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Homogenization of fish assemblages in an endemic biodiversity hot spot: Evidence from 70-year data from the Yun-Gui Plateau, China

Lei Shi[1] | **Tao Xiang**[2] | **Xianghong Dong**[3] | **Chi Xu**[4] | **Haijun Wang**[1,5] | **Erik Jeppesen**[1,6,7,8] | **Ping Xie**[1,9]

[1]Institute for Ecological Research and Pollution Control of Plateau Lakes, School of Ecology and Environmental Science, Yunnan Key Laboratory of Ecological Protection and Resource Utilization of River-lake Networks, Qilu Lake Field Scientific Observation and Research Station for Plateau Shallow Lake in Yunnan Province, Ministry of Education Key Laboratory for Transboundary Ecosecurity of Southwest China, Yunnan University, Kunming, China

[2]Nanjing Institute of Geography and Limnology, Chinese Academy of Sciences, Nanjing, China

[3]College of Animal Science, Guizhou University, Guiyang, China

[4]School of Life Sciences, Nanjing University, Nanjing, China

[5]Institute of Yunnan Plateau Indigenous Fish, Kunming, China

[6]Department of Ecoscience, Aarhus University, Aarhus, Denmark

[7]Sino-Danish Centre for Education and Research, Beijing, China

[8]Department of Biological Sciences, Middle East Technical University, Ankara, Turkey

[9]Donghu Experimental Station of Lake Ecosystems, State Key Laboratory of Freshwater Ecology and Biotechnology, Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan, China

Correspondence
Haijun Wang and Ping Xie, Institute for Ecological Research and Pollution Control of Plateau Lakes, School of Ecology and Environmental Science, Qilu Lake Field Scientific Observation and Research Station for Plateau Shallow Lake in Yunnan Province, Ministry of Education Key Laboratory for Transboundary Ecosecurity of Southwest China, Yunnan University, Kunming 650500, China.
Email: wanghaijun@ynu.edu.cn and xieping@ihb.ac.cn

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Abstract

1. The combined impacts of anthropogenic activities and global climate changes threaten native fish communities. Such threats are particularly critical in biodiversity hot spot areas with many endemic species, as exemplified by the isolated Yun-Gui Plateau, China. The risk of biotic homogenization is also expected to be high in such areas, but this risk and its underlying drivers remain poorly studied.
2. Here, we established a database of fish distributions and used environmental filtering for spatial clusters ($n=3759$) in river basins located at Yun-Gui Plateau. This database was based on public data sources and a comprehensive review of relevant literature ($n=481$) covering the period from 1950 to 2021. We divided the plateau into nine subbasins for spatial comparison and into two periods for temporal comparison—before and after the start of rapid economic growth development in 1978.
3. We found: (a) a marginal increase in replacement (species exchange in different subbasins) and similarity index but a decrease in richness difference index, indicating homogenization and the loss of natural barriers across the entire plateau; (b) an increase in species richness accompanied by a discernible decline in phylogenetic diversity, also indicating homogenization; (c) the increase in species richness by species loss-gain analyses was associated with climatic variables (temperature and precipitation), elevation and human activities in all subbasins.

4. Temporal and spatial comparisons indicated that homogenization of fish assemblages in the Yun-Gui Plateau was exacerbated by climatic and anthropogenic pressures.
5. The observed homogenization of fish species is of great concern, and we call for systematic assessments and precautionary mitigation actions to maintain the uniqueness of biodiversity in the Yun-Gui Plateau region.

KEYWORDS
beta diversity, biotic homogenization, fish assemblages, isolated plateau, species losses and gains

1 | INTRODUCTION

With industrialization and a major rise in the Earth's population, we might already have entered the sixth mass extinction in the Anthropocene due to threats from multiple stressors; no less than 1 million species (accounting for one eighth of all species) are currently at risk of becoming extinct (Barnosky et al., 2011; Pievani, 2014). In this scenario, non-native species that have evolved high competitive, defensive and reproductive abilities may frequently replace native species, causing serious ecological effects, such as loss of endemic species and biotic homogenization (Olden & Rooney, 2006; Vermeij, 1991). Biotic homogenization is defined as a multifaceted ecological process that leads to an increase in taxonomic, phylogenetic or functional similarity over temporal and spatial scales (McKinney & Lockwood, 1999; Olden & Poff, 2003; Olden & Rooney, 2006). Homogenization may in some cases lead to drastic changes in ecosystems, for example, a collapse of Wallace's faunal realms happened a century ago due to homogenization in the region following global human interference (Leprieur et al., 2008; Olden, 2006).

Biotic homogenization may become uneven, with a skew towards dominant elements between or within communities (Olden, 2006; Olden et al., 2004; Olden & Rooney, 2006; Petsch, 2016). Taxonomic homogenization (the main focus of earlier research studies) is a process of increasing similarity of species composition at different spatial or temporal scales due to the establishment of non-native species and extinction of native species (Olden, 2006; Olden & Rooney, 2006; Petsch, 2016)—it erodes regional taxonomic distinctiveness, creating vulnerable ecosystems with reduced resistance and resilience to perturbations (Rosenzweig, 2001; Villéger et al., 2011). Functional homogenization refers to the replacement of unique (endemic) functional species with non-native widespread ones that have similar ecological functions over time (Olden, 2006; Olden & Rooney, 2006), and may serve as an indicator of ecosystem function and stability and provide a greater understanding of the impacts of biodiversity change than traditional index (Villéger et al., 2014). Phylogenetic homogenization is defined as the increase of similarity in genotypes at the molecular level due to the dilution and replacement of unique native genes by non-native genes (Petit, 2004; Petsch, 2016). As closely related phylogeny between introduced and native species may not co-occur within the same communities, phylogenetic homogenization may be scale-dependent (Lambdon & Hulme, 2006; Winter et al., 2009). Non-native species can exhibit functional redundancy with native species even when phylogenetically divergent, increasing phylogenetic dissimilarity while decreasing functional dissimilarity (Su et al., 2021). Therefore, homogenization can occur without species invasion, species loss or addition, species extinction or even a gradually increasing replacement and turnover (Olden & Rooney, 2006; Rahel, 2000).

Biotic homogenization has been extensively examined for various groups or organisms, such as fish, plants, birds, amphibians and reptiles (Britton et al., 2009; Chen et al., 2018; Menezes et al., 2015; Radomski & Goeman, 1995; Rooney et al., 2004; Xu et al., 2017). Various strong effects of homogenization have been widely reported, such as the collapse of functions, resistance and resilience in different ecosystems, and negative economic impacts on tourism, fishery and recreational activities (Lee, 2002; Olden et al., 2004). For example, phylogenetic homogenization, representing a loss of evolutionary diversity, may drive the loss of functional diversity and uniqueness in species and ecosystems (Cavender-Bares et al., 2009; Harrison et al., 2018; Winter et al., 2009). In Europe, biotic homogenization due to non-native species invasion and local species extinction reduced the host resources of freshwater species for local affiliated species, for example, bivalve larvae (Douda et al., 2013). When loss of regional uniqueness happens everywhere, the travel demand for adventurers, species researchers and fishers diminishes, indirectly resulting in economic losses in tourism (Olden et al., 2005). However, some previous studies on biotic homogenization have methodological or conceptual problems that bias the outcome, for example, using political rather than natural units (disregarding geographical characteristics), and ignoring extirpation and species identities (Carlson & Daniels, 2004; Olden, 2006; Walters et al., 2003). Therefore, to quantify biotic homogenization, the establishment of databases on the historical presence and absence of species, explicitly including extinct species, has been recommended (Olden, 2006; Petsch, 2016; Villéger et al., 2015; Xu et al., 2015).

Rapid uplift of the Yun-Gui Plateau created heterogeneous habitats and geographical barriers, which contributed to the great biodiversity and exceptional concentrations of endemic species (Myers et al., 2000; Xie et al., 2017). However, this ‘biodiversity kingdom’ is also facing increasing anthropogenic pressure and climate change, which could lead to biotic homogenization, species invasions and endemic species loss (Ding et al., 2017; Jiang et al., 2015). For instance, the trend of homogenization and endemic species loss began to appear following fish species invasions in 15 isolated lakes of the Yun-Gui Plateau over 1940–2015 (Ding et al., 2017), but so far information is limited in space and time (Myers et al., 2000).

We used beta-diversity partitioning, the temporal beta-diversity index and random forest (RF) on data from a literature data review (*n* = 481; 1950–2021) to examine the changes and patterns of fish assemblages in the Yun-Gui Plateau. We tested the hypothesis that fish communities have homogenized in the Yun-Gui Plateau due to anthropogenic disturbance and climate change. By analysing the spatial–temporal homogenization of fish communities in the plateau, we provide a fresh perspective on the homogenization trends of fish communities and the underlying drivers, particularly focusing on the breakdown of natural geographical barriers resulting from increased human activity.

2 | MATERIALS AND METHODS

2.1 | Study area

The formation of the special geomorphology of the Yun-Gui Plateau with a high level of geographical isolation originating from orogeny and alluvial denudation dates back to the late Pliocene period (Ding et al., 2017; Zhao & Chen, 1999). Located in southwest China with a vast Karst Landform and lower connectivity between subbasins, the plateau includes 65 isolated lakes greater than 1 km^2 (13 lakes >10 km^2) (Ma et al., 2011). According to geographical features and literature reviews (Kapos et al., 2000; Meybeck et al., 2001), the baselines of altitude were 500, 800, 1000 and 1500 m above sea level. The use of the 500 m baseline includes some low-altitude hills, whereas the use of the 1000 or 1500 m baselines cuts off some mountains and basins, so 800 m is the optimal criterion that maintains the topographical and hydrological features of the plateau, which is essential for our study. Therefore, we defined the boundary of the Yun-Gui Plateau as having an average altitude >800 m, encompassing parts of the adjacent provinces and the entire Yunnan Province and Guizhou Province (Zhao & Chen, 1999). The Chinese secondary river basin dataset from National Earth System Science Data Center takes into account multiple factors, such as the drainage divide, water flow and river length, ensuring accurate and temporally stable water resource zoning (Xu et al., 2012). Based on this nationally representative dataset, the Yun-Gui Plateau was divided into nine subbasins, including the upper Yangtze River Basin (UYR-YRB), the Mingjiang River Basin (MJR-YRB), the Wujiang River Basin (WJR-YRB), the Dongting Lake Basin (DTL-YRB), the Yalongjiang River Basin (YLJR-YRB), the Xijiang River Basin (XJR-PRB), the Yuanjiang River Basin (YJR-YHRB), the Lancangjiang River Basin (LCJR-LMRB) and the Nujiang River Basin (NJR-NYRB) (Figure 1). All geographic analyses were completed in ArcGIS Pro 2.5.

2.2 | Fish database construction

All records of fish assemblages were obtained from published literature reviews (*n* = 481) for the period 1950–2021. After censoring duplicate, synonym and erroneous inventories by Fishbase (https://www.fishbase.se/search.php) and the International Union for Conservation of Nature (IUCN; https://www.iucnredlist.org/), the fish database included 4026 non-repeating distributed records. In this database, detailed information of all fish species were found, including ID, the site and time of discovery, latitude, longitude (WGS-84), synonym and reference. To account for the uneven sampling

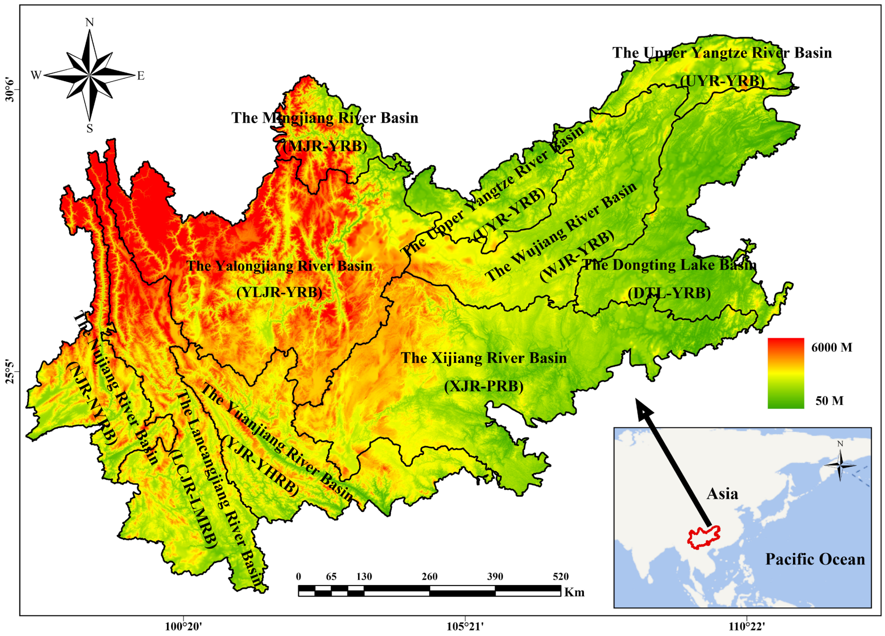


FIGURE 1 The distribution of the nine studied subbasins in the Yun-Gui Plateau.

effort across subbasins with unequal original occurrence numbers, we employed an environmental filtering approach to balance the occurrence records (Boakes et al., 2010; Phillips et al., 2009; Shipley et al., 2022). We first divided the environmental values (shown in Table S1) for each species occurrence record into a number of bins. For each n-dimensional bin, we randomly extracted a single occurrence record for subsequent analysis (Castellanos et al., 2019). This filtering method allowed us to reduce spatially and environmentally oversampled records and balanced sampling effort, while keeping the representation of full environmental gradients where species occurred (Varela et al., 2014). Compared to random subsampling or spatial filtering, this approach improves model performance (Varela et al., 2014).

After processing, the conservation status of the fish species in the nine subbasins was determined by the IUCN red list, the world's most widely used system for gauging the extinction risk faced by species, to obtain the present number of threatened species in the Yun-Gui Plateau. The number of records ($n=3759$ totally) was highest from XJR-PRB ($n=894$), followed by LCJR-LMRB ($n=888$), while only three records existed from MJR-YRB, the least recorded and smallest subbasin (Figure S1). Among the nine subbasins (Figure S1), a total of 793 species belonging to 224 genera, 49 families and 15 orders were recorded. The most prominent order among them was Cypriniformes, representing 74.7% of the total, followed by Siluriformes at 15.7%; the least orders were Salmoniformes, Myliobatiformes and Anabantiformes (0.13%). Additionally, Cyprinidae with 346 species accounted for the most dominant family at 43.0%. From 1950 to 2020, the fish community richness of the Yun-Gui Plateau exhibited an overall increasing trend. However, the beta diversity underwent an overall decline during this temporal stretch (every 10 years) (Figure S2b).

2.3 | Beta-diversity partitioning

The total beta diversity was decomposed into richness difference (*RichDiff*) and replacement (*Repl*) using the Sørensen and Jaccard indices in the Podani family (Carvalho et al., 2013; Legendre, 2014; Podani & Schmera, 2011). The equations of the Jaccard index including dissimilarity indices (D) and similarity indices (S) are:

$$D_J = (b + c) / (a + b + c) \tag{1}$$

$$\mathrm{RichDiff}_J = 2 \min(b, c) / (a + b + c) \tag{2}$$

$$\mathrm{Repl}_j = \mid b - c \mid / (a + b + c) \tag{3}$$

$$S_J = 1 - D_J \tag{4}$$

and the equations of Sørensen index are:

$$D_S = (b + c) / (2a + b + c) \tag{5}$$

$$\mathrm{RichDiff}_S = 2 \min(b, c) / (2a + b + c) \tag{6}$$

$$\mathrm{Repl}_S = \mid b - c \mid / (2a + b + c) \tag{7}$$

$$S_S = 1 - D_S \tag{8}$$

where a is the number of common species in the compared sites, b is the number of species only present in the first sites and c is the number of species only occurring in the second sites. For any method, the total beta diversity ($\mathrm{BD}_{\mathrm{total}}$) was calculated by replacement and richness difference, and the relationship can be expressed as follows:

$$\mathrm{BD}_{\mathrm{total}=}\ \mathrm{RichDiff}_{\mathrm{total}} + \mathrm{Repl}_{\mathrm{total}} \tag{9}$$

$$\mathrm{Repl}_{\mathrm{total}} = \sum_{h=1}^{n-1} \sum_{i=h+1}^{n} \mathrm{Repl}_{hi} / \left[n(n-1)\right] \tag{10}$$

$$\mathrm{RichDiff}_{\mathrm{total}} = \sum_{h=1}^{n-1} \sum_{i=h+1}^{n} \mathrm{RichDiff}_{hi} / \left[n(n-1)\right] \tag{11}$$

where h and i are any research sites.

Since $S + \mathrm{Repl} + \mathrm{RichDiff} = 1$, these pairwise subbasins were shown in the triangular plot, where similarity (S) is on the bottom line with zero on the left, richness difference (RichDiff) is on the right edge with zero at the top and replacement (Repl) is on the left edge with zero at the bottom. This plot is recommended to interpret the component of partitioning beta diversity and similarity (Podani & Schmera, 2011). The 'adespatial' and 'vegan' packages were used for statistical analysis in R software (https://cran.r-project.org/web/packages/adespatial/index.html; https://cran.r-project.org/web/packages/vegan/index.html).

We divided the data into two periods, before and after the start of Chinese economic reform in 1978, when human activities intensified rapidly due to the economic and industrial revolution in China. Consequently, the periods 1950–1978 and 1979–2021 were compared for beta-diversity changes and to elucidate the change of fish assemblage in the Yun-Gui Plateau. To ensure proper comparison, richness rather than abundance was used.

2.4 | Phylogenetic diversity

We constructed the phylogeny of fish species based on the phylogenetic tree proposed by Rabosky (presenting the most comprehensive phylogenies of fish species and including all species in our research except from one unidentified species) using the 'FishPhyloMaker' package by R software (Rabosky et al., 2018). The phylogenetic diversity was calculated by the Faith index ($\mathrm{PD}_{\mathrm{Faith}}$), mean pairwise distance (MPD) and mean nearest taxon distance (MNTD) (Faith, 1992; Webb et al., 2002). Specifically, $\mathrm{PD}_{\mathrm{Faith}}$ quantifies the phylogenetic diversity of a set of species R represented as leaf nodes on a phylogenetic tree T as the total phylogenetic branch length spanned by R; MPD is calculated as the average cost of all phylogenetic paths between all pairs of nodes in R; MNTD measures the average phylogenetic distance from each species to its nearest relative in R, excluding self-distances (Faith, 1992; Gilbert & Parker, 2022;

Honorio Coronado et al., 2015; Tsirogiannis & Sandel, 2014). *T*-test and Wilcoxon-Mann–Whitney test (prioritize *t*-test when the data satisfy the assumptions) were used to calculate the difference in phylogenetic diversity between the two time periods shown by box plot and scatter plot (grey line).

According to the MNTD value separating two subbasins, which is a measure of phylogenetic beta diversity, the nearest taxon index (NTI) was calculated by comparing the difference between a null model of random phylogenetic community and our subbasins to determine whether the basin was phylogenetically influenced by a deterministic process or a stochastic process (Evans & Wallenstein, 2014; Jiang et al., 2021; Weiblen et al., 2006; Zhu et al., 2016). Beta mean nearest taxon distance (βMNTD) between communities was calculated using phylogeny trees. A null distribution of βMNTD was then generated under a stochastic spatial null model (tip-shuffling method), which randomizes phylogeny identities to break down evolutionary relationships (Huang et al., 2022; Stegen et al., 2013). This approach produces randomized community assemblages to compare against observations. Calculation of the beta nearest taxon index (βNTI) as the standard effect size between observed and null βMNTD followed after 999 randomizations. βNTI values >+1.96 or <−1.96 (95% confidence interval) indicate the dominance of deterministic assembly, because observed phylogenetic turnover exceeds stochastic expectations; βNTI values between +1.96 and −1.96 suggest phylogenetic turnover primarily arising from stochastic factors (Chase et al., 2011; Stegen et al., 2012, 2013).

All phylogenetic diversity indices were derived by the 'picante' package in R (https://cran.r-project.org/web/packages/picante/index.html).

2.5 | Local contribution to beta diversity

The local contribution to beta diversity (LCBD) represents the uniqueness of each research site regarding assemblage composition (Legendre & De Cáceres, 2013). The index can also be tested for significance using random and independent permutations (Legendre & De Cáceres, 2013). In a species (n)×sampling sites (p) matrix, the LCBD was calculated by:

$$\mathrm{LCBD}_i = \mathrm{SS}_i / \mathrm{SS}_{\mathrm{total}} = \sum_{i=1}^{p} \left(y_{ij} - \overline{y_j}\right)^2 \Big/ \sum_{i=1}^{n} \sum_{j=1}^{p} \left(y_{ij} - \overline{y_j}\right)^2 \quad (12)$$

where SS_i is the contribution of site i to the total beta diversity ($\mathrm{SS}_{\mathrm{total}}$). y_{ij} is the number of the ith site and jth species, and $\overline{y_j}$ is the mean value in the column of the jth site in the species-site matrix. LCBD represents the uniqueness of the study location, providing a quantitative measure of its conservation value. However, due to the lower richness, also being a type of 'uniqueness', the LCBD and the number of species were used to preferentially determine the conservation value of the subbasins. Therefore, we consider the LCBD index and species richness for the evaluation of subbasin conservation comprehensively.

2.6 | Species losses and gains

B–C plots (temporal beta-diversity index) show the detail and whole process of species losses and gains and reveal the dominant position (losses or gains) and relative importance at the research sites (Legendre, 2019). In a species-site matrix, these variables can be calculated by the following vectors:

1. $A_j = \min(y_{1j}, y_{2j})$ where y_{1j} and y_{2j} are the numbers of species at sites 1 and 2, respectively. A can be calculated by the sum of A_j for all species.
2. If $y_{1j} > y_{2j}$, $B_j = y_{1j} - y_{2j}$; $B_j = 0$ when y_{1j} and y_{2j} are similar to (1), and B is the sum of B_j for all species.
3. If $y_{1j} < y_{2j}$, $C_j = y_{2j} - y_{1j}$; $C_j = 0$ when y_{1j} and y_{2j} are similar to (1), and C is the sum of C_j for all species.

We used the Sørensen dissimilarity index (presence–absence data) for percentage dissimilarity ($D_{\%\mathrm{diff}}$), that is, $D_{\%\mathrm{diff}} = (B+C)/(2A+B+C)$. In this equation, the $B+C$ was the unscaled dissimilarity and the denominator can be scaled by B and C by division, that is, $\mathrm{den}_{\%\mathrm{diff}} = (2A+B+C)$. In B–C plot, coordinates consist of $D_{\mathrm{loss}} = B/\mathrm{den}_{\%\mathrm{diff}}$ (in the abscissa) and $D_{\mathrm{gain}} = C/\mathrm{den}_{\%\mathrm{diff}}$ (in the ordinate), representing species losses and gains, respectively. The B–C plot shows how species gains and losses vary across study sites in two time slots. The blue line represents equal species gains and losses (slope = 1 and intercept = 0). The red line is parallel to the blue line (slope = 1) and passes through the centroid of all points. When the red line is above the blue line, species gains are dominant, when below, species losses are dominant.

2.7 | The driving factors determined by random forest

Based on previous studies and four hypotheses (energy availability, water availability, habitat heterogeneity and intermediate disturbance hypothesis), we selected four types of 26 environmental variables to serve as candidate variables in light of the ecological significance (Table S1) (Kerr & Packer, 1997; Rahbek & Graves, 2001; Tognelli & Kelt, 2004). To ensure the same resolution for these variables and to reduce the dimension effects, a bilinear interpolation method was used to resample the raster variable layers (2.5 arc-minutes, approximately 4.5 km^2) and standardize the geographical coordinates (WGS 1984 datum) (Dong et al., 2020; Fletcher et al., 2016). Then, the value of different variables was extracted by the unified layers. To minimize overfitting and multicollinearity, the candidate predictor variables were reselected by the variance inflation factor (*VIF*) and removed step by step if the value was >10 to obtain a brief and scrutable model (Dormann et al., 2013; Duque-Lazo et al., 2018; Júnior & Nóbrega, 2018; Li et al., 2015). Consequently, 10 representative environmental factors were selected as the final predictive variables: mean temperature of driest quarter (BIO9), precipitation of driest month (BIO14), precipitation of warmest quarter (BIO18), elevation

(Elev), geomorphic type (Geo), global human influence index (HII), population density (PopD), aquaculture pressure (AquC), terrestrial evapotranspiration (TE) and global reservoir and dam (ResDam) (Table S1). In the 2.5 arc-minute map raster, the species richness of each cell grid was used as the response variable for RF. We then ran a RF model to determine the importance of each variable by Mean Decrease Gini using the randomForest packages in R (https://cran.r-project.org/web/packages/randomForest/index.html). R software version 4.0.5 (R Core Team, 2022) was used for all statistical analyses.

3 | RESULTS

3.1 | Assessment information of fish species

Based on assessment information from the IUCN (version 3.1 checked date by 2022), 69.6% of the present species (793 fish species) were 'Not Evaluated' (NE) and 'Data Deficient' (DD), and the level of 'Near Threatened' (NT) and above was 9.8% (78 fish species). Due to a lack of comprehensive data, the IUCN assessment levels of 218 fish species remain unknown in the XJR-PRB, followed by YLJR-YRB with 138 fish species. At the evaluated level, the XJR-PRB and LCJR-LMRB needed to focus on the issues of protection with more threatened species (classified as 'Near Threatened' and above), and the YLJR-YRB was the following one with the second number of species (only one less than LCJR-LMRB; Figure 2). Among the assessment information, *Anabarilius macrolepis* and *Cyprinus yilongensis* were deemed to extinct in the Yilonghu Lake by IUCN red list category and criteria.

3.2 | Beta-diversity partitioning of fish assemblages

A marked disparity in the beta-diversity partitioning of pairwise subbasins was found between the periods prior to and after 1978 (Figure 3). Results from the Jaccard index analysis revealed a marginal increase in replacement and similarity and a decrease in richness difference according to the coordinate values (Figure 3a,b). Meanwhile, mean value of diversity partitioning variables (the red point) moved to the upper right and each subbasin point became more dispersed compared to the periods before and after 1978. The total similarity index from 2.6% to 9.3% between the two periods (Figure 3a,b), and the overall similarity of the pairwise subbasins across the plateau was found to increase (Tables S2 and S3). A similar trend was found for the Sørensen index (Figure S4). However, the similarity of the pairwise subbasin comparisons for both indices did not surpass 20% in the triangular plots and remained a limited proportion (Figure 3c, Figure S4c).

3.3 | Phylogenetic diversity of fish assemblages

Species richness increased significantly from before to after 1978 for all subbasins (*t*-test results, $p < 0.05$; Figure 4a). A similar pattern was observed for the phylogenetic diversity as measured by the PD_{Faith} ($p < 0.05$, Figure 4b). Compared to the PD_{Faith}, the MPD index did not show a significant increase in phylogenetic diversity in pairwise subbasins, with some subbasins exhibiting a decreasing trend (Figure 4c). The MNTD index revealed a larger decrease in phylogenetic diversity in most of the pairwise subbasins and a minimal increase in only two (Figure 4d). Furthermore, the non-parametric test results, excluding the PD_{Faith} in phylogenetic diversity, failed to demonstrate significant differences in phylogenetic diversity from before to after 1978.

A null model was employed to ascertain the underlying determinant of the subbasins within the phylogenetic system. XJR-PRB displayed a discrete distribution with a minimum median, while MJR-YRB, with a smaller area and lower species richness, exhibited an aggregated pattern with a maximum median across all subbasins (Figure 5). In general, the median of the βNTI index for all subbasins was outside the 95% confidence interval (the range [−1.96, 1.96]), and below the −1.96 threshold, indicating that the fish assemblages in the Yun-Gui Plateau were primarily shaped by deterministic processes rather than stochasticity.

3.4 | The temporal beta-diversity index and driving factors

In the B–C plot, the red line was overall above the blue line, and all the values of species gain were greater than those for species loss, providing evidence for a preponderance of species gains over species losses in the Yun-Gui Plateau from before to after 1978 (Figure 6). A more in-depth examination of the subbasin plots and their geographical locations revealed that when the subbasins were far away from the middle and lower reaches of the Yangtze River, which is characterized by higher levels of economic development and consequent anthropogenic disturbance, the more noticeable was the decline in the proportion of species gain and the increase in the proportion of species losses (e.g. YJR-YHRB, LCJR-LMRB and NJR-NYRB).

According to the richness of each cell grid RF model, the spatial–temporal fish distribution and biotic homogenization were predominantly influenced by three abiotic factors: BIO14, Elev and BIO9 (as displayed in Figure S5; maps of environmental characteristics were shown in Figure S6). However, nine abiotic and anthropogenic factors contributed to the construction of fish communities, albeit not all to a significant extent.

3.5 | Local contribution to beta diversity

In conservation biology, higher values of LCBD are indicative of a site possessing an ecological distinctiveness with an unusual species composition (i.e. endemic species) and high conservation value, or a site characterized by degraded and poor species pools with the tide of biodiversity loss (i.e. the species uniqueness whether

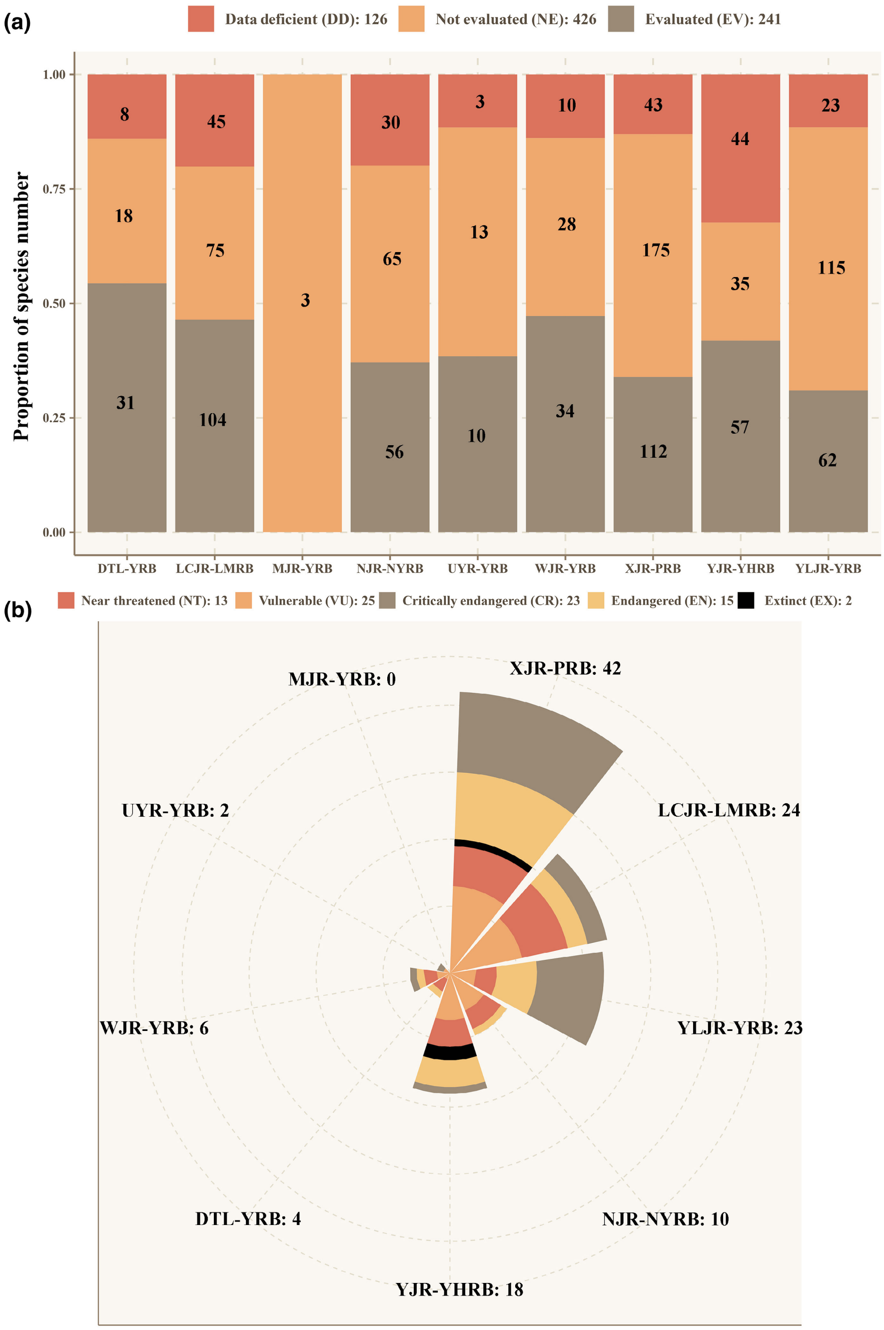
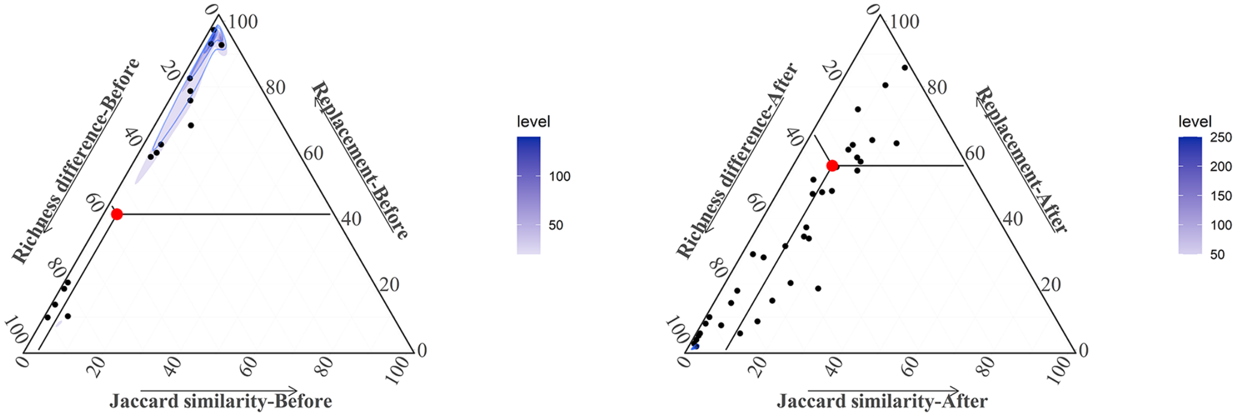


FIGURE 2 Fish assessment information in Yun-Gui Plateau. (a) IUCN assessment information for fish composition to data deficient (DD), not evaluated (NE) and evaluated (EV) in different subbasins; (b) threatened fish species (classified as near threatened and above) in nine subbasins based on IUCN red list categories and criteria.

best or worst). We found that the Upper Yangtze River Basin (UYR-YRB) and the MJR-YRB (significant difference $p < 0.05$) had higher LCBD values than the other basins due to a lower number of fish species (i.e. an atypical species composition); thus, they are merely descriptive but not an in-depth analysis (Figure 7). Furthermore, most subbasins exhibited high LCBD values. YLJR-YRB subbasins had a high richness of fish species, but a low contribution to beta diversity due to the predominance of widespread species. By contrast, YJR-YHRB, LCJR-LMRB and NJR-NYRB subbasins had a significant proportion of endemic fish species and high LCBD values ($p < 0.05$).

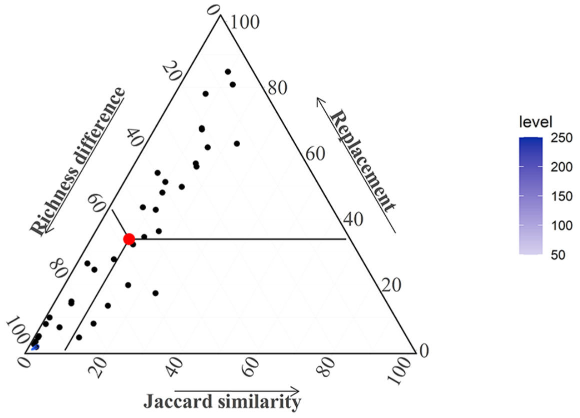
4 | DISCUSSION

We found a marginal increase in replacement and similarity but a decrease in richness difference by beta-diversity partitioning from before to after 1978. This pattern occurred in all subbasins in the Yun-Gui Plateau, suggesting biotic homogenization across the region. The observed increase in the replacement of fish species was accompanied by a discernible decline rather than a proportional increase in phylogenetic diversity, indicating homogenization also of phylogenetic diversity. Meanwhile, this increase revealed that the isolation of the Yun-Gui Plateau had started to erode. Similar



(a) Jaccard-based indices before 1978

(b) Jaccard-based indices after 1978



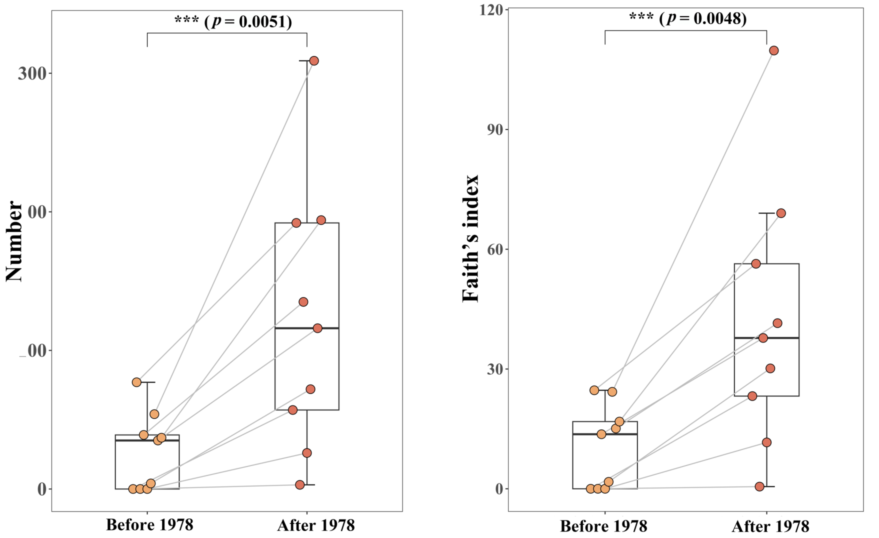
(c) Jaccard-based indices (1950–2021)

FIGURE 3 Triangular plots of the beta diversity of fish assemblages in Yun-Gui Plateau based on beta diversity partitioning. Each point represents a pair of subbasins and the red point represents the mean value for similarity, replacement and richness difference in each subbasin. (a) Was calculated by Jaccard indices before 1978 and (b) after 1978, respectively; (c) show differences in fish assemblage structure in the Podani family from 1950 to 2021 between the nine studied subbasins based on Jaccard indices.

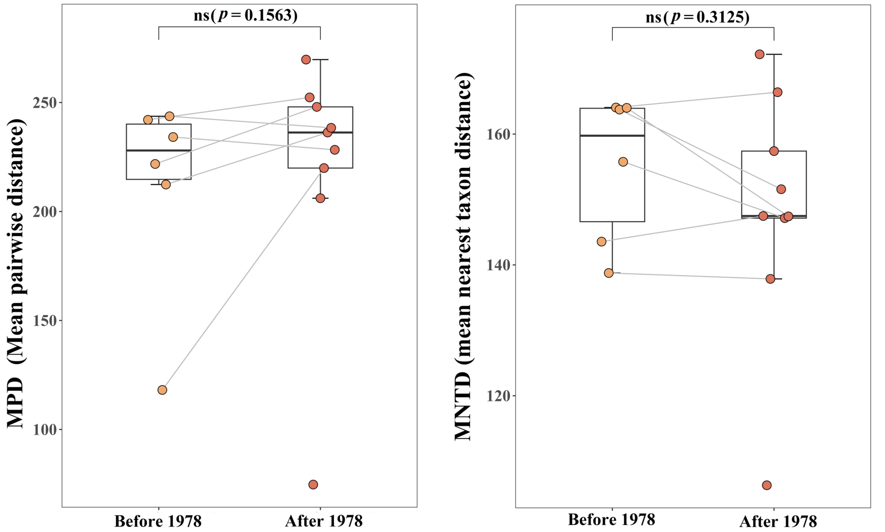
patterns have been reported earlier for 15 lakes at this plateau (Ding et al., 2017; Jiang et al., 2019). Fortunately, about 9.0% and 15.9% values for the Jaccard and Sørensen similarity indices indicated a low degree of homogenization from before to after 1978. The lower similarity may partly result from the geographical isolation limiting the species exchange, despite eroding and causing endemism at lake level, for example, for *Sinocyclocheilus grahami*. The characteristics of the Yun-Gui Plateau are similar to those characterizing isolated islands in the tropical Pacific that harbour a rich and local biota shaped by island biogeography; these are vulnerable to prolonged disturbance due to their evolutionary isolation and missing functional groups (Gillespie et al., 2008; Keppel et al., 2014). In addition, our results support the suggestion that high environmental heterogeneity and dispersal ability at the subbasin level (e.g. LCJR-LMRB) lead to higher beta diversity and dissimilarity, as also found in previous similar types of studies (Córdova-Tapia et al., 2018; Soininen, 2014).

Globally, the biotic homogenization marked by the erosion of unique biodiversity is occurring in freshwater ecosystems, with fish serving as prime indicators across diverse biogeographical realms (Brito et al., 2020; Daga et al., 2020; Magalhães et al., 2020). The observed homogenization in the plateau ecosystem was consistent across temporal and spatial dimensions, as indicated by the metrics of species and phylogenetic diversity. The results align with observations from other biogeographically distinct regions, such as the Neotropical reservoirs, where fish assemblages have undergone taxonomic homogenization but functional differentiation at broader spatial scales (Daga et al., 2020). The unique geological history of the Yun-Gui Plateau has fostered a distinctive species pool, highlighting the significance of geographic isolation and evolutionary processes in preserving regional biodiversity. The pivotal role of geographical barriers in maintaining endemism became evident when the Itaipu Dam at the border of Brazil and Paraguay was formed, as it led to a marked increase in taxonomic similarity (more than 50%) between previously separated ecoregions (Vitule et al., 2012). Despite the overall trend of biotic homogenization, our study revealed the persistence of local variations.

FIGURE 4 Differences in (a) species richness, (b) Faith's index, (c) mean pairwise distance and (d) mean nearest taxon distance between subbasins relative to phylogenetic diversity from before to after 1978. The grey lines denote similar changes of subbasin before and after 1978.



(a) Species richness (b) Faith's index of phylogenetic diversity(PD)



(c) PD based on mean pairwise distance (d) PD based on mean nearest taxon distance

These differences may be influenced by habitat modification and intensifying human disturbance (Figure 6), ultimately contributing to a decrease in beta diversity over time (Figure S2b). Similar results were observed in 20 reservoirs in the State of Paraná, Southern Brazil, which might share geographical features with our study area, including strong isolation (Daga et al., 2015). Human activities (e.g. aquaculture) have led to an increase in non-native species and intra-country established alien species in these reservoirs (Daga et al., 2015; Vitule et al., 2019). The interactions of invasive species within freshwater ecosystems, particularly predatory and competitive relationships, further aggravated the biotic homogenization (Bezerra et al., 2019).

Richness difference indices were the main determinants of beta diversity patterns in the fish assemblages across the Yun-Gui Plateau. We found a high degree of nestedness among subbasins, and less diverse subbasins contained subsets of species from the most diverse ones (Legendre, 2014). Our results challenge the prevailing view that replacement is the dominant mechanism underlying beta diversity in fish assemblages and other aquatic taxa across various habitats (e.g. ponds, lakes and wetlands) (da Silva et al., 2021; López-Delgado et al., 2020). Previous studies have assumed that both environmental and spatial factors significantly influence the species turnover while spatial factors alone explain significant variations in richness difference, possibly reflecting the dispersal limitations of some species (Córdova-Tapia et al., 2018; Heino et al., 2015; Su et al., 2024). The discrepancy may stem from the different spatial scales used as biodiversity is multidimensional and scale-dependent (Chase et al., 2018). We examined differences between subbasins with low connectivity and dispersal potential, whereas previous studies have typically focused on a single basin with high connectivity and dispersal. In addition, the temporal comparison from before to after 1978 revealed altered dominance of beta diversity from richness difference (i.e. nestedness) to replacement, possibly caused by the broken barrier property and the gain of widespread species and loss of endemic species with disproportionate effects in all subbasins (Ding et al., 2017).

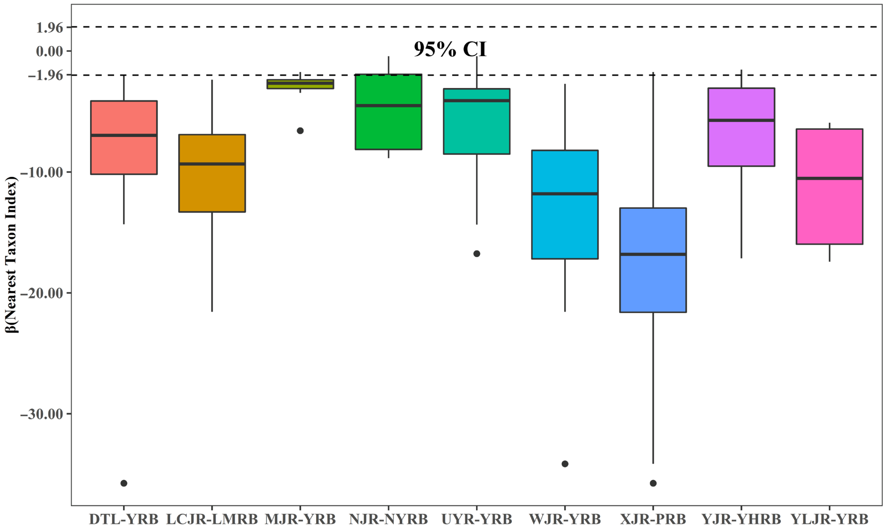


FIGURE 5 The nearest taxon index between a null model of random phylogenetic community for all subbasins. The codes are the same as in Figure 1.

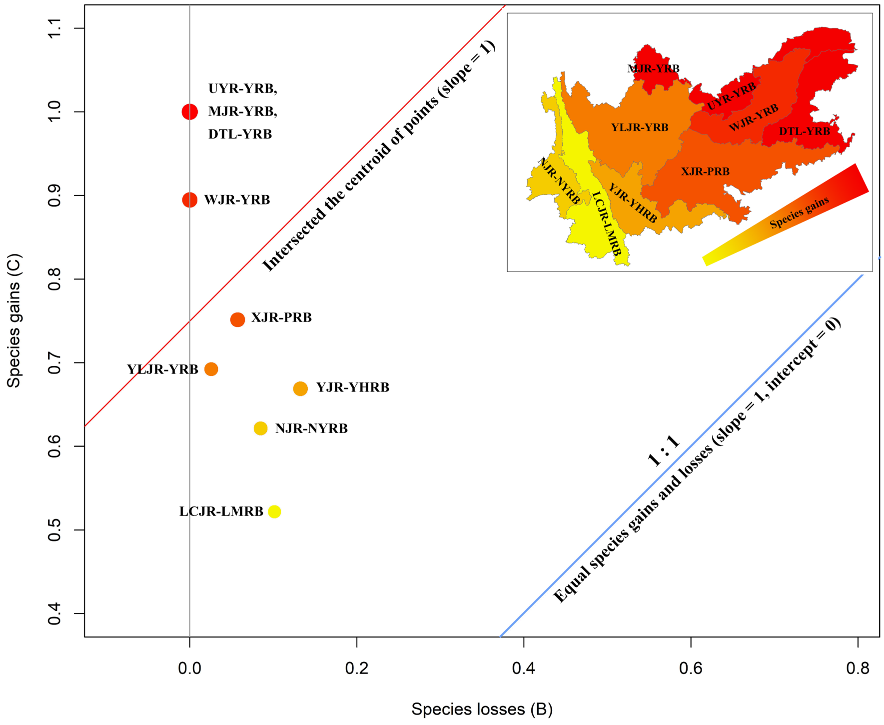


FIGURE 6 B–C plot for fish richness data in the Yun-Gui Plateau. The red line (passed through the centroid of subbasin points and parallel to the blue line with a slope of 1) above the blue line shows that the species gains were greater than losses in most subbasins, indicating that species gains dominated between the periods from before to after 1978. The codes are the same as in Figure 1.

The causes of biotic homogenization vary and may include non-native species introductions, climate change and land use changes (Devictor et al., 2008; Magurran et al., 2015; Winter et al., 2009). Here, we showed that the phylogenetic diversity of the fish communities was primarily driven by deterministic factors. Both external and internal factors were important. The internal factors included variation in landscape characteristics, for example, NJR-NYRB had high biodiversity including many endemic species and larger areas, while the smaller subbasins (MJR-YRB and UYR-YRB) had fewer and more cosmopolitan species. In addition, geographical isolation creates heterogeneous habitats and prevents gene flow, which enhances biodiversity (Albert et al., 2011). Loss of isolation, mainly due to human activities, may drive biological invasion and ecosystem degradation (loss of endemic species). For example, *Cyprinus yilongensis* and *Anabarilius macrolepis*, endemic species in Lake Yilong, have gone extinct, likely due to the impacts of power stations and agriculture developments since the 1950s (the lake dried up completely for 20 days in 1984) (Xie & Chen, 1999). Furthermore, the possible reason for the increase in species may be the continuous discovery of native species always present but undetected in earlier surveys. Due to the lack of research in the past, the original species pool may not have been thoroughly documented. Since 1978, based on the available literature (72 research articles), nearly 120 previously unknown fish species have been discovered in this plateau, revealing that the identification of previously undetected native species may be one of the factors contributing to the observed increase in species diversity (Chen, 2013). Thus, we have conducted a sensitivity analysis (Figures S7 and S8), removing two subbasins where species richness

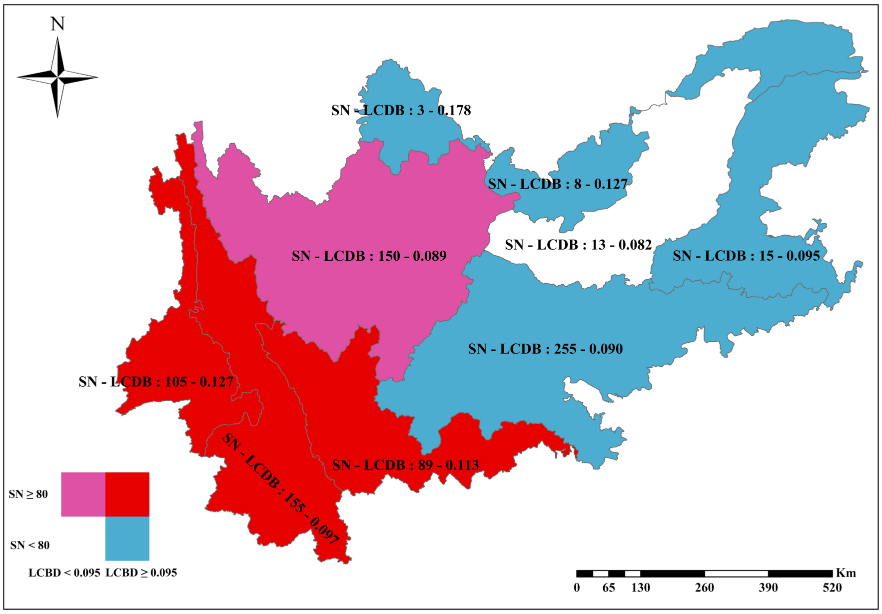


FIGURE 7 The number of fish species (SN) and the contribution of nine subbasins to beta diversity (LCBD). Three basins had a significant LCDB index by multiple testing ($\alpha = 0.05$) after Holm correction: UYR-YRB ($p = 0.027$), MJR-YRB ($p = 0.042$) and NJR-NYRB ($p = 0.027$). For codes, see Figure 1.

increased by more than 150 species. After recalculating beta diversity and phylogenetic diversity, the results were consistent with our original findings. Even when excluding the subbasins with substantial species growth, we still observed the basin-level homogenization. As for external factors, the main drivers appeared to be BIO14, Elev and BIO9, indicating that the climate variables and geographical characteristics were those most important for the temporal–spatial distribution of the fish species. The differences in elevation and landform features create diverse habitats boosting the heterogenization at the local scale (Rahbek et al., 2019), while changes in temperature and precipitation (i.e. climate change) force species to adapt by migrating or cause their disappearance, leading to biotic homogenization in both cases (Petsch, 2016; Xu et al., 2014, 2020). Fish are poikilotherms and thus are highly sensitive to temperature and precipitation changes (Dong et al., 2020; Perrin et al., 2022). Moreover, human disturbance, measured by HII and PopD with high values of mean decrease Gini, had a significant impact on the species distribution in the Yun-Gui Plateau. The index of species gain increased near economically developed areas (Figure 6), suggesting that human activities contributed to homogenization through, for example, conscious or unconscious introduction of species (e.g. aquaculture and aquarium market). In the Yun-Gui Plateau, intensive human introductions have caused a dramatic loss of endemic species (Ding et al., 2017). For example, *Neosalanx taihuensis*, a commercial fish was introduced in the 1980s, producing eutrophication and displacement of endemic species (predation on fish eggs and niche competition) (Qin et al., 2007; Zhang et al., 2005). Eutrophication can also act as an environmental filter, leading to increasing homogenization (Menezes et al., 2015).

We found an increase in replacement (i.e. species turnover from one subbasin to another) and a decrease in richness difference but the dominant part still was the richness difference from 1950 to 2022, indicating that the contribution of some subbasins to diversity had increased (i.e. some subbasins were subsets of others relative to species richness). Considering their significant uniqueness and species contributions according to the LCBD and species richness (Result 3.3), YJR-YHRB, LCJR-LMRB and NJR-NYRB are suggested as high-priority areas of protection. Among Chinese river basins, LCJR-LMRB has a high diversity of freshwater fish species (0.76 species per 1000 km^2; followed by NJR-NYRB with 0.38), endemics and threatened species (0.08 per 1000 km^2 of basin area) (Xing et al., 2016). Restoration of homogenized ecosystems may be possible if countermeasures are implemented before invasions or predicted extirpation of species (Essl et al., 2011; Hanski, 2000; Kuussaari et al., 2009; Rouget et al., 2016). Fortunately, the degree of homogenization has so far been relatively modest, and the plateau lakes have retained large alpha and beta diversity (similarity index from 0.01 to 0.40; Tables S2 and S3), for example, compared to the Pearl River (from 0.30 to 0.60 over the past few decades) (Zeng et al., 2017).

Based on our findings, we suggest some strategies for biological conservation. (1) If funding is limited, the focus should be directed at protecting specific subbasins rather than the whole region. Contrary to our study, a dominance of replacement processes of birds, lizards and spiders in Thousand Island Lake, Eastern China, suggests that an optimal conservation strategy should be directed at all islands instead of a particular one (Si et al., 2015; Wu et al., 2017). Due to the dominant richness difference index, YJR-YHRB, LCJR-LMRB and NJR-NYRB with high biodiversity and uniqueness might, if protected, become a new national germplasm resource bank for fish species. (2) Unnecessary human activities should be reduced in some areas to avoid species invasions. Anthropogenic activities such as overfishing, excessive sand mining, fish introduction for aquaculture and reclaiming lakes for farming pose significant threats to aquatic habitats and biodiversity, leading to severe disruptions in native species populations and facilitating invasive species proliferation (Chen et al., 2024; Rentier & Cammeraat, 2022; Wu et al., 2008; Xing et al., 2016). Managers of waters adjacent to urbanized areas (such as WJR-YRB and DTL-YRB), exhibiting high levels of species introductions, should implement measures to minimize human disturbances and mitigate invasion risks. (3) Coordination and cooperation on conservation and management among neighbouring countries should be enhanced. Cooperation on international river basin management can yield sustainable ecosystems, increased food and energy outputs, reduced tensions and costs and potential economic integration between states, generating manifold benefits beyond the rivers themselves (Luo et al., 2024; Sadoff & Grey, 2002). To prevent the collapse of freshwater fish in international rivers and subbasins such as LCJR-LMRB and NJR-NYRB, countries should share experiences from their management practices and develop scientific protection plans.

We found increased species similarity and declined phylogenetic diversity across the Yun-Gui Plateau from before to after 1978, indicating increasing biotic homogenization. As climate variables and human disturbance were identified as the key drivers impacting fish community composition over time, protecting priority subbasins from further habitat degradation while also managing human activities is critical to safeguard the exceptional fish diversity, despite the current relatively low degree of biotic homogenization. By comprehensive literature integration, we strived for maximal consistency to minimize inflated diversity from the sampling effort. While providing an important baseline and guidance for long-term monitoring and developing targeted conservation strategies in this critical biodiversity hot spot, further investigation of how climate change may impact biotic homogenization patterns may add valuable insights. Balancing development and conservation is essential to preserve the uniqueness of Yun-Gui Plateau freshwater ecosystems into the future.

AUTHOR CONTRIBUTIONS

Conceptualization: Haijun Wang, Erik Jeppesen and Ping Xie; Developing methods: Lei Shi, Tao Xiang, Xianghong Dong and Chi Xu; Data analysis: Lei Shi, Tao Xiang and Xianghong Dong; Preparation of figures and tables: Lei Shi; Conducting the research, data interpretation and writing: Lei Shi.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest and have observed all ethical guidelines.

DATA AVAILABILITY STATEMENT

The corresponding author can provide the data upon reasonable request.

ORCID

Lei Shi https://orcid.org/0000-0003-3132-2320

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