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Assessing the impact of river connectivity on fish biodiversity in the Yangtze River Basin using a multi-index evaluation framework

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ABSTRACT

The Yangtze River Basin, the world's third-largest river basin and a hot spot for global biodiversity conservation, is facing biodiversity crisis caused by reduced river connectivity. The deterioration arises from four dimensions: longitudinal, lateral, vertical and temporal. However, limited research has quantified the spatiotemporal connectivity of the Yangtze River Basin and further evaluated the consequent impact on fish biodiversity. In our study, a multi-index evaluation framework was developed to assess the variations in the four-dimensional connectivity of the Yangtze River Basin from 1980 to 2020, and fish biodiversity affected by reduced connectivity was detected by environmental DNA metabarcoding. Our results showed that the Yangtze River Basin suffers from a pronounced connectivity reduction, with 67% of assessed rivers experiencing deteriorated connectivity in recent years. The lost fish biodiversity along the river reaches with the worst connectivity was likely attributed to the construction of hydropower plants. The headwaters and the downstreams of most hydropower plants had a higher fish biodiversity compared with reservoirs. The free-flowing reaches in the downstream of the lowest hydropower station, had higher lotic fish abundance compared with that in the upstream. As for the entire Yangtze River Basin, 67% of threatened fish species, with 70% endemic species, were threatened by reduced river connectivity. Our result indicates that the massive loss of river connectivity changes the spatiotemporal patterns of fish community and threatens protected fish. More effective measures to restore the populations of affected fish in rivers with reduced river connectivity are required.

1. Introduction

The concept of river connectivity, which describes the shift of matter and organisms in the spatial units of natural systems (Wohl, 2017), derives from the concept of river continuum (Vannote et al., 1980). River connectivity is a four-dimensional structure (Grill et al., 2019), including longitudinal, lateral, vertical and temporal connectivity. Longitudinal connectivity refers to the flow of water along the river continuum, while lateral connectivity is the shift of water between the stream and riverine areas. Vertical connectivity describes the movement of water in the vertical direction, and temporal connectivity demonstrates discharge changes in time scales (Ward and Stanford, 1995). While river connectivity plays a key role in maintaining aquatic biodiversity, the global river connectivity is strongly disturbed by human activities (Grill et al., 2019). In Europe, at least 1,200,000 barriers have obstructed the water flow of rivers in 36 countries (Belletti et al., 2020). A global research based on the longitudinal connectivity (fragmentation) and the temporal connectivity (flow regulation) shows that 48% of rivers worldwide have been impeded (Grill et al., 2015). Another study based on the four-dimensional connectivity illustrates that the water flow in 63% of rivers longer than 1000 km is hindered globally (Grill et al., 2019). However, the Global Reservoir and Dam Database used in the above two global studies underestimates the number of dams in China (Hennig et al., 2017), which may underrate the deterioration of river connectivity in China.

The degraded river connectivity threatens freshwater biodiversity

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worldwide (Vorosmarty et al., 2010), particularly disrupting the migration of aquatic species directly (He et al., 2021a). In the meantime, hydrological and water-quality conditions changed by reduced river connectivity, alter the habitat suitability of some species and have an indirect impact on communities (Barbarossa et al., 2020; Guo et al., 2023; Yan et al., 2023; He et al., 2021a). For instance, α-diversity of macroinvertebrates reaches its maximum at a moderate level of hydrological connectivity, while β-diversity decreases as the improvement of connectivity (Chi et al., 2018). This phenomenon is consistent with the intermediate disturbance hypothesis, which describes that the diversity of species is higher in sites with intermediate disturbance (Collins and Glenn, 1997). In order to investigate the impact of longitudinal connectivity on aquatic species, the model given by the river continuum concept (Vannote et al., 1980), which depicts the gradual change of macroinvertebrate communities as a result of gradual alteration in habitats along the river, is widely used. Recently, this model is confirmed to explain the longitudinal pattern of fish community (Ferreira and Petrere, 2009).

The Yangtze River Basin is the world's third-largest basin (Chen et al., 2020), and its water resource accounts for 35% of the total river runoff in China (Tang et al., 2022). The basin provides habitats for more than 140 species of amphibian and 400 species of fish (Zhang et al., 2022a). From 1980 to 2020, the Yangtze River Basin suffered from enhanced anthropogenic disturbances, e.g. the increasing number of hydropower plants. These disturbances impacted the connectivity status of the Yangtze River Basin, and resulted in serious biodiversity loss (Xie, 2017). For instance, the reproduction of Chinese sturgeon (*Acipenser sinensis*) has been hindered by the Three Gorges Hydropower Station (Chen et al., 2020). However, previous studies about the Yangtze River Basin mainly focused on the longitudinal connectivity and haven't reflected the spatiotemporal deterioration in the connectivity of the entire Yangtze River Basin, which may obstruct the formulation of protection policy.

Therefore, we aimed to develop a multi-index evaluation framework based on the four-dimensional connectivity to quantify the spatiotemporal connectivity of the Yangtze River Basin from 1980 to 2020 and further evaluate the consequent impact on fish biodiversity. We hypothesized that patterns of fish communities in a natural river without hydropower stations showed a gradual change from headwater to downstream (the River Continuum Concept), whereas the fish communities in a river blocked by dams may exhibit significant community shift and biodiversity loss.

2. Materials and methods

2.1. Study area

The Yangtze River is the third-longest river in the world, flowing for 6300 km from the Qinghai-Tibet Plateau to the sea, entirely within China (Fig. 1A and B) (Chen et al., 2009), with the area 1,800,000 km^2. Due to the human demand for electricity, hydropower plants have been proliferated in the Yangtze River Basin, acting as the major barriers to disrupt river connectivity. In 2020, nearly 100 hydropower plants have been built in the Yangtze River and its main tributaries (Fig. 1C) (Lehner et al., 2011; Mulligan et al., 2021). By 2030, nearly 20 hydropower plants are planned for construction (Cui et al., 2022; He et al., 2021b; Ja and Huang, 2011; Li et al., 2013; Zarfl et al., 2015).

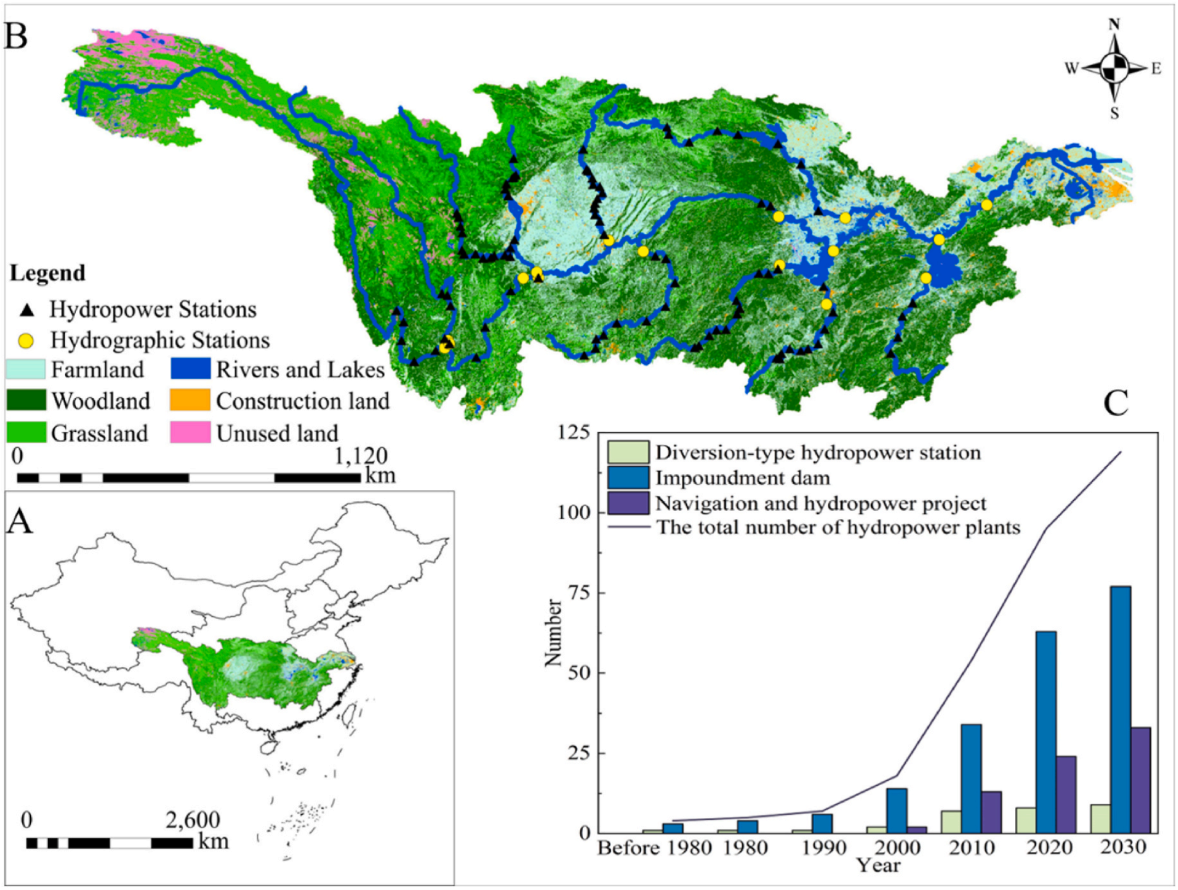

Fig. 1. A: Yangtze River Basin. B: Main stream, major tributaries, connected lakes, hydropower plants and selected hydrographic stations in the Yangtze River Basin. C: The cumulative number of hydropower plants in the Yangtze River and major tributaries from 1980 to 2030. Projected hydropower plant data from 2020 to 2030 is taken from (Cui et al., 2022; He et al., 2021b; Ja and Huang, 2011; Li et al., 2013; Zarfl et al., 2015).

2.2. Data collection

2.2.1. Geographic and discharge data

The hydropower station dataset was generated using the Global Reservoir and Dam Database (GRanD, v1.3) (Lehner et al., 2011; Mulligan et al., 2021), supplemented with data derived from Google Earth and comprehensive report of the national water conservancy census (Ministry of Water Resources of the People's Republic of China, 2013). This database includes all hydropower stations in the Yangtze River and major tributaries.

Databases for Chinese multi-period land use and spatial distribution of primary rivers were provided by the Data Center for Resources and Environmental Sciences, Chinese Academy of Sciences (Xu et al., 2018). The China multi-period land use land cover data set (Yang and Jiang, 2021) included six primary classes: farmland, woodland, grassland, water area, construction land and unused land.

Hydrologic discharge data was obtained from the Hydrological Yearbook of the Yangtze River Basin (Changjiang Water Resources Commission, 2020). Hydrographic stations close to stream outlets were selected based on proximity to study and data availability. Changes in flow regime in the Yangtze River Basin were evaluated by comparing historic discharge data (1961–1975) to three five-year periods (Fig. 2).

2.2.2. Biological data

Based on the analysis of our hydropower station database, we found that the Wu River, with annual average flow roughly equal to the second-longest river (the Yellow River) in China (Cheng et al., 2023; Yang et al., 2010), was one of the rivers most severely affected by infrastructure development. Eleven sites located in the main stream of the Wu River were sampled during July 2022 (Fig. 3). S1 is the site at the headwater. S2 is the site 5 km in front of the Dongfeng Hydropower Station. S3 is the site 5 km behind the Dongfeng Hydropower Station. S4 is the site 7 km in front of the Yinpan Hydropower Station. S5 is the site 1 km in front of the Yinpan Hydropower Station. S6 is the site 1 km behind the Yinpan Hydropower Station. S7 is the site 3 km behind the Yinpan Hydropower Station. S8 is the site 7 km behind the Yinpan Hydropower Station. S9 is the site 10 km behind the Yinpan Hydropower Station. S10 is the site 15 km behind the Yinpan Hydropower Station. S11 is the site at the stream outlet of the Wu River.

At each site, the 5-L mixed water of the left, middle and right sections were collected. Each sample was filtered using a 0.22 μm hydrophilic polycarbonate filter membrane within 6 h after sampling. At the same time, a blank control in each site was set by getting 5 L distilled water filtered using a 0.22 μm hydrophilic polycarbonate filter membrane. After filtering, membranes were frozen at −80 °C. The eDNA in membranes was extracted using Qiagen DNeasy PowerWater kit, and was used as templates for Polymerase chain reaction (PCR) approach through gene primers MiFish-F (5′-GTCGGTAAAACTCGTGCCAGC-3′) and MiFish-R (5′-CATAGTGGGGTATCTAATCCCAGTTTG-3′) (Miya et al., 2015). The high-throughput sequencing was operated by the MiSeq sequencing platform (Illumina, San Diego, USA).

The threatened fish directory and species status at the catchment scale were counted on the basis of China's Red List of Biodiversity (Zhang and Cao, 2021) and literatures (Chang et al., 2016; Chen et al., 2022; Liu et al., 2021a; Lv et al., 2019; Shao et al., 2020; Wang et al., 2005; Yang et al., 2023; Zhang et al., 2022b).

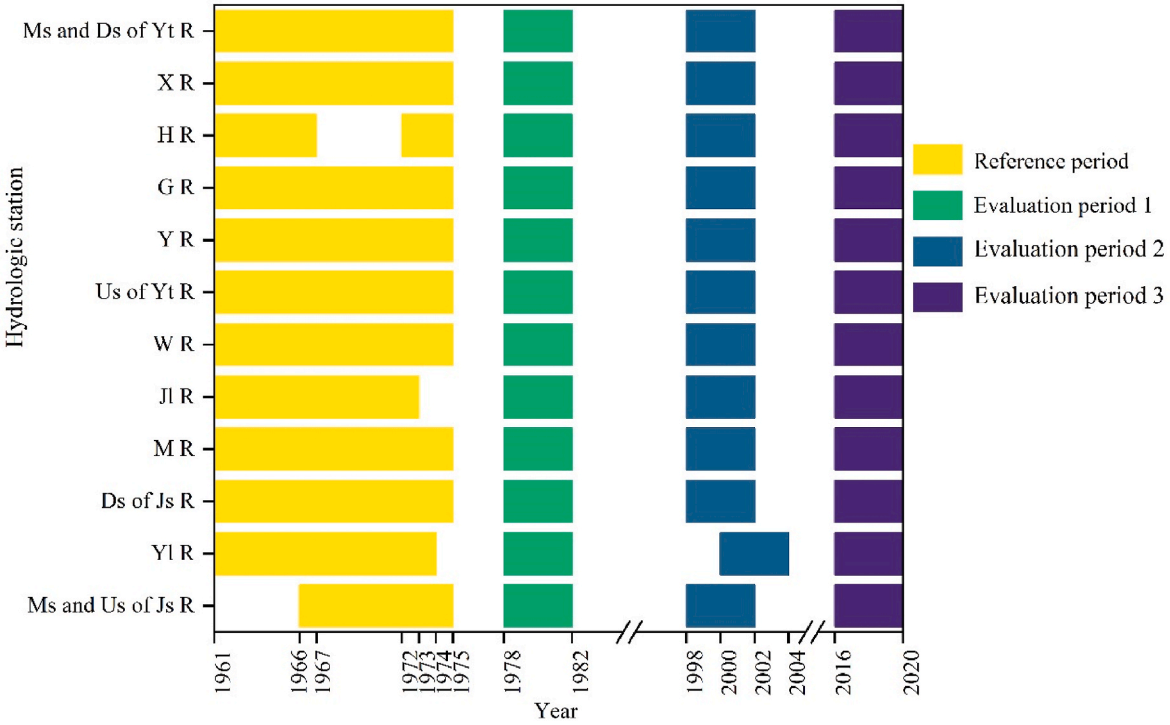

Fig. 2. The hydrologic stations and years of flow data for rivers are as follows: (1) The midstream and upstream of the Jinsha River (Ms and Us of Js R) at the Panzhihua Station, year 1966–1975, 1978–1982, 1998–2002, and 2016–2020. (2) The Yalong River (Yl R) at the Xiaodeshi Station (year 1961–1974, 1978–1982, 2000–2004) and the Tongzilin Station (year 2016–2020). (3) The downstream of the Jinsha River (Ds of Js R) at the Pingshan Station (year 1961–1975, 1978–1982, 1998–2002) and the Xiangjiaba Station (year 2016–2020). (4) The Min River (M R) at the Gaochang Station, year 1961–1975, 1978–1982, 1998–2002, and 2016–2020. (5) The Jialing River (Jl R) at the Beibei Station, year 1961–1973, 1978–1982, 1998–2002, and 2016–2020. (6) The Wu River (W R) at the Wulong Station, year 1961–1975, 1978–1982, 1998–2002, and 2016–2020. (7) The upstream of the Yangtze River (Us of Yt R) at the Yichang Station, year 1961–1975, 1978–1982, 1998–2002, and 2016–2020. (8) The Yuan River (Y R) at the Taoyuan Station, year 1961–1975, 1978–1982, 1998–2002, and 2016–2020. (9) The Gan River (G R) at the Waizhou Station, year 1961–1975, 1978–1982, 1998–2002, and 2016–2020. (10) The Han River (H R) at the Xiantao Station, year 1961–1967, 1972–1975, 1978–1982, 1998–2002, and 2016–2020. (11) The Xiang River (X R) at the Xiangtan Station, year1961–1975, 1978–1982, 1998–2002, and 2016–2020. (12) The midstream and downstream of the Yangtze River (Ms and Ds of Yt R) at the Datong Station, year 1961–1975, 1978–1982, 1998–2002, and 2016–2020.

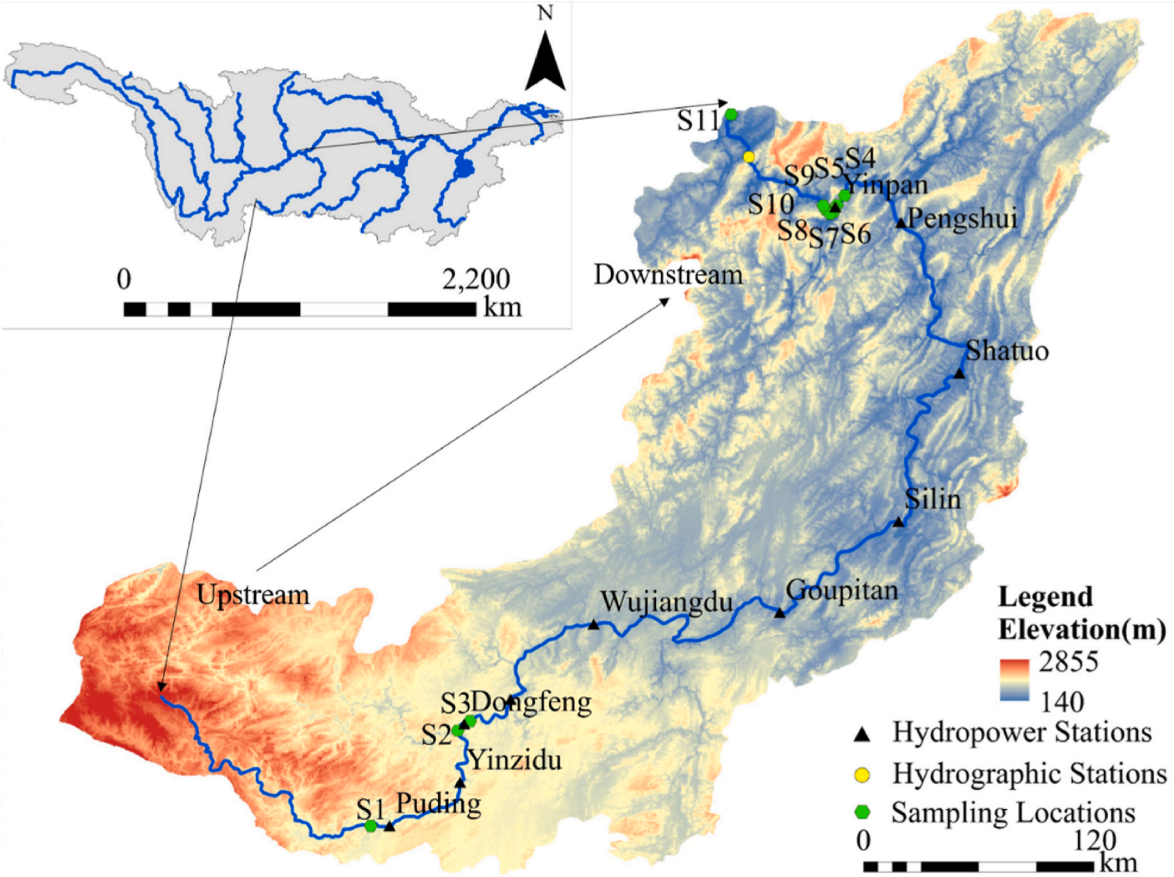

Fig. 3. The DEM of Wu River. Eleven sampling sites were located in the Wu River during July 2022, including one site (S1) at the headwater of the Wu River, one site (S2) at the upstream of the Dongfeng Hydropower Station, one site (S3) at the downstream of the Dongfeng Hydropower Station, two sites (S4 and S5) at the upstream of the Yinpan Hydropower Station, five sites (S6–S10) at the downstream of the Yinpan Hydropower Station, and one site (S11) at the stream outlet of the Wu River.

2.3. Statistical analysis

2.3.1. Multi-index evaluation framework of river connectivity

To assess the integrated connectivity of the Yangtze River and major tributaries, a multi-index evaluation framework was developed according to the four structural dimensions. Six parameter indices were set in the framework, including barrier coefficient, the ratio of longest continuous river reach, riparian construction land, constant water surface area, annual discharge variation coefficient and monthly average discharge variation coefficient (Table 1).

(1) Longitudinal connectivity

Hydropower plants persistently impede the free flow of water, which profoundly affect the longitudinal connectivity and obstruct the migration of aquatic organisms. In order to eliminate the barrier effect of water conservancy facilities, the fish passage is built. However, the efficiency of fishway is limited (Noonan et al., 2012).

In this study, the barrier coefficient (A1) was used to estimate the average fragment processing of the longitudinal connectivity (Tang et al., 2022), represented by:

$$B_j = \left(\sum_{i=1}^{n} N_i a_i \middle/ L_j \right) \times 100\% \quad (i = 1, 2, \cdots, n) \tag{1}$$

where B_j is the barrier coefficient of a certain river reach j, L_j is the length of a certain river, N_i is the total number of the i-type hydropower plant, n is the total kinds of hydropower plants, and a_i is the barrier coefficient of the i-type hydropower plant.

The barrier coefficient of facilities with fishways was set lower than similar facilities without fish lanes (Table 2) (Li et al., 2018; Tang et al.,

Table 1
List of connectivity aspects and parameter indices (A1-A6) in our multi-index evaluation framework.

Multi-index evaluation framework	Connectivity aspect	Parameter index
	Longitudinal	A1Barrier coefficient
		A2 The ratio of longest continuous river reach
	Lateral	A3 Riparian construction land
	Vertical	A4 Constant water surface area
	Temporal	A5 Annual discharge variation coefficient
		A6 Monthly average discharge variation coefficient

Table 2
List of the barrier coefficient of different hydropower plants. The hydropower stations with fishway and fairway has lower barrier coefficient.

The kinds of hydropower stations	Barrier coefficient
Diversion-type hydropower stations	0.5
Impoundment dam (without fishway but having fairway)	0.75
Impoundment dam (without fishway and fairway)	1
Impoundment dam (with fishway)	0.5
Navigation and hydropower project (with fishway)	0.75
Navigation and hydropower project (without fishway)	0.5

2022).

The ratio of longest continuous river reach (A2) was adopted to assess the optimal longitudinal connectivity. It was expressed as (Tang et al., 2022):

$$W_j = (I_{\max} / L_j) \times 100\% \tag{2}$$

whereW_j is the ratio of the longest continuous river reach for a certain river j, $I_{\max}$ is the longest continuous river length between two adjacent hydropower stations in the certain river j, and L_j is the total length of the certain river j.

(2) Lateral and vertical connectivity

Considering the different geographical background of rivers, the lateral and vertical connectivity status in 1980, which was less disturbed, was used as the reference. The area of 800 m on both sides of rivers was classified as riparian zone (Xu et al., 2021).

Under the anthropogenic interference, some parts of riparian zone tends to be applied as construction land, which may have a narrow effect on the riverbed (Tessler et al., 2016). In our study, the riparian construction land (R_{Ct}, A3) was calculated as:

$$R_{Ct} = (S_{iCt} / A_t) \div (S_{iC1980} / A_{1980}) \tag{3}$$

where S_{iCt} is the area of construction land in t period, and A_t is the total area of riparian zone in t period.

The constant water surface area is the water area below the annual water level, which affects the movement of water in the vertical direction. The constant water surface area was used to reflect the vertical connectivity. The constant water surface area (R_{wt}, A4) was counted as follows:

$$R_{Wt} = W_t / W_{1980} \tag{4}$$

where W_t is the surface area of constant water in t period.

(3) Temporal connectivity

The temporal connectivity of rivers without anthropogenic intervention depends on climatic variables, especially the spatiotemporal distribution of precipitation. Considering the variability of runoff caused by climatic factors, the flow data from 1961 to 1975 was set as the reference, the flow data of evaluation period 1, period 2 and evaluation period 3 was applied to indicate the flow conversion. The annual discharge variation coefficient β_t (A5) and the monthly average discharge variation coefficient φ_t (A6) were calculated to illustrate annual flow changes and monthly flow alteration, which were represented by:

$$\beta t = ((dr - dt) / dr) \times 100\% \tag{5}$$

$$\varphi_t = \sqrt{\sum_{m=1}^{12} ((q_m - Q_m)/dr)^2} \tag{6}$$

where d_r is the multi-year average flow for the reference period, d_t is the mean multi-year flow for the evaluation period, m is the serial number of months, q_m is the measured average monthly discharge in the m month of the evaluation period, and Q_m is the measured average monthly discharge in the m month of the reference period.

(4) The integrated connectivity

The Pearson correlation coefficient |r | was used to indicate the relevance between two parameter indices. Only indices with $|r| \geq 0.8$ would be chosen based on their indicator roles. For the purpose of standardization, the ratio method, which was considered to be the most accurate and effective in the standardization approach of aquatic ecosystem health assessment (Xie et al., 2023), was applied.

The weight of selected indices and connectivity aspects were determined by the Analytic Hierarchy Process (AHP) (Sun et al., 2021). The main process is as follows (Sun et al., 2021):

Firstly, the judgment matrix is established by sorting out the relative importance. Secondly, the eigenvalues λ and corresponding eigenvectors ω of each judgment matrix are calculated. Finally, the consistency ratio CR is counted based on the largest eigenvalue λ_{max}, the order n of the judgment matrix, and the random consistency index RI (formula (7))

$$CR = \frac{\lambda_{max} - n}{n-1} \times \frac{1}{RI} \tag{7}$$

When all matrices meet $CR < 0.1$, it's considered that the judgment matrix passes the consistency test, and the eigenvector ω corresponding to the largest eigenvalue λ_{max} is the weight.

The integrated connectivity scores were calculated as follows:

$$Q = \sum_{i=1}^{n} Q_i C_i \tag{8}$$

where Q is the total score, Q_i is the score for the i parameter index, and C_i is the weight for the i parameter index.

River reaches whose integrated connectivity scores ≥95% of quantiles were classified as the degree of excellent (Xie et al., 2023). The other were evenly divided into 4 degree, including good, fair, poor and very poor degree.

In order to detect whether the landscape of the riparian zone around dams has an impact on connectivity status, the land use of the riparian zone within 800 m of dams was counted. The ratio of construction land in riparian zone around dams was standardized by the ratio method (Xie et al., 2023). The Pearson correlation coefficient |r | (Liu et al., 2020; Liu et al., 2023a) was calculated among the standardized ratio of construction land in riparian zone around dams, scores of the longitudinal connectivity, scores of the lateral connectivity, scores of the vertical connectivity, scores of the temporal connectivity and scores of the integrated connectivity.

2.3.2. *Ecological impact analysis*

The raw data of eDNA metabarcoding was filtered by VSEARCH (Rognes et al., 2016) in order to eliminate adapter contamination and reads of low quality. The OTUs was determined at the 97% identity level (Fan et al., 2020; Shi et al., 2023). Metabarcoding annotation was conducted according to the MitoFish dataset (Iwasaki et al., 2013; Sato et al., 2018; Zhu et al., 2023). The relative abundance of the OTUs was calculated using the VEGAN package in RStudio (Dixon, 2003).

In order to confirm our hypothesis, the One-way analysis of variance (ANOVA) (Gao et al., 2023; Yu et al., 2023a) was conducted to investigate the difference of fish composition at the upstream and the downstream of the Yinpan Hydropower Station (S4–S10). The T-test (Huang et al., 2022; Zeng et al., 2022) was applied to detect the difference of fish composition at the upstream and downstream of the Dongfeng Hydropower Station (S2–S3). Further, the fish composition in sampling sites was clustered based on the Jaccard coefficient to detect the difference of fish composition along the Wu River. Besides, the OTUs relative abundance of lotic fish, the Shannon-Wiener index, the Pielou's evenness index and the Margalef's richness index were calculated to indicate the difference of fish composition among sampling sites.

At the catchment scale, the conservation status of threatened fish species was counted. Simultaneously, the impact of connectivity on threatened fish was analyzed according to the water layer of habitat, feeding habit, reproductive conditions and geographical distribution range (Chang et al., 2016; Chen et al., 2022; Liu et al., 2021a; Lv et al., 2019; Shao et al., 2020; Wang et al., 2005; Yang et al., 2023; Zhang et al., 2022b).

3. Results

3.1. The status of connectivity

Our result showed that the Pearson correlation coefficient |r | among parameter indices did not meet the threshold value. All parameter indices passed the correlation testing.

The *CR* value of Analytic Hierarchy Process matrices was less than 0.1, which indicated the weight was reasonable. The weight of the connectivity in different aspects was: 0.6130 (longitudinal), 0.2050 (lateral), 0.1177 (vertical) and 0.0643 (temporal). The weight of parameter indices was as: 0.3065 (A1), 0.3065 (A2), 0.2050 (A3), 0.1177 (A4), 0.0161 (A5) and 0.0482 (A6).

The four-dimensional and integrated connectivity status is illustrated in Fig. 4. The standardized scores are represented in Fig. 5A and B, and monthly average runoff in rivers with greater variation is showed in Fig. 5C.

3.1.1. Longitudinal connectivity

The longitudinal connectivity of assessed rivers deteriorated over time (Figs. 4A and 5A). In 1980, only 5 hydropower plants were built in the Dadu River (the main tributary of the Min River), the upper Min River, the upper Han River and the upper Xiang River. Such few hydropower plants maintained high longitudinal connectivity. In 2000, the longitudinal connectivity of the lower Yalong River, the middle Jialing River, the upper Han River, the upper and middle Wu River, the lower Yuan River and the upper Xiang River were significantly reduced due to the construction of hydropower plants. In 2020, the deterioration in the

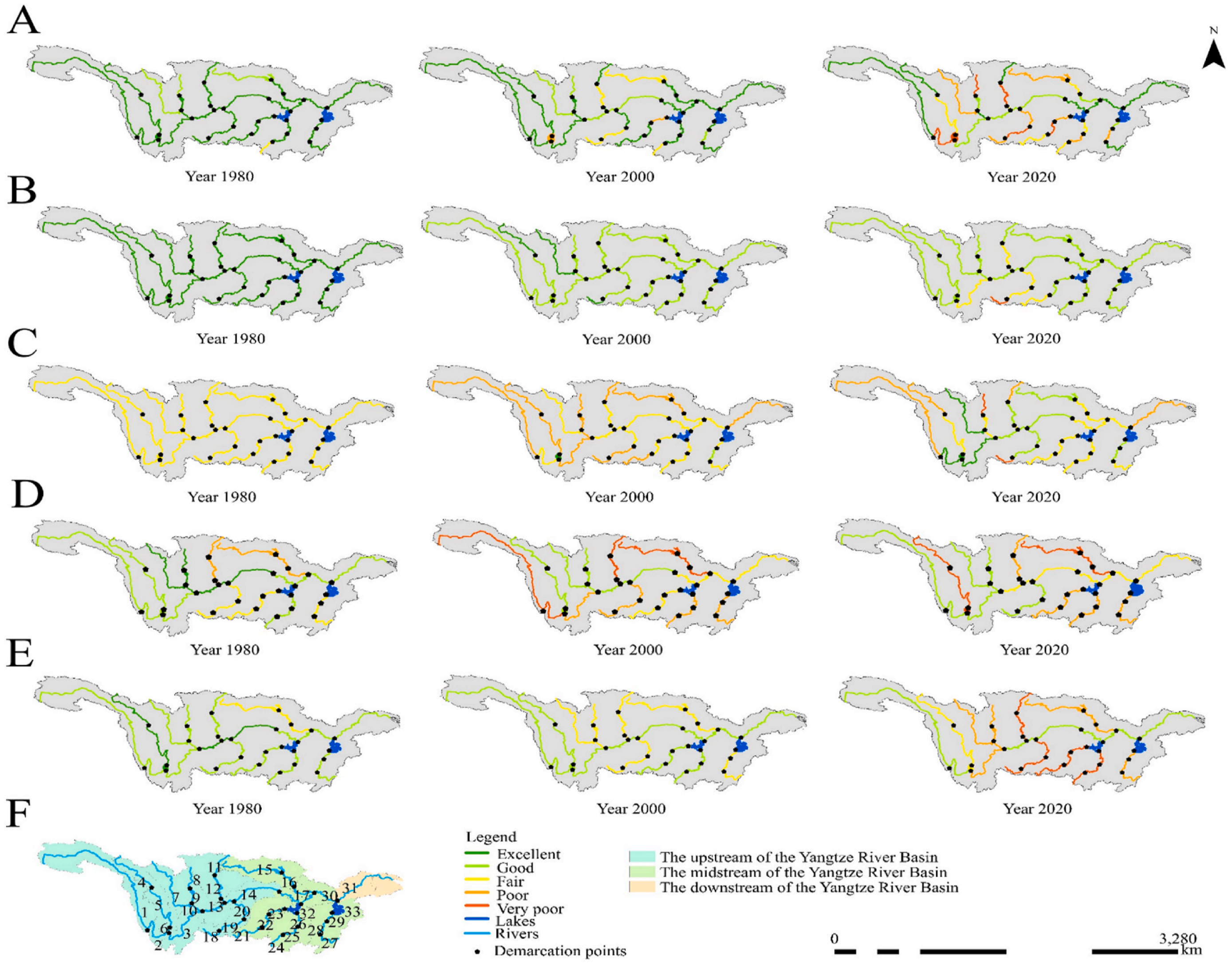

Fig. 4. A: the longitudinal connectivity status. B: the lateral connectivity status. C: the vertical connectivity status. D: the temporal connectivity status. E: the integrated connectivity status. F: the code and legend. The meaning of number in F is as follows: 1. The upstream of the Jinsha River (Us of Js R). 2. The midstream of the Jinsha River (Ms of Js R). 3. The downstream of the Jinsha River (Ds of Js R). 4. The upstream of the Yalong River (Us of Yl R). 5. The midstream of the Yalong River (Ms of Yl R). 6. The downstream of the Yalong River (Ds of Yl R). 7. The Dadu River (D R). 8. The upstream of the Min River (Us of M R). 9. The midstream of the Min River (Ms of M R). 10. The downstream of the Min River (Ds of M R). 11. The upstream of the Jialing River (Us of Jl R). 12. The midstream of the Jialing River (Ms of Jl R). 13. The downstream of the Jialing River (Ds of Jl R). 14. The upstream of the Yangtze River (Us of Yt R). 15. The upstream of the Han River (Us of H R). 16. The midstream of the Han River (Ms of H R). 17. The downstream of the Han River (Ds of H R). 18. The upstream of the Wu River (Us of W R). 19. The midstream of the Wu River (Ms of W R). 20. The downstream of the Wu River (Ds of W R). 21. The upstream of the Yuan River (Us of Y R). 22. The midstream of the Yuan River (Ms of Y R). 23. The downstream of the Yuan River (Ds of Y R). 24. The upstream of the Xiang River (Us of X R). 25. The midstream of the Xiang River (Ms of X R). 26. The downstream of the Xiang River (Ds of X R). 27. The upstream of the Gan River (Us of G R). 28. The midstream of the Gan River (Ms of G R). 29. The downstream of the Gan River (Ds of G R). 30. The midstream of the Yangtze River (Ms of Yt R). 31. The downstream of the Yangtze River (Ds of Yt R). 32. The Dongting Lake. 33. The Poyang Lake.

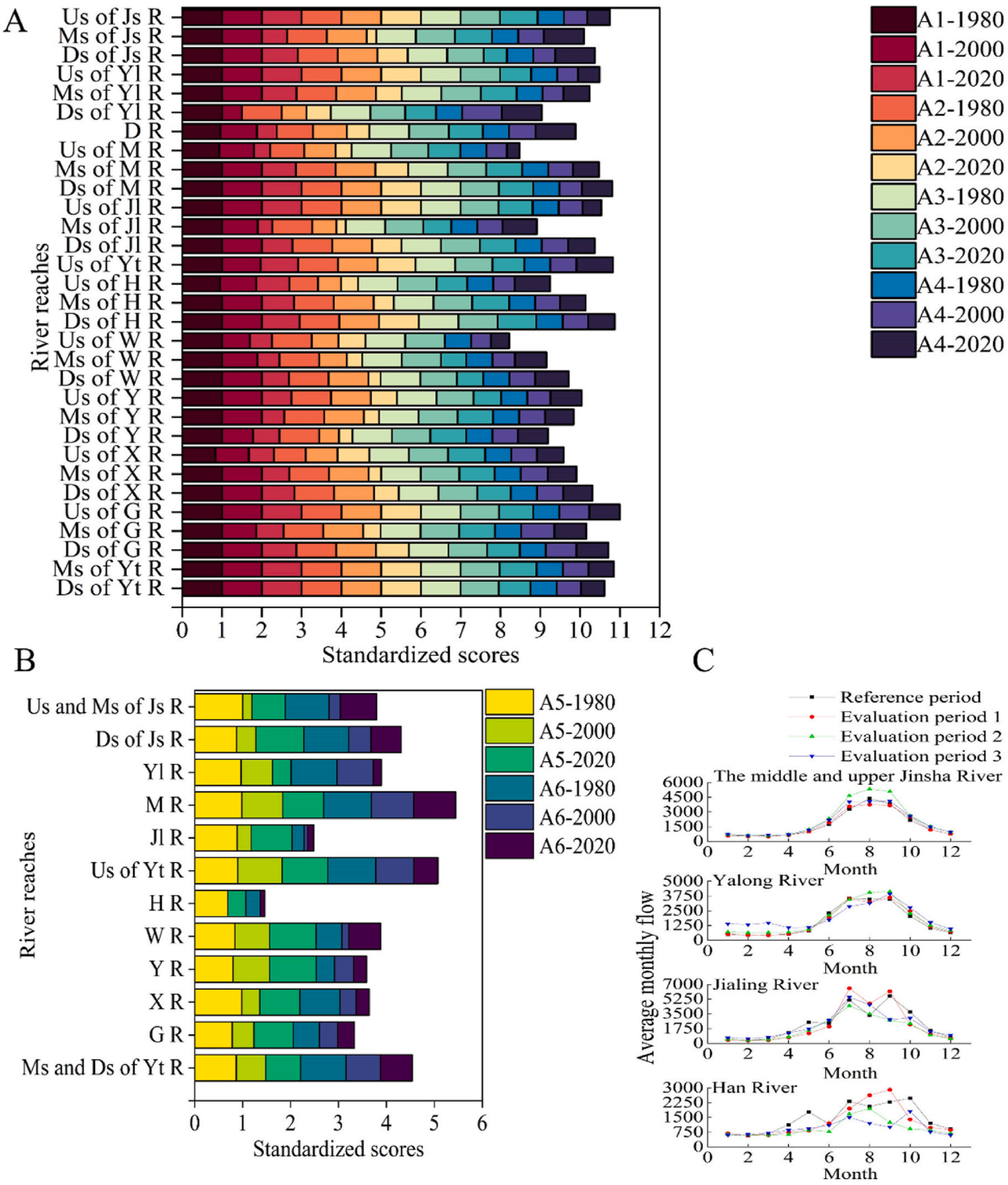

Fig. 5. A: the standardized scores of A1 (Barrier coefficient), A2 (The ratio of longest continuous river reach), A3 (Riparian construction land) and A4 (Constant water surface area). The meaning of abbreviation in Y-axis of Fig. 5A is equal to Fig. 4. B: the standardized scores of A5 (Annual discharge variation coefficient) and A6 (Monthly average discharge variation coefficient). The meaning of abbreviation in Y-axis of Fig. 5B is as follows: 1. Us and Ms of Js R, the upstream and midstream of the Jinsha River. 2. Ds of Js R, the downstream of the Jinsha River. 3.Yl R, the Yalong River. 4. M R, the Min River. 5. Jl R, the Jialing River. 6. Us of Yt R, the upstream of the Yangtze River. 7. H R, the Han River. 8. W R, the Wu River. 9. Y R, the Yuan River. 10. X R, the Xiang River. 11. G R, the Gan River. 12. Ms and Ds of Yt R, the midstream and downstream of the Yangtze River. C: the monthly average runoff in rivers with greater variation.

longitudinal connectivity of the middle Wu River, the middle Jinsha River, the lower Yalong River, the upper Min River, the middle Jialing River and the middle Yuan River was the most tremendous because of the rapid increasing of hydropower development in these areas.

3.1.2. Lateral connectivity

In 1980, the lateral connectivity of assessed rivers was all at the excellent level (Figs. 4B and 5A). In 2000, despite that the area of construction land had expanded to a certain extent, the lateral connectivity of assessed rivers remained good conditions. However, in 2020, the lateral connectivity in most rivers degraded, especially in the Wu River, the upper Yuan River, the middle Jialing River and the lower Jinsha River.

3.1.3. Vertical connectivity

The vertical connectivity altered significantly as the result of hydropower stations storage and changes in annual runoff, especially in the midstream of the Jinsha River, the downstream of the Jinsha River and the Dadu River (Figs. 4C and 5A). By 2020, 5 cascade hydropower stations had been constructed in the midstream of the Jinsha River, with a total utilizable capacity of 1.683 billion cubic meters (Ministry of Water Resources of the People's Republic of China, 2013; Mulligan et al., 2021). As for the lower Jinsha River, the Xiluodu Hydropower Station and other hydropower stations had been built, which led to the widening of the reservoir (Wang et al., 2018). In the Dadu River, 14 impoundment dams had been constructed (Ministry of Water Resources of the People's Republic of China, 2013; Mulligan et al., 2021).

3.1.4. *Temporal connectivity*

The main driving force in the reduction of temporal connectivity was the change of monthly runoff (Fig. 5C). Compared with the reference period, the discharge of the Jialing River, the Han River and the Yuan River showed giant variation in 1980 (Figs. 4D and 5C). In 2000, the flow of the evaluated rivers generally changed at a large scale. The deterioration of the Han River, the Jialing River, and the midstream and upstream of the Jinsha River was the most obvious. Although the temporal connectivity of some rivers in 2020 showed obvious improvement, the whole temporal connectivity was significantly altered, compared with the reference period.

3.2. *Ecological impact*

3.2.1. *The fish diversity in the Wu River*

A total of 17,494 OTU sequences belonging to 7 orders, 16 families, 41 genera and 54 species were identified after annotation (Fig. 6A). The Cypriniformes was the dominant order. Six exotic species such as the Mrigal (*Cirrhinus mrigala*) and the Rainbow Trout (*Oncorhynchus mykiss*) were contained. Eight threatened species were detected, including the *Scaphesthes macrolepis* and the *Gymnodiptychus pachycheilus*.

The results about One-way analysis of variance and T-test showed that species composition owned abrupt variation along the Wu River. The composition of fish species at the upstream and the downstream of the Yinpan Hydropower Station (S4–S10) had significant difference (One-way ANOVA, $P < 0.05$). In addition, sampling sites at the upstream and the downstream of the Dongfeng Hydropower Station (S2–S3) were also significantly different (T-test, $P < 0.05$) in fishes' composition.

The result of Shannon-Wiener index indicated that the headwater, the stream outlet and the downstream of dams tended to own higher biodiversity, while the upstream of dams had lower biodiversity (Fig. 6B). This tendency was dominated by the species' richness, since the tendency of Margalef's richness index was more consistent to the Shannon-Wiener index, while the Pielou's evenness index remained stable.

The result of cluster (Fig. 6C) showed that sites (S2 and S5) at the upstream of hydropower stations had lower species composition similarity with sites at the downstream of hydropower stations (S3 and S6). Overall, sites in the upper and middle reaches of the Wu River shared more difference than the lower reach. Besides, the stream outlet of the Wu River, which was indirectly controlled by the water storage in the Three Gorges Reservoir (Gao et al., 2010), had the lowest species composition similarity with any other sites.

The consequence of the OTUs relative abundance of lotic fish showed that the Yinpan Hydropower Station significantly affected the distribution of lotic fish (Fig. 6D).

3.2.2. *The threatened fishes at the basin scale*

Vulnerable species took the largest part in the threatened species (Fig. 7). Among the total 94 threatened species, 70 species were endemic to Yangtze River Basin. However, 87% of endemic species only existed in the upstream of the Yangtze River Basin with numerous in-stream infrastructure. Overall, the life cycles of 63 species (67%), were hindered by the connectivity status (Fig. 7.)

4. Discussion

4.1. *The impacts of anthropogenic activities on river connectivity*

The anthropogenic impact on river connectivity mainly includes hydropower development and land use alteration in riparian zone. Hydropower plants induce enormous decrease in the longitudinal

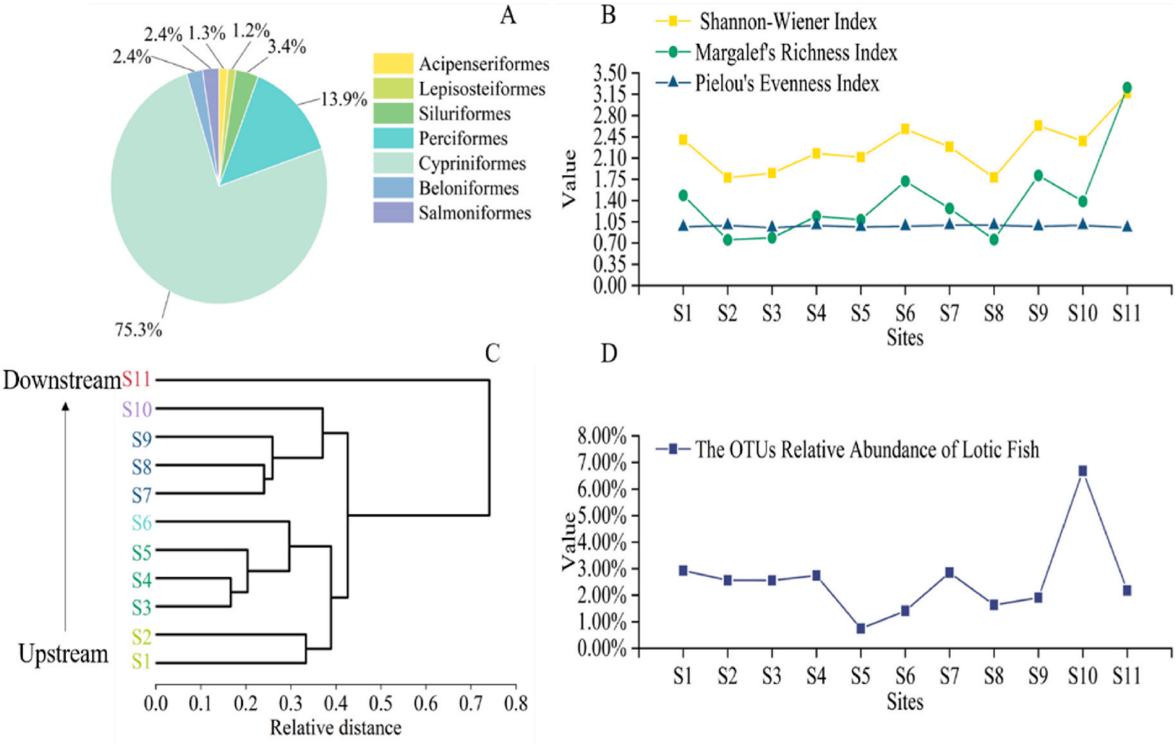

Fig. 6. A: the composition of fish in the order level. B: the result of biodiversity indices. C: the result of cluster. D: the OTUs relative abundance of lotic fish.

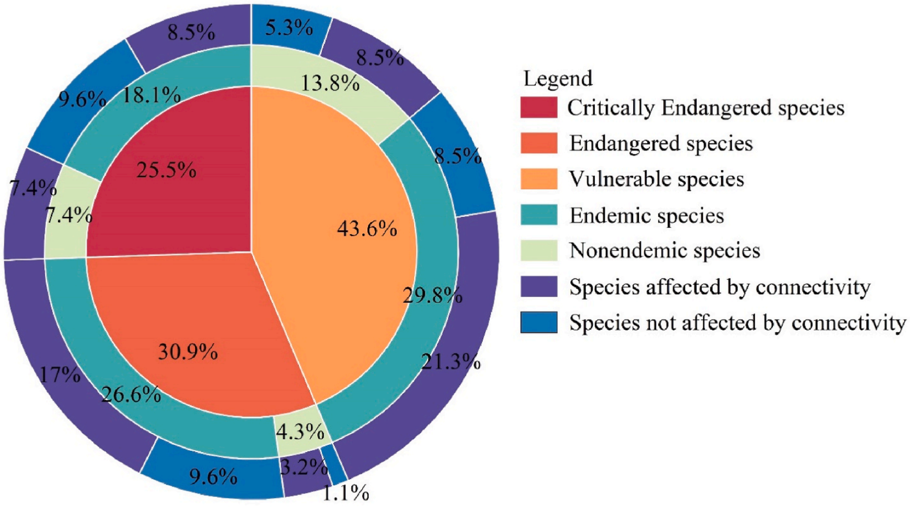

Fig. 7. The proportion of fish species with different protected levels, endemic species and species affected by deteriorated connectivity.

connectivity. In the Yangtze River Basin, with more than 2400 hydropower plants constructed (Li et al., 2019), the density of hydropower plants is 0.007 per km. Although the density is lower than Europe (0.74 per km) (Belletti et al., 2020), hydropower plants in the Yangtze River Basin have significantly blocked the longitudinal connectivity. Previous findings show that the value of two dendritic longitudinal connectivity indices of the Yangtze River Basin decreased by over 60% from 1980 to 2010 (Table 3) (Yi et al., 2022). Another study shows that at the catchment scale, the value of the river connectivity index based on the sediment longitudinal movement decreased by over 50% from 1950 to 2019 (Table 3) (Yang et al., 2019). As for the mainstream and main tributaries, our work illustrates that the degree of deterioration in the longitudinal connectivity was slightly lower. Our study indicates that 42% of assessed rivers had deteriorated connectivity in the longitudinal dimension.

Table 3
List of studies on river connectivity in the Yangtze River Basin, Europe and the whole world.

Study area	Reference	Connectivity status
Yangtze River Basin	Yi et al. (2022)	From 1980 to 2010, the value of the two dendritic longitudinal connectivity indices of the Yangtze River Basin decreased by over 60%.
	Yang et al. (2019)	For the whole Yangtze River Basin, the value of the river connectivity index based on the sediment longitudinal movement decreased by over 50%, from 1950 to 2019.
	This work	The density of hydropower plants in the Yangtze River and major tributaries is 0.007 per km. The result of the four-dimensional connectivity indices indicates that the Yangtze River Basin is facing a pronounced connectivity reduction from 1980 to 2020. Forty-two percent of assessed rivers own deteriorated connectivity in the longitudinal dimension. Three percent of assessed rivers own deteriorated connectivity in the lateral dimension. Sixty-seven percent of assessed rivers suffer from deteriorated integrated connectivity in 2020, especially the Wu River.
Europe	Belletti et al. (2020)	For 36 European countries, the density of dams in rivers is 0.74 per km.
	Duarte et al. (2021)	The result of longitudinal connectivity metrics based on diadromous fish, indicates that the connectivity of more than 66% of large rivers is impaired by large dams.
The whole world	Grill et al. (2019)	Worldwide, the result of the four-dimensional connectivity indices illustrates that 63% of rivers longer than 1000 km and 44% of rivers with length of 500–1000 km own deteriorated connectivity.

The land use alteration in riparian zone affects the lateral connectivity, with construction land in riparian zone deeply obstructing the lateral movement of water. However, previous study shows factors like infrastructure development in riparian zone had limited impact on the river connectivity worldwide (Grill et al., 2019). Our evaluation result was consistent with this result and indicated that only 3% of assessed rivers had deteriorated connectivity in the lateral dimension. The result of the Pearson correlation coefficient $|r|$ showed that there was no strong correlation among the standardized ratio of construction land in riparian zone around dams, scores of the longitudinal connectivity, scores of the lateral connectivity, scores of the vertical connectivity, scores of the temporal connectivity and scores of the integrated connectivity ($|r| < 0.8$). The construction land in riparian zone around dams had no significant impact on longitudinal, lateral, vertical, temporal and integrated connectivity, since hydropower stations were mainly built in areas with relatively small populations and the ratio of construction land in riparian zone around dams was lower than the ratio of construction land in the whole riparian zone.

In addition, anthropogenic interference affects the vertical connectivity in combination with other factors. For instance, although hydropower plants had been built in the Wu River and the Han River, the reduced annual runoff still caused the reduced vertical connectivity in 2000. Besides, the increase in annual runoff (Huang and Luo, 2012) and the operation of hydropower stations in the Gan River improved the vertical connectivity. As for the temporal connectivity, even only few hydropower plants were built in the Yangtze River Basin in 1980, climate change still boosted the temporal variation in monthly and annual flow. After the construction of hydropower plants, the average monthly discharge was mainly affected by the regulation and storage of hydropower stations. For instance, the Three Gorges Hydropower Station adopts the flow regulation rule of "winter storing and summer releasing", which increases the runoff in dry season (Guo et al., 2020). Similarly, the average runoff in the dry season of the lower Yalong River increases significantly after the construction of the Tongzilin Hydropower Station (He et al., 2023).

As for integrated river connectivity, our study shows that 67% of assessed rivers suffer from deteriorated connectivity, especially the Wu River. This ratio is higher than the degree of global deterioration in connectivity of rivers longer than 1000 km and rivers with length of 500–1000 km (Table 3) (Grill et al., 2019). The result suggests more attention should be paid to the status of connectivity in the Yangtze River Basin.

4.2. Connectivity status and conservation of aquatic biodiversity

Reduced river connectivity impedes the movement of migratory fish and changes the hydrological conditions of fish habitat (Carvajal-Quintero et al., 2019; Van Puijenbroek et al., 2019). The changed hydrological conditions may weaken the biological signals required for fish reproduction and affect the hatching of drifting eggs (Barbarossa, 2020; Yu, 2023b). Besides, reduced river connectivity has an indirect influence on fish diversity at the community level (Shao et al., 2019). Hydropower development is the main reasons for the decrease in global river connectivity (Grill et al., 2019). Hydropower dams highly threaten global fish habitats (Barbarossa et al., 2020). A study shows that global dams threatened 20% of 9000 freshwater fish species in the past 100 years (Table 4) (Chen et al., 2009).

While the ecological impact of dams in Yangtze River Basin has attracted large attention, current studies focus on the influence of giant hydropower stations in the upper Yangtze River. Our study confirms that hydropower stations in major tributaries also exerted tremendous pressure on fish communities. The hydropower stations in the Wu River indeed disrupted the pattern of fish distribution and caused abrupt variation in fish communities. The headwater, the stream outlet and the downstream of dams tended to own higher biodiversity, while the upstream of dams had lower biodiversity. Besides, hydropower stations led to reduced abundance of lotic fish, with reservoirs of dams having lower relative abundance of lotic fish. This phenomenon has been confirmed by a recent study on the Wu River (Cheng et al., 2023). In contrast, the fish composition pattern of the Chishui River, the tributary without dams in the upper Yangtze River Basin, has more gradual variations along the Chishui River (Liu et al., 2021a). It's worth noting that even at the downstream of the lowest hydropower station (the Yinpan Hydropower Station), there was not enough space for lotic fish to restore, since the stream outlet of the Wu River was also impacted by the storage of the Three Gorges Hydropower Station (Gao et al., 2010).

At the catchment scale, the Yangtze River had more than 200 fish species in the mainstream, before the 1980s. However, there were only 84 fish species in the main stream of the Yangtze River in the tenth year after the completion of the Three Gorges Hydropower Station (Table 4) (Yi et al., 2022). Nowadays, the Yangtze River Basin is the home to 94 threatened fish species (Yang et al., 2023; Zhang and Cao, 2021). A recent study shows that the change of connectivity in the Yangtze River Basin may affect about 30 fish species which lay drifting eggs (Table 4) (Xu and Pittock, 2021). Another study on endemic fish in the upper Yangtze River Basin shows that 24 fish species suffered from moderate or above interference caused by dams (Table 4) (Zhang et al., 2015). Our result indicates that 63 threatened fish species (67%) in the Yangtze River Basin were influenced by reduced connectivity. This proportion was a bit lower than the result of Xie's (Table 4) (Xie, 2017), but was still enormous. Besides, 70% of threatened fishes affected by the reduced connectivity were endemic species and mainly live in the upper Yangtze River Basin. However, the link between the only fish nature reserve in the upper Yangtze River Basin (the Upper Yangtze River Rare Endemic Fish National Nature Reserve) and other protected areas is blocked by hydropower stations without any fishway. The survival crisis of indicator species, the Chinese sturgeon (*Acipenser sinensis*), whose life cycle is impeded by the Three Gorges Hydropower Station, fully reflects this dilemma (Chen et al., 2020). This dilemma needs more effective management measures, such as increasing the frequency of ecological flow regulation to meet the flow demand of threatened fish (Ban et al., 2022). Although quantities of hydropower stations have been built in the Yangtze River and its major tributaries, it's worth noting that the upper Yalong River, the upper Jialing River and the upper Gan River haven't been blocked by any hydraulic structure. These areas have more advantages in protecting the upstream species. In addition, because of the negative impact of hydropower development on aquatic ecology in the Yangtze River Basin, solar energy (Liu et al., 2021b; Liu et al., 2021c; Liu et al., 2023b; Tayyab, 2022a,b) and other forms of clean energy should be considered for the purpose of producing energy and avoiding larger scale hydropower development.

Table 4
List about the status of fish affected by the reduced river connectivity in the Yangtze River Basin and the whole world.

Study area	Reference	Status of fish affected river connectivity
Yangtze River Basin	Yi et al. (2022)	The Yangtze River owned more 200 fish species in the mainstream, before the 1980s. However, there were only 84 fish species in the main stream of the Yangtze River in the tenth year after the completion of the Three Gorges Hydropower Station.
	Xu and Pittock (2021)	A recent study shows that the change of connectivity in the Yangtze River Basin may affect about 30 fish species which lay drifting eggs.
	Zhang et al. (2015)	A study on endemic fishes in the upper Yangtze River Basin shows that 24 fish species suffer from moderate or above interference caused by dams.
	Xie (2017)	The study roughly estimates that gates and hydropower stations bear 70% of the responsibility for the fish biodiversity crisis in the Yangtze River Basin.
	This work	In the Yangtze River Basin, 67% of threatened fish species, with 70% endemic species, are in a survival dilemma governed by reduced connectivity.
The whole world	Chen et al. (2009)	A study shows that in the world, dams threatened 20% of 9000 freshwater fish species in the past 100 years.
	Barbarossa et al. (2020)	Hydropower dams highly threaten fish habitats worldwide.

5. Conclusion

Our work developed a multi-index evaluation framework quantifying the four-dimensional connectivity of Yangtze River and its major tributaries in 1980, 2000 and 2020. Our study can fill in the gap in quantifying the spatiotemporal river connectivity status of the Yangtze River Basin and offer target areas for biodiversity conservation and restoration in the Yangtze River Basin. Our results indicate the Yangtze River Basin suffers from a pronounced connectivity reduction, with 67% of assessed rivers experiencing deteriorated connectivity in 2020, especially the Wu River. This ratio is higher than the degree of global deterioration in connectivity of rivers longer than 1000 km and rivers with length of 500–1000 km (Grill et al., 2019). The environmental DNA metabarcoding in the Wu River indicates that hydropower stations disrupt the pattern of fish communities and severely affect the abundance of lotic species. At present, 67% of threatened fish species in the Yangtze River Basin are in a survival dilemma governed by reduced connectivity. Although the proportion is a bit lower than the previous rough estimation (Xie, 2017), the number of affected species is still enormous. Our study illustrates that the massive connectivity reduction changes the pattern of fish community and threatens protected fish. The status of river connectivity in the Yangtze River Basin calls for more effective measures to maintain or restore populations of fish biodiversity.

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Credit author statement

The manuscript was written through contributions of all authors. All authors have given approval to the final version of the manuscript.Aopu Li: Conceptualization, Methodology, Visualization, Investigation and Writing-Original Draft and Writing-Review & Editing. Juntao Fan: Conceptualization, Supervision, Project administration, Funding acquisition and Writing-Review & Editing. Fen Guo: Investigation and Writing-Review & Editing. Luke Carpenter-Bundhoo: Investigation and Writing-Original Draft. Guoxian Huang: Investigation and Writing-Original Draft. Yue Shi: Investigation and Formal analysis. Yuying Ao: Methodology, Writing-Review & Editing. Jingfu Wang: Methodology, Investigation and Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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