Conservation Biology

Boosting freshwater fish conservation with high-resolution distribution mapping across a large territory

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Abstract

The lack of high-resolution distribution maps for freshwater species across large extents fundamentally challenges biodiversity conservation worldwide. We devised a simple framework to delineate the distributions of freshwater fishes in a high-resolution drainage map based on stacked species distribution models and expert information. We applied this framework to the entire Chinese freshwater fish fauna (>1600 species) to examine high-resolution biodiversity patterns and reveal potential conflicts between freshwater biodiversity and anthropogenic disturbances. The correlations between spatial patterns of biodiversity facets (species richness, endemicity, and phylogenetic diversity) were all significant ($r = 0.43$–0.98, $p < 0.001$). Areas with high values of different biodiversity facets overlapped with anthropogenic disturbances. Existing protected areas (PAs), covering 22% of China's territory, protected 25–29% of fish habitats, 16–23% of species, and 30–31% of priority conservation areas. Moreover, 6–21% of the species were completely unprotected. These results suggest the need for extending the network of PAs to ensure the conservation of China's freshwater fishes and the goods and services they provide. Specifically, middle to low reaches of large rivers and their associated lakes from northeast to southwest China hosted the most diverse species assemblages and thus should be the target of future expansions of the network of PAs. More generally, our framework, which can be used to draw high-resolution freshwater biodiversity maps combining species occurrence data and expert knowledge on species distribution, provides an efficient way to design PAs regardless of the ecosystem, taxonomic group, or region considered.

KEYWORDS
China, conservation priorities, expert-based information, freshwater fish diversity, protected areas, species distribution models

Potenciación de la conservación de peces de agua dulce con mapeos de distribución de alta resolución a lo largo de un territorio extenso

Resumen: La falta de mapas de distribución en alta resolución para las especies de agua dulce en grandes extensiones es un reto importante para la conservación mundial de la biodiversidad. Diseñamos un marco simple para delinear la distribución de los peces de agua dulce en un mapa de drenaje en alta resolución basado en los modelos apilados de la distribución de las especies y la información de expertos. Aplicamos este marco a toda la ictiofauna de agua dulce en China (>1600 especies) para analizar los patrones en alta resolución de la biodiversidad y revelar los conflictos potenciales entre la biodiversidad de agua dulce y las perturbaciones antropogénicas. Todas las correlaciones entre los patrones espaciales de las facetas de la biodiversidad (riqueza de especies, endemismo y diversidad filogenética) fueron importantes ($r = 0.43$-0.98, $p < 0.001$). Las áreas con valores altos de diferentes facetas de la biodiversidad se traslaparon con las perturbaciones antropogénicas. Las áreas protegidas existentes que actualmente cubren el 22% del territorio de China, protegen 25-2% del hábitat de los peces, 16–23% de las especies y 30–31% de las áreas de conservación prioritarias. Además, 6–21% de las especies se encontraban totalmente desprotegidas. Estos resultados sugieren que se necesita extender la red de áreas protegidas para asegurar la conservación de los peces de agua dulce de China y los bienes y servicios que proporcionan. En concreto, los niveles medio a bajo de los grandes ríos y sus lagos asociados del noreste al suroeste de China albergaron los ensambles de especies más diversos y por lo tanto deberían ser el objetivo de las futuras expansiones de la red de áreas protegidas. De forma más generalizada, nuestro marco, el cual puede usarse para trazar mapas en alta resolución de la biodiversidad de agua dulce al combinar los datos de presencia de las especies y el conocimiento de los expertos sobre su distribución, proporciona un método eficiente para diseñar las áreas protegidas sin importar el ecosistema, región o grupo taxonómico considerado.

PALABRAS CLAVE
áreas protegidas, China, diversidad de peces de agua dulce, información de expertos, modelos de distribución de especies, prioridades de conservación

【摘要】

摘要 大尺度淡水物种高分辨率分布图的匮乏从根本上挑战了全球的生物多样性保护。我们设计了一个简单的框架, 基于堆叠物种分布模型和基于专家的信息将淡水鱼类的分布描绘到高分辨率的水系图上。我们将这一框架应用于整个中国淡水鱼类(>1600种), 以探究高分辨率的生物多样性模式, 并揭示淡水生物多样性与人为干扰之间的潜在冲突。生物多样性不同方面(物种丰富度、特有性和系统发育多样性)的空间模式之间的相关性都很显著($r = 0.43$-0.98, $p < 0.001$)。不同生物多样性方面的高值区域与人类活动干扰相重叠。现有的保护区占中国领土的22%, 保护了25–29%的鱼类栖息地、16–23%的物种和30–31%的优先保护区域。此外, 6–21%的物种完全没有受到保护。这些结果表明, 需要扩大保护区网络, 以确保中国淡水鱼类及其提供的商品和服务的保护。具体地, 从中国东北到西南的大江大河的中下游及其附属湖泊承载了最多样化的物种组合, 因此应成为未来扩大保护区网络的目标区域。总之, 我们的框架结合物种发生数据和关于物种分布的专家知识绘制高分辨率的淡水生物多样性地图, 为保护区设计提供了一种有效的途径, 并适用于不同的生态系统、分类群或区域。

关键词: 淡水鱼类多样性, 中国, 物种分布模型, 基于专家的信息, 保护区, 保护优先

INTRODUCTION

Freshwater ecosystems support approximately 9.5% of all described animal species and 35% of vertebrates, yet they cover <1% of the globe (Balian et al., 2008). Freshwater biodiversity is rapidly declining due to prevailing threats, such as overexploitation, habitat degradation, pollution, invasive species, and climate change (Albert et al., 2021; Heino et al., 2021; Reid et al., 2019). These anthropogenic disturbances have caused drastic environmental and biodiversity changes in more than two thirds

of rivers worldwide (Grill et al., 2019; Su et al., 2021). Extinction rates of freshwater species are generally higher than those of terrestrial species and far exceed natural rates (Collen et al., 2014; WWF, 2020).

Protected areas (PAs) are widely regarded as an effective way to bend the curve of current biodiversity loss, particularly in terrestrial ecosystems (Hermoso et al., 2016; Tickner et al., 2020; WWF, 2020). To ensure sufficient species representativeness in PAs, their delineation needs to be based on robust mapping of species distributions (Hermoso & Kennard, 2012; McManamay et al., 2018). However, the development of high-resolution distribution maps for freshwater species is incomplete for large areas of the globe and remains much less developed than for terrestrial species (Abell et al., 2008; McManamay et al., 2018). Besides, conventional PAs do not always protect the dynamics and connectivity essential for functioning freshwater ecosystems, and they rarely address exogenous threats, such as upstream dams and pollution or terrestrial changes (e.g., deforestation and land conversion) that affect aquatic ecosystems (Abell et al., 2017; Hermoso et al., 2016; Higgins et al., 2021). Consequently, most PAs were designed for terrestrial ecosystems and have been shown to be of limited value for the conservation of freshwater biodiversity (Abell et al., 2017; Acreman et al., 2019; Azevedo-Santos et al., 2019; Leal et al., 2020). Designing PAs and including other effective area-based conservation measures (OECMs) for freshwater ecosystems under a durable protection framework are therefore urgently needed (IUCN–WCPA, 2019; Higgins et al., 2021). Boosting freshwater biodiversity conservation requires high-resolution distribution maps for freshwater species, which are currently lacking for most species and most regions of the world. Adequate occurrence data for freshwater fishes are only available for a few regions (e.g., Western Europe, North America) and represent only a small amount of the world's fishes. Inadequate occurrence data on most species means useful species distribution models (SDMs) cannot be developed for them (Domisch et al., 2016; Elith & Leathwick, 2009). In particular, data are lacking for species with narrow niches and small spatial ranges (i.e., species that tend to be threatened) (Le Feuvre et al., 2021).

We sought to address this issue by combining SDMs built on species with sufficient occurrence data and expert-based information (e.g., range descriptions in the literature and empirical estimations of dispersal distance) for use with species with insufficient data. This approach allowed us to draw high-resolution distribution maps of all freshwater fishes over large areas. Such maps can inform PA designs (Domisch et al., 2016; Ellis-Soto et al., 2021). Recently published freshwater-specific environmental data (Domisch et al., 2015; Zanaga et al., 2021) were used to develop relevant SDMs; these allow species distributions to be mapped by drainage system. We used freshwater fishes of China as a mapping case study because China has a land area of over 9.6 million km^2, contains some of the world's largest rivers, and has a high diversity of freshwater habitat types, including rivers, lakes, and wetland systems, that host over 1600 freshwater fish species (approximately 10% of the global freshwater fish fauna) (He et al., 2020). Long years of research on China's fishes have yielded a large amount of species occurrence data and expert information on species distribution in the literature (He et al., 2020), although the data are scattered and require a systematic compilation and curation. This fundamental knowledge combined with recent information in freshwater environmental databases opens novel opportunities for the development of a high-resolution map of China's freshwater fishes' distribution to inform their conservation.

Based on long-term field surveys and exhaustive literature data extractions, we built the largest occurrence database for China's freshwater fishes. We used this data set to visualize biodiversity patterns in a high-resolution drainage map of the entire country. We then used these high-resolution distributions to measure the spatial congruence among different biodiversity facets (e.g., species richness, endemicity, and phylogenetic diversity). We paid special attention to threatened species, because of their conservation value, and aquaculture species (i.e., commercial fishes with scaled aquaculture), because of their critical economic value in China and elsewhere in Asia (FAO, 2020; Wang et al., 2015). We also analyzed spatial patterns of potential overlap between freshwater fish occurrence and anthropogenic disturbance to identify priority areas for conservation. We expected large areas of overlap between fish biodiversity and anthropogenic disturbances because of the particularly high dependency of humans on freshwater resources in Asia. Finally, we aimed to assess the representativeness of the current network of PAs, mainly designated to protect terrestrial fauna and flora, for freshwater fish biodiversity. These assessments are crucial for identifying representation gaps and informing future development of adequate conservation frameworks for aquatic ecosystems and for ensuring the sustainability of freshwater resources and their associated ecosystem services.

METHODS

Fish occurrence data set

We compiled and curated the occurrence data of China's freshwater fishes (Actinopterygii) from all the data sources systematically reviewed in a previous study (He et al., 2020), from the Global Biodiversity Information Facility (GBIF), and from our recent field survey data and literature searches. We confirmed that all data were associated with the correct drainage systems. Here, we considered only freshwater fishes and migratory species that use freshwaters for growth or reproduction (e.g., sturgeons, salmonids, and eels). Non-native species were not considered because our major objective was to predict the distribution patterns of native species. The final database included 32,203 occurrence points for 1658 species across all watersheds in China (Appendices S1 & S2). All species names were checked and further confirmed using Eschmeyer's Catalog of Fishes (Fricke et al., 2021). Although there may be some heterogeneity in sampling efforts, such bias was reduced by considering only species occurrences (quantitative data were transformed as occurrence data), and our data set represents the most comprehensive distribution of freshwater fish species in China.

Environmental variables data set

All key environmental variables (e.g., climate, geography, hydrology) that potentially affect freshwater fish distribution were considered. This data set comprised 24 environmental layers (raster data) (Appendix S3), including elevation, slope, flow discharge, river length, water area, and 19 bioclimatic variables extracted from WorldClim (Fick & Hijmans, 2017). All environmental layers were matched to a 30-arcsec spatial resolution raster-based map of China projected with Lambert conformal conic projection. This resolution is equivalent to approximately 0.86 km^2 at the equator and is commonly referred to as the 1-km^2 spatial resolution. Because interdependencies exist among the 19 bioclimatic variables, 9 of them were excluded to avoid overrepresenting problems based on pairwise Spearman's correlations and variable relationship descriptions ($|r| > 0.70$) (Dormann et al., 2013). The 10 less-correlated variables (i.e., BIO1, BIO3-6, BIO12, BIO15, and BIO17-19) were retained, and a principal component analysis (PCA) was used to reduce data dimensionality. The first 3 principal components (i.e., Bio pca1, Bio pca2, and Bio pca3 with an eigenvalue >1), representing a cumulative contribution of 99.69% (Appendix S4), were retained for the SDM predictions. Elevation data were derived from the Shuttle Radar Topography Mission (Farr et al., 2007). The slope raster was generated with the percent rise measurement calculated with the spatial analyst tool in ArcMap 10.4.1 (ESRI, 2016). The flow discharge and river length data were sourced from Domisch et al. (2015). Water area was considered because fish movements can be constrained to drainage systems and because it can be indicative of available habitats for fish and, thereby, affect fish distribution. The water area raster was generated from the 100-m^2 resolution WorldCover 2020 version 100 product (Zanaga et al., 2021). To determine the percentage of water area in each 1-km^2 cell, we resampled and reduced the raster resolution from 100 m^2 to 1 km^2. Finally, 8 environmental layers were included in SDM predictions. All data processing, analyses, and visualizations were conducted in ArcMap and R (R Core Team, 2021).

Mapping species distributions with SDMs and expert information

To overcome potential bias resulting from the heterogeneity of occurrence data, we predicted the distribution of each species based either on SDMs when the number of occurrences was sufficient or on expert information for rare species. Predicting distributions included 4 major steps (see below and Appendix S5).

First, we snapped occurrence data points of all species to the drainage system with the near analysis toolbox in ArcMap. The snapping results were carefully checked, especially in confluence areas of tributaries and mainstems and neighboring areas of different drainage basins. Occurrence data for each species were spatially thinned to 1 record per cell of the environmental layers to avoid overrepresentative problems related to samplings in some cells (Schmitt et al., 2017).

Second, we developed stacked species distribution models (SSDMs) for species with ≥11 occurrence records after thinning. The SSDMs ensemble many single SDMs to eliminate biases and uncertainties from different algorithms and to obtain more robust results and insights (Schmitt et al., 2017). Eight models were included: artificial neural networks, classification tree analysis, generalized additive models, generalized linear models, multivariate adaptive regression splines, maximum entropy, support vector machines, and random forest. The processes and settings strictly followed the overview, data, model, assessment, and prediction protocol (Zurell et al., 2020) (Appendix S6). For each species and algorithm, 10 model replicates were fitted using random training data subsets (70% training, 30% test) and cross-validated with holdout data. We used the area under the curve, kappa, proportion of correctly predicted occurrences, sensitivity, and specificity to evaluate the models, and the included models were based on thresholds of these values >0.7. The results of the included models were then ensembled by an unweighted mean to obtain the final distribution for each species (Schmitt et al., 2017). To convert the ensembled model results into binary maps, we used the threshold of the true skill statistic, which maximizes the sum of sensitivity and specificity. Ensembled SDMs that included multiple algorithms were built using the R package SSDM (Schmitt et al., 2017).

Third, for species with <11 occurrence records after thinning, we used expert-based information to predict their distribution. Two strategies were adopted: occurrence point buffering and watershed clipping. The buffering distances (i.e., dispersal distances) for each occurrence point of each species were based on fish dispersal capacity and river order and were determined with a method developed from empirical data (Radinger & Wolter, 2014). Briefly, key dispersal-related functional traits (i.e., total length [TL] and aspect ratio of the caudal fin [AR]) of each species were extracted from FISHMORPH (Brosse et al., 2021) and FishBase (Froese & Pauly, 2021). The river order of each occurrence point was downloaded from HydroRIVERS (Lehner & Grill, 2013). For specific species, the dispersal distance at each occurrence point was estimated from the TL, AR, and river order with the R package fishmove (Radinger & Wolter, 2014). The estimated dispersal distance was used as the diameter of the buffer zone for each occurrence point. The area of overlap between buffer zones of all occurrence points and the 1-km^2 drainage map were taken as the predicted distribution for that species. For watershed clipping, each sampling point was expanded to the watershed level according to the literature and limited to a small area (e.g., town to county level) to avoid overestimating the species distribution range. Therefore, the SSDMs plus either prediction strategy based on expert information generated 2 distribution results: one was rigorous (i.e., SSDMs + occurrence point buffering) and the other was tolerant (i.e., SSDMs + watershed clipping).

Fourth, the distribution of each species in both prediction strategies was further refined and validated with expert information. The distribution of each species was cropped to its native drainage basin to exclude predictions that were out of range. Based on the occurrence points, records from the

literature, and expert information, 3 distribution elevation limits (i.e., 2600, 4600 and 5250 m asl) were applied for different taxonomic groups to correct overestimations (Ellis-Soto et al., 2021) (Appendix S2; He et al., 2020). For large species (e.g., *Acipenser sinensis*) (Appendix S2), their distribution was cropped to the mainstems and large tributaries of rivers because they rarely inhabit small tributaries during most of their life history. The final distribution area for all species was checked visually.

Biodiversity measures

Based on the distribution of all 1658 species, we calculated indices of different biodiversity facets for each cell on the drainage map, including species richness (SR), weighted endemicity (WE), coldspots and hotspots (CH), and phylogenetic diversity (PD). Weighted endemicity was measured as the species richness inversely weighted by species range (Daru et al., 2020). The identification of hotspots and coldspots was based on the weighted endemicity threshold of the top and bottom 2.5% (Daru et al., 2020). Phylogenetic diversity represents the length of evolutionary pathways that connect a given set of taxa on a rooted phylogenetic tree (Nakamura et al., 2021). The phylogeny of 1658 China's freshwater fishes was generated based on taxonomic information and using the method developed in the R package FishPhyloMaker (Nakamura et al., 2021) (Appendix S7). We also considered threatened species richness (TSR) and aquaculture species richness (ASR) because these species are of high societal concern (e.g., conservation) and provide ecosystem services (e.g., edible protein and fishery economics). The threat category of each species was sourced from the International Union for Conservation of Nature (IUCN) and Cao et al. (2016). Threatened species included those categorized as vulnerable, endangered, and critically endangered (317 species, 19% of the total) (Appendix S2). The list of aquaculture species (115 species, 7%) (Appendix S2) was generated from a literature review and expert consultation (Wang et al., 2015; China Fisheries Year Books, 1981−2020). The congruences among different facets, except for coldspots and hotspots, because they were binary data, were assessed using pairwise spatial correlation. We used the R package phyloregion (Daru et al., 2020) to calculate indices of different biodiversity facets (e.g., SR, WE, CH, and PD; Appendix S2).

Overlap between biodiversity and anthropogenic disturbance

Identifying areas where anthropogenic activity affects biodiversity is also important for conservation planning, including the identification of areas requiring strict protection and restoration (Heino & Koljonen, 2022). Therefore, we assessed the spatial overlap between anthropogenic disturbances and fish occurrence by correlating biodiversity facets with the human footprint index (HFI), which is the best available index for indicating the intensity of anthropogenic disturbances at the same spatial resolution as our fish data (i.e., 1-km^2 cell). The

1-km^2-resolution HFI data were sourced from Venter et al. (2016).

Representativeness of existing PAs

To evaluate the freshwater fish representativeness in existing PAs by habitat, we overlapped the distribution of each species with these PAs. To estimate how many species were protected, we established a maximum representation target of 100% for narrowly distributed species (<1000–10 km^2) and a minimum target of 10% for widespread species (<250,000–2500 km^2) and set a linear decline target between these 2 extremes (Rodrigues et al., 2004) (Appendix S8). Area targets were adjusted up to 1% of those developed for terrestrial species because fishes are mapped into drainages and freshwaters occupy a tiny fraction of the global surface (Balian et al., 2008). To evaluate the coverage of existing PAs in priority areas, we defined the 5% of cells with the most conservation value for each biodiversity facet, except CH, as priority conservation cells (PCCs) (Tang et al., 2006), and then the PCCs were overlapped with existing PAs. The PCCs were categorized into 4 grades (i.e., I–IV), with quarterly ranking by the HFI (e.g., HFI = 0.75–1.0 for grade I PCCs).

The location and range of PAs were sourced from the Protected Area Platform of China (PAPC, http://www.papc.cn), GeoServer (https://geoserver.travelxj.cn), and key biodiversity areas (KBAs) (http://www.keybiodiversityareas.org). Considering the importance of freshwater fish in inland fisheries and aquaculture, we also specifically included China's aquatic germplasm reserves (CAGRs), which were accessed from the Ministry of Agriculture and Rural Affairs of the People's Republic of China (http://www.moa.gov.cn). For PAs without spatial data, their locations and areas were obtained from reliable sources (e.g., PA websites, local government websites, and Baidu Maps [https://map.baidu.com]), and the extent of each PA was demarcated as a circle constrained by its total area. After duplicates were removed, the retained PAs were visually checked. We obtained valid data for 4104 PAs (PAPC and GeoServer, 2980; KBA, 606; CAGR, 518).

RESULTS

Model results and map coverage

Among the 1658 species, 480 met the criteria for the development of SSDMs after spatial thinning. Model evaluation metrics, including the area under the curve (0.90 [SD 0.04] for ensembled SDMs), kappa (0.60 [0.10]), proportion of correctly predicted occurrences (0.87 [0.05]), sensitivity (0.92 [0.04]), and specificity (0.85 [0.06]), indicated that all algorithms fit the data well (Appendix S9). The mean true skill statistic threshold of the ensemble SDMs was 0.41 (0.04). The leading environmental predictor in SSDMs was Bio pca1 (mostly contributed by Bio 4 [i.e., temperature seasonality], mean relative importance 21%), followed by the rest (9–13%), although they varied among species (Appendix S10). The remaining 1178 species

had insufficient occurrence records for SDM application. The mean point-buffering radius for a species was 24.45 km (16.23), which was significantly and positively correlated with its maximum total body length ($r = 0.66$, $p < 0.01$) (Appendix S11). The average area for watershed clipping was 7955 km^2 (18,980) (Appendix S11). The rigorous and the tolerant strategies covered most areas of the drainage system of China; 85.20% (1,070,311 cells) and 99.13% (1,245,472 cells) of the total 1,256,362 cells had at least 1 species, respectively.

Biodiversity distribution patterns

The predicted distribution patterns of different biodiversity facets (i.e., SR, WE, CH, PD, TSR, and ASR) based on the 2 mapping strategies and on species with SSDMs only were similar (Figure 1; Appendix S12), but the upper range values of the tolerant strategy were generally higher than those of the rigorous strategy (except for the WE). For instance, the rigorous SR ranged from 1 to 160, whereas the tolerant SR ranged from 1 to 200. The upper limits for the tolerant TSR and ASR were 32 and 68, respectively, which were slightly higher than those of the rigorous strategy (i.e., 28 and 64).

The overall biodiversity distribution patterns at both coarse and fine spatial scales were clear (Figure 1). At the coarse spatial scale, high species richness was generally observed from northeastern to southwestern China, particularly in the middle to lowland areas of large rivers (e.g., the Amur, Yellow, Yangtze, and Pearl Rivers). The species richness in the southern area was higher than that in the northern area. Species richness was generally low in the northwestern area (e.g., Xinjiang, Xizang, and Qinghai), despite large numbers of lakes and dense river networks in the Qinghai–Tibetan Plateau. Large river basins generally possessed higher species richness than small river basins (e.g., Yangtze River vs. Huaihe River). At the fine spatial scale within a drainage basin, the lower reaches of the mainstem and large associated lakes generally had the highest species richness (e.g., Hulunhu Lake of the Amur River, Weishanhu Lake of the Huaihe River, and Dongting, Poyang, Chaohu, Hongze, and Taihu Lakes of the Yangtze River). Small tributaries generally had fewer species than the mainstems and large tributaries. Thus, species richness increased along the upstream–downstream longitudinal gradient. Large lakes within floodplains of large rivers (e.g., Yangtze River) often had more species than or at least a comparable number of species in their mainstems, revealing lateral fish diversity gradients.

The longitudinal and lateral patterns were consistent with the elevation, temperature, and water area gradients. For indices other than species richness, WE and CH showed similar patterns; high-value areas of WE (e.g., Southwest China) coincided with hotspots, and low-value areas of WE (e.g., Qinghai–Tibetan Plateau) co-occurred with coldspots. Hotspots were primarily distributed in areas with rich biodiversity from eastern to southwestern China, including the 2 large islands, Taiwan and Hainan. The hotspots were also outstanding in the southern area of the Himalayas and the downstream areas of the Lancang and Nu Rivers. The PD, TSR, and ASR showed a similar spatial pattern to that of the SR. High TSR was primarily present in the northeast, center to southeast, and northwest of China, and high ASR occurred in the center to southeast part.

Spatial correlations between different biodiversity facets demonstrated strong congruence for most biodiversity facets (Figure 2), which was consistent with the biodiversity distribution patterns. The correlations between SR and PD were all significant ($p < 0.01$) and had the highest r values (0.98 for rigorous and tolerant), followed by SR and ASR ($r = 0.95$–0.87, $p < 0.01$) and SR and TSR ($r = 0.73$–0.71, $p < 0.01$). In contrast, WE had significant ($p < 0.01$) but low correlations with all the other biodiversity facets; r varied from 0.50 to 0.57 (rigorous) and from 0.43 to 0.75 (tolerant).

Overlap between biodiversity and anthropogenic disturbances and conservation representativeness

In both rigorous and tolerant strategies, areas with high species richness (i.e., SR, TSR, and ASR) generally overlapped with areas of high HFI; for example, large tributaries, lower reaches of the mainstem, and associated lakes of large rivers with high fish diversity showed the highest anthropogenic disturbance values (Figure 3). For instance, the upper Yangtze River area (e.g., Jinsha River, Yalong River) showed a strong concordance between anthropogenic disturbances and biodiversity. A similar situation was found for the western half of Taiwan and the fringe areas of Hainan Island. In contrast, most areas in northwestern China had less overlap between fish biodiversity and anthropogenic disturbances, apart from the mainstem of the Ertix River and a small area in the southern Himalayas (Figure 3). Similar patterns were observed for WE and PD. Overall, all biodiversity facets were significantly and positively correlated with the HFI ($p < 0.001$) (Figure 3f,l). Spearman's r ranged from 0.20 to 0.39 (rigorous) and from 0.14 to 0.39 (tolerant).

The PAs in China covered 2.09 million km^2 and accounted for approximately 21.64% of China's terrestrial territory (Figure 4a). The northwestern part of China (e.g., Xizang and Qinghai), which had low fish species richness, also had large PAs, whereas PAs were generally small and scattered in the northeastern to southwestern areas with high fish species richness. A total of 136,690 PCCs (accounting for 10.88% of the total drainage cells) were identified based on the 2 strategies, and the PCCs were primarily distributed from the east to southwest of China (Figure 4b). The representativeness of PAs estimated using predicted distributions from the rigorous and tolerant strategies were similar; overall 25% (rigorous) and 29% (tolerant) of habitats covered for SR, WE, hotspots, PD, TSR, and ASR (Figure 4b,d). However, the fish coldspots were unexpectedly well covered in PAs (55% [rigorous] and 59% [tolerant] of coldspots were included within PAs). At the species level, 6% (rigorous) and 21% (tolerant) of the species were not protected at all (distribution range entirely out of PAs), and 38% (rigorous) and 45% (tolerant) of the species benefitted from protection in <10% of their distribution
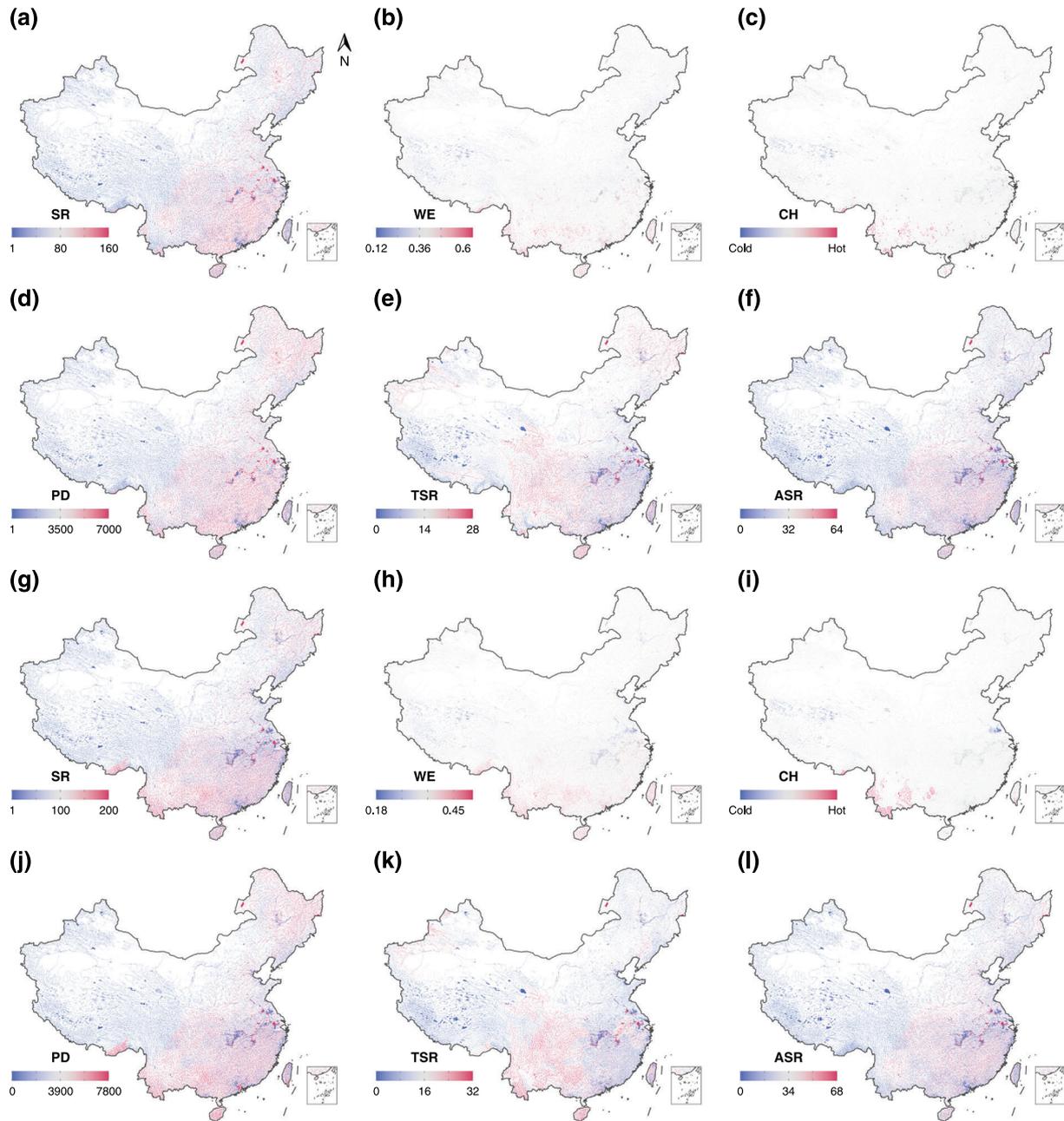
FIGURE 1 Distribution patterns of biodiversity facets (species richness [SR], weighted endemicity [WE], coldspots and hotspots [CH], phylogenetic diversity [PD], threatened species richness [TSR], and aquaculture species richness [ASR]) of China's freshwater fishes based on 2 distribution prediction strategies: (a–f) rigorous (i.e., stacked species distribution models [SSDMs] + occurrence point buffering) and (g–l) tolerant (i.e., SSDMs + watershed clipping)

range. According to different area threshold combinations, an average of 16% (rigorous) to 23% (tolerant) of all species, 19% (rigorous) to 25% (tolerant) of threatened species, and 58% (rigorous) to 64% (tolerant) of species of aquacultural value were considered protected (Figure 4c,e; Appendix S13). Regarding the PCCs, 30% (rigorous) to 31% (tolerant) of them were covered by existing PAs, and the value ranges for different biodiversity facets were 26–45% (rigorous) and 26–43% (tolerant) (Figure 4g,h). A total of 2% (both rigorous and tolerant), 12% (rigorous) and 11% (tolerant), 44% (rigorous) and

45% (tolerant), and 43% (rigorous) and 42% (tolerant) PCCs were in grades I to IV, respectively. Coverage by existing PAs ranged from 18% to 37% (rigorous) and 18% to 36% (tolerant) (Figure 4i,j). The higher the grade of the PCCs, the fewer of them were covered by PAs. The PCCs with high grades (i.e., I & II) that were not protected generally surrounded megacities (e.g., Wuhan, Shanghai, and Guangzhou) in lowland areas of large rivers (e.g., Yangtze and Pearl Rivers), and those with low grades were spread throughout eastern to southwestern China (Figure 4b).
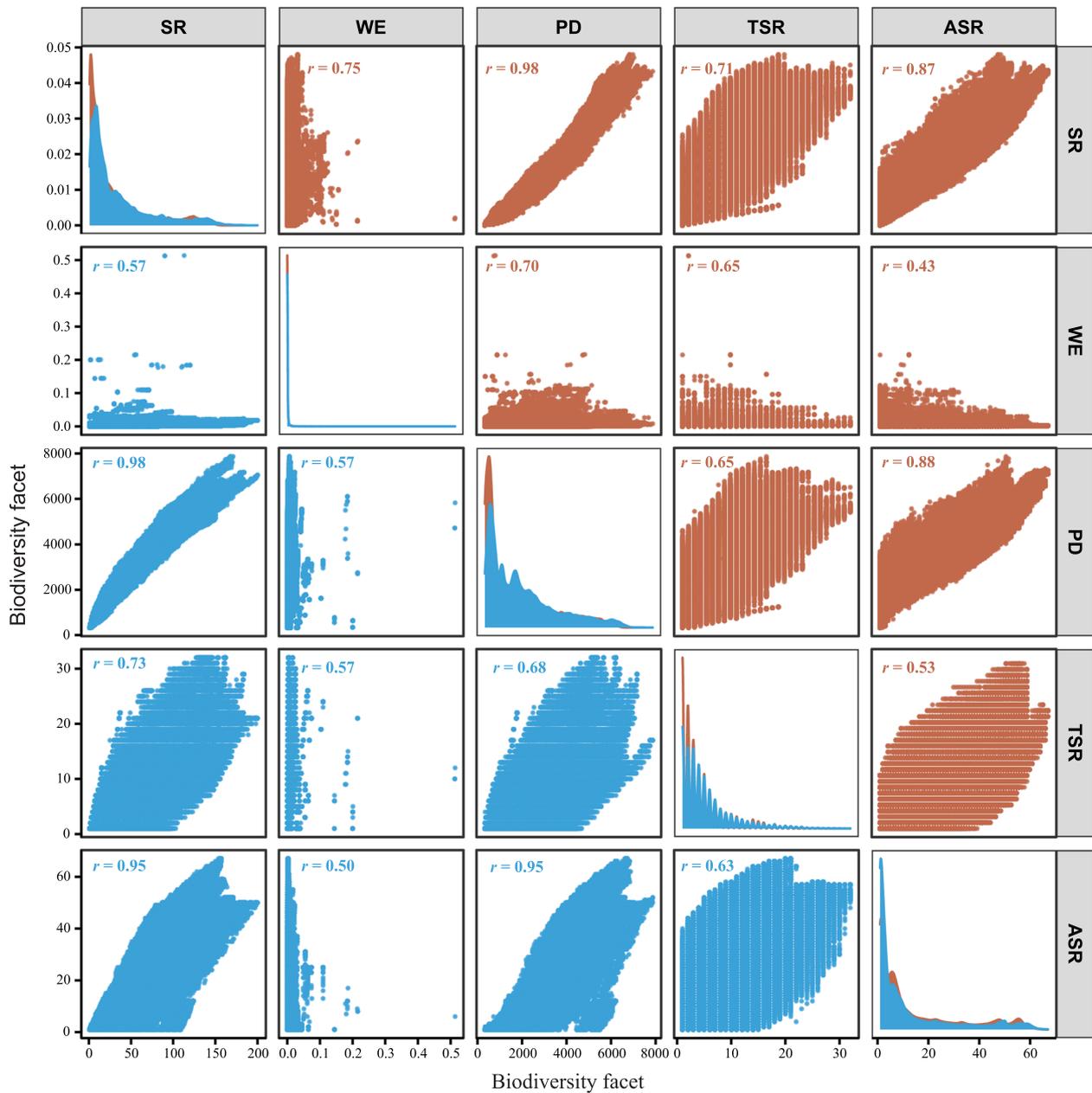
FIGURE 2 Congruences among biodiversity facets for China's freshwater fishes (blue, results of the rigorous prediction strategy; brown, results of tolerant prediction strategy; 2-color plots, diagonal shows original data distribution of each facet; biodiversity facets and strategies defined in text and in legend of Figure 1). All *p* values <0.001 (Spearman correlations).

DISCUSSION

We provided the first high-resolution distribution map for freshwater fishes for all of China. Freshwater ecosystems are spatially constrained to a small fraction of the land surface (Balian et al., 2008), and most obligatory freshwater organisms occur throughout their entire lives only in wetted areas. Therefore, high-resolution maps are essential for efficiently delineating PAs for freshwater organisms. With the help of global environmental databases for freshwaters (Domisch et al., 2015; Zanaga et al., 2021), we successfully developed high-resolution distributions

in drainages for 1658 native freshwater fishes in China. These distributions were based on the occurrence database we built (largest of its kind). We combined SSDMs and expert-based information to overcome the high data heterogeneity (Domisch et al., 2016; Ellis-Soto et al., 2021). Using these distribution maps, we found a limited representativeness of existing PAs (i.e., 25–29% of fish habitats, 16–18% of species, and 30–31% of PCCs) for China's freshwater fishes. Our distribution maps are valuable not only for identifying conservation gaps, but also for designing efficient conservation strategies in the future. Our study can be a guide for conservation studies worldwide because
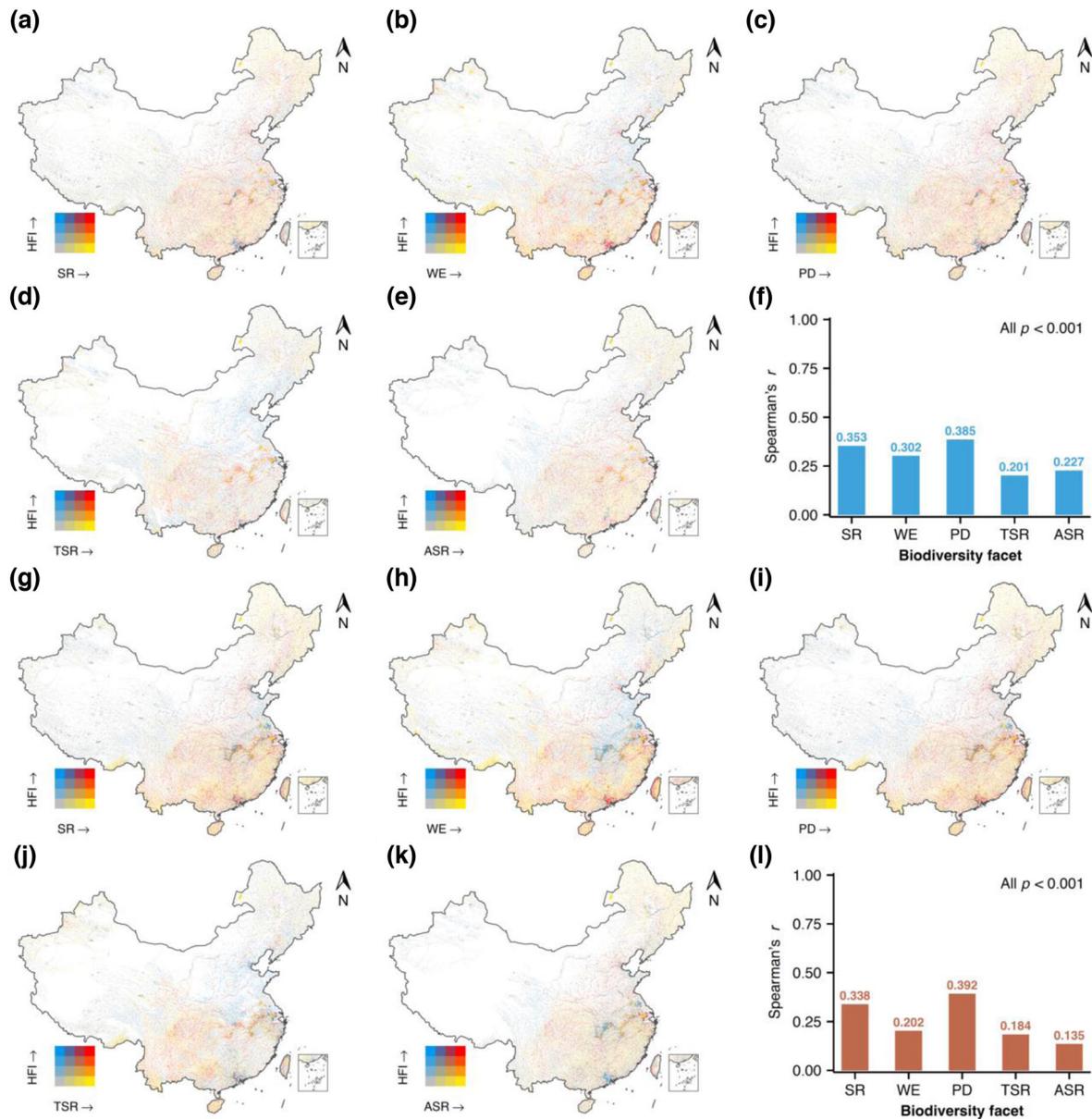
FIGURE 3 Overlap of China's freshwater fish biodiversity facets with human activity as indicated by the human footprint index (HFI) and predicted based on (a–f) rigorous and (g–l) tolerant strategies (biodiversity facets and strategies defined in text and in legend of Figure 1): (a–e, g–k) spatial overlaps and (f, l) Spearman correlations

we provide a framework for producing high-resolution maps for freshwater organisms for which occurrence data are limited .

Coarse-scale (e.g., latitudinal and elevational gradients) and fine-scale patterns in drainage basins (e.g., longitudinal and lateral gradients) revealed in the 1-km²-resolution map (Figure 1) are consistent with current knowledge of freshwater organisms' diversity patterns and underlying determinants measured across global, continental, and regional spatial extents (Collen et al., 2014; He et al., 2020). For instance, the decline in species richness as latitude and elevation increase (Collen et al., 2014; Zhao et al., 2006) and the increase in river basin species richness as basin area increases (Oberdorff et al., 2011) were shown in our data. Moreover, distinct longitudinal and lateral gradients of

fish species richness were found in drainage basins (Figure 1). Downstream reaches harbored more species than upstream reaches, mainstems had more species than tributaries, and lakes supported more species than associated river channels. These fine-scale patterns conformed to the results of many investigations conducted in single drainage basins (Muneepeer-akul et al., 2008) and to theoretical predictions (e.g., river continuum concept [Vannote et al., 1980]). All the biodiversity patterns we found across China were consistent with theoretical and applied knowledge on rivers. Therefore, the framework we propose to reconstruct fish assemblages from the combined use of SSDMs and expert knowledge appears to be robust.
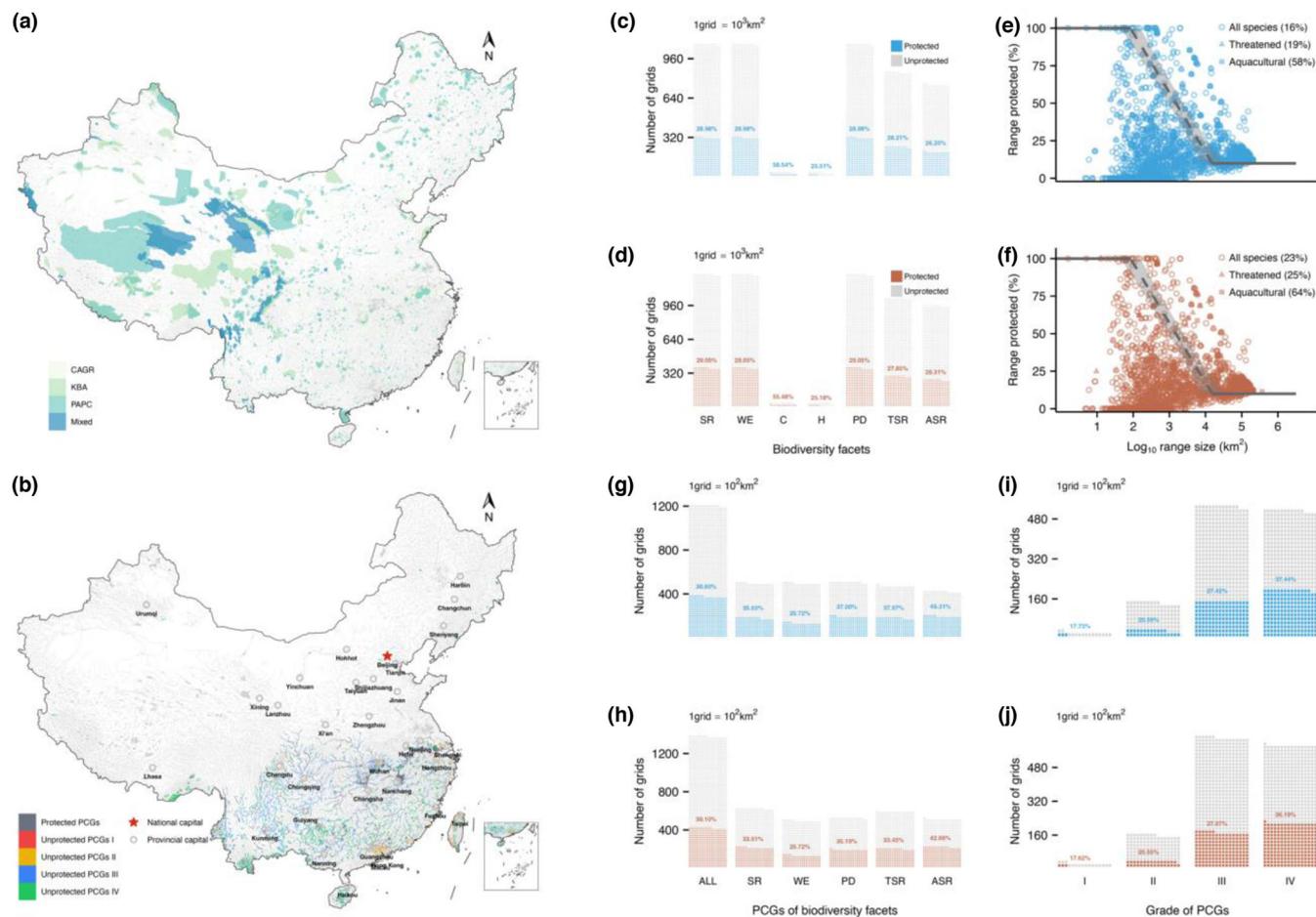
FIGURE 4 China's freshwater fishes' representation in existing protected areas predicted based on rigorous (blue) and tolerant (brown) predicting strategies: (a) distribution of existing protected areas, (b) distribution of priority conservation cells (PCCs), (c, d) habitat coverage of biodiversity facets in protected areas, (e, f) species range in protected areas, (g, h) PCC coverage of biodiversity facets, and (i, j) PCC coverage of different grades (I–IV). The PCCs were categorized into 4 grades (i.e., I–IV), with quarterly ranking based on the human footprint index (HFI), for example, HFI = 0.75–1.0 for grade I PCCs. CAGR, China's Aquatic Germplasm Reserve; KBA, key biodiversity area; PAPC, Protected Area Platform of China. Biodiversity facets and strategies defined in text and in legend of Figure 1

The distribution patterns of freshwater fish at both the coarse and fine scales confirmed spatial mismatches between terrestrial and freshwater biodiversity as previously reported (Abell et al., 2017; Acreman et al., 2019; Tickner et al., 2020; Xu et al., 2017). The priority conservation gaps (i.e., unprotected PCCs) (Figure 4) we identified did not fully overlap with those identified for terrestrial species (Tang et al., 2006; Xu et al., 2017). For instance, the biodiversity (e.g., richness of all species, endemic species, and endangered species) of terrestrial plants and vertebrates peaks in the low- to mid-elevation mountainous areas of southwestern China (e.g., Hengduan Mountains and Xishuangbanna area) and Hainan and Taiwan Island (Tang et al., 2006; Xu et al., 2017), whereas we found freshwater fish biodiversity (e.g., SR, TSR, ASR) peaked in the lowland reaches of large rivers and their associated lakes in eastern China. Fish biodiversity hotspots with high endemism were mostly in southwestern mountain areas and the 2 large islands (Figure 1), in accordance with previous findings (He et al., 2020; Xing et al., 2016). These mismatches between terrestrial and freshwater biotas are probably rooted in habitat availability, which is low in mountain

streams and high in the lowland reaches of large rivers for freshwater species (Muneepeerakul et al., 2008; Vannote et al., 1980). In contrast, the steep elevational gradient in mountainous areas can generate a great variety of habitats for terrestrial organisms (Rahbek et al., 2019; Tang et al., 2006).

Given the traditional designation of PAs for terrestrial biodiversity, the mismatch between terrestrial and freshwater biodiversity at coarse and fine scales inevitably resulted in conservation insufficiencies for freshwater species and explains the limited representativeness of them in current PAs for freshwater fishes in China. Overall, less than one third of freshwater fish habitats and PCCs and less than one fourth of fish species were covered in PAs (Figure 4), a result consistent with the low effectiveness of PAs for freshwater organisms across the globe (Abell et al., 2017; Acreman et al., 2019; Azevedo-Santos et al., 2019). For example, using ecological niche models and modified targets of Rodrigues et al. (2004), Frederico et al. (2018) found only 5 out of the 138 stream fish species (i.e., 4%) were completely protected by strictly PAs in the Brazilian Amazon. We found that areas of high fish species richness in southeastern

China are still largely unprotected (Figures 1 & 4) and are greatly affected by anthropogenic disturbances (Figure 3). The designation of freshwater PAs is urgently needed in the face of current and emerging pressures on freshwater ecosystems, such as overexploitation, climate change, biological invasions, and habitat degradation (Guo et al., 2019; He et al., 2020; Reid et al., 2019; Tao et al., 2018). Moreover, China is currently involved in the development of renewable sources of energy, implying the development of hydropower electricity production to achieve carbon neutrality. Damming for electricity production is therefore forecasted to increase in the next decades (Reid et al., 2019; Zarfl et al., 2015), which would further aggravate disturbances in freshwater biodiversity. It is therefore pivotal to design effective freshwater conservation frameworks to sustain freshwater biodiversity and the associated goods and services they provide to humans (Acreman et al., 2019; Harper et al., 2021). Additionally, designing freshwater PAs could also have positive repercussions for terrestrial biodiversity (Heino et al., 2021; Leal et al., 2020), which is reported to be declining rapidly in Asia (Toussaint et al., 2021; WWF, 2020).

The way subjects of conservation are evaluated by humans, their distribution patterns, and threats to them collectively determine what strategies should be used to determine which species should be conserved and where and how to prioritization their conservation (Mace, 2014). Although conservation perception has shifted to "people and nature" in seeking a balance between conservation and human needs, it has not yet been sufficiently considered in freshwater research, management, and conservation (Harper et al., 2021; Mace, 2014). We provide a basis for efficient development of biodiversity-based conservation priorities that will complement the conservation of emblematic species with umbrella effects. The consideration of distinct biodiversity facets of different socioeconomic relevance, as we demonstrated here, could also allow the design of conservation plans according to the diverse ecosystem functions of freshwater fishes, such as providing food, economic, cultural, and recreational services, which are essential to achieving sustainable development goals (FAO, 2020). Although most of the freshwater biodiversity facets were spatially congruent, the richness of endemic fish species displayed a distinct pattern and peaked in the mountainous areas in southwestern China (He et al., 2020; Xing et al., 2016), whereas aquacultural species were centrally distributed in the lowland areas of East China (Figure 1). In China and most other Asian countries, the food and economic values of freshwater fishes are particularly prominent. For instance, inland aquacultural production in China reached 30 million t/year, with a gross value of approximately US\$100 billion in 2019 (data from the Ministry of Agriculture and Rural Affairs of the People's Republic of China). Freshwater fishes provide at least 50% of people's average per capita intake of animal proteins in many developing Asian countries and regions (e.g., Bangladesh, Cambodia, and inland Sri Lanka) (FAO, 2020). Thus, more than 500 of CAGRs have been designated for the conservation of biodiversity with socioeconomic value. Future revision of these CAGRs could benefit from the biodiversity distribution maps we developed. However, CAGRs are directed toward the conservation of potential aquaculture resources, and other species, including most of the endemic fish species, remain overlooked. Adequate planning must, therefore, play a key role when designing management strategies that aim to fulfil the diversity of objectives for freshwater ecosystems. This future planning must also help reduce potential trade-offs between objectives (e.g., exploitation of freshwater resources and biodiversity conservation) and maximize cobenefits.

Despite the fact that PAs in China have experienced rapid expansion in recent decades (Xu et al., 2017), freshwater fishes did not strongly benefit from existing PAs due to the spatial incongruence between terrestrial and freshwater biodiversity (Figure 4). Our high-resolution maps suggest that freshwater-specific PAs should primarily be designated in lowland areas of eastern China that host diverse fauna and plentiful aquaculture resources. Although these areas overlap with areas of high human population densities (Figures 3 & 4), they can provide essential protein resources to human populations and should thus be protected from the ecosystem services point of view. Little-affected mountainous areas (e.g., Yunnan, Guangxi, and Guizhou) should also be prioritized because they host evolutionarily invaluable species and unique genetic diversity (i.e., rare and endemic species) (Figures 1 & 4). Within river basins, lower reaches, large tributaries, and associated lakes should be protected to maximize the number of species benefitting from conservation programs, and the upper tributaries and lakes in mountainous areas should be considered to protect endemic species. Overlaps between freshwater fish biodiversity and anthropogenic disturbances should be highlighted in the improvement of conservation effectiveness (Figure 4). The central and southeastern parts of China and areas surrounding megacities in lowlands of large rivers, which harbor diverse fish fauna and where most of the species are heavily threatened by anthropogenic disturbances, should be considered a conservation priority (Figures 1, 3, & 4). A conservation approach should be adapted that promotes coexistence with widespread anthropogenic stressors (e.g., dams and pollution) because these stressors persist even in PAs through dendritic connections (Harper et al., 2021; Hermoso et al., 2016). Inclusive conservation incorporating more public interests and engagement (Acreman et al., 2019; Wu et al., 2019) and a conservation network of small reserves is practical and resource saving and may produce efficient results (Koning et al., 2020).

Our framework for mapping high-resolution distributions of freshwater fish is highly transferable to other taxonomic groups, ecosystems, and geographical regions. Using either the rigorous or tolerant strategies depends on the availability of species occurrence data and expert information on distribution ranges, which require relevant efforts (e.g., field sampling, fisher interviews, and expert consultation). Although watershed clipping errors in the tolerant strategy may occur at linking points (e.g., randomly clipping a mainstem species to a headwater stream), they would not change the overall distribution patterns at large scales, and their influences can be reduced through decreasing the watershed size used in the analyses. The produced maps could inform IUCN assessments, KBA delineations, PA representativeness evaluations, and systematic conservation planning because species distribution ranges are

essential inputs in these activities. PAs for freshwater ecosystems must consider the needs of organisms for longitudinal and lateral connectivity within the landscape, provide multifunctional services, and account for the intensity of anthropogenic disturbances. Therefore, PAs for freshwater ecosystems should be more diverse in form (e.g., designing based on objectives, catchment zoning, classifying PAs into different protection levels, and OECMs) and integrated with each other to optimize multiobjective achievements (Hermoso et al., 2018; IUCN–WCPA, 2019; Higgins et al., 2021). Alternatively, strengthening the effectiveness of existing PAs through multiple measures (e.g., funding, staffing, and equipping) and restorations (e.g., river habitat rehabilitation, and connectivity restoration) is also important (Coad et al., 2019; Heino & Koljonen, 2022) in cases where expanding PAs is difficult or where it is not possible to meet the expected PA coverage requirements.

The biodiversity distribution patterns and gaps in protection of priority conservation areas we identified provide a roadmap for protecting China's freshwater fishes. Our high-resolution mapping of freshwater fish distributions also provides a historical benchmark for future studies; changes in fish distribution throughout China can now be measured. Besides the importance of our results for China's freshwater fish conservation, our framework, which combines occurrence data and expert knowledge on species distribution, provides an efficient way to design PAs regardless of ecosystem, taxonomic group, or geographical area.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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