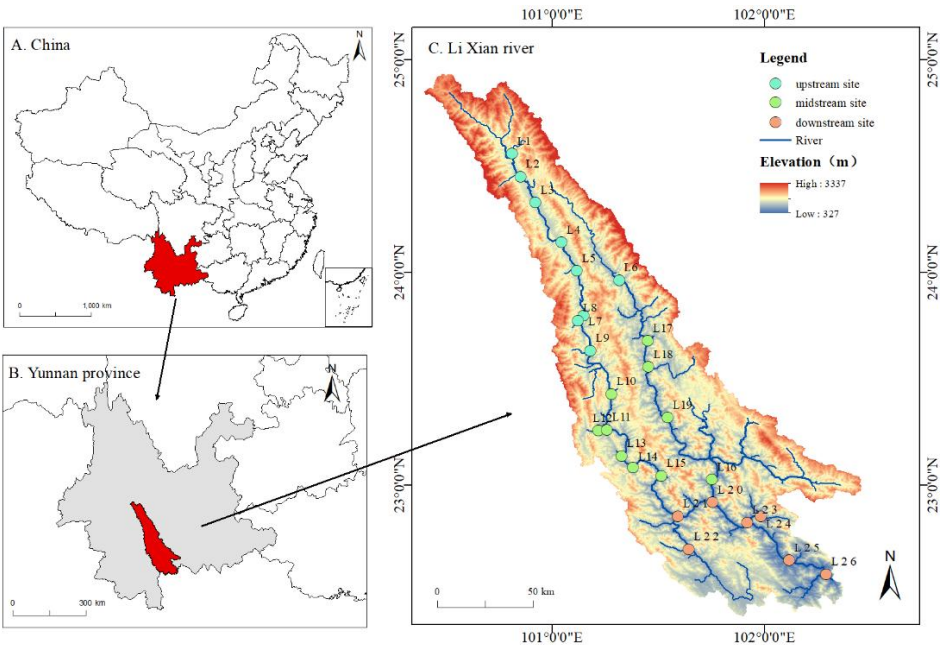


Figure 1. Distribution of eDNA water sampling sites in the Lixian River. A: Map of China, with the Yunnan Province in red. B: Map of Yunnan Province, with Lixian River basin in red. C: Map of the Lixian River basin, where L1-L26 indicates the sampling sites, with filling color of blue, green and organe indicating the up-, mid-, and downstream sites, respectively.

2.2. Total eDNA Extraction and Sequencing

eDNA was extracted from the filtered membranes using the Fast DNA[®] SPIN Kit for Soil (MP Biomedicals, USA) following the manufacturer's protocol. The integrity and quality of each extracted DNA were evaluated by agarose gel electrophoresis, and quantification was performed using a NanoDrop 2000 Spectrophotometer (Thermo Fisher Scientific, USA) and Qubit 3.0 Fluorometer (Thermo Fisher Scientific, USA). The mitochondrial 12S rRNA gene hypervariable region was amplified using Tele02_F/R (Tele02-F: 5'-AAACTCGTGCCAGCCACC-3'; Tele02-R: 5'-GGGTATCTAATCCCAGTTTG-3'[30]). The PCR was carried out in a 10 µL volume, consisting of 1 µL 10× Toptaq Buffer (Transgen, China), 0.8 µL dNTPs (2.5 mM), 2 µL template DNA, 0.2 µL each of forward and reverse primers (10 µM) and 0.2 µL Toptaq DNA Polymerase (Transgen, China). The thermal conditions consisted of an initial denaturation at 95°C for 2 min, followed by 30 cycles of 95°C (30 s), 55°C (30 s), and 72°C (1 min), and a final extension at 72°C for 10 min. Each sample was amplified in triplicate, including negative controls (no template) and filter blanks. PCR products were purified using Agencourt AMPure XP Beads (Beckman Coulter, USA), and then followed by indexed libraries construction, repurification, quantification, normalization, and finally sequencing on an Illumina NovaSeq 6000 platform (Illumina, USA) using a paired-end 250 bp (PE250) SP-Xp strategy.

2.3. Economic Data Collection of Yunnan's Counties and Districts in the Lixian River Basin

A total of 19 economic indicators during 2013–2022 were selected to characterize the level of overall economic, agricultural, breeding industrial and industrial across the upper, middle, and lower reaches of the Lixian River basin (Table S2). Provincial-level data were sourced from the Yunnan Statistical Yearbook (2013–2022), while national-level datasets were obtained from the China Regional Economic Database and China Urban and Rural Construction Database (<https://www.epsnet.com.cn>). Hydrological data were provided by the Pu'er City Water Conservancy Department, and climatic records were accessed via the Xihe Energy Big Data Platform (<https://xihe-energy.com>).

2.4. Bioinformatic Analyses

After removing of adapter and primer sequences by QIIME2 software [31], the DADA2 plugin [32] was employed for quality control, noise reduction, sequence splicing, and chimera removal. Species accumulation and rarefaction curves were generated to evaluate the sampling rationality (Figure S1). The Usearch (V.10.0) was used to cluster the sequences into Operational Taxonomic Units (OTUs) at a 97% sequence similarity threshold (Rognes T et al., 2016), and blast with the MitoFish database was also performed. What's more, manual corrections were made based on the fish historical distribution information in the Lixian River basin, referring to the Atlas of Yunnan Fishes [33], Color Atlas of Native Fishes in Pu'er [34], Fauna Sinica, and Species and Distribution of Inland Fishes in China [35] to ensure the accuracy of species annotation. A fish species was only considered present in a sample when the number of its sequence was equal to or greater than 3 [36].

2.5. Statistics

To ensure consistent relative sequence abundances (read proportions) for all taxa across samples, the amplicon sequence variant (ASV) abundances were normalized using Phyloseq V1.2.6 based on a previous report [37]. Relative abundances of fish species were calculated based on OTUs abundance. α -diversity including the Chao 1, Shannon-Wiener index, Simpson's diversity, and Pielou's evenness index were computed using the vegan package V2.6.8 [38] in R.

One-way ANOVA was performed to test differences among different reaches of the Lixian River, and differences were considered significant when $P < 0.05$. Redundancy analysis (RDA) based on Bray-Curtis dissimilarity matrices [39] was conducted to investigate spatio-temporal variations in fish community structure, and the permutational multivariate analysis of variance (PERMANOVA) was applied to assess the significance.

As less economically developed region is a relative concept, Yunnan Province's per capita GDP was used as the benchmark, with regions below this threshold being classified as less economically developed. The per capita GDPs of all mentioned six counties were significantly lower than the provincial value (Figure S2, one-way ANOVA, $P < 0.05$), confirming the basin's status as less economically developed. Pearson correlation analysis was performed on 19 selected economic indicators, and those with strong correlations ($r > 0.7$, $P < 0.05$) were excluded (Figure S3). Finally, variables including GDP, population, agricultural population, total grain output, aquatic product yield, number of hogs slaughtered and industrial gross output were retained representing overall economy, agriculture, aquaculture, animal husbandry, and industrial development for subsequent analysis.

To explore the nexus between economic development and fish diversity, a three-step analytical framework was employed. First, independent multiple regression tree models were constructed for the four α -diversity indices to identify the underlying determinants, and 10-fold cross-validation and the one-standard-error (1-SE) rule [11] was used to prune regression trees. Next, generalized linear models (GLMs) were applied to test the effects of economic factors while controlling for dominant natural drivers. Finally, a total of 17 key indicators were selected in a partial least-squares path model (PLS-PM) analysis to reveal the mechanism how economic development affects fish diversity. Specifically, permanganate index, total phosphorus, total nitrogen, pH value, and water temperature were included as water quality variables. In terms of overall economic variables, GDP and total population were incorporated. For breeding-industry, the aquatic product output and the number of hogs slaughtered were chosen. The grain yield and the total industrial output were selected as the agricultural and industrial variables, respectively. Regarding the climate variables, precipitation, maximum temperature, and average temperature were included.

In this study, all data analyses were completed by R4.3.2 [40]. Specifically, the multiple regression tree was carried out using the mvpart V1.6-2 [41], and the GLM was performed using the MASS [42]. The PLS-PM fitting analysis was conducted by plsrm V0.5.1 [43] and semPlot V1.1.6 [44]. Finally, ggplot2 [45] was used to visualization.

3. Results

3.1. Species Identification and Composition in the Lixian River

55 species/genera belonging to 45 genera 16 families and 6 orders in summer, and 51 species/genera belonging to 40 genera 13 families and 4 orders in winter were identified, respectively. In both seasons, the order of Cypriniformes was the most dominant, with species accounting for proportions more than 55%, and followed by the Siluriformes (more than 20%), and then the Perciformes (14.55% and 19.61 in summer and winter, respectively). The other three orders, including Acipenseriformes, Synbranchiformes and Cyprinodontiformes, each was comprised of only 1 species (Figure 2A-B).

Combining data from the two seasons, a total of 65 species/genera, belonging to 49 genera 17 families and 6 orders were identified. The Cypriniformes remained to be the most diverse order, with 36 species (55.38%), followed by the Siluriformes with 15 species (23.08%), and the Perciformes with 11 species (16.92%). Three orders, Acipenseriformes, Synbranchiformes and Cyprinodontiformes, each comprised just 1 species, accounting for 1.54% of the total (Figure 2C). The dominant species were *C. carpio*, *C. gachua* and *Schistura* sp. (Figure 2D).

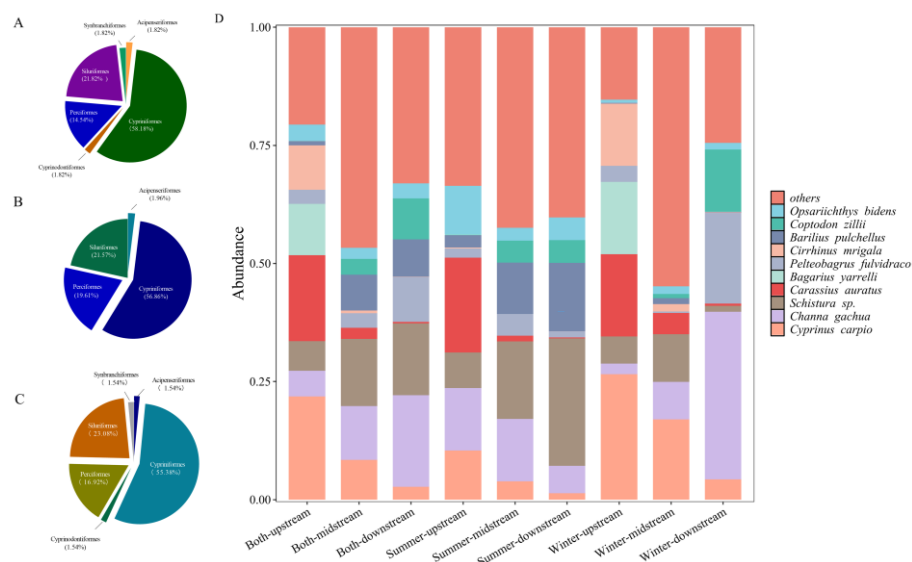


Figure 2. Fish species composition in the Lixian River. A: Fish composition at the order level during the summer; B: Fish composition at the order level during the winter; C: Fish composition at the order level across both seasons; D: Relative sequence abundance of fish species during the summer, winter, and across both seasons in the upstream, midstream, and downstream.

3.2. Fish Diversity and Spatial Distribution Pattern in the Lixian River

3.2.1. Fish Diversity in the Upstream, Midstream and Downstream of the Lixian River

To reveal the spatial distribution of fish in the Lixian River, α -diversities in both seasons in the upper, middle, and lower reaches of this river were calculated respectively (Figure 3). During summer, significantly higher Chao1 indices were observed in both the upper and lower reaches than in the middle reach ($P=0.0031, 0.0062$, respectively; Figure 3A), highlighting pronounced longitudinal variations in species richness. Notably, the Simpson and Shannon-Wiener indices of the downstream were significantly greater than those of the midstream ($P=0.0235, 0.0351$, respectively; Figure 3B, C). The Pielou index exhibited the highest value in the upstream and the lowest in the downstream, but without significance (Figure 3D). During winter, the Chao1 index of the upstream was significantly higher than those of both the midstream and downstream in winter ($P<0.0001$, Figure 3E), reflecting notably greater species richness in the upstream section. However, the Shannon-Wiener index of the downstream was significantly higher than that of the upstream ($P=0.0015$, Figure 3F). The Simpson index in the downstream was significantly lower than those in both the midstream and upstream ($P=0.0128$ and 0.0154 , respectively; Figure 3G), while the Pielou index in the midstream was significantly higher than that in the downstream ($P=0.0272$, Figure 3H). These results indicted a time and space dependent effects of fish diversity in the Lixian River.

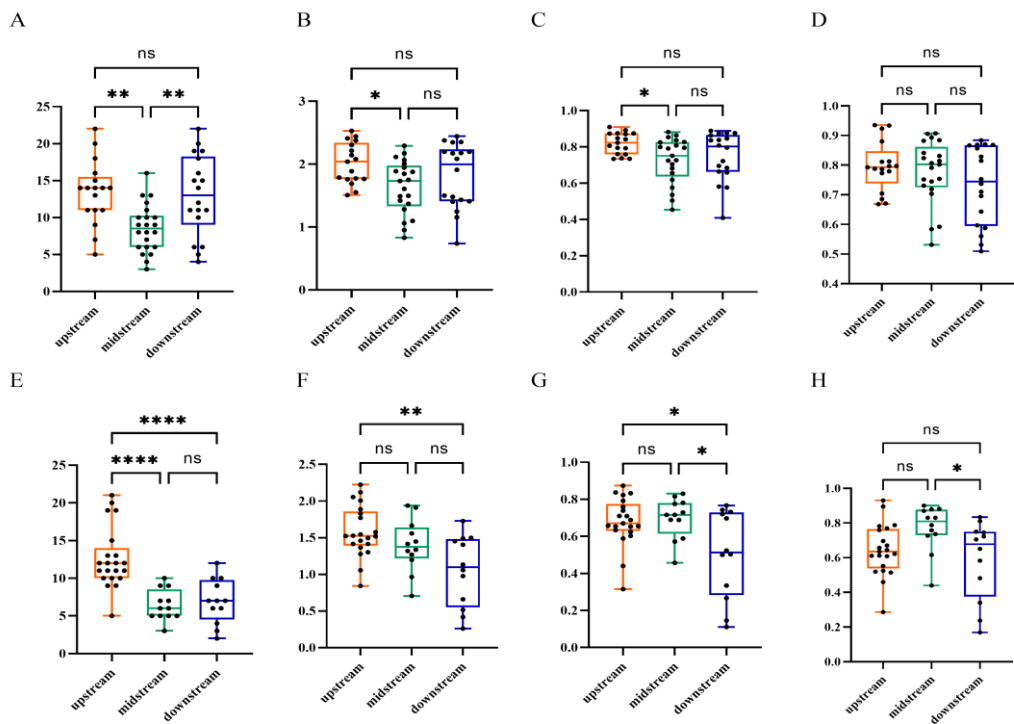


Figure 3. Fish α -diversity in the upstream, midstream, and downstream of the Lixian River. A-D: Chao1 index, Shannon-Wiener index, Simpson index, Pielou index during summer; E-H: Chao1 index, Shannon index, Simpson index, Pielou index during winter. ***: $P < 0.001$, **: $P < 0.01$, *: $P < 0.05$.

3.2.2. Relationship Between the Spatial Distribution Pattern of Fish and Natural Environmental Factors

To verify the reach-dependent effects on fish diversity, the β -diversity was also analyzed in the three reaches of this river. As expected, fish communities differed significantly among the upstream, midstream, and downstream reaches of the Lixian River ($P < 0.01$), forming a obvious longitudinal gradient from upstream to downstream (Figure 4A, C). Besides, effects of water quality indicators on the spatial distribution pattern of fish communities in the Lixian River showed a season-dependent manner. Specifically, the key driving factors in summer were pH ($R^2=0.4286$, $P=0.001$) and dissolved oxygen (DO, $R^2=0.4075$, $P=0.001$), while in winter those were shifted to water temperature (Temp, $R^2=0.8299$, $P<0.001$) and pH ($R^2=0.6029$, $P=0.009$) (Figure 4B, D).

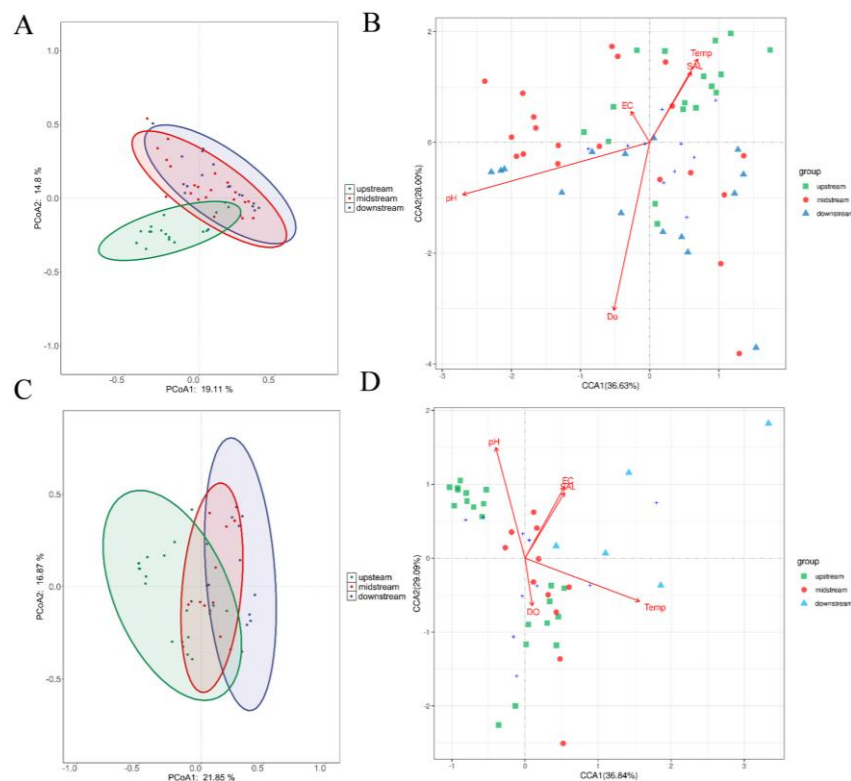


Figure 4. Drivers of fish community spatial patterns and key water quality variables in the Lixian River. A-B: PCoA analysis results and CCA analysis results during summer; C-D: PCoA analysis results and CCA analysis results during winter.

3.3. The Impacts of Economic Development Level on the Fish Diversity in the Lixian River

3.3.1. Economic Development and Climate Status of the Upper, Middle and Lower Reaches of the Lixian River

To address multicollinearity among potential economic indicators, Pearson correlation analysis was performed on the selected 19 indicator factors, and 7 core factors with strong correlations ($r > 0.7$, $P < 0.05$) were screened out. These 7 indicators included GDP, total population, agricultural population, grain yield, aquatic product output, number of hogs slaughtered and total industrial output value, which represented the levels of overall economy, agriculture, breeding industry and industry of the Lixian River basin.

The development levels of overall economy, agriculture, and breeding industry in the Lixian River basin presented a gradually decreasing trend from the upstream to the downstream. However, industrial development is more pronounced in the middle reach. Specifically, GDPs and the total populations of both the upstream and midstream were significantly higher than that of the downstream ($P < 0.05$; Figure 5A-B). In the agricultural sector and breeding industry, except agricultural population, all other indices including grain output, number of hogs slaughtered, and aquatic product output exhibited a distinct gradient: the upstream significantly outperformed the midstream, which in turn surpassed the downstream significantly ($P < 0.05$, Figure 5C-F). For industrial index, the total industrial output value revealed that both the upstream and middle reaches were significantly more developed than the downstream ($P = 0.0006$ and 0.0013 , respectively), whereas the difference between the upstream and middle reaches was nonsignificant ($P = 0.8802$, Figure 5G).

In terms of climatic indices, there was no significant difference in daily precipitation across the basin; however, the downstream region showed a significantly higher daily temperature than the upstream ($P = 0.0311$, Figure 5H-I).

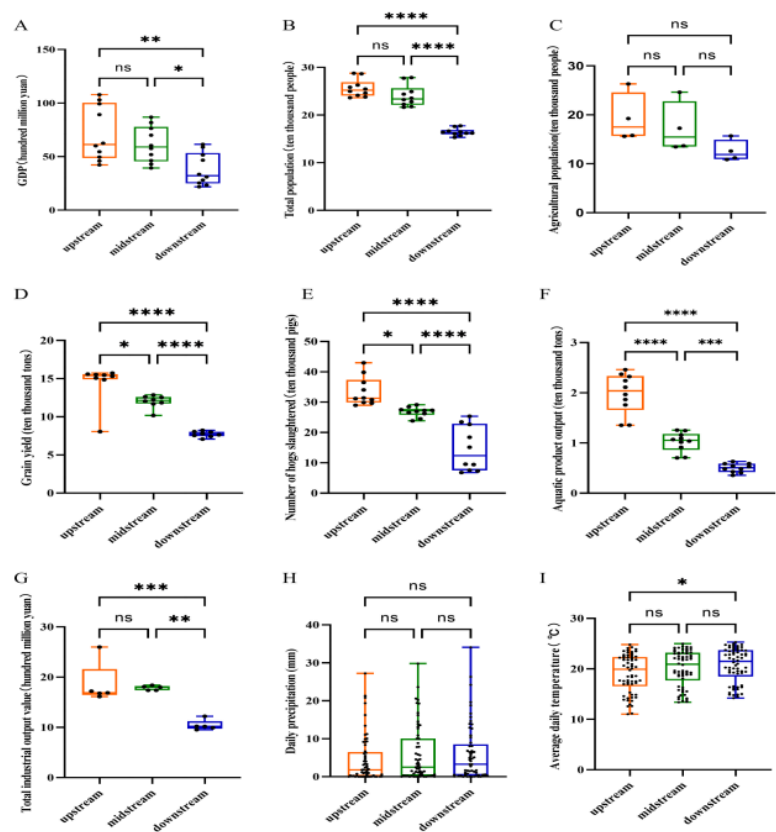


Figure 5. Economic development and climate in the Lixian River. A: GDP ; B: Total population; C: Agricultural population; D: grain yield; E: number of hogs slaughtered; F: aquatic product output; G: Total industrial output value; H: Daily precipitation; I: Average daily temperature. ****: $P < 0.001$, **: $P < 0.01$, *: $P < 0.05$).

3.3.2. The Relationship Between the Fish Diversity and Economic Development in the Lixian River

The regression tree analyses were separately conducted for each of the four aforementioned diversity indices (Figure 6). In terms of Chao1 index, the primary split was defined by the number of hogs slaughtered, followed by the precipitation. While the Shannon-Wiener index was firstly divided by the maximum temperature (T_{max}), and then by the agricultural population. Similarly, the Simpson index was initially divided by the maximum temperature (T_{max}), and further subdivided by factors such as total population and agricultural population. The primary split of the Pielou index was defined by the maximum temperature (T_{max}), followed by the total industrial output value (industrial output). These results suggested that, climatic factors, particularly the maximum temperature, exhibited stronger predictive power compared to human-driven factors. However, the impacts of human-driven factors, such as agriculture and breeding industry, on fish diversity remained significant and nonnegligible.

In order to explore the impacts of economic development factors on fish diversity, T_{max} was selected as the key controlling factor based on the regress tree analysis, and the data were divided into two subsets. One subset was the group with a higher maximum temperature and the other one was that with a lower maximum temperature. Generalized linear models were then fitted to analyze the relationships between anthropogenic economic factors and fish diversity indices within each subset (Figures 7 and 8).

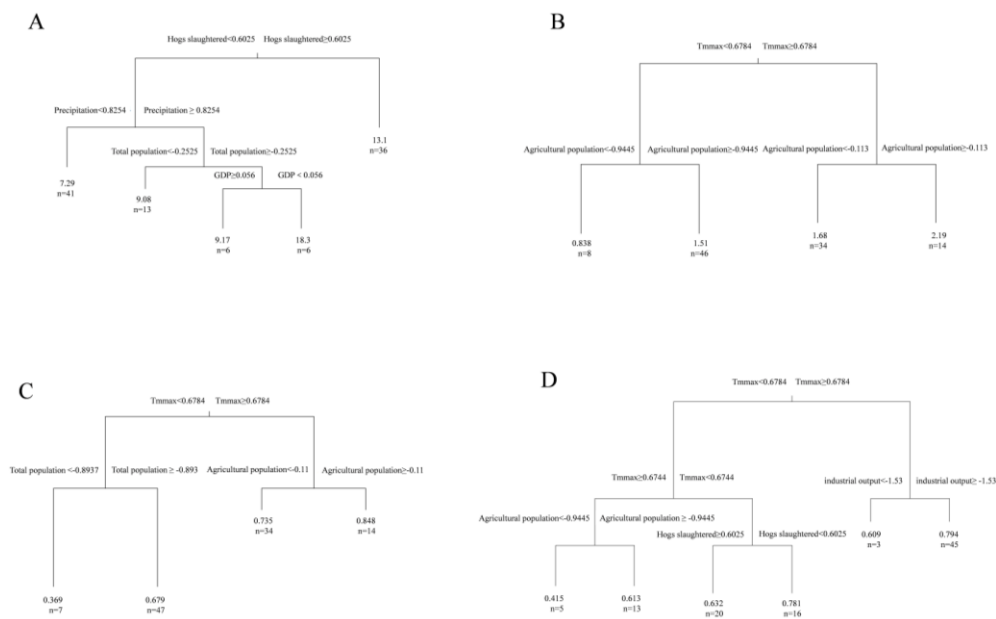


Figure 6. Multiple regression trees based on fish diversity. A: Regression tree analysis based on Chao1 index; B: Regression tree analysis based on Simpson index; C: Regression tree analysis based on Shannon-wiener index; D: Regression tree analysis based on Pielou index.

In the group with lower maximum temperature, the number of hogs slaughtered showed significant positive correlations with all three fish diversity indexes ($P < 0.05$, Figure7, AE-DE). Grain yield exhibited significant positive correlations with both Shannon-Wiener ($P = 0.0282$, Figure7, BD) and Simpson indexes ($P = 0.0211$, Figure7, CD). Agricultural population just showed a significant positive correlation with Simpson index ($P = 0.0269$, Figure7, CC). GDP showed a positive but insignificant correlation with Chao 1 index ($P = 0.164$, Figure7, AA), while aquatic product output showed a negative correlation with Chao 1 index ($P = 0.0277$, Figure7, AF).

In the group with higher maximum temperature, GDP, total population, agricultural population, grain yield demonstrated significant positive correlations with all three fish diversity indexes ($P < 0.05$, Figure8, AA-CD). While the industrial output showed significant positive correlations with both the Shannon-Wiener index ($P = 0.0352$, Figure8, BG) and the Pielou index ($P = 0.0496$, Figure8, DG).

Based on the above results, it is obvious that, local economic activities, particularly the agricultural and breeding industrial aspects, have positive influences on fish diversity in the Lixian River basin, which exhibits a less economically developed level.

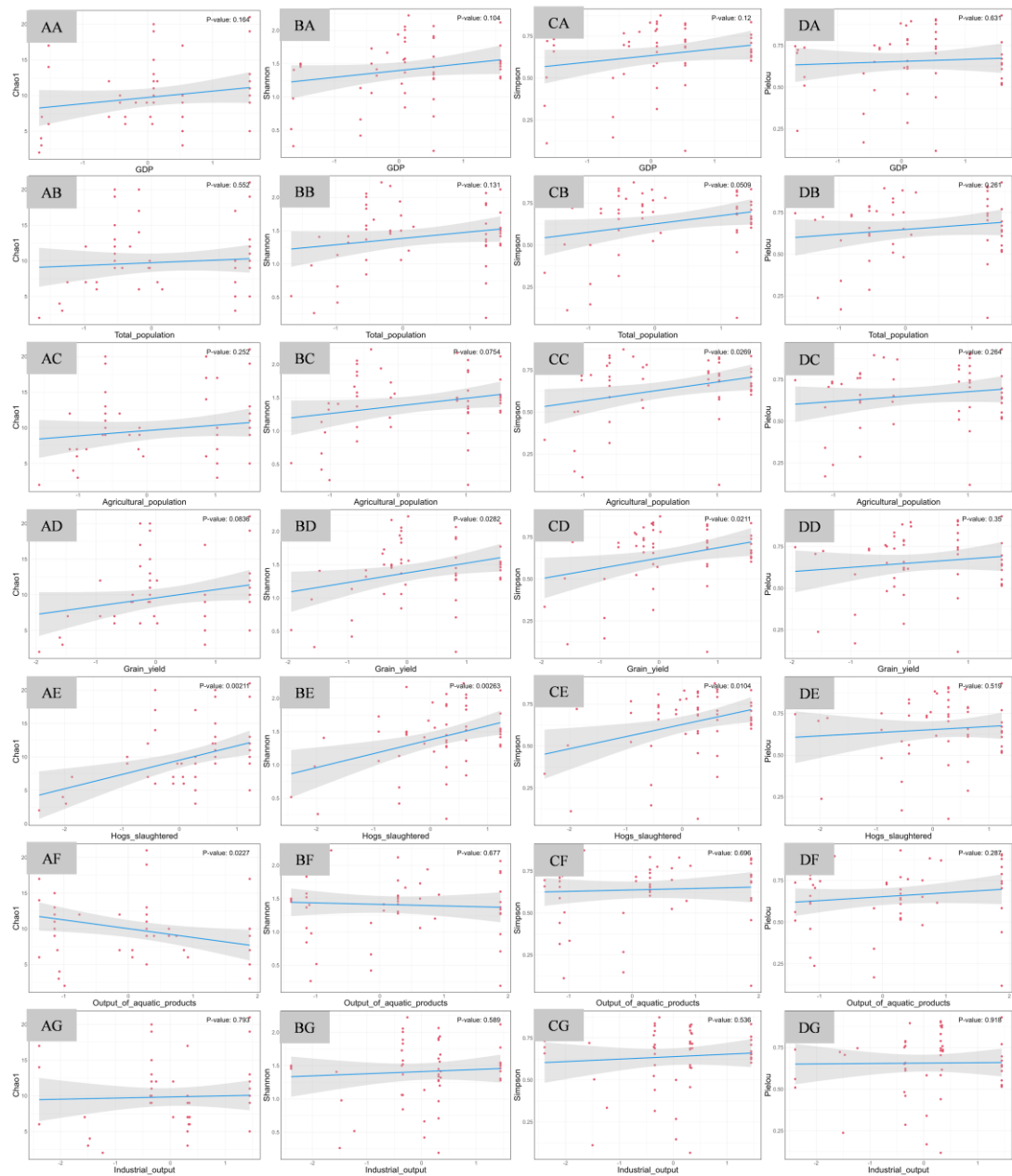


Figure 7. Generalized linear model analysis of fish diversity indices and indicators of economic activities in the group with lower maximum temperature. The horizontal axis represents economic indicator factors, and the vertical axis represents the four diversity indices. AA-AF: Generalized linear model of 7 economic indicators and Chao 1 index; BA-BF: Generalized linear model of 7 economic indicators and Shannon-wiener index; CA-CF: Generalized linear model of 7 economic indicators and Simpson index; DA-DF: Generalized linear model of 7 economic indicators and Pielou index.

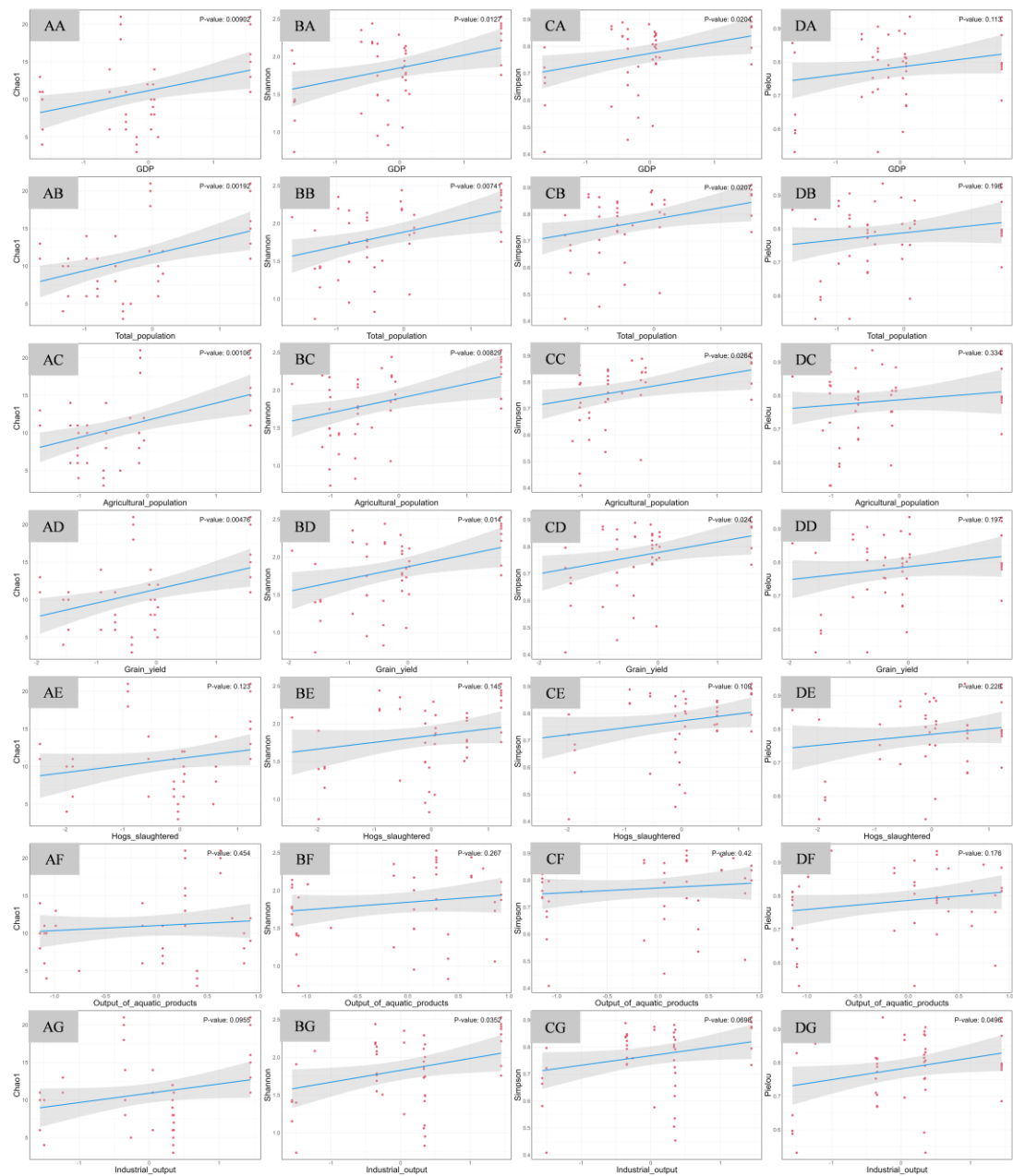


Figure 8. Generalized linear model analysis of fish diversity indices and indicators of economic activities in the group with higher maximum temperature. The horizontal axis represents economic indicator factors, and the vertical axis represents the four diversity indices. AA-AF: Generalized linear model of 7 economic indicators and Chao 1 index; BA-BF: Generalized linear model of 7 economic indicators and Shannon-wiener index; CA-CF: Generalized linear model of 7 economic indicators and Simpson index; DA-DF: Generalized linear model of 7 economic indicators and Pielou index.

3.4. Mechanisms of Effects of Economic Development Level on the Fish Diversity in the Lixian River

To explore the mechanism how economic factors affect fish diversity in the Lixian river basin, a partial least-squares path model (PLS-PM) was conducted (Figure 9). The overall economy showed a direct positive relationship with agriculture, aquaculture, and industry ($P<0.0001$). The agriculture and breeding industry positively related with fish diversity, while the industry showed a negative relationship. Climate exhibited a weak negative impact on fish diversity, while water quality had a significant positive direct effect ($P=0.01465$), indicating its importance as a critical factor in shaping fish diversity. Agriculture exerted a negative influence on both water quality and climate, as indicated by path coefficients of -0.363 and -0.331, respectively. In contrast, breeding husbandry

demonstrated a positive effect on these two aspects, with path coefficients of 0.325 and 0.204, respectively. Regarding industry, although without significance, it exhibited a trend of positive impact on water quality (path coefficient: 0.246) and a negative one on climate (path coefficient: -0.031).

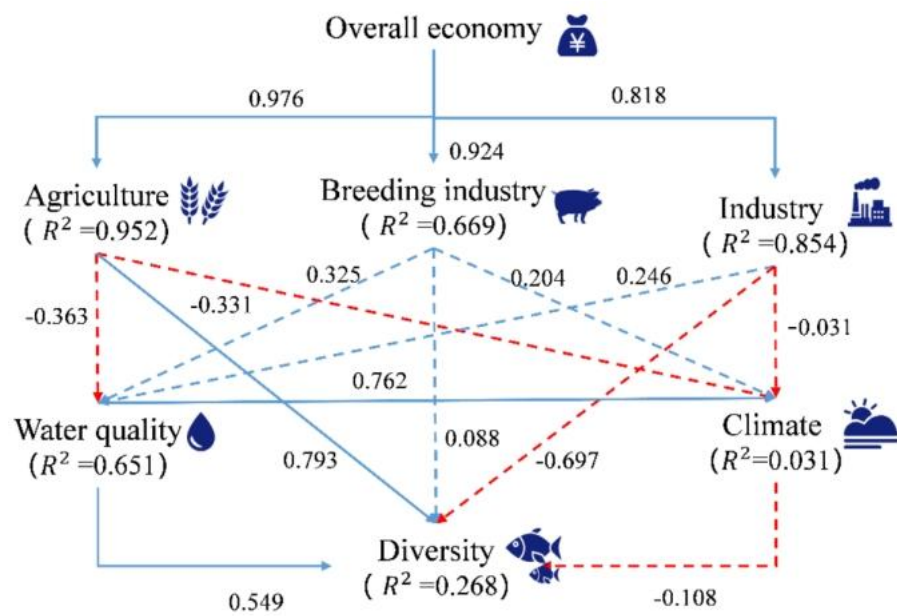


Figure 9. Partial least-squares path model based on the economy, fish diversity, and environment of the Lixian River. Red and blue arrows represent negative and positive impacts, respectively. Solid lines indicate significance ($P < 0.05$), and dashed lines indicate non-significance ($P > 0.05$). The goodness-of-fit (GoF) of the model is 0.633.

4. Discussion

4.1. Changes in the Fish Composition of the Lixian River Basin

In the present study, a total of 65 fish were identified by eDNA in the Lixian River, and 29 of which were also historically recorded in data from fish capture in this river approximately 15 year ago [27]. Among these identified fish, it was hard to distinguish *Schistura callichroma* and *Schistura fasciolatus* at the species level, due to the primer discrimination which resulted in the matching degrees of these two fish both were above 97%, and with a difference between them less than 1%. When comparing the species composition, a notable increase in the proportion of non-native fish was found in the present study. In 2010, the number of non-native fish individuals just accounted a small proportion (3%) of all fish catches, while the current relative sequence abundance of non-native fish has risen to 18.28%. Besides, there were three species of tilapia identified in the present study, including *Oreochromis niloticus*, *O. mossambicus*, and *Coptodon zillii*, and all three fish ranked among the top 10 species in terms of relative sequence abundance during the winter (Figure 2). The tilapias are known for their strong adaptability and reproductive capacity [46], and Yunnan Province is one of the main farming regions of tilapia in China (Yuan et al., 2017), and escape of tilapia from farms to natural rivers is inevitable. Based on the recorded data of water temperature during sample collection, and those retrieved from official database, the minimum water temperature in winter in the Lixian River is higher than 18oC, which provides a suitable environment for the escaped tilapia from farming populations, and consequently lead to a rapidly establishment of a dominant community of these invasive fish in Lixian River within just over a decade.

4.2. *Effects of Climate on the Fish Diversity in the Lixian River*

In the present study, both CCA and regression tree analyses supported that, natural factors were important in shaping fish diversity in the Lixian River (Figure 4, 6). The Climate change is the one that received most extensive attention, and it has been widely recognized as a key driver of biological shifts in natural systems [47]. As climate change progresses, the frequency of floods and droughts is increasing, which inevitably leads to a rise in water engineering projects [48]. This, in turn, intensifies alterations in water flow patterns and exerts a profound impact on fish populations [49]. Not just water flow, climate change mediated alterations in many other natural factors, including temperature, precipitation, augmented drought occurrences, and early-onset floods, have been reported to result in a decline of 21.25% in fish biodiversity in Bangladesh [50]. Climate change can directly affect physiological activities of fish as well [51]. For instance, the raised water temperature driven by increased air temperature, can elevate fish metabolic rate, thereby results in a higher oxygen demand; however, higher water temperature is always accompanied by a decline of dissolved oxygen. This dual effects finally result in a insufficiency of dissolved oxygen, which constrains fish growth, reproductive capabilities and changes of other physiological activities [52]. Besides, under the challenge of global climate change, alterations on frequency and intensity of extreme climate events (such as heavy rainfall, droughts, extreme high temperatures, etc.) can also profoundly affect fish reproduction [53], migration [54], and even survival (Kragh et al., 2020). Moreover, climate-mediated environmental indicators are also closely related to changes in fish distribution. For example, in response to the rising water temperature, the distribution ranges of many fish species along the coastline of Texas have expanded from relatively southern regions towards the north over the past 35 years [55]. Also driven by climate change, the geographic redistribution of marine fish species has been reported, with an increase in species richness in Arctic within the past 20 years [56]. In Norway, climate warming has led to a poleward shift in fish distribution, changing the fish community from an obvious latitudinal pattern to a more homogeneous one [57]. Similarly in the Nordic Seas, the raising seawater temperature has caused fish distributions to shift toward more northerly or deeper waters [58]. What's more, the redistribution of invasive fish species has become a highly concerning issue in recent years, and the impacts of invasive fish on local biodiversity will be amplified or exacerbated due to the climate warming [59].

4.3. *The Impact of Economic Development on Fish Diversity in the Lixian River*

In this study, although the overall economic and agricultural development levels in the Lixian River basin showed gradually decrease pattern from the upstream to the downstream regions, higher fish diversity was observed in both the upstream and downstream areas (Figure 3-4), showing a nonlinear relationship between economic development and fish diversity, the PLS-PM analysis here also indicates a complex relationship between economic levels and fish diversity. This is consistent with a previous view that the relationship between economic development and fish richness and diversity is influenced by multiple complex mechanisms [15].

Contrary to the traditional view that economic development often has a detrimental impact on fish diversity [11,60], the present study found that in regions with relatively low level of economic development, local economic activities, especially those related to agriculture and aquaculture, can positively influence fish diversity (Figure 7-8); and this was verified by the significant and positive impacts of agriculture on fish diversity in the PLS-PM analysis (Figure 9). Although the degradation of river connectivity by dams or other human activities globally threatens the freshwater biodiversity [5], moderate agricultural activities, such as rational management of irrigation water, may maintain the hydrological connectivity of rivers, thus providing suitable habitats and migration environments for fish [61,62], and thereby sustaining biodiversity [63]. Freshwater ecosystems encompass not only the humid peripheries but also the catchment areas that serve as sources of water and nutrients [2]. Moreover, some pond aquaculture systems, to a certain extent, simulate the natural wetland ecology, offering diverse habitats and food sources for fish [64]. Available research has shown that low-intensity agriculture, the characteristic of many rural landscapes around the world, promotes the

high diversification of species and habitats, particularly at small spatial scales [65]. Being located in an underdeveloped area, the low overall intensity of agricultural development may contribute to the high diversification of species and habitats in this River.

However, it should be noted that although positive impacts of agriculture and aquaculture on fish diversity in the Lixian River was observed, this does not mean that all agricultural and aquaculture activities will yield similar effects. Here, a negative correlation was observed between the aquatic product output and the Chao 1 index (Figure 7). Increase of aquatic product output often implies the intensified fishing activities and/or fish farming. Overfishing can directly reduce the fish populations, especially for some economically valueble fish species, whose populations struggle to recover and stabilize under extensive fishing pressure, thereby reducing overall fish species richness [66]. At the same time, fishing may lead to the loss of diversity within ecosystem, with particularly greater impacts observed when fishing targets are some specific species rather than random ones [67]. Under the intensified fish farming, abuse of antibiotics and other drugs can lead to serious deleterious ecological problems, including decline of fish diversity[68]. In pursuit of high yields, just one or limited number of species will be commonly selected in aquatic farming, which may change the ecological environment of both the aquaculture area and surrounding natural water bodies [69]. Besides, escaped farmed fish can compete with wild fish for food and habitats, introduce diseases and parasites as well, posing threats to the survival and reproduction of wild fish and reducing fish diversity ultimately [70,71]. In the present study, tilapia were found to have established a stable populations and become the dominant species in the Lixian River (Figure 2). Therefore, although the appropriate development of economic levels, especially agriculture related activities, relates to higher fish diversity in the less economic developed regions, the overfishing, improper fish farming, and invasive species are still risks that needs attention.

4.4. Pathways Under the Effects of Economical Development on Fish Diversity in the Lixian River

Based on the PLS-PM analysis in the present study, we can conclude that, except agriculture that directly pointed to the fish diversity, all these three parameters of socioeconomical development pointed to water quality and climate, and which interacted with each other (Figure 9), suggesting a fundamental effects of water quality on river fish diversity. Indeed, the pH value and dissolved oxygen were key factors affecting fish diversity in this river (Figure 6). With the development of rural economic, decreased level of forestry, increased industrial activity, the intensity and type of agricultural activity has reported to be all critical factors affecting the freshwater quality [72], and water qualities such as total nitrogen (TN), dissolved oxygen (DO) and so on have been widely recognized as critical factors in shaping the diversity and biomass of both the phytoplankton and zooplankton [73–75]. As key elements in the aquatic biosystem, phytoplankton function as the primary producers, which support zooplankton populations, and all planktons serve as trophic resources of many fish species [76,77]. Thus biomass and diversity of planktons can directly affect fish community and biodiversity via trophic cascades [75,78,79]. To reveal whether effects of the development of socioeconomic in this river was mediated by the water quality-plankton pathway, analyses on the biomass, diversity of plankton and the factors that affecting their distribution were also performed. The results showed that, both phytoplankton and zooplankton densities and biomass demonstrated higher values in the upper reaches compared to the lower reaches, and total nitrogen (TN) and dissolved oxygen (DO) represented the primary environmental drivers shaping plankton community structure in this system (Figure S4). Combined with what we have discussed above, this provides a proof that economic activities can systematically alter aquatic community structures in the Lixian River basin through water quality-mediated ecological pathways.

5. Conclusions

Based on the eDNA technology and multiple statistical analyses, a higher fish diversity was observed in the upper and lower reaches of Lixian River, which located in the economic underdeveloped areas. Climatic factors are the key factors affecting the fish diversity in the Lixian

River. However, in this less economically developed river basin, local economic activities, especially the development of agriculture and aquaculture, have an indirect positive effect on the fish diversity. Water quality-plankton might be the mediators of both climate and economic activities on fish diversity in the Lixian River.

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Abbreviations

The following abbreviations are used in this manuscript:

eDNA	Environmental deoxyribonucleic acid
OTUs	Operational taxonomic units
RDA	Redundancy analysis
Temp	Water temperature
Tmax	Maximum temperature
Tmin	Minimum temperature
DO	Dissolved oxygen
SAL	Salinity
EC	Electrical conductivity
TN	Total nitrogen
PERMANOVA	Permutational multivariate analysis of variance
PCR	Polymerase chain reaction
ASVs	Amplicon sequence variants
PCoA	Principal Co-ordinates Analysis
CCA	Canonical Correlation Analysis
PLS-PM	Partial Least Squares Path Modeling

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