Global diversity patterns and threats of cave fish

Bai, X.; Zhang, P.; Gan, L.; Brosse, S.; Shipley, B.R.; Grenouillet, G.; ... ; Dong, X.

Citation

Bai, X., Zhang, P., Gan, L., Brosse, S., Shipley, B. R., Grenouillet, G., ... Dong, X. (2025). Global diversity patterns and threats of cave fish. *Global Ecology And Biogeography*, *34*(11). doi:10.1111/geb.70160

Global Ecology and Biogeography

WILEY

Global Ecology and Biogeography A Journal of Macroecology

RESEARCH ARTICLE

Global Diversity Patterns and Threats of Cave Fish

Xiongfeng Bai[1] | Peng Zhang[1] | Lei Gan[2] | Sébastien Brosse[3] | Benjamin R. Shipley[4] | Gaël Grenouillet[3,5] | Tao Ju[6] | Yahui Zhao[7] | Valerio Barbarossa[8,9] | Guohuan Su[10] | Lihua Xiong[1] | William R. Jeffery[11] | Sovan Lek[3] | Xianghong Dong[2]

[1]State Key Laboratory of Water Resources Engineering and Management, Wuhan University, Wuhan, People's Republic of China | [2]Department of Fisheries Sciences, College of Animal Science, Guizhou University, Guiyang, People's Republic of China | [3]Centre de Recherche sur la Biodiversité et l'Environnement (CRBE), UMR5300, Université de Toulouse, CNRS, IRD, INPT, Toulouse, France | [4]Department of Earth Sciences, University of Oxford, Oxford, UK | [5]Institut Universitaire de France, Paris, France | [6]Guangxi Academy of Marine Sciences, Guangxi Academy of Sciences, Nanning, People's Republic of China | [7]Institute of Zoology, Chinese Academy of Sciences, Beijing, People's Republic of China | [8]Institute of Environmental Sciences, Leiden University, Leiden, the Netherlands | [9]Global Sustainability, PBL Netherlands Environmental Assessment Agency, The Hague, the Netherlands | [10]Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan, People's Republic of China | [11]Department of Biology, University of Maryland, College Park, Maryland, USA

Correspondence: Peng Zhang (zhang1230@whu.edu.cn) | Xianghong Dong (xhdong@gzu.edu.cn)

Received: 16 April 2025 | **Revised:** 12 October 2025 | **Accepted:** 10 November 2025

Handling Editor: Fabien Leprieur

Funding: This study was financially supported by the National Natural Science Foundation of China (no. 52179142) and the Basic Project of Guizhou University (no. [2023]14).

Keywords: cave fish | climate change | exposure risk | maximum entropy | species richness

ABSTRACT

Aim: Cave fish have long fascinated biologists due to their unusual morphology, biology and physiology. Here, we developed the first database of cave fish occurrences, provided the first map of cave fish diversity patterns and evaluated how environmental changes are threatening cave fish diversity across the globe.

Location: Global.

Time Period: 21st century.

Major Taxa Studies: Cave fish, classified as Stygobionts and Stygophiles, are widespread across the phylogeny of freshwater fish, with more than one-third of fish orders (17/45) and one-fifth of freshwater fish families (37/185).

Methods: We collected 1017 records of cave fish through a review of 378 publications and field surveys. We then used species distribution models to project the current and future global distribution of cave fish under varying climatic and geomorphic conditions, while assessing threats posed by multiple environmental stressors.

Results: We show that a few places in South America and Asia host a striking richness in cave fish species, whereas other regions are almost free from such species. We moreover reveal that almost two-thirds of the species are not formally named and that knowledge of cave fish diversity is lacunary in several regions from the Global South. Limited dispersal capacities of cave fish are expected to result in substantial habitat loss, as newly suitable or restored habitats remain inaccessible, thereby pushing species at risk of extinction across the globe. Arsenic contamination in groundwater and dam construction were identified as further threats to cave fish in karst and non-karst regions, respectively.

Conclusions: We mapped the global patterns of cave fish diversity and richness, assessed exposure risks under changing environmental conditions and revealed substantial knowledge gaps. Our work constitutes a primer for cave fish ecology and paves the way for further studies on the impact of global changes on the fragile but unique subterranean ecosystems.

1 | Introduction

With more than 17,000 species, freshwater fish account for one fourth of all vertebrates (Su et al. 2021). They are found in all freshwater environments with the exception of the poles and colonise almost all habitats, from temporary pools to large rivers and deep lakes (Matthews 2012). Caves are among the most extreme habitats colonised by freshwater fishes (Zhao and Zhang 2006), where they represent the most species-rich group of vertebrates, with 460 species currently identified (Culver and Pipan 2019; Niemiller et al. 2019). Due to their long-term adaptation to stable, aphotic and food-limited cave environments, cave fishes have evolved a range of adaptive traits, such as reduced or absent eyes, loss of pigmentation, decreased metabolic rates, and the absence of circadian rhythms (Howarth 1993; Jeffery 2001; Rétaux and Casane 2013; Borowsky 2018; Soares and Niemiller 2020). The unique biological traits and evolutionary characteristics of cave fish have long fascinated biologists (von Rintelen et al. 2012; Protas and Jeffery 2012). Although a few species, such as *Astyanax mexicanus*, have become leading models in various biological fields, including evolution, development and neuroscience (Keene et al. 2015), knowledge of cave fish ecology and biogeography remains lacunary, with a lack of understanding of the global patterns of diversity of cave fish species.

Cave fish are often local endemics with small population sizes living in the environmentally stable environment of caves, probably making them highly sensitive to global changes (Zhao et al. 2022). Among them, the rise of cave temperatures, environmental pollution and non-native species invasions has been listed as potential detrimental effects to cave fish ecology (Mermillod-Blondin et al. 2013; Proudlove 2001; Zhao et al. 2022). As a result, there remains a notable lack of global-scale studies on cave fish distribution and on their exposure risks to multiple environmental stressors. In particular, fluoride and arsenic pollutants are recognised as a major global threat to groundwater ecosystems (Podgorski and Berg 2022, 2020), along with extreme heat waves that can cause thermal instability (Mermillod-Blondin et al. 2013) and dams that disturb water availability and dispersal for non-obligatory cave fish (stygophile) species (Zhao et al. 2011; Barbarossa et al. 2020).

To fill this gap, we developed a global database of cave fish diversity, and projected the spatial patterns of this diversity under climate change and exposure risk to environmental threats. Based on an extensive literature review, we collected more than 350 literature sources and online databases to provide the first map of cave fish species diversity across the globe. We then modelled habitat requirements of the cave fish genera through species distribution models (SDMs) using the widely employed Maximum Entropy (MaxEnt) algorithm (Phillips et al. 2006) that allows assessing ecological niches for numerous taxa across terrestrial, freshwater, and marine environments (Guisan and Thuiller 2005; Elith and Leathwick 2009; Guisan et al. 2013; Robinson et al. 2017; Hao et al. 2019; Sofaer et al. 2019). Finally, we used these models to predict how climate and land use changes will affect cave fish richness across the world. We further assessed how other major globally recognised threats to groundwater ecosystems, including chemical (fluoride, arsenic), and physical (dams and extreme heat risk) disturbances will put at risk cave fish diversity.

2 | Methods

2.1 | Cave Fish Occurrences

Cave fish occurrence data were primarily collected through a literature review of scientific peer-reviewed articles. We conducted a literature search using the keywords cavefish, cavefishes, cave fish, cave-dwelling fish, blind fish, hypogean fish and subterranean fishes across Web of Science (WOS), Google Scholar and the Chinese CNKI database. In total, 378 articles and books were selected for data extraction (Appendix S2), from which information on species taxonomy and locality of occurrence was compiled. Details of the search process, inclusion/exclusion criteria and screening steps are provided in Note S1 in Appendix S1. Additional occurrence data were also extracted from GBIF (https://www.gbif.org/), FishBase (https://fishbase.se/) and grey literature, and included in the database after a careful quality check. Taxonomy was checked for all records using the latest literature, monographs, FishBase (Froese and Pauly 2024) and Eschmeyer's Catalogue of Fishes (Fricke et al. 2024), and the spatial accuracy of the records was also verified by checking the consistency between the textual description and the coordinates of each record in Google Earth (https://earth.google.com/). To buffer the possible heterogeneity in sampling effort, occurrence data records were thinned (Boria et al. 2014; Aiello-Lammens et al. 2015), retaining a single record per grid cell at a spatial resolution of 2.5 arc minutes (Steen et al. 2021).

For occurrence data with specific coordinates, we evaluate the survey status of regional sites in conjunction with the IUCN Red List (https://www.iucnredlist.org/). For cave fish survey events without specific coordinates, we integrate them with the occurrence data at the national scale to conduct species diversity statistics and analysis.

2.2 | Predictor Variables Selection

The selection of predictor variables can significantly affect the quantification of niches, thereby impacting the temporal and spatial transferability of individual SDMs (Peterson et al. 2007). Here we retained environmental variables known as influential on cave ecology, namely annual mean temperature (BIO1), annual precipitation (BIO12), land cover (LC) and karst topography (KRT).

Cave temperatures are relatively stable, and little influenced by seasonal variations of surface temperatures, but they are highly correlated with BIO1 (Moore and Sullivan 1964; Mammola et al. 2019). The situation is similar for water supply, which is correlated to BIO12. LC is related to the food sources of cave fish because subterranean ecosystems are highly dependent on external ecosystems for essential energy and organic matter inputs (Gibert and Deharveng 2002), that can reach the caves through the water input (Wilhelm et al. 2006) or be actively transported in the caves environment by bat defecation (guano) and corpses (Ferreira and Martins 1999; Culver and Pipan 2019). Because bat distributions are influenced by LC (Razgour et al. 2016), LC can therefore also indirectly affect cave ecosystems. KRT directly indicates the presence of cave environments, which are thus crucial for cave fish as a higher spatial extent of karsts in a region will increase habitat availability of cave fishes.

To ensure consistency with the occurrence data grid, categorical variables (LC, KRT) were resampled to 2.5 arc minutes using the nearest-neighbour method, which is recommended for preserving class values (Appelhans et al. 2022). The BIO1 and BIO12 climate factors at a resolution of 2.5 arc minutes were obtained from the WorldClim database (http://www.worldclim.org) (Hijmans et al. 2005). The LC data are derived from 2010 MODIS data at a resolution of 500 m and include 12 land use types such as grassland, shrubland, cropland, various forest types, urban land and so on (Rolf 2023). KRT represents karst landscape data (Goldscheider and Drew 2007; Hartmann and Moosdorf 2012; Chen et al. 2017), which we simplified into binary data (1 for karst landscape, 0 for non-karst landscape) for modelling purposes. To avoid overfitting and collinearity effects (De Marco and Nóbrega 2018), we tested for collinearity among BIO1, BIO12, LC and KRT across the seven study regions. To balance statistical rigour with ecological relevance, variables were deemed suitable for modelling when the variance inflation factor (VIF) was below 10 (Table S1 in Appendix S1) and the absolute value of the Pearson correlation coefficient ($|r|$) was below 0.8 (Figure S1 in Appendix S1), thresholds that are widely adopted in species distribution modelling as indicators of acceptable multicollinearity (Naimi et al. 2014; Yu et al. 2013; Liu et al. 2019; Bai et al. 2024, 2025; Zhou et al. 2025). Although stricter criteria (e.g., VIF < 3 or $|r| < 0.7$) may further reduce collinearity, they could also exclude ecologically relevant predictors and compromise model interpretability and performance (Alves-Ferreira et al. 2024; Li et al. 2025).

2.3 | MaxEnt Modelling and Prediction

Prior to model construction, and to avoid the model overfitting, we considered cave fish diversity at the genera level and retained for modelling fish genera with more than five occurrence records (Mi et al. 2023). The final database used to build the models counts 31 genera and 263 species distributed over five continents and seven study regions (Table S2 in Appendix S1). The delineation of the study regions is based on the first-level basin divisions of GRNWRZ Version 2.0, which is based on a comprehensive consideration of the basin area and whether river connectivity within the water resource zone can be fully highlighted (Yan et al. 2022).

We used the megaSDM package (Version 2.0.0; Shipley et al. 2022) on the R platform to build the MaxEnt model for cave fish at the genus level. This framework incorporates several recent advancements in SDMs, including using background points instead of pseudo-absence points to replace true absence points more efficiently, and applying geographical and environmental filtering to species occurrence records and/or background points (Shipley et al. 2022; Dong et al. 2024). These techniques effectively reduce inherent sampling bias in presence records and background points, thereby significantly improving the model's predictive performance (Kramer-Schadt et al. 2013; Varela et al. 2014; Castellanos et al. 2019). Unlike many studies that rely solely on the MaxEnt software (Yu et al. 2013; Zhang et al. 2014; Makki et al. 2023) to generate background points, the megaSDM package generates background points in two steps. The first step randomly selects 50% of the background points from the entire study area, while the second step draws the remaining 50% from buffers (with a radius equal to twice the 95% quantile of the minimum distance between each occurrence point) around true occurrence points (Shipley et al. 2022). In contrast, using MaxEnt software alone typically performs only the first step. Our model-building process consists of generating up to 10,000 background points, ensuring this number was significantly larger than the number of occurrence points. We then randomly split the filtered occurrence dataset into a training set (70%) and a testing set (30%) using the 'bootstrap' method. Model performance was evaluated using the area under the receiver operating characteristic (ROC) curve (AUC) (Shipley et al. 2022). Finally, we repeated the dataset splitting and model performance evaluation steps 10 times to reduce the bias caused by data partitioning and increase the robustness of the results.

This study initially modelled cave fish distribution for the 2000–2020 period (2010s). Subsequently, predictions were made using future climate data for the 2050s (average values for 2041–2060) and 2090s (average values for 2081–2100), while keeping all factors except climate variables unchanged. LC and KRT were held constant in future projections due to the lack of reliable future data for LC and the near-constancy of KRT over the study's time scale. The use of static non-climatic variables in predicting the impacts of climate change is widely accepted (Peterson et al. 2002). Moreover, previous studies have demonstrated that models incorporating both static and dynamic variables perform better than those that obscure or exclude static variables (Iverson and Prasad 1998; Stanton et al. 2012). To reduce uncertainty in future projections, we selected climatic data from three widely used global circulation models (CanESM5, CNRM-ESM2-1 and MIROC-ES2L) (Table S3 in Appendix S1) and averaged the cave fish richness distributions derived from these climate models (Hole et al. 2009; Mi et al. 2023). Considering the impact of human carbon emissions and societal development pathways on meteorological outcomes, we predicted cave fish habitat distribution under two scenarios: SSP1-2.6 (a sustainable development pathway; by the end of this century, the temperature is projected to rise by 2.0°C compared to pre-industrial levels, which is still higher than the Paris Agreement goal) and SSP5-8.5 (a fossil fuel-intensive pathway; by the end of this century, the temperature is forecasted to ascend by

5.4°C compared to pre-industrial levels) (Zhou et al. 2021; Urban 2024).

2.4 | Species Richness Gap Assessment Under Dispersal Limitations for Cave Fish

Freshwater fish are generally poor dispersers (Shurin et al. 2009), which makes it challenging for them to track suitable climate conditions beyond their existing river networks (Bush and Hoskins 2017; Comte and Grenouillet 2015; Lenoir et al. 2020). The underground cave environment exacerbates this issue by creating an 'island effect' (Wu 1993), which may further restrict the dispersal ability of cave fish compared to typical freshwater species. As a result, cave fish have limited dispersal opportunities and must either persist in situ or face local extinction if environmental conditions fail to meet their ecological requirements (Mammola et al. 2019). To evaluate the impact of dispersal limitations, we considered two extreme dispersal scenarios: (1) cave fish can reach any suitable habitat within the study region; and (2) cave fish cannot move from their current spatial range. Based on these two scenarios, we calculated the annual richness gap of cave fish for each study region due to dispersal limitations over the 21st century using the following formula:

$$\mathrm{RG} = \mathrm{SR}_{\mathrm{I}} - \mathrm{SR}_{\mathrm{II}}$$

$$\mathrm{SR}_{\mathrm{I}} = \sum_{i=1}^{n} \mathrm{HS}_{i,2090\mathrm{s}}$$

$$\mathrm{SR}_{\mathrm{II}} = \sum_{i=1}^{n} \min\left(\mathrm{HS}_{i,2010\mathrm{s}}, \mathrm{HS}_{i,2050\mathrm{s}}, \mathrm{HS}_{i,2090\mathrm{s}}\right)$$

where RG is the abbreviation of richness gap; SR_{I} and $\mathrm{SR}_{\mathrm{II}}$ represent the cave fish richness in 2090s under dispersal scenarios (1) and (2) over this century, respectively; $\mathrm{HS}_{i,2010\mathrm{s}}$, $\mathrm{HS}_{i,2050\mathrm{s}}$ and $\mathrm{HS}_{i,2090\mathrm{s}}$ correspond to the richness of the ith genus of cave fish during the years 2010s, 2050s and 2090s, where $i = 1, 2, \dots, n$; $n = 31$.

Richness gap is therefore defined as a specific form of habitat loss, representing the number of species in each grid cell that cannot persist in their current habitat under future climate conditions because dispersal limitations prevent them from reaching newly suitable or restored habitats (Robinson and Handel 1993; Baur 2014; Di Musciano et al. 2020).

2.5 | Multiple Exposure Risk Assessment

Cave fishes are intrinsically linked to groundwater (Zhao and Zhang 2006), making them vulnerable to groundwater pollution, which poses a remarkable threat to cave fish. Here, we considered the concentrations of fluoride and heavy metals, such as arsenic, that are a global concern to subterranean ecology (Podgorski and Berg 2022, 2020). High fluoride levels can have detrimental effects on fish, including inhibited growth (Chen et al. 2013; Shi et al. 2009; Yoshitomi and Nagano 2012), developmental disorders (Camargo 2003), metabolic diseases (Bajpai and Tripathi 2010; Chen et al. 2012) and behavioural changes (Camargo 2003; Tripathi et al. 2004). Similarly, arsenic exposure can disrupt the skin, vascular and nervous systems of species living in groundwater and increase cancer risk (Smith et al. 2000; Hughes 2002). Furthermore, stygophiles may occasionally leave the nearly temperature-stable cave environment to inhabit river systems where they would be exposed to extreme high temperatures, which could be fatal for these sensitive species (Mermillod-Blondin et al. 2013). Artificial reservoirs and dams utilise groundwater, and the frequent and irregular water level changes in these reservoirs affect the subterranean habitat of cave fish (Zhao et al. 2011). Additionally, they can block the foraging and migration of stygophiles entering surface river systems (Barbarossa et al. 2020). Therefore, we selected the probability of fluoride ($> 1.5\,\mathrm{mg/L}$) presence (Podgorski and Berg 2022) and the probability of arsenic ($> 10\,\mu\mathrm{g/L}$) presence (Podgorski and Berg 2020) to represent groundwater exposure factors, and selected dam density (Vörösmarty et al. 2010) and the probability of extreme heat (> 30°C) presence (Tuholske et al. 2021) to represent surface water exposure factors.

For this study, we used global karst landscape data (Goldscheider and Drew 2007; Hartmann and Moosdorf 2012; Chen et al. 2017) to delineate cave environments. Since karst cave water systems are typically connected to groundwater (Chen et al. 2017), the exposure factors inside and outside the cave environment are represented by groundwater and surface water exposure factors, respectively. To maintain consistency in future assessments, the exposure factors were kept unchanged, and the exposure risk of cave fish was evaluated using the following equation:

$$\mathrm{ER} = \mathrm{SR} \times \left[\mathrm{KRT} \times \max\left(\mathrm{EG}_i\right) + (1 - \mathrm{KRT}) \times \max\left(\mathrm{ES}_j\right)\right]$$

where SR represents the species richness of cave fish; KRT denotes whether a grid is karst topography ($\mathrm{KRT}=1$) or not ($\mathrm{KRT}=0$); EG and ES are the groundwater and surface water exposure factors, respectively, each ranging between 0 and 1; The subscripts i and j represent the ith groundwater exposure factor and the jth surface water exposure factor, respectively. The resulting exposure risk (*ER*) was calculated as the product of species richness and the maximum value of multiple exposure factors in karst or non-karst landscape. For the purpose of statistical analysis, areas where cave fish were at risk of exposure to the considered environmental stressors ($\mathrm{ER} \geq 1$) were categorised as CARE.

3 | Results

3.1 | Global Patterns of Cave Fish Diversity

Synthesis of global occurrence information of cave fish revealed at least 398 described species worldwide, belonging to 17 orders, 37 families and 115 genera. Of these species, 284 are strictly living in caves (stygobionts) and 104 are also found in the surface waters (stygophiles). In addition, 73 putative unnamed species are also known, leveraging cave fish global diversity to 471 species in 17 orders, 40 families and 124 genera, with 347 stygobionts and 114 stygophiles (Figure 1b).

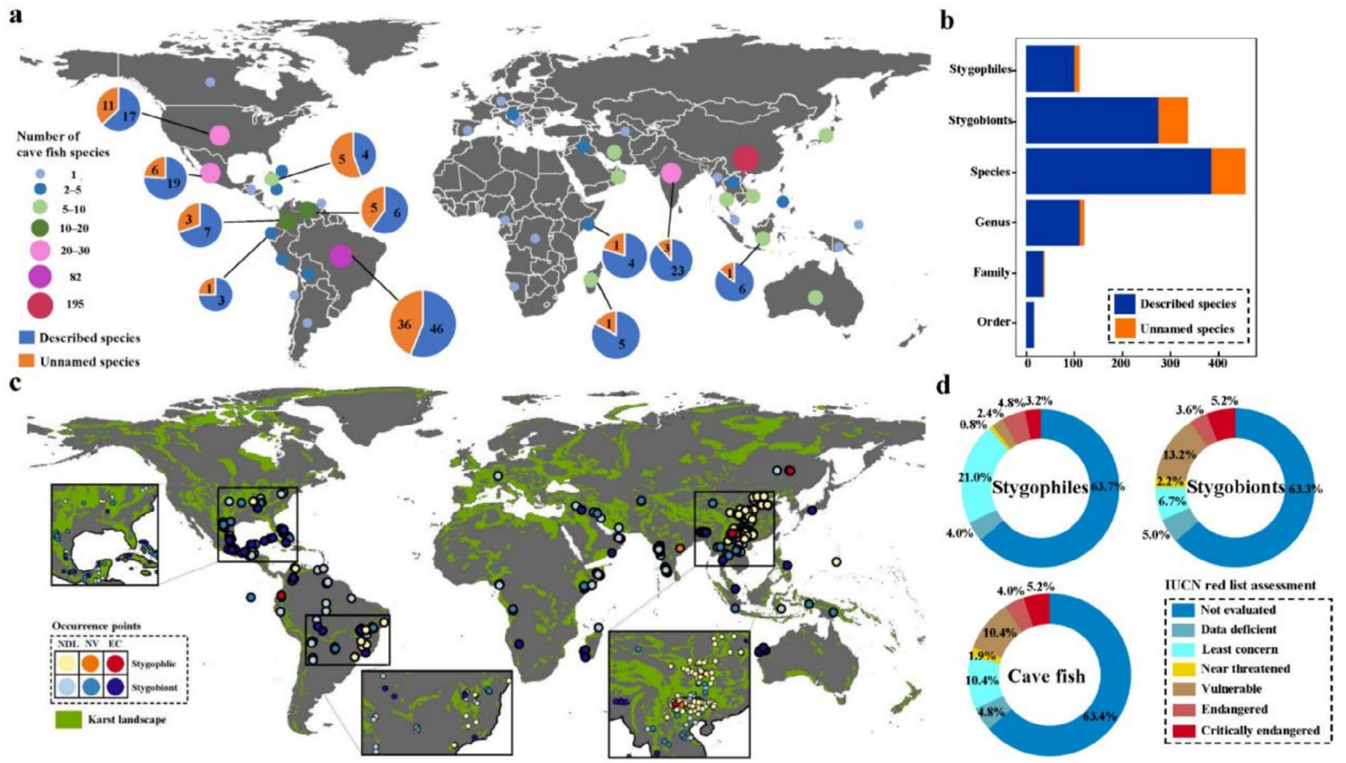

FIGURE 1 | Global survey results of cave fish. (a) Distribution of cave fish species by country; the size and colour of the dot indicates the number of species; Countries without pie charts means all cave fish species within them belong to described species to the exception of Germany where the sole cavefish species is unnamed. (b) Number of stygophiles, stygobionts, Species, Genus, Family and Order of cave fish, as reported from Described and Unnamed species, respectively. (c) Occurrence points of cave fish across different IUCN Red List assessment categories and classifications, along with the global karst landscape distribution represented in light green; NDL represents the IUCN Red List assessment categories of Not Evaluated, Data Deficient and Least Concern; NV represents the IUCN Red List assessment categories of Near Threatened and Vulnerable; EC represents the IUCN Red List assessment categories of Endangered and Critically Endangered. (d) Proportion of cave fish species in different IUCN Red List assessment categories; Unnamed species are considered as Not Evaluated. No species was to date recorded as Extinct in the wild or Extinct.

China holds the highest diversity of cave fish species globally, with a total of 195 described species, followed by Brazil with 46 described and 36 unnamed species. Most cave fish are concentrated in mid to low-latitude regions, while only a few species have been reported from high-latitude areas. Cave fish have been reported in 43 countries, but 27 of these countries host fewer than five species, and more than 10 cave fish species have been documented in only seven countries (Figure 1a).

The highest number of cave fish sites is found around the Gulf of Mexico, in central and eastern South America, the Yunnan-Guizhou Plateau in China and the Indian Peninsula (Figure 1c). According to the International Union for Conservation of Nature (IUCN) Red List assessments, cave fish around the Gulf of Mexico are predominantly classified as Endangered or Critically Endangered, while the living conditions of those in the Yunnan-Guizhou Plateau of China are mostly Not Evaluated or Data Deficient. On a global scale, 63.4% of cave fish species—including stygophiles and stygobionts—have not been evaluated and an additional 21.5% of them are threatened (Figure 1d). Moreover, the proportion of threatened species for stygobionts is higher than stygophiles, with the former being 24.2% and the latter being 11.2%.

3.2 | Current Species Distribution

SDMs, built using MaxEnt for the 31 most occurring genera, yielded a mean AUC of 0.91. All models are reliable for predicting the current and future spatial distribution of the species, reaching AUC values greater than 0.72 (Figure S2 in Appendix S1). Fish distributions were primarily influenced by karst landscape (KRT), annual mean temperature (BIO1), annual precipitation (BIO12) and land cover (LC) contributing on average 37.3%, 34.2%, 15.8% and 12.5%, respectively (Table S4 in Appendix S1).

The potential global species richness (SR) of cave fish, as predicted by the MaxEnt models across 31 genera, is depicted in Figure 2a. It can be clearly observed that nearly all occurrences were successfully forecasted by our models and cave fish could occupy a broader range than that which has been recorded worldwide (Figure 1c). Moreover, our results indicated that southwestern China (part of AS1; details of the study regions can be found in Figure 2b) hosts the highest species richness, with SR of greater than 100 covering areas up to $5.29 \times 10^5\,\text{km}^2$. In contrast, Oceania (OC) contained no regions suitable for more than five cave fish species. South America (SA) exhibited the widest distribution of cave fish spanning $1.59 \times 10^7\,\text{km}^2$.

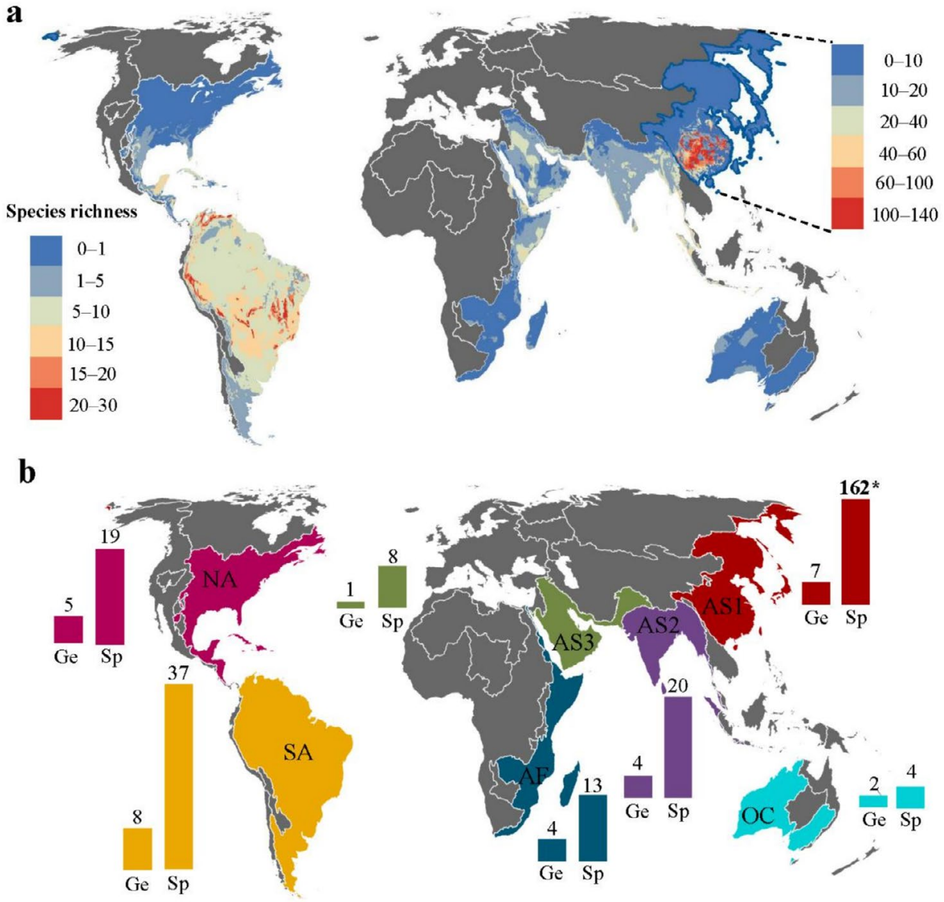

FIGURE 2 | Global cave fish species richness and study regions (NA, North America; SA, South America; AF, Africa; AS1, Eastern Asia, AS2, Central Asia; AS3, Western Asia; OC, Oceania). The values shown are estimates based on MaxEnt modelling. (a) Distribution of species richness; note the distinct colour scale for AS1. (b) Study regions for modelling, showing the number of species (Sp) and genera (Ge); note that the number of Sp in AS1 is not proportional to the length of the bar.

Additionally, Coastal Africa (AF), India and surrounding areas (AS2) and North America (NA) host more than 10 cave fish species, across areas of 6.53×10^4, 1.67×10^5 and $1.33 \times 10^5\,\text{km}^2$, respectively.

3.3 | Richness Gap Under Climate Change

The cave fish richness gap defined as the number of species unable to persist in their current habitat under future climate conditions over a 100-year period (see Section 2) is peaking in Asian regions with a predicted loss of more than five species per site in India and China. South America also appears sensitive to global changes, with predicted species losses throughout the region (Figure 3). Under the SSP1-2.6 scenario, the largest area with a richness gap of cave fish (richness gap > 1) was found in South America, covering $1.54 \times 10^7\,\text{km}^2$. Additionally, areas with a richness gap > 10 were mostly confined to eastern Asia (AS1), covering $5.68 \times 10^5\,\text{km}^2$, while other regions had areas smaller than $1.00 \times 10^2\,\text{km}^2$. The area and degree of cave fish richness gap increased substantially under the SSP5-8.5 scenario. The area with a richness gap > 5 expanded in AS1, AS2, AS3 and SA, with increases of 0.66, 1.50, 3.02 and 4.90 times, respectively. The area with a richness gap > 5 in AF and NA expanded even more sharply, with increases of 34.95 and 13.72 times. Furthermore, the area with a richness gap > 10 in AS1 also increased by 0.40 times (Table S5 in Appendix S1).

3.4 | Exposure Risk of Cave Fish

The temporal variation of exposure risks for cave fish to combined stressors including fluoride and arsenic pollution, dam-driven fragmentation and extreme heatwaves is illustrated in Figure 4. SA contained the largest area where cave fish are at risk of exposure to the considered environmental stressors (CARE), averaging $1.24 \times 10^7\,\text{km}^2$ across the three periods. Except for AS3, all regions showed an increase in CARE area over time, with greater expansion under the SSP5-8.5 than the SSP1-2.6 scenario. Under the SSP5-8.5 scenario, CARE areas experienced the largest increase in OC (981.3%) by the 2090s, followed by AF (269.3%) and NA (113.3%). In contrast, the SSP1-2.6 scenario resulted in smaller increases, with OC rising by 644.6%, AF by 92.7% and NA by 38.8%. The increases in AS1, AS2 and SA were generally lower across both scenarios, with the SSP5-8.5 scenario showing slightly higher overall increases (Table S6 in Appendix S1).

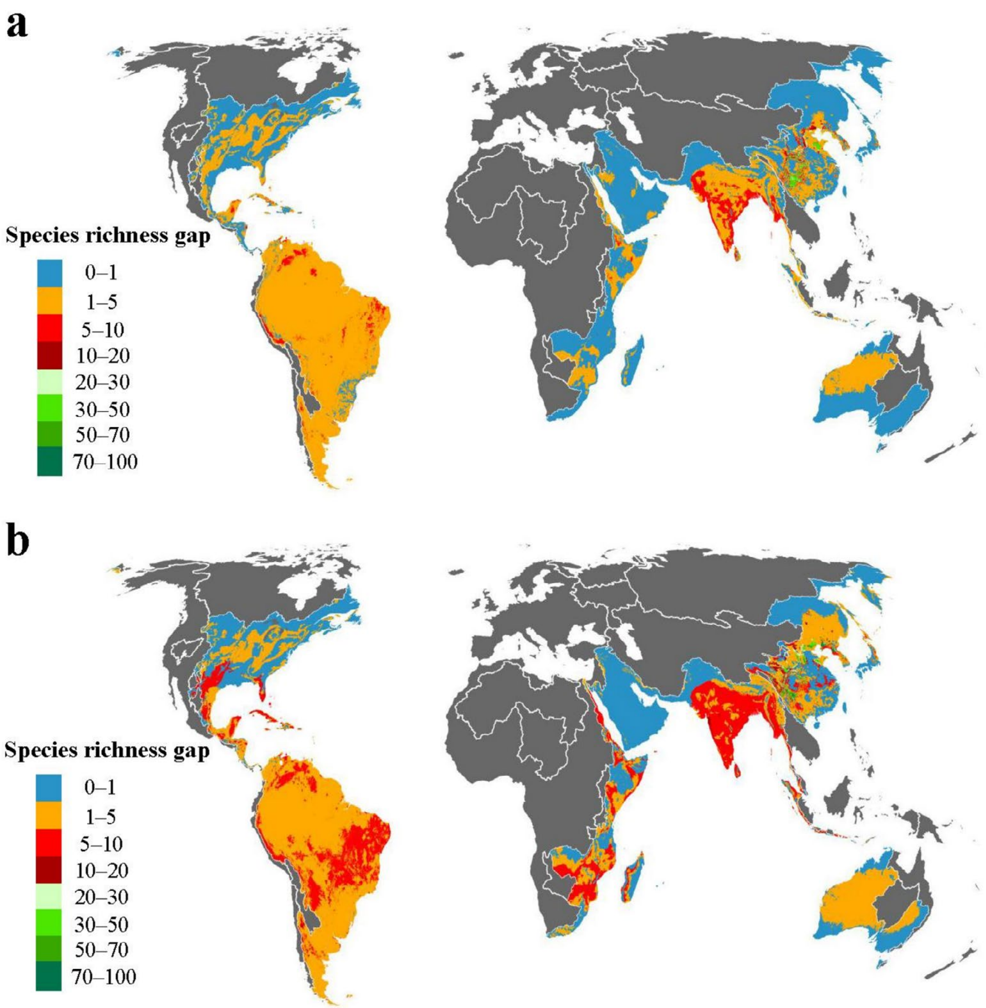

FIGURE 3 | Species richness gaps of cave fish under dispersal limitation for (a) SSP1-2.6 and (b) SSP5-8.5 scenarios.

4 | Discussion

Synthesis of global occurrence information of cave fish revealed at least 398 described species worldwide, accounting for about 2% of the freshwater fish species. Surprisingly, they are widespread across the phylogeny of freshwater fish with more than a third of fish orders (17/45) and a fifth of freshwater fish families (37/185) counting cave species. Among them, 71% of the species (284/398) are only found in caves (stygobionts), whereas the remaining are also found in surface waters (stygophiles). Although individual caves usually host only a few species, cave ecosystems as a whole gather unique lineages that constitute a substantial part of the freshwater fish tree of life. This perspective contrasts with the common belief that caves are species-poor environments with only a few trapped fishes. Our study also confirms the potential existence of many undescribed fish species in caves (Zhao and Zhang 2009; Zhao et al. 2011; Niemiller et al. 2019). Caves are thus an extreme but very important environment harbouring an underestimated fish diversity (Riesch et al. 2015), with at least 15% (73/471) of the known cave fish diversity still unnamed (Figure 1a,b).

Combining cave fish sites with the IUCN Red List, it was revealed that the Chinese Yunnan–Guizhou Plateau is the most densely concentrated area for cave fish sites. For most of those species, conservation status is unknown (Figure 1c), probably because most of them were recently discovered due to their small populations and sparse distributions. In contrast, around the Gulf of Mexico, where stygobiont sites are the most concentrated, IUCN evaluation reveals the unsustainable conservation status of most described species (59.6% are threatened), (Figure 1c). This may indicate that more scientific and conservation efforts in this region are needed.

Although cave fish have been reported in 43 countries around the globe, species diversity peaks in China with almost half of the described species (195/398), most of them being concentrated in the southwestern province of Yunnan-Guizhou Plateau and its surrounding areas (Zhao and Zhang 2006, Figure 2a). This may be attributed to the extensive limestone karst landscapes in the region, which provide abundant habitats for cave fishes, combined with the extensive exploration of caves since the 1980s, leading to the discovery of numerous species (Proudlove et al. 2010; Niemiller and Soares 2014). Additionally, the rapid uplift of the Tibetan Plateau may have promoted species radiation in certain cave fish genera, such as *Triplophysa* (Qian et al. 2023). Still North, Central and South America, together with India harbour an important species diversity with more than 20 species per country. In contrast the Western Palearctic (Europe) counts no more than five described species, with most countries hosting no or a single recently described species by 2024 (Behrmann-Godel et al. 2017,

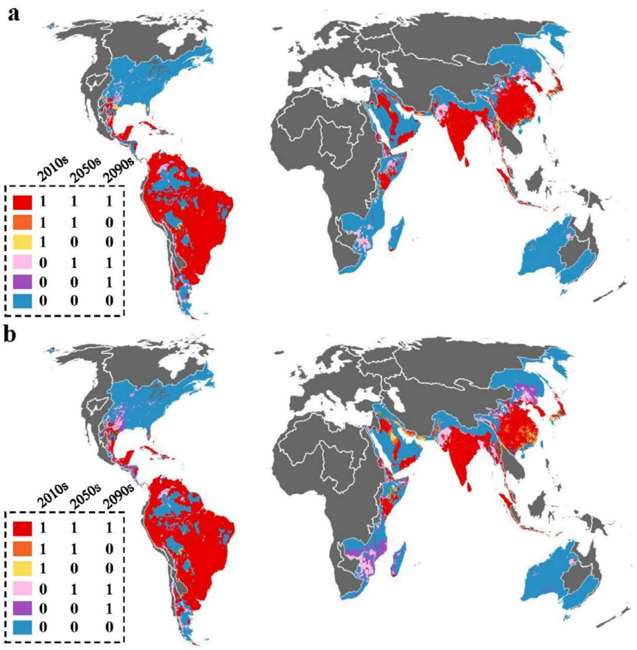

FIGURE 4 | Cave fish's historical and future exposure risk. (a, b) The distribution of areas where cave fish are at risk of exposure to the considered environmental stressors (CARE) under SSP1-2.6 and SSP5-8.5, respectively; 1 indicates an extinction of risk, while 0 represents areas not considered at risk. For example, '1 1 1' for a single grid in figure a or b means that CARE exists in the 2010s, 2050s and 2090s, while '1 1 0' means that CARE exists in the 2010s and 2050s, but does not exist in the 2090s.

2024; Kleinschmidt et al. 2024). Africa also counts very few cave fish species, despite extensive karst landscapes, for instance in the non-desert coastal areas of northern Africa (Chen et al. 2017). As African caves remain understudied, the scarcity of cave fishes there should be considered with caution, and further studies on African cave ecosystems are necessary. Interestingly, the amounts of unnamed species remain high in the areas richest in species, with the exception of China and India where relatively more research efforts were devoted to cave fish (Zhao and Zhang 2006), indicating that further taxonomic efforts are required to formally name these fishes, as a prerequisite to conservation actions (Mace 2004) (Figure 1).

One-quarter of freshwater species are currently found at risk of extinction (Sayer et al. 2025), and this proportion is expected to increase in the future due to climate change (Urban 2024). The diversity of freshwater fish becomes one of the aspects that human beings are most concerned about. However, surface-water fish species have received significantly more attention than subterranean species, the latter being considered as protected from global changes due to their remote habitats. Yet, climate change is altering the microclimate of underground environments (Domínguez-Villar et al. 2015; Šebela et al. 2015; Pipan et al. 2019), exacerbating the survival crisis faced by cave organisms including cave fish.

The global CARE distribution pattern differs from the richness pattern of cave fish species (Figures 1a and 3a,b), primarily due to the uneven spatial distribution of exposure sources (Figure S3 in Appendix S1). For instance, although the cave fish species richness in India and surrounding areas is moderate, the high density of dams and frequent extreme temperatures in non-karst landscapes make it one of the three regions (AS1, SA and AS2) with the most widespread exposure risk for cave fish. From a temporal perspective, both the habitat centre and CARE are projected to expand towards higher latitudes in the forthcoming decades. Under the SSP5-8.5 scenario, this trend becomes more pronounced (Figure S4a in Appendix S1; Figure 4). Yet, the expansion of the habitat centre and CARE should be considered with caution, because it implies an unlimited dispersal of the species, which is likely unrealistic, explaining differences between predicted and observed spatial shifts, as shown for *Onychostoma macrolepis* in Chinese caves (Dong et al. 2024).

Although the dispersal capacities of cave fish remain largely unknown, most cave-dwelling animals cannot adapt to changing conditions through dispersal and microhabitat utilisation, as long-distance dispersal is unfeasible for them. Consequently, their only viable strategy in response to climate change is to remain and adapt in situ (Mammola et al. 2019). Considering dispersal and no-dispersal hypotheses thus appears reasonable. Under both hypotheses, we found that cave fish will lose a substantial amount of habitat (Figure 3). This loss is exacerbated under the SSP5-8.5 scenario. In addition to their limited dispersal capability, the ability of cave fish to respond to and recover from habitat perturbations is also quite restricted due to the stable environmental conditions found in caves. Thus, cave fish generally do not adapt well to environmental changes; they are for instance highly sensitive to low temperature variations, and a temperature variation of only 2°C (e.g., in terms of global warming, it is equivalent to the output of SSP1-2.6 by the end of this century) may be fatal to them (Mermillod-Blondin et al. 2013).

Given the isolation of cave habitats and the low dispersal capacity of cave fishes, the non-dispersal hypothesis appears to be the most plausible one. Under such a hypothesis, the habitat centre of cave fish does not actually exhibit a significant trend of shifting towards higher latitudes (Figure S4b in Appendix S1). Our results also indicate that some local extinctions might occur. It is for instance the case for species from the *Sinocyclocheilus* and *Triplophysa* genera in AS1, as well as for loaches from the *Nemacheilus* genus in AS2 (Figure 2b), that are predicted to be pushed to extinction before the end of the century under the SSP5-8.5 climate change scenario.

Given their limited distribution, the fragile balance of subterranean habitats, anthropogenic pressures (Zhao et al. 2011), and our findings, cave fish should be prioritised at the forefront of conservation agendas. To ensure targeted measures for conservation, attention should be given to the arsenic exposure that threatens all cave environments with the exception of the eastern part of SA (Figures S5 and S6 in Appendix S1). Additionally, the distribution of CARE due to dam construction closely aligns with areas where cave fish species richness is peaking (Figure S7 in Appendix S1). Under future scenarios, exposure risks from dams are expected to decline in China, but increase in India and surrounding regions. This is mainly attributed to the fact that cave fish communities in China are projected to move towards higher latitudes with lower dam density, whereas this trend is not as evident in India. Cave fish in these areas also face disproportionately high threats from extreme high temperatures (Figure S8 in Appendix S1). To mitigate these risks, groundwater quality monitoring must be strengthened, and tolerance thresholds of cave fish to pollutants should be assessed to ensure that cave fish can better resist harmful contaminants like arsenic and fluoride. In addition, more attention should be given to the stygophiles, which intermittently leave the stable cave environments and appear on the surface, as they may be more vulnerable to extreme temperatures and to the effects of dams compared to typical surface freshwater fish.

Limited research and data in this field constrain our study, and caution is thus needed on the models' outputs. We modelled cave fish at the genus level, which may overlook species-specific behavioural differences, due to the lack of occurrence data. The difficulty in sampling subterranean fish, including both stygobionts and stygophiles, highlights this issue. This study assessed the impact of dispersal limitations on cave fish richness using two extreme dispersal scenarios. Although the megaSDM package (Version 2.0.0; Shipley et al. 2022) allows for species-specific dispersal rates, we excluded this due to a lack of reliable estimation methods. Future studies should consider species-specific dispersal limitations, as suggested for surface freshwater fish (Manjarrés-Hernández et al. 2021). H_2S is also a common toxic substance in caves (Hose et al. 2000), alongside arsenic and fluoride. However, *Poecilia mexicana* from the Cueva del Azufre cave in the tropical region of Mexico can adapt to this toxicity, although it sacrifices some body condition and reduces high-energy behaviours to enhance its ability to cope with metabolic toxicity (Tobler et al. 2006). This suggests that cave fish may adapt to environmental toxicity through unique evolutionary traits or behavioural changes, and the specific mechanisms warrant further attention in future studies.

Even if there are limitations and uncertainties, this study provides a comprehensive, global-scale assessment of species richness patterns of cave fish and their current and future exposure risks to environmental stressors. The results reveal a striking imbalance in the global distribution of cave fish species richness and underscore considerable knowledge gaps. Our findings also provide an early warning of the potential exposure risks faced by cave fish amid global changes. Global-scale assessments on the impact of global change (e.g., IPBES) overlook such ecosystems that sustain unique and vulnerable faunas. Therefore, we urge the inclusion of subterranean ecosystems monitoring and conservation into intergovernmental policies, in order to protect these ecosystems and the unique biodiversity they support.

Acknowledgements

This study was financially supported by the National Natural Science Foundation of China (no. 52179142) and the Basic Project of Guizhou University (no. [2023]14).

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All information about cave fish (including occurrence, IUCN Red List classification, taxonomy and references) has been listed in Appendix S1. Appendix S1 and Appendix S2 and R code used to conduct this study has been submitted to Figshare (https://figshare.com/s/11e455c7008e497bed88). BIO1(annual mean temperature) and BIO12 (annual precipitation) data are available at https://www.worldclim.org/data/worldclim21.html. LC (land cover) data is available at https://zenodo.org/records/8367523. KRT (karst landscape) data is available at https://www.whymap.org/whymap/EN/Maps_Data/Wokam/wokam_node_en.html. The delineation of the study regions from GRNWRZ Version 2.0 is available at https://figshare.com/articles/dataset/A_data_set_of_global_river_networks_and_corresponding_water_resources_zones_divisions_V2_0/17430749. Fluoride presence data is available at https://opendata.eawag.ch/dataset/global-analysis-and-prediction-of-fluoride-in-groundwater. Arsenic presence data is available at https://opendata.eawag.ch/dataset/global-threat-of-arsenic-in-groundwater. Extreme heat data is available at https://www.earthdata.nasa.gov/data/catalog/sedac-ciesin-sedac-sdei-gehe-1.00. Dam density data is available at https://www.riverthreat.net/data.html.

References

Aiello-Lammens, M. E., R. A. Boria, A. Radosavljevic, B. Vilela, and R. P. Anderson. 2015. "spThin: An R Package for Spatial Thinning of Species Occurrence Records for Use in Ecological Niche Models." *Ecography* 38, no. 5: 541–545.

Alves-Ferreira, G., F. M. M. Mota, D. Custódio Talora, C. V. Oliveira, M. Solé, and N. M. Heming. 2024. "'Phyloraster': An R Package to Calculate Measures of Endemism and Evolutionary Diversity for Rasters." *Ecography* 2024, no. 4: e06902.

Appelhans, T., F. Detsch, C. Reudenbach, S. Woellauer, S. Forteva, and T. Nauss. 2022. "Package 'mapview'."

Bai, X., P. Zhang, X. Cao, et al. 2024. "Incorporating Implicit Information to Disentangle the Impacts of Hydropower Dams and Climate Change on Basin-Scale Fish Habitat Distribution." *Ecology and Evolution* 14, no. 10: e70412.

Bai, X., P. Zhang, L. Xiong, et al. 2025. "River Network Connectivity Reductions Dominate Declines in the Richness of Plateau Fish Species Under Climate Change in the Upper Yangtze River Basin." *Water Resources Research* 61, no. 6: e2024WR037557.

Bajpai, S., and M. Tripathi. 2010. "Effect of Fluoride on Growth Bioindicators in Stinging Catfish, *Heteropneustes fossilis* (Bloch)." *Fluoride* 43, no. 4: 232–236.

Barbarossa, V., R. J. Schmitt, M. A. Huijbregts, C. Zarfl, H. King, and A. M. Schipper. 2020. "Impacts of Current and Future Large Dams on the Geographic Range Connectivity of Freshwater Fish Worldwide." *Proceedings of the National Academy of Sciences of the United States of America* 117, no. 7: 3648–3655.

Baur, B. 2014. "Dispersal-Limited Species–a Challenge for Ecological Restoration." *Basic and Applied Ecology* 15, no. 7: 559–564.

Behrmann-Godel, J., A. W. Nolte, J. Kreiselmaier, R. Berka, and J. Freyhof. 2017. "The First European Cave Fish." *Current Biology* 27, no. 7: R257–R258.

Behrmann-Godel, J., S. Roch, A. Böhm, J. W. Jolles, and A. Brinker. 2024. "Genetic Differentiation and Phenotypic Plasticity Drive Troglomorphic Character Development in European Cavefish." *Evolution* 78, no. 4: 734–745.

Boria, R. A., L. E. Olson, S. M. Goodman, and R. P. Anderson. 2014. "Spatial Filtering to Reduce Sampling Bias Can Improve the Performance of Ecological Niche Models." *Ecological Modelling* 275: 73–77.

Borowsky, R. 2018. "Cavefishes." *Current Biology* 28, no. 2: R60–R64.

Bush, A., and A. J. Hoskins. 2017. "Does Dispersal Capacity Matter for Freshwater Biodiversity Under Climate Change?" *Freshwater Biology* 62, no. 2: 382–396.

Camargo, J. A. 2003. "Fluoride Toxicity to Aquatic Organisms: A Review." *Chemosphere* 50, no. 3: 251–264.

Castellanos, A. A., J. W. Huntley, G. Voelker, and A. M. Lawing. 2019. “Environmental Filtering Improves Ecological Niche Models Across Multiple Scales.” *Methods in Ecology and Evolution* 10, no. 4: 481–492.

Chen, J., J. Cao, J. Wang, et al. 2013. “Effects of Fluoride on Growth, Body Composition, and Serum Biochemical Profile in a Freshwater Teleost, *Cyprinus carpio*.” *Environmental Toxicology and Chemistry* 32, no. 10: 2315–2321.

Chen, Q., L. Yu, L. Yang, and B. Zhou. 2012. “Bioconcentration and Metabolism of Decabromodiphenyl Ether (BDE-209) Result in Thyroid Endocrine Disruption in Zebrafish Larvae.” *Aquatic Toxicology* 110: 141–148.

Chen, Z., A. S. Auler, M. Bakalowicz, et al. 2017. “The World Karst Aquifer Mapping Project: Concept, Mapping Procedure and Map of Europe.” *Hydrogeology Journal* 25, no. 3: 771–785.

Comte, L., and G. Grenouillet. 2015. “Distribution Shifts of Freshwater Fish Under a Variable Climate: Comparing Climatic, Bioclimatic and Biotic Velocities.” *Diversity and Distributions* 21, no. 9: 1014–1026.

Culver, D. C., and T. Pipan. 2019. *The Biology of Caves and Other Subterranean Habitats*. Oxford University Press.

De Marco, P., and C. C. Nóbrega. 2018. “Evaluating Collinearity Effects on Species Distribution Models: An Approach Based on Virtual Species Simulation.” *PLoS One* 13, no. 9: e0202403.

Di Musciano, M., V. Di Cecco, F. Bartolucci, F. Conti, A. R. Frattaroli, and L. Di Martino. 2020. “Dispersal Ability of Threatened Species Affects Future Distributions.” *Plant Ecology* 221, no. 4: 265–281.

Domínguez-Villar, D., S. Lojen, K. Krklec, A. Baker, and I. J. Fairchild. 2015. “Is Global Warming Affecting Cave Temperatures? Experimental and Model Data From a Paradigmatic Case Study.” *Climate Dynamics* 45: 569–581.

Dong, X., T. Ju, L. Shi, et al. 2024. “Evaluating Effects of Climate Change on the Spatial Distribution of an Atypical Cavefish *Onychostoma macrolepis*.” *Journal of Environmental Management* 350: 119643.

Elith, J., and J. R. Leathwick. 2009. “Species Distribution Models: Ecological Explanation and Prediction Across Space and Time.” *Annual Review of Ecology, Evolution, and Systematics* 40, no. 1: 677–697.

Ferreira, R. L., and R. P. Martins. 1999. “Trophic Structure and Natural History of Bat Guano Invertebrate Communities, With Special Reference to Brazilian Caves.” *Tropical Zoology* 12, no. 2: 231–252.

Fricke, R., W. N. Eschmeyer, and R. Van der Laan. 2024. “Eschmeyer's Catalog of Fishes: Genera, Species, References.” http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp.

Froese, R., and D. Pauly, eds. 2024. “FishBase. World Wide Web Electronic Publication, Version (06/2024).” www.fishbase.org.

Gibert, J., and L. Deharveng. 2002. “Subterranean Ecosystems: A Truncated Functional Biodiversity: This Article Emphasizes the Truncated Nature of Subterranean Biodiversity at Both the Bottom (No Primary Producers) and the Top (Very Few Strict Predators) of Food Webs and Discusses the Implications of This Truncation Both From Functional and Evolutionary Perspectives.” *Bioscience* 52, no. 6: 473–481.

Goldscheider, N., and D. Drew. 2007. *Methods in Karst Hydrogeology: IAH: International Contributions to Hydrogeology*, vol. 26. 1st ed. CRC Press.

Guisan, A., and W. Thuiller. 2005. “Predicting Species Distribution: Offering More Than Simple Habitat Models.” *Ecology Letters* 8, no. 9: 993–1009.

Guisan, A., R. Tingley, J. B. Baumgartner, et al. 2013. “Predicting Species Distributions for Conservation Decisions.” *Ecology Letters* 16, no. 12: 1424–1435.

Hao, T., J. Elith, G. Guillera-Arroita, and J. J. Lahoz-Monfort. 2019. “A Review of Evidence About Use and Performance of Species Distribution Modelling Ensembles Like BIOMOD.” *Diversity and Distributions* 25, no. 5: 839–852.

Hartmann, J., and N. Moosdorf. 2012. “The New Global Lithological Map Database GLiM: A Representation of Rock Properties at the Earth Surface.” *Geochemistry, Geophysics, Geosystems* 13, no. 12: Q12004. https://doi.org/10.1029/2012GC004370.

Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones, and A. Jarvis. 2005. “Very High Resolution Interpolated Climate Surfaces for Global Land Areas.” *International Journal of Climatology: A Journal of the Royal Meteorological Society* 25, no. 15: 1965–1978.

Hole, D. G., S. G. Willis, D. J. Pain, et al. 2009. “Projected Impacts of Climate Change on a Continent-Wide Protected Area Network.” *Ecology Letters* 12, no. 5: 420–431.

Hose, L. D., A. N. Palmer, M. V. Palmer, D. E. Northup, P. J. Boston, and H. R. DuChene. 2000. “Microbiology and Geochemistry in a Hydrogen-Sulphide-Rich Karst Environment.” *Chemical Geology* 169, no. 3–4: 399–423.

Howarth, F. G. 1993. “High-Stress Subterranean Habitats and Evolutionary Change in Cave-Inhabiting Arthropods.” *American Naturalist* 142: S65–S77.

Hughes, M. F. 2002. “Arsenic Toxicity and Potential Mechanisms of Action.” *Toxicology Letters* 133, no. 1: 1–16.

Iverson, L. R., and A. M. Prasad. 1998. “Predicting Abundance of 80 Tree Species Following Climate Change in the Eastern United States.” *Ecological Monographs* 68, no. 4: 465–485.

Jeffery, W. R. 2001. “Cavefish as a Model System in Evolutionary Developmental Biology.” *Developmental Biology* 231, no. 1: 1–12.

Keene, A., M. Yoshizawa, and S. E. McGaugh. 2015. *Biology and Evolution of the Mexican Cavefish*. Academic Press.

Kleinschmidt, Y., A. Ros, J. Behrmann-Godel, and A. Brinker. 2024. “Navigation in the Dark: Early Behavioural Adaptation of Europe's Only Native Cave Fish.” *Animal Behaviour* 215: 111–124.

Kramer-Schadt, S., J. Niedballa, J. D. Pilgrim, et al. 2013. “The Importance of Correcting for Sampling Bias in MaxEnt Species Distribution Models.” *Diversity and Distributions* 19, no. 11: 1366–1379.

Lenoir, J., R. Bertrand, L. Comte, et al. 2020. “Species Better Track Climate Warming in the Oceans Than on Land.” *Nature Ecology & Evolution* 4, no. 8: 1044–1059.

Li, C., Y. H. Fang, G. P. Ren, et al. 2025. “Monsoon Climate and Anthropogenic Influences Shape Primate Distributions Across the Southeastern Edge of the Qinghai-Tibet Plateau.” *Global Change Biology* 31, no. 4: e70178.

Liu, Y., P. Huang, F. Lin, et al. 2019. “MaxEnt Modelling for Predicting the Potential Distribution of a Near Threatened Rosewood Species (Dalbergia Cultrata Graham ex Benth).” *Ecological Engineering* 141: 105612.

Mace, G. M. 2004. “The Role of Taxonomy in Species Conservation.” *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* 359, no. 1444: 711–719.

Makki, T., H. Mostafavi, A. A. Matkan, et al. 2023. “Impacts of Climate Change on the Distribution of Riverine Endemic Fish Species in Iran, a Biodiversity Hotspot Region.” *Freshwater Biology* 68, no. 6: 1007–1019.

Mammola, S., E. Piano, P. Cardoso, et al. 2019. “Climate Change Going Deep: The Effects of Global Climatic Alterations on Cave Ecosystems.” *Anthropocene Review* 6, no. 1–2: 98–116.

Manjarrés-Hernández, A., C. Guisande, E. García-Roselló, et al. 2021. “Predicting the Effects of Climate Change on Future Freshwater Fish Diversity at Global Scale.” *Nature Conservation* 43: 1–24.

Matthews, W. J. 2012. *Patterns in Freshwater Fish Ecology*. Springer Science & Business Media.

Mermillod-Blondin, F., C. Lefour, L. Lalouette, et al. 2013. “Thermal Tolerance Breadths Among Groundwater Crustaceans Living in a Thermally Constant Environment.” *Journal of Experimental Biology* 216, no. 9: 1683–1694.

Mi, C., L. Ma, M. Yang, et al. 2023. “Global Protected Areas as Refuges for Amphibians and Reptiles Under Climate Change.” *Nature Communications* 14, no. 1: 1389.

Moore, G., and G. Sullivan. 1964. “Out of Phase Seasonal Temperature Fluctuations in Cathedral Cave, Kentucky.” *Geological Society of America* 76: 313.

Naimi, B., N. A. Hamm, T. A. Groen, A. K. Skidmore, and A. G. Toxopeus. 2014. “Where Is Positional Uncertainty a Problem for Species Distribution Modelling?” *Ecography* 37, no. 2: 191–203.

Niemiller, M. L., and D. Soares. 2014. “Cave Environments.” In *Extremophile Fishes: Ecology, Evolution, and Physiology of Teleosts in Extreme Environments*, 161–191. Springer International.

Niemiller, M. L., S. J. Taylor, M. E. Slay, and H. Horton. 2019. *Encyclopedia of Caves*. 3rd ed. Academic Press.

Peterson, A. T., M. A. Ortega-Huerta, J. Bartley, et al. 2002. “Future Projections for Mexican Faunas Under Global Climate Change Scenarios.” *Nature* 416, no. 6881: 626–629.

Peterson, A. T., M. Papeş, and M. Eaton. 2007. “Transferability and Model Evaluation in Ecological Niche Modeling: A Comparison of GARP and Maxent.” *Ecography* 30, no. 4: 550–560.

Phillips, S. J., R. P. Anderson, and R. E. Schapire. 2006. “Maximum Entropy Modeling of Species Geographic Distributions.” *Ecological Modelling* 190, no. 3–4: 231–259.

Pipan, T., M. Petrič, S. Šebela, and D. C. Culver. 2019. “Analyzing Climate Change and Surface-Subsurface Interactions Using the Postojna Planina Cave System (Slovenia) as a Model System.” *Regional Environmental Change* 19, no. 2: 379–389.

Podgorski, J., and M. Berg. 2020. “Global Threat of Arsenic in Groundwater.” *Science* 368, no. 6493: 845–850.

Podgorski, J., and M. Berg. 2022. “Global Analysis and Prediction of Fluoride in Groundwater.” *Nature Communications* 13, no. 1: 4232.

Protas, M., and W. R. Jeffery. 2012. “Evolution and Development in Cave Animals: From Fish to Crustaceans.” *Wiley Interdisciplinary Reviews: Developmental Biology* 1, no. 6: 823–845.

Proudlove, G. S. 2001. “The Conservation Status of Hypogean Fishes.” *Environmental Biology of Fishes* 62: 201–213.

Proudlove, G. S., E. Trajano, M. E. Bichuette, and B. G. Kapoor. 2010. “Biodiversity and Distribution of the Subterranean Fishes of the World.” In *Biology of Subterranean Fishes*, 41–63. Science Publishers.

Qian, Y., M. Meng, C. Zhou, et al. 2023. “The Role of Introgression During the Radiation of Endemic Fishes Adapted to Living at Extreme Altitudes in the Tibetan Plateau.” *Molecular Biology and Evolution* 40, no. 6: msad129.

Razgour, O., H. Rebelo, M. Di Febbraro, and D. Russo. 2016. “Painting Maps With Bats: Species Distribution Modelling in Bat Research and Conservation.” *Hystrix* 27, no. 1: 1–8.

Rétaux, S., and D. Casane. 2013. “Evolution of Eye Development in the Darkness of Caves: Adaptation, Drift, or Both?” *EvoDevo* 4: 1–12.

Riesch, R., M. Tobler, and M. Plath. 2015. “Extremophile Fishes.” In *Ecology, Evolution, and Physiology of Teleosts in Extreme Environments*. Springer.

Robinson, G. R., and S. N. Handel. 1993. “Forest Restoration on a Closed Landfill: Rapid Addition of New Species by Bird Dispersal.” *Conservation Biology* 7, no. 2: 271–278.

Robinson, N. M., W. A. Nelson, M. J. Costello, J. E. Sutherland, and C. J. Lundquist. 2017. “A Systematic Review of Marine-Based Species Distribution Models (SDMs) With Recommendations for Best Practice.” *Frontiers in Marine Science* 4: 421.

Rolf, S. 2023. “MODIS MCD12Q1 Land Cover and Land Use Time Series Global Mosaics 2001-2022 (500 m).” [Dataset]. Zenodo.

Sayer, C. A., E. Fernando, R. R. Jimenez, et al. 2025. “One-Quarter of Freshwater Fauna Threatened With Extinction.” *Nature* 638: 1–8.

Šebela, S., J. Turk, and T. Pipan. 2015. “Cave Micro-Climate and Tourism: Towards 200 Years (1819–2015) at Postojnska Jama (Slovenia).” *Cave and Karst Science* 42, no. 2: 78–85.

Shi, X., P. Zhuang, L. Zhang, et al. 2009. “Growth Inhibition of Siberian Sturgeon (*Acipenser baerii*) From Dietary and Waterborne Fluoride.” *Fluoride* 42, no. 2: 137.

Shipley, B. R., R. Bach, Y. Do, H. Strathearn, J. L. McGuire, and B. Dilkina. 2022. “megaSDM: Integrating Dispersal and Time-Step Analyses Into Species Distribution Models.” *Ecography* 2022, no. 1: 1–12.

Shurin, J. B., K. Cottenie, and H. Hillebrand. 2009. “Spatial Autocorrelation and Dispersal Limitation in Freshwater Organisms.” *Oecologia* 159: 151–159.

Smith, A. H., E. O. Lingas, and M. Rahman. 2000. “Contamination of Drinking-Water by Arsenic in Bangladesh: A Public Health Emergency.” *Bulletin of the World Health Organization* 78, no. 9: 1093–1103.

Soares, D., and M. L. Niemiller. 2020. “Extreme Adaptation in Caves.” *Anatomical Record* 303, no. 1: 15–23.

Sofaer, H. R., C. S. Jarnevich, I. S. Pearse, et al. 2019. “Development and Delivery of Species Distribution Models to Inform Decision-Making.” *Bioscience* 69, no. 7: 544–557.

Stanton, J. C., R. G. Pearson, N. Horning, P. Ersts, and H. Reşit Akçakaya. 2012. “Combining Static and Dynamic Variables in Species Distribution Models Under Climate Change.” *Methods in Ecology and Evolution* 3, no. 2: 349–357.

Steen, V. A., M. W. Tingley, P. W. Paton, and C. S. Elphick. 2021. “Spatial Thinning and Class Balancing: Key Choices Lead to Variation in the Performance of Species Distribution Models With Citizen Science Data.” *Methods in Ecology and Evolution* 12, no. 2: 216–226.

Su, G., M. Logez, J. Xu, S. Tao, S. Villéger, and S. Brosse. 2021. “Human Impacts on Global Freshwater Fish Biodiversity.” *Science* 371, no. 6531: 835–838.

Tobler, M., I. Schlupp, K. U. Heubel, et al. 2006. “Life on the Edge: Hydrogen Sulfide and the Fish Communities of a Mexican Cave and Surrounding Waters.” *Extremophiles* 10, no. 6: 577–585.

Tripathi, A., A. Kumar, A. Rani, and M. Tripathi. 2004. “Fluoride Induced Morphological and Behavioural Changes in Fresh Water Fish *Channa punctatus*.” *Journal of Ecophysiology and Occupational Health* 4, no. 1: 83–88.

Tuholske, C., K. Caylor, C. Funk, et al. 2021. “Global Urban Population Exposure to Extreme Heat.” *Proceedings of the National Academy of Sciences of the United States of America* 118, no. 41: e2024792118.

Urban, M. C. 2024. “Climate Change Extinctions.” *Science* 386, no. 6726: 1123–1128.

Varela, S., R. P. Anderson, R. García-Valdés, and F. Fernández-González. 2014. “Environmental Filters Reduce the Effects of Sampling Bias and Improve Predictions of Ecological Niche Models.” *Ecography* 37, no. 11: 1084–1091.

von Rintelen, K., T. J. Page, Y. Cai, et al. 2012. “Drawn to the Dark Side: A Molecular Phylogeny of Freshwater Shrimps (Crustacea: Decapoda: Caridea: Atyidae) Reveals Frequent Cave Invasions and Challenges Current Taxonomic Hypotheses.” *Molecular Phylogenetics and Evolution* 63, no. 1: 82–96.

Vörösmarty, C. J., P. B. McIntyre, M. O. Gessner, et al. 2010. "Global Threats to Human Water Security and River Biodiversity." *Nature* 467, no. 7315: 555–561.

Wilhelm, F. M., S. J. Taylor, and G. L. Adams. 2006. "Comparison of Routine Metabolic Rates of the Stygobite, *Gammarus Acherondytes* (Amphipoda: Gammaridae) and the Stygophile, *Gammarus Troglophilus*." *Freshwater Biology* 51, no. 6: 1162–1174.

Wu, Z. 1993. *Proceedings of the Yunnan Biodiversity Symposium* (In Chinese). Yunnan Science and Technology Press.

Yan, D., C. Li, X. Zhang, et al. 2022. "A Data Set of Global River Networks and Corresponding Water Resources Zones Divisions v2." *Scientific Data* 9, no. 1: 770.

Yoshitomi, B., and I. Nagano. 2012. "Effect of Dietary Fluoride Derived From Antarctic Krill (*Euphausia superba*) Meal on Growth of Yellowtail (*Seriola quinqueradiata*)." *Chemosphere* 86, no. 9: 891–897.

Yu, D., M. Chen, Z. Zhou, R. Eric, Q. Tang, and H. Liu. 2013. "Global Climate Change Will Severely Decrease Potential Distribution of the East Asian Coldwater Fish Rhynchocypris Oxycephalus (Actinopterygii, Cyprinidae)." *Hydrobiologia* 700: 23–32.

Zhang, X. S., Z. Lü, and Y. Chen. 2014. "A Prediction of the Global Habitat of Two Invasive Fishes (Pseudorasbora Parva and *Carassius Auratus*) From East Asia Using Maxent." *Biodiversity Science* 22, no. 2: 182.

Zhao, Y., A. G. Gluesenkamp, J. J. Wynne, et al. 2022. "Diversity, Distribution, and Conservation of Cavefishes in China." *Cave Biodiversity: Speciation and Diversity of Subterranean Fauna* 271: 22.

Zhao, Y. H., R. Gozlan, and C. G. Zhang. 2011. "Out of Sight out of Mind: Current Knowledge of Chinese Cave Fishes." *Journal of Fish Biology* 79, no. 6: 1545–1562.

Zhao, Y., and C. Zhang. 2006. "Cavefishs: Concept, Diversity, and Research Progress (In Chinese)." *Biodiversity Science* 14, no. 5: 451–460.

Zhao, Y., and C. Zhang. 2009. *Endemic Sinocyclocheilus Fish in China: Species Diversity, Cave Adaptation, Phylogeny, and Zoogeography* (In Chinese). Science Press.

Zhou, Y., X. Dong, T. Ju, et al. 2025. "Urgent Conservation Actions Are Needed for Qinling Lenok *Brachymystax Lenok* tsinlingensis Li, 1966: Enlightenment From Model Simulations." *Ecology and Evolution* 15, no. 5: e71427.

Zhou, Y., Z. Zhang, B. Zhu, et al. 2021. "MaxEnt Modeling Based on CMIP6 Models to Project Potential Suitable Zones for *Cunninghamia lanceolata* in China." *Forests* 12, no. 6: 752.

Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Appendix S1:** geb70160-sup-0001-AppendixS1.docx. **Appendix S2:** geb70160-sup-0002-AppendixS2.docx.