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Dam Construction Impacts Fish Biodiversity in a Subtropical River Network, China

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Abstract: Dams and diversions are a primary threat to freshwater fish biodiversity, including the loss of species and restructuring of communities, often resulting in taxonomic homogenization (increased similarity) over time. Mitigating these impacts requires a strong scientific understanding of both patterns and drivers of fish diversity. Here, we test whether different components of fish biodiversity have changed in response to major dam construction, and whether these patterns are predictable as a function of key environmental factors in the Gan River Basin, China. The results showed that total and native species alpha diversity have declined from the historical period (pre-dam) to the current period (post-dam). A total of 29 native species are lost, while 6 alien species were gained over time. We found evidence for fish faunal homogenization in the Gan River Basin, with a slight (1%) increase in taxonomic similarity among river basins from the historical period to the current period. Additionally, we revealed significant associations between drainage length, drainage area, and average air temperature, and alpha and beta fish diversity. This study provides new insight into the patterns and drivers of fish biodiversity change in the broader Yangtze River Basin and helps inform management efforts seeking to slow, and even reverse, current trajectories of biodiversity change.

Keywords: long-term biodiversity changes; biodiversity loss; regional homogenization; dams; river network

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1. Introduction

Dams and diversions are a persistent threat to freshwater biodiversity and ecosystem functioning [1–4]. Dams cause habitat fragmentation and lead to altered hydrological and water quality regimes that compromise the structure and function of freshwater ecosystems [5,6]. Ecological impacts of dams are widespread, ranging from nutrient declines, loss or change in biodiversity, and the complete reshaping of food webs and energy pathways [7–9]. Dams are also major barriers to species movement [3].

Freshwater fish are the most diverse group of vertebrates, playing a number of important roles in freshwater ecosystems [10,11], while concurrently rapidly declining across the world [4]. Fragmentation and river regulation by dams remain a central threat to fish biodiversity by altering downstream environmental conditions and blocking migratory paths [12–14]. In addition to the local extinction of many fish species after dam construction is the establishment and spread of aquatic invasive species [15–18]. Changes in fish community structure resulting from species gains and losses can subsequently alter river ecosystem function [19]. Therefore, understanding how dam construction affects fish biodiversity is crucial to inform freshwater management strategies.

Beta diversity, a measure of the amount of change in species composition from one location to another, is a fundamental consideration in fish conservation efforts [20]. Species gains and losses (nestedness) and species replacement (turnover) over time contribute to spatial patterns in beta diversity [21]; together these two components provide important insight into the formation and maintenance of biodiversity [22–24]. Additionally, beta diversity is key to detecting the processes of shaping metacommunity dynamics [22,25]. Past research has reported distinct patterns in beta diversity driven by both natural and human-impacted environmental processes [22,26–28]. For example, a study of freshwater fishes across Europe found evidence that large-scale patterns of spatial turnover for exotic fishes were generated by human-mediated dispersal limitation, whereas patterns of spatial turnover for native fishes result from both dispersal limitation relative to historical events (isolation by mountain ranges, glacial history) and environmental filtering [29].

The Gan River Basin supports considerable fish diversity in the broader Yangtze River Basin, China. However, the construction of large dams over the past five decades has led to significant impacts to aquatic habitats and fish biodiversity [30–32]. Negative associations between the alpha diversity (local richness) of fish communities and sources of anthropogenic disturbance are evident in the Gan River Basin [30,31,33–38], although it remains unclear whether patterns of fish beta diversity have been similarly altered after major periods of dam construction. Such explorations are important, given that changes in species composition, and not systematic reductions in species richness, are being witnessed in response to global change [39]. The primary objective of this study is to evaluate the effects of dam constructions and environmental change on the fish diversity. We test whether different dimensions of fish biodiversity have changed in response to major dam construction, and whether the patterns are predictable as a function of key environmental factors. Results from this study aim to provide new insight into the patterns and drivers of fish biodiversity change in the Yangtze River Basin and inform management efforts seeking to slow, and even reverse, current trajectories of biodiversity change [27,40].

2. Material and Methods

2.1. Study Area

The Gan River is the largest river in Jiangxi Province and among the most important tributaries of the Yangtze River Basin with higher fish biodiversity (Figure 1) [31]. The total catchment area and the total length in the Gan River is 82,809 km^2 and 766 km, respectively. It has an average annual precipitation of 1580.8 mm. Its average annual air temperature is 18.3 °C and average annual surface runoff is 686 × 10^8 m^3, According to Bureau of Hydrology in Jiangxi Province (http://www.jxssw.gov.cn/ (accessed on 1 February 2021)), the length of upper reach (from Shicheng County to Ganzhou city), middle reach (from Ganzhou city to Xingan County), and lower reach (from Xingan County to Wucheng town) of the Gan River is 255 km, 303 km, and 208 km, respectively [31]. In 1990, the Wanan Dam was constructed in the upper reach of the Gan River; many dams, including Shihutang Dam in 2009, Xiajiang Dam in 2016, and Xingan Dam in 2018, were constructed in the middle reach; and the Longtoushan Dam was constructed in the lower reach in 2021 (Figure 1). These dams are part of large-scale water control projects with power generation and ship navigation as their primary purposes. Dam construction in the basin continues today, albeit at a smaller extent.

2.2. Data Collection

Fish species presence and absence in 13 rivers of the Gan River Basin were collected from published books and literature (Table S1). The literature search was systematic and followed protocols to ensure legitimacy and reproducibility based on Xiao and Watson (2019) [41]. Relevant studies published from 1965 to 2021 were obtained from three databases (i.e., Web of Science (WoS), CNKI (https://www.cnki.net/ (accessed on 1 January 2021)), and Scopus) using the following search keywords: fish diversity AND Gan River Basin; fish biodiversity AND Gan River Basin; aquatic biodiversity AND Gan River Basin;

aquatic diversity AND Gan River Basin; freshwater biodiversity AND Gan River Basin; freshwater diversity AND Gan River Basin. Our dataset is the most complete freshwater fish distribution of the Gan River Basin. FishBase [42] was used to update all scientific names of fish species to accepted nomenclature in the historical and current list. Species origin (native or alien) was defined according to Liu et al. (2017) [40] and Liu et al. (2019) [27], where a species was classified as "non-native" if it was not native to the Gan River Basin. Two datasets were collated representing the historical pre-dam period (1965–1990; Table S2) and current post-dam period (1990–2021; Table S3), according to the construction of the Wanan Dam in 1990. These fish data were obtained from standardized fish inventories according to a variety of fishing gears, gill nets and trawl nets. We calculated a number of basin descriptors for each river, including: drainage length (DL; km), drainage area (DA; km^2), average altitude (AA; m), average annual total precipitation (AP; mm), and average annual air temperature (AAT; °C) in the current period, as well as a suite of water chemistry parameters that included: dissolved oxygen (DO; mg/L), hydrogenions (pH), turbidity (TURB; NTU), water temperature (T; °C), chlorophyll-a (Chl-a; mg/L), total nitrogen (TN; mg/L), total phosphorus (TP; mg/L) ammonium nitrogen (NH_4^+; mg/L), and nitrate nitrogen (NO_3^-; mg/L) in the current period from published online databases, books, and literature (Zou, 2011; Su et al., 2012; Liu et al., 2017; Guo et al., 2018; Liu et al., 2019; Wang et al., 2019; Tong et al., 2019; Shi et al., 2020; World Clim-Global Climate Data (http://www.worldclim.org/bioclim (accessed on 24 January 2021); Bureau of hydrology in Jiangxi Province (http://www.jxssw.gov.cn/ (accessed on 1 February 2021)); Table S4) [30–32,35–38,43].

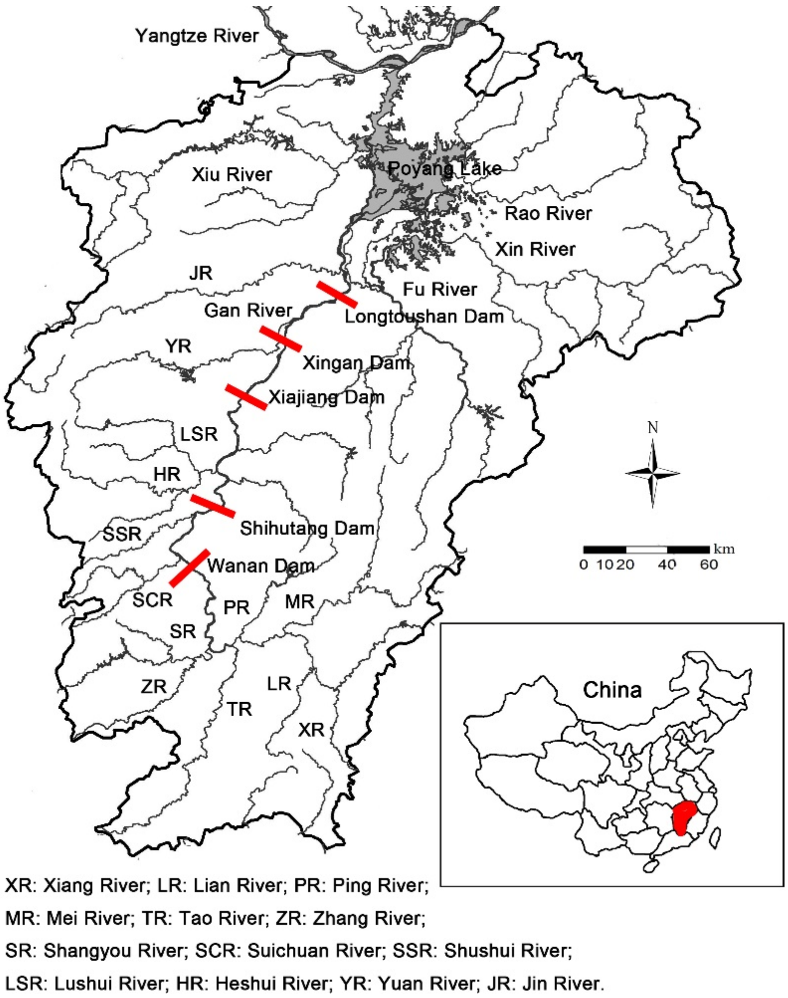

Figure 1. Map showing the study area and locations of river sites in the Gan River Basin, China. The red symbols represent the dams.

2.3. Data Analysis

Alpha diversity (species richness), beta (species turnover and nestedness), and gamma diversity (total species richness in Gan River Basin) was calculated for each river in both historical and current time periods [44]. The Sørensen dissimilarity index (β_{sor}), spatial turnover component (β_{sim}) and nestedness component (β_{sne}) between fish community of each pair of rivers were used to describe patterns of fish beta-diversity [21,45]. Changes in pairwise compositional dissimilarity among regions, calculated as $\Delta\beta_{sor} = \beta_{sor\text{-}historical} - \beta_{sor\text{-}current}$, indicates either taxonomic homogenization (i.e., positive $\Delta\beta_{sor}$) or taxonomic differentiation (i.e., negative $\Delta\beta_{sor}$) [46]. Mantel tests [47] were used to assess the correlations between beta diversity (β_{sor}) and the suite of environmental factors. All the analysis was performed in R [48] using BETAPART package [49], VEGAN package, and CMDSCALE package [50]. One-way analysis of variance (ANOVA) was used to detect differences in the alpha diversity between each period. The hierarchical cluster analysis of species composition was analyzed using the Bray–Curtis similarity index, performed in PRIMER 6 [51]. Fish community composition was also summarized using non-metric multidimensional scaling (NMDS) and the Sørensen dissimilarity index as performed in PRIMER 6 [51]. To evaluate the correlation between geographical and environmental factors and community composition of fish, a redundancy analysis (RDA) with 999 Monte Carlo permutations was performed using CANOCO version 4.5 [52,53]. All geographical and environmental factors and community composition of fish were log10(x + 1) transformed to meet the assumptions of multivariate normality and to moderate the influence of extreme data [54].

3. Results

3.1. Changes in Species Diversity

The total number of fish species in the historical period (176 species) exceeded that found in the current period (172 species) in the Gan River Basin (Figure 2A). Cypriniformes and Cyprinidae were the most common order and family (Figure 2B; Tables S2 and S3). The number of species of nine families declined and ten families increased when comparing the current and past time period (Figure 2B). Species in the families Acipenseridae, Cluoeidae, Anguillidae, Cynoglossidae, and Teraodontidae were not present in the current time period (Figure 2B). The number of native species declined after dam construction, whereas the number of alien species increased over time (Figure 2A). The number of total and native species in the middle reach was greater than in the upper reach and lower reach in the current period (Tables S2 and S3). In addition, species richness (both total and native species) was higher in the tributaries compared to the mainstem in the current period (Table 1). Hierarchical clustering and the NMDS showed that the 16 rivers tended to cluster into three groups in the current period according to species composition (Figure 3). The first group was TR, MR, TSU, ZR, SR, and PR, and the second group was JR, SCR, YR, TSL, and TSM, with the remaining rivers making up the third group.

Current-period alpha diversity in the Gan River Basin is lower compared to the historical period for total and native species, indicating a decrease in local species diversity after major dam constructions (ANOVA, $F_{df1,\,df2} = 756.23$, $p = 0.0001 < 0.05$; Figure 2). Similarly, beta-diversity (β_{sor}) decreased for total, native, and alien species in the Gan River Basin (Figure 4A). Changes in beta-diversity were predominantly driven by spatial turnover ($\beta_{sim} = 0.60$) compared to species nestedness ($\beta_{sne} = 0.16$; Figure 4A). Differences between historical and current Sørensen dissimilarity index indicated an overall homogenization of species composition over time ($\Delta\beta_{sor} = 0.10$ (0.03)). In addition, the total value of Sørensen dissimilarity index in the whole middle reach was greater than those in the whole upper and lower reaches, indicating an increasing biological homogenization in the whole middle and lower reaches (the whole middle reach vs. the whole upper reach: $\Delta\beta_{sor} = 0.06$; the whole middle reach vs. the whole lower reach: $\Delta\beta_{sor} = 0.17$). The spatial turnover component was always greater than its nestedness component in each area, indicating spatial turnover was major driver of beta diversity (Figure 4B). The total value of Sørensen dissimilarity index of

17 families was high, spatial turnover was major pattern of beta diversity in seven families and the nestedness was major pattern of beta diversity in nine families (Figure 4C).

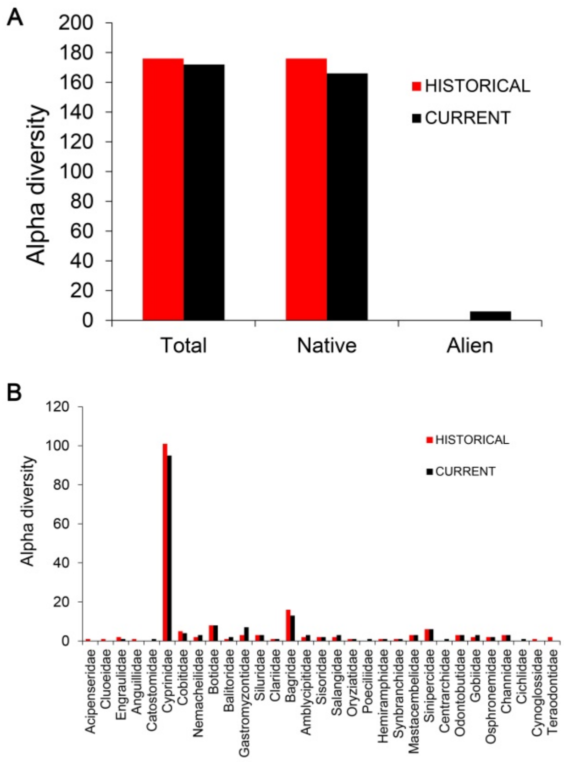

Figure 2. Alpha diversity (# of species) according to origin (**A**) and family (**B**) in the Gan River Basin for the historical (red) and current (black) time periods.

Table 1. The alpha diversity and gamma diversity of total, native, and alien fish species in the current period from the Gan River Basin.

River	Code	Total Species	Native Species	Alien Species
Xiang River	XR	47	46	1
Lian River	LR	31	31	0
Ping River	PR	62	62	0
Mei River	MR	87	86	1
Tao River	TR	91	91	0
Zhang River	ZR	73	73	0
Shangyou River	SR	73	73	0
Yuan River	YR	107	104	3
Jin River	JR	93	92	1
Suichuan River	SCR	107	107	0
Shushui River	SSR	42	42	0
Lushui River	LSR	66	65	1
Heshui River	HR	67	66	1
Mainstem of middle reach of the Gan River	TSM	117	117	0
Mainstem of upper of the Gan River	TSU	88	86	2
Mainstem of lower reach of the Gan River	TSL	111	111	0
Tributary of upper reach of the Gan River	TU	120	119	1
Tributary of middle reach of the Gan River	TM	126	125	1
Tributary of lower reach of the Gan River	TL	120	116	4
Upper reach of the Gan River	BU	124	121	3
Middle reach of the Gan River	BM	147	146	1
Lower reach of the Gan River	BL	143	139	4
All tributaries	T	158	153	5
All mainstems	TS	146	144	2

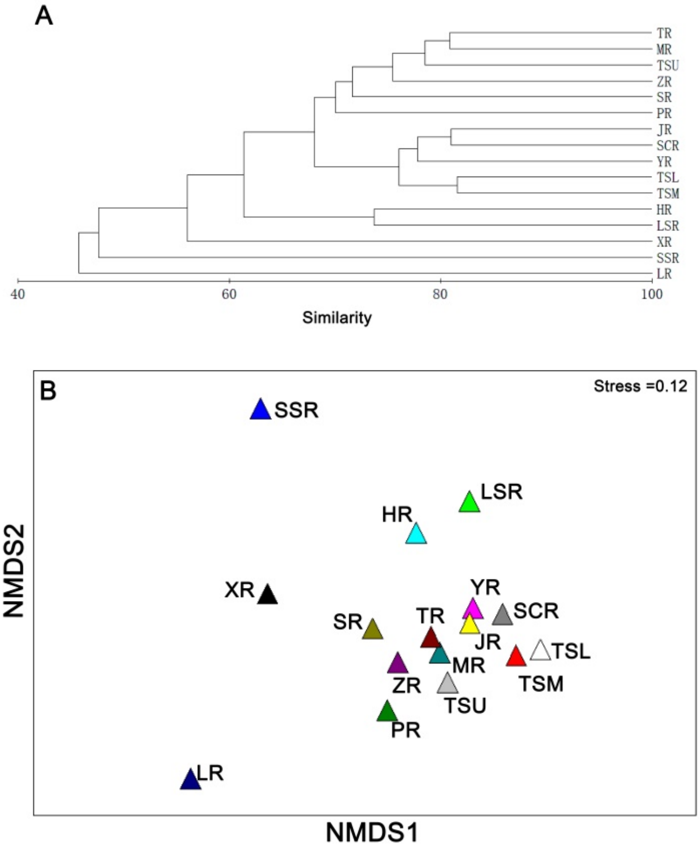

Figure 3. Dendrogram from a hierarchical cluster analysis of species composition (**A**) and non-metric multidimensional scaling (NMDS) ordination (**B**) of community composition in the Gan River Basin for the current period. River codes are the same as in Table 1.

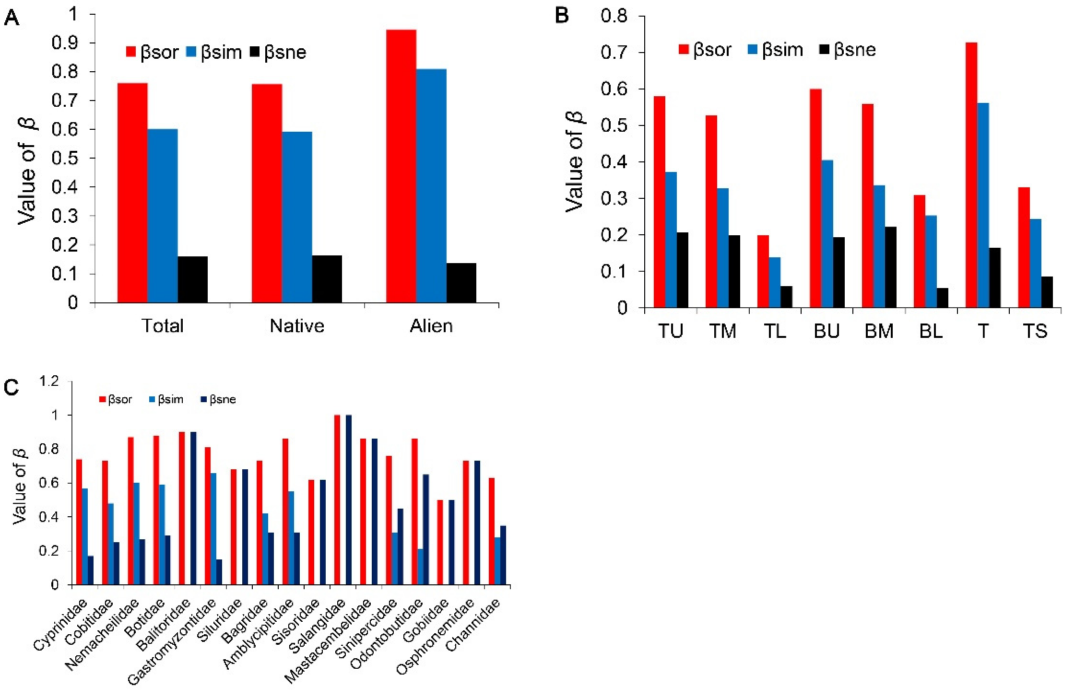

Figure 4. Beta diversity according to origin (**A**), basins of the Gan River Basin (**B**), and families (**C**) quantified by the Sørensen index (β_{sor}) and its species spatial turnover (β_{sim}) and nestedness components (β_{sne}) in the current period. River codes are the same as in Table 1.

3.2. Threatened Status of Fish

A total of 16 Chinese red-listed fish species identified as threatened or near-threatened to extinction were recorded in the historical period, compared to 11 fish species in the current period (Tables S2 and S3). The number of these imperiled species (i.e., CR, EN, VU or NT) in the Suichuan River was the highest, followed by the Tao River and Mei River, and the number of these imperiled species in the Shushui River was the lowest (Figure 5). The number of these imperiled species in the middle and lower reaches of the Gan River Basin were greater than those that in the upper reach (Figure 5).

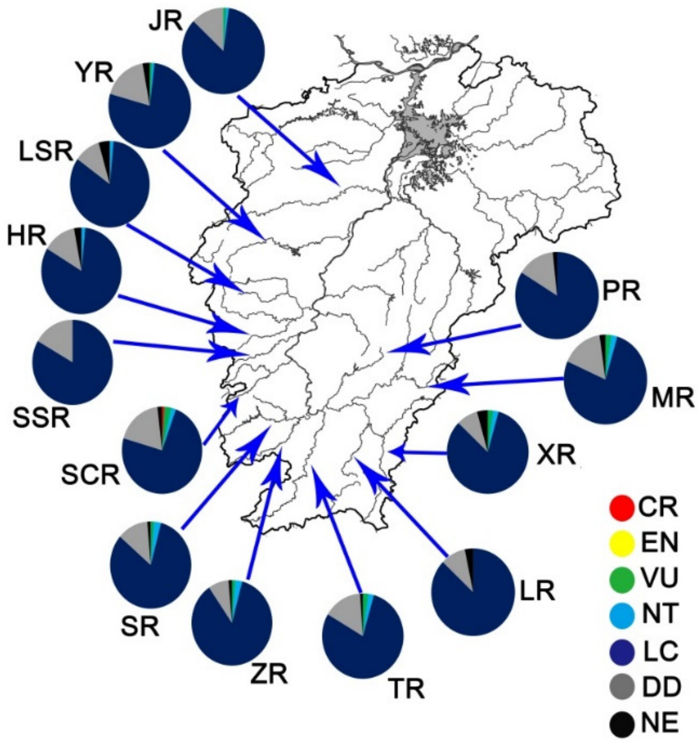

Figure 5. Fish species composition according to threatened status based on Chinese Red-list results in river basins of the Gan River Basin in the current period. Abbreviations include CR, Critically Endangered; EN, Endangered; VU, Vulnerable; NT, Near Threatened; LC, Least Concern; DD, Data Deficient; and NE, Not evaluated. River codes are the same as in Table 1.

3.3. Environmental Drivers of Fish Diversity

Environmental factors explained significant variation in fish composition according to the redundancy analysis (RDA), with the global model explaining 40.1% of the variation. The community structure of fish was significantly correlated with average precipitation, water temperature, pH, chlorophyll-a, and total nitrogen (Figure 6). A significant effect of drainage length, drainage area, and average air temperature on alpha and beta diversity was found in the Gan River Basin (Table 2). Water temperature, pH, and total nitrogen were significantly associated with alpha diversity, and water temperature significantly associated with beta diversity (Table 2).

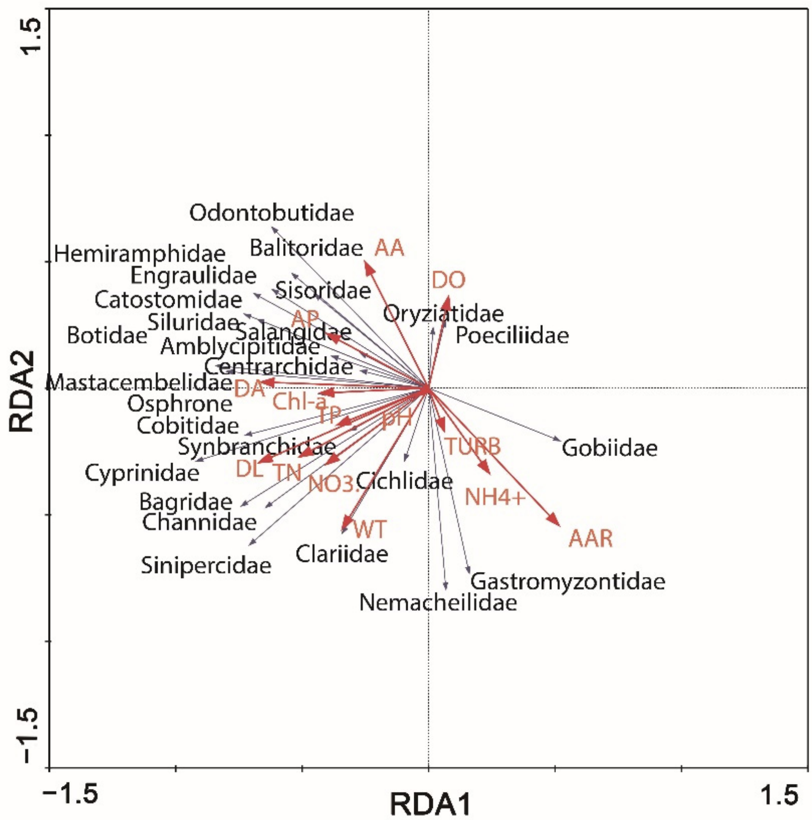

Figure 6. Ordination biplot of composition of fish species and geographical and environmental variables based on redundancy analysis in the Gan River Basin (rivers not shown). Variables include DL, drainage length (km); DA, drainage area (km^2); AA, average altitude (m); AP, average precipitation (mm); AAT, average air temperature (°C); DO, dissolved oxygen (mg/L); pH, hydrogenions; TURB, turbidity (NTU); WT, water temperature (°C); Chl-a, chlorophyll-a (mg/L); TN, Total nitrogen (mg/L); TP, total phosphorus (mg/L); NH_4^+, ammonium nitrogen (mg/L); and NO_3^-, nitrate nitrogen (mg/L).

Table 2. Effects of geographical and environmental factors on α and β diversity of total and native fish species in the Gan River Basin based on Mantel tests in the current period. Variables include DL, drainage length (km); DA, drainage area (km^2); AA, average altitude (m); AP, average precipitation (mm); AAT, average air temperature (°C); DO, dissolved oxygen (mg/L); pH, hydrogenions; TURB, turbidity (NTU); WT, water temperature (°C); Chl-a, chlorophyll-a (mg/L); TN, Total nitrogen (mg/L); TP, total phosphorus (mg/L); NH_4^+, ammonium nitrogen (mg/L); and NO_3^-, nitrate nitrogen (mg/L). Significant results are in bold (* $p < 0.05$; ** $p < 0.01$).

		α Diversity		**β Diversity**					
				All Species			**Native Species**		
		All Species	**Native Species**	β_{sor}	β_{sim}	β_{sne}	β_{sor}	β_{sim}	β_{sne}
Geographica factors	DL	**0.729 ****	**0.725 ****	**0.562 ****	**−0.306 ****	**0.713 ****	**0.563 ****	**−0.286 ****	**0.708 ****
	DA	**0.737 ****	**0.736 ****	**0.625 ****	−0.205	**0.698 ****	**0.626 ****	**−0.190 ***	**0.696 ****
	AP	0.033	0.030	−0.060	−0.152	0.055	−0.061	**−0.151 ***	0.053
	AAT	**0.170 ***	**0.167 ***	**0.327 ****	**0.224 ****	**0.130 ***	**0.327 ***	**0.230 ***	0.128
	AA	0.018	0.021	0.090	0.111	0.001	0.095	0.111	0.006
Environmental factors	WT	**0.260 ***	**0.259 ***	**0.456 ***	**0.286 ***	**0.200 ***	**0.461 ***	**0.301 ***	0.197
	pH	**−0.218 ***	**−0.220 ***	−0.142	0.136	**−0.222 ***	−0.147	0.128	**−0.223 ***
	DO	−0.025	−0.023	−0.031	0.014	−0.037	−0.025	0.018	−0.035
	TURB	−0.106	−0.113	−0.001	0.166	−0.118	0.008	0.192	−0.129
	Chl-a	−0.003	0.001	−0.071	−0.104	0.011	−0.069	−0.105	0.013
	NH_4^+	0.053	0.053	0.150	0.151	0.026	0.146	0.146	0.027
	NO_3^-	0.176	0.180	0.019	**−0.267 ****	0.206	0.024	**−0.262 ****	0.209
	TP	−0.018	−0.021	0.040	0.075	-0.018	0.046	0.091	−0.024
	TN	**0.249 ***	**0.250 ***	0.152	−0.192	**0.271 ****	0.152	−0.191	**0.272 ***

4. Discussion

Dams continue to have innumerable impacts on freshwater fishes and ecosystems [2,12]. This study found that major dam construction in the Gan River Basin has resulted in dramatic changes to multiple dimensions of fish diversity. Comparisons of historical (pre-dam) to current (post-dam) periods found that the number of total and native species have declined. Most notably, 29 native species were lost in the present-day, including the extirpation of all species from the families Acipenseridae, Cluoeidae, Anguillidae, Cynoglossidae and Teraodontidae (Tables S2 and S3). By contrast, six alien species were gained.

Our results suggest that the construction of major dams have affected the composition and alpha diversity of fish in the Gan River Basin, although we recognize that other environmental changes independent of dams have occurred. Previous research has shown that after construction of Wanan Dam, Chinese sturgeon (*Acipenser sinensis*), Reeves shad (*Tenualosa reevesii*), and long spiky-head carp (*Luciobrama macrocephalus*) were extirpated, and population sizes of Japanese grenadier anchovy (*Coilia nasus*) and yellowcheek (*Elopichthys bambusa*) rapidly declined in the Gan River Basin [30,31]. Total reproductive output of four major Chinese carps rapidly declined from 2.5 billion in the 1960s to 20 million in 2000 [30,31], and the 12 spawning grounds of four major Chinese carps and three spawning grounds of Reeves shad (*Tenualosa reevesii*) were degenerated and disappeared [31,55].

River ecosystems have experienced hydrological disconnection and habitat fragmentation due to dam constructions, resulting in biological homogenization [17,20,56]. For example, flow regimes, water quality, and habitat conditions of Yangtze River Basin are significantly affected by the Three Gorges Dam, which resulted in the extinction of many native and endemic fish species and leading to fish faunal homogenization [17,57,58]. Similar effects of dam constructions in the Yellow River Basin have also manifested [59]. This study also demonstrated a homogenization trend, with a general increase in fish taxonomic similarity among regions of the Gan River Basin. Past studies also showed that dams caused habitat fragmentation and loss in many river ecosystems, resulting in the loss of native and endemic species and the introduction of non-native fish species, leading to a decline in beta diversity and increase in biological homogenization [17,46,60,61].

A rich body of literature points to the negative effects of dam operations on downstream fish faunas [62]. Dam operations often result in altered magnitude, variability, and timing of flow, with subsequent impacts on fish populations and communities. Furthermore, altered thermal regimes, due to dam management operations, have led to significant ecological impacts around the world (reviewed in Olden and Naiman, 2010) [6]. The frequent discharge of warm or cold water and other environmental variables in the downstream areas is unfavorable to the survival and reproduction of some fish species [63]. In this study, water temperature was an important predictor of fish diversity and composition. For example, four major Chinese carps and Reeves shad were lost because of thermal or flow sensitivities [31]. Furthermore, biogeographic patterns of fish faunas are shaped by zoogeographic history, geographical factors, climate factors, and anthropogenic disturbance [29,64,65]. Our results showed that a significant effect of drainage length, drainage area and average air temperature on alpha and beta fish diversity in the Gan River Basin.

Many freshwater ecosystems in China have experienced massive fish declines in recent decades; a pattern also observed in this study. Other threats, such as water pollution, overfishing, invasive species, and climate change, have also affected fish diversity in the Gan River Basin. For example, the yield of *Tenualosa reevesii* rapidly declined from 309–584 t in 1960, 74–157 t in 1970, and 12 t in 1986 due to overfishing [17,66,67]. The continuous input of industrial wastewater and domestic sewage has caused the gradual deterioration of the water quality and indirectly affected fish diversity [67–69]. In many instances, freshwater fish may be under multiple pressures and, at the same time, may act synergistically, exposing the species to greater risks [70]. Therefore, further research on the interaction between unknown or poorly understood stressors (pollution, invasive species, and climate change) and multiple stressors deserves further attention.

As human activities continue to alter freshwater ecosystems globally, a critical conservation goal is to develop dynamic fish diversity conservation management strategies that can adapt to changing environmental conditions while maintaining natural biogeographic patterns [20]. Investigations of beta-diversity components over space and time are considered pivotal for pinpointing factors driving community variability and can help inform conservation prioritization and planning [21]. In light of the mounting threats to China's freshwater fishes [40,71], we offer the following two recommendations. First, we call for systematic conservation planning efforts that seek to efficiently select a comprehensive and representative set of areas for conservation management to ensure the long-term persistence of fish biodiversity. Second, changing socio-economic activities and climate change is only further intensifying the risk of species invasion risk across China [27,72]. We call for enhanced biosecurity frameworks that incorporate the risks from species invasions on fish biodiversity, including improved monitoring programs for invasive alien species.

Supplementary Materials: The following are available online at https://www.mdpi.com/article/10.3390/d14060476/s1, Table S1: Literature used to buildup fish species lists in the historical (1965–1990), and the current (1990–2021) periods in the Gan River Basin. Table S2: Species composition in the Gan River Basin during the historical period (1965–1990). Table S3: Species occurrence in the Gan River Basin during the current period (1990–2021). Table S4: Mean value of geographical factors and environmental factors in the Gan River Basin.

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