Diversity and Distributions

WILEY

Diversity and Distributions

RESEARCH ARTICLE OPEN ACCESS

Bat Migration Intensifies Cave Fish Richness Loss Under Climate Change in China

Xiongfeng Bai[1] | Peng Zhang[1] | Benjamin R. Shipley[2] | Tao Ju[3] | Yiran Zhang[1] | Guohuan Su[4] | Xianghong Dong[5]

[1]State Key Laboratory of Water Resources Engineering and Management, Wuhan University, Wuhan, People's Republic of China | [2]Department of Earth Sciences, University of Oxford, Oxford, UK | [3]Guangxi Academy of Marine Sciences, Guangxi Academy of Sciences, Nanning, People's Republic of China | [4]Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan, People's Republic of China | [5]Department of Fisheries Sciences, College of Animal Science, Guizhou University, Guiyang, People's Republic of China

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

Received: 1 August 2025 | **Revised:** 28 December 2025 | **Accepted:** 15 January 2026

Keywords: biodiversity loss | cave bats | cave ecosystems | cave fish | China | climate change | karst landscape | species distribution model | trophic interaction | vertebrate conservation

ABSTRACT

Aim: Cave fish, the largest aquatic vertebrates in karst ecosystems, rely heavily on bat guano as a nutrient source. However, ongoing environmental change is degrading cave habitats and altering bat distributions. This study aims to assess how climate-driven bat migration affects cave fish distributions in China, providing insights for biodiversity conservation.

Location: China.

Methods: We developed ensemble species distribution models (ensemble SDMs) for cave bats and cave fish, integrating current and projected climate data to simulate historical and future distributions. Cave bat richness was used as a proxy for food resource availability for cave fish. We then quantified changes in cave fish richness under different climate scenarios and evaluated the amplifying effect of bat migration.

Results: Both cave bats and cave fish exhibit overlapping richness hotspots in southern China, strongly associated with fragmented karst landscapes. Under future climate scenarios, the cave bat richness center is projected to shift northwestward, with greater displacement under high-emission conditions. Cave fish richness is predicted to decline due to climate stress alone, but when accounting for bat migration, losses are amplified by 12–40 times.

Main Conclusions: Climate-induced shifts in cave bat distributions may drastically intensify habitat and nutrient limitations for cave fish, exacerbating biodiversity loss. These findings highlight the importance of integrating biotic interactions and trophic dependencies in species distribution modelling and conservation planning. The study provides a framework for prioritising cave ecosystem protection under future environmental change.

1 | Introduction

Caves are critical habitats for endemic and threatened species, harbouring high levels of endemism (Deharveng 2005) and genetic uniqueness (Gibert and Deharveng 2002). These subterranean ecosystems support diverse specialised taxa, including cave-dwelling fish, crustaceans, insects, worms, and various other troglobionts (Gunn 2004). Among these, cave fish—rare freshwater species dependent on subterranean habitats to complete all or part of their life history stages (Zhao and Zhang 2006)—represent the most diverse vertebrate group in cave environments (Culver and Pipan 2019; Niemiller et al. 2019). Through evolutionary adaptation to perpetual darkness, cave fish have developed a series of striking morphological and physiological traits, including degenerated or absent eyes, depigmentation, lowered metabolic rates, and attenuated circadian rhythms (Jeffery 2001; Rétaux and Casane 2013; Borowsky 2018; Soares and Niemiller 2020). These extraordinary evolutionary characteristics have captivated biologists for decades (von Rintelen et al. 2012; Protas and Jeffery 2012), with species such as *Astyanax mexicanus* established as leading model organisms in diverse biological disciplines, from evolutionary and developmental biology to neurophysiology (Keene et al. 2015). Furthermore, cave fish adaptations may provide critical insights into addressing complex human pathologies including cancer progression (Gatenby et al. 2011) and metabolic disorders such as diabetes (Riddle et al. 2018).

Cave fishes are predominantly local endemics, typically constrained by small population sizes and highly restricted distributions (Zhao and Zhang 2006). Most species inhabit karst regions and exhibit extremely narrow ranges—for example, nearly 50 *Sinocyclocheilus* species are confined to only one or a few caves (Zhao and Zhang 2009). Despite the karst region being recognised as a World Heritage site, it is subject to unprecedented human disturbances, yet these fishes remain poorly known and are rarely listed as protected species (Wen et al. 2022). Like other troglobionts, cave fish rely critically on external energy subsidies as subterranean habitats lack photosynthetic production (Gibert and Deharveng 2002). Most cave systems are therefore resource-limited, and cave communities depend largely on external organic inputs—typically dissolved and particulate organic carbon transported underground via hydrological pathways, or the occasional influx of animals that enter caves accidentally and subsequently die, thereby fueling subterranean food webs (Niemiller and Soares 2014). Cave bats, acting as symbiotic species of cave fish in the same habitats, are pivotal ecological vectors in cave ecosystems (Ferreira and Martins 1999; Ferreira 2019; Culver and Pipan 2019; Wen et al. 2022). They transport essential organic nutrients—primarily via guano and carcass—into caves during nightly foraging excursions to provide food to cave fish (Ferreira and Martins 1999; Culver and Pipan 2019; Iskali and Zhang 2015). Beyond nutrient provisioning, cave bats influence cave microhabitats, with their ecological presence directly linked to the survival of cave fish populations (Meierhofer et al. 2024). Unfortunately, the habitats of both taxa have been increasingly degraded due to climate change and anthropogenic disturbances (Furey and Racey 2016; Festa et al. 2023; Proudlove 2001; Dong et al. 2024). While bats exhibit range shifts toward climatically suitable areas in fragmented cave networks (Ke et al. 2025), cave fish—constrained by minimal dispersal capacity—remain geographically trapped (Mammola et al. 2019). This disparity elevates extinction risks for cave fish as dwindling bat-mediated energy subsidies and disrupted microhabitat dynamics may lead to underestimated population collapses, posing profound threats to global diversity conservation. China harbours the planet's richest cave fish diversity (Zhao et al. 2011; Bai, Zhang, Gan, Brosse, et al. 2025) and approximately 10% of global bat species—77% of which are cave-dwelling (Tinglei et al. 2020; Luo et al. 2013; Medellin et al. 2017). Furthermore, its extensive karst landscapes provide widely distributed cave environments across the country (Wang et al. 2019). Understanding how climate-driven bat range shifts alter cave fish habitat viability through indirect cave trophic cascades is therefore imperative for targeted conservation planning.

Species distribution models (SDMs) have served as a foundational methodology in recent decades for predicting how changing environmental conditions influence species' spatial and temporal distributions (Booth et al. 2014; Elith and Leathwick 2009; Bai, Zhang, Xiong, Yang, et al. 2025). These models have been widely employed to quantify ecological niches and project species occurrences across terrestrial, freshwater, and marine ecosystems (Guisan and Thuiller 2005; Elith and Leathwick 2009; Robinson et al. 2017; Hao et al. 2019; Sofaer et al. 2019; Bai et al. 2024). By forecasting species distributions across space and time, SDMs provide critical tools for anticipating biological invasions, delineating key habitats, guiding conservation planning, and informing translocation for imperilled species (Guisan et al. 2013). This study investigates the poorly understood impacts of cave bat migration on cave fish habitats in China under global change using an ensemble SDMs framework, which can produce consensus projections that outperform single SDMs (Araújo and New 2007; see methods). We modelled habitat suitability and species richness for both cave-dwelling bats and fish by integrating climatic, anthropogenic, and geomorphological variables. We then examined the migration trends of cave bats and their subsequent effects on spatial patterns of cave fish richness. Our study provides a foundational methodological framework for the conservation of cave fish habitats amid environmental change while delivering critical insights into the ecology and protection of rare freshwater taxa.

2 | Methods

2.1 | Cave Fish and Cave Bat Occurrences

Occurrence data for cave bat were sourced from the global cave bat database compiled by Tanalgo et al. (2022). Cave fish occurrence records (listed in Appendix S1) were collected from three sources: (1) a systematic literature review using the keywords cavefish, cavefishes, cave fish, blind fish, hypogean fish, and cave-dwelling fish across Web of Science (WOS), Google Scholar, and the Chinese CNKI database; (2) digitised records from the Global Biodiversity Information Facility (GBIF, https://www.gbif.org/) and FishBase (https://fishbase.se/); and (3) field surveys from January 2023 to December 2024 in Guizhou Province, China (Figure S8; Appendix S1). All records were validated for taxonomic consistency (resolving synonymies and errors) and georeferenced for spatial accuracy prior to modelling (Da Mata et al. 2017). To reduce spatial autocorrelation, occurrence data were processed through spatial thinning at a 30 arc-second resolution grid, retaining a single record per grid cell (Boria et al. 2014; Aiello-Lammens et al. 2015; Steen et al. 2021). To prevent model overfitting, we only retained cave fish genera or cave bat species with at least five occurrence records (Pearson et al. 2007; Mi et al. 2023; Bai, Zhang, Yang, Grenouillet, et al. 2025). Following data curation, 329 occurrence records were retained for modelling six cave fish genera (occurrences of cave fish are particularly sparse in both space and time), and 1245 records were used to model distributions for 34 cave bat species (Figure S1).

As highlighted by Elith et al. (2006), presence (occurrence)–absence algorithms typically provide more robust predictions than presence-only methods. Because verified absence data were not available for cave fish and bat species, we employed a pseudo-absence strategy. For each species, pseudoabsence points were randomly drawn in numbers equal to their presences, excluding grids where presences occurred (Barbet-Massin et al. 2012; Bai, Zhang, Yang, Zhang, et al. 2025). These pseudoabsence and presence records were subsequently combined and randomised to create the final dataset for model construction (Senay et al. 2013).

2.2 | Predictor Variables Selection

The selection of predictor variables critically determines the quantification of ecological niches and the spatiotemporal transferability of SDMs (Townsend Peterson et al. 2007). To ensure model reliability, variables must demonstrate clear ecological relevance to the target species (Sillero et al. 2021). For cave bats, we selected six predictor variables: annual mean temperature (BIO1), temperature seasonality (BIO4), annual precipitation (BIO12), precipitation seasonality (BIO15), land cover (LC), and karst landscape (KRT). All variables were processed to a uniform 30 arc-second resolution (~1 km^2 grid) to align with occurrence data. BIO1, BIO4, BIO12, and BIO15 were obtained from the WorldClim database (http://www.worldclim.org; Hijmans et al. 2005). LC was sourced from a spatial land cover dataset developed by Xin Lin (https://zenodo.org/records/7417369; Lin et al. 2023), which includes six categories: Cropland, Forest, Grassland, Water, Urban, and Barren. KRT data (Hartmann and Moosdorf 2012; Goldscheider and Drew 2014; Chen et al. 2017) were reclassified as a categorical variable with three classes: 0 (non-karst); 1 (discontinuous carbonate karst); 2 (continuous carbonate karst). For cave fish, predictors included BIO1, BIO12, KRT, and bat species richness (BSR), all at the same uniform resolution of 30 arc-seconds. BSR was generated by aggregating the habitat suitability projections from SDMs of 34 cave bat species.

BIO1, BIO12, and KRT are ecologically critical predictors for cave-dwelling organisms, due to their direct relevance to survival mechanisms. While cave temperatures exhibit relative stability throughout the year, they remain strongly correlated with regional surface temperatures (Moore and Sullivan 1964) and are often approximated by BIO1 in ecological models (Mammola et al. 2019). BIO1 thus serves as a proxy for thermal regimes influencing both cave bat and cave fish. BIO12 governs cave humidity and groundwater dynamics, which regulate key ecological processes such as nutrient transport and physiological tolerance in these taxa. KRT directly reflects the presence or absence of karst caves, which are essential habitats for cave bat (Furey and Racey 2016; Tanalgo et al. 2022) and cave fish (Zhao et al. 2011), as they depend heavily on stable subterranean environments. Seasonal climatic variability (BIO4 and BIO15) further explains cave bat distributions, as many species exhibit seasonally temperature- and resource-driven behaviours (Whitaker Jr and Rissler 1992; Agosta et al. 2005; Ramanantsalama et al. 2019). In addition, land cover (LC) constrains cave bat occupancy by defining foraging habitat quality and prey availability (Razgour et al. 2016). Crucially, cave fish—with their limited dispersal capacity—rely on cave bat to mediate nutrient inputs (e.g., guano, carcasses) into the subterranean ecosystem (Ferreira and Martins 1999; Culver and Pipan 2019). To account for this species symbiosis, we included BSR as a predictor variable in cave fish distribution models.

To mitigate overfitting and address collinearity among predictors (De Marco and Nóbrega 2018), we performed collinearity diagnostics on predictor variables for both cave bat and cave fish models. Weak collinearity was confirmed, with all variables showing VIF values below 10 (Table S1). This threshold has been widely adopted as an indicator of low multicollinearity in ecological modelling (Naimi et al. 2014) and is recommended in numerous recent SDM studies (Bai et al. 2024; Bai, Zhang, Xiong, Yang, et al. 2025; Zhou et al. 2025). Retaining variables under this criterion not only allows the inclusion of ecologically relevant predictors, thereby maintaining model interpretability and performance (Alves-Ferreira et al. 2024; Li et al. 2025), but also enhances the transferability of SDMs, that is, their ability to predict species' adaptability in novel environments (Biancolini et al. 2024).

2.3 | Ensemble Modelling and Prediction

Ensemble modelling approaches are widely recognised for their superior predictive performance compared to individual algorithms (Friedman and Popescu 2008; Seni and Elder 2010), offering a robust framework to address uncertainties in species distribution projections (Araújo and New 2007; Marmion et al. 2009; Thuiller et al. 2009). For this study, we implemented four established algorithms—Generalised Linear Models (GLMs; McCullagh 2019), Random Forest (RF; Breiman 2001), Multivariate Adaptive Regression Splines (MARS; Friedman 1991), and Maximum Entropy (MaxEnt; Phillips et al. 2006)—to generate ensemble models. All algorithms were executed using default parameters in the "biomod2" package (Thuiller et al. 2016) within R 4.3.1. Model performance was evaluated using the Area Under the Curve (AUC) of the Receiver Operating Characteristic (ROC; Huang and Ling 2005) and the True Skill Statistic (TSS; Allouche et al. 2006) calculated from independent evaluation datasets. The ROC curve illustrates the trade-off between a model's true positive rate and false positive rate at different thresholds. A higher AUC value indicated by the ROC curve bending toward the upper-left corner reflects better model prediction performance. The TSS, calculated as $TSS = Specificity + Sensitivity - 1$, ranges from -1 to 1, with higher TSS values denoting robust model performance (Allouche et al. 2006). To ensure model reliability, we employed repeated split-sample and cross-validation techniques: 70% of the total presence and pseudo-absence records were randomly selected as the training set for fitting the algorithms, with the remaining 30% used to evaluate the algorithm's performance (Bai, Zhang, Gan, Brosse, et al. 2025). This process was repeated 10 times to reduce variability caused by the splitting of datasets and increase the rigour of the results (Bai et al. 2024; Zhou et al. 2025). Only models achieving $AUC > 0.75$ were retained, with final ensemble predictions weighted by individual AUC scores (Araújo and New 2007; Buisson et al. 2010).

In this study, we first simulated historical distributions of cave bat and cave fish for the baseline period of 2010s (2001–2020).

Future projections for 2050s (average from 2041 to 2060) and 2090s (average from 2081 to 2100) were generated by integrating future bioclimatic variables and non-climatic predictors (LC, BSR), while holding KRT constant. KRT remains static in the future projections due to its negligible temporal variability in the time scale of this study—a standard practice for non-climatic variables in climate impact modelling (Peterson et al. 2002). This approach aligns with evidence that models combining static and dynamic variables outperform those relying solely on dynamic predictors (Iverson and Prasad 1998; Stanton et al. 2012). To minimise uncertainty in future projections, we utilised outputs from four widely validated global circulation models (GCMs: ACCESS-CM2, BCC-CSM2, CanESM5, and CNRM-ESM2 – 1; Table S2), averaging species richness projections across all GCM ensembles (Hole et al. 2009; Mi et al. 2023; Bai et al. 2024; Bai, Zhang, Yang, Zhang, et al. 2025). We selected two Shared Socioeconomic Pathways (SSP) scenarios (SSP1-2.6 that represents low-emission mitigation and SSP5-8.5 denoted by high-emission baseline) from the IPCC Sixth Assessment Report (AR6) to address different levels of shared socioeconomic pathway and human carbon emissions (O'Neill et al. 2017). Separate distribution models for cave bat and cave fish were developed under each scenario to assess habitat shifts under varying degrees of emission.

2.4 | Richness for Cave Bat and Cave Fish

In the R package biomod2, species richness is generally calculated by stacking individual output in two ways: (1) bssdm—summing the binary maps obtained after thresholding; (2) pssdm—directly summing the habitat suitability maps. Previous studies have found that the bssdm method tends to overestimate species richness per unit area (Algar et al. 2009; Dubuis et al. 2011; Mateo et al. 2012), as this method does not account for factors that limit the maximum number of species that can occupy the same geographic unit (Guisan and Rahbek 2011). In contrast, the pssdm method is less likely to overestimate species richness (Dubuis et al. 2011; Calabrese et al. 2014). However, the pssdm method does not account for species' dispersal abilities, and when applied to populations with limited dispersal capacity, species richness may still be overestimated. Unlike the cave bats (which can fly), the underground cave environment creates an "island effect" (Wu 1993) for cave fish, which may result in them having much lower dispersal abilities compared to surface freshwater fish. In the face of climate change, these species may only be able to persist locally (Mammola et al. 2019), making it necessary to incorporate dispersal limitations into the calculation of cave fish species richness. Therefore, this study calculates the species richness of cave bat and cave fish for each grid using the pssdm and dl-pssdm (pssdm under dispersal limitation) methods, respectively. Among these two, dl-pssdm implements dispersal limitations by excluding the emergence of new habitats and the restoration of old habitats. The calculation formulas are as follows:

$$R_t^b = \sum_{i=1}^{34} HS_{i,t}^b$$

$$R_{2010}^f = \sum_{j=1}^{6} HS_{j,2010}^f$$

$$R_{2050}^f = \sum_{j=1}^{6} \min\left(HS_{j,2010}^f, HS_{j,2050}^f\right)$$

$$R_{2090}^f = \sum_{j=1}^{6} \min\left(HS_{j,2010}^f, HS_{j,2050}^f, HS_{j,2090}^f\right)$$

where R_t^b and R_t^f represent the species richness of cave bat and cave fish in period t; t can be 2010, 2050, or 2090; $HS_{i,t}^b$ represents the habitat suitability of the i-th cave bat species in period t, $i = 1, 2, \ldots, 34$; $HS_{j,t}^f$ represents the habitat suitability of the j-th cave fish genus in period t, $j = 1, 2, \ldots, 6$.

2.5 | Richness Change for Cave Bat and Cave Fish

Under future scenarios, changes in climate and LC will alter the distribution of cave bat richness, which in turn may influence the spatial pattern of cave fish richness under climate change. The changes in species richness for cave bat and cave fish are calculated as follows:

$$RC_t^b = R_t^b - R_{2010}^b$$

$$RC_{t(C)}^f = R_{t(C)}^f - R_{2010}^f$$

$$RC_{t(C,B)}^f = R_{t(C,B)}^f - R_{2010}^f$$

where RC_t^b represents the change in cave bat species richness in period t relative to the historical baseline year 2010, $R_{t(C)}^f$ and $R_{t(C,B)}^f$ represent the projected cave fish genera richness in period t when only climate variables (C) are changed, and both climate variables and cave bat richness (C, B) are changed, t can be 2050 or 2090; $RC_{t(C)}^f$ and $RC_{t(C,B)}^f$ represent the changes in cave fish genera richness in period t when only climate variables (C) are changed, and both climate variables and cave bat richness (C, B) are changed.

3 | Results

3.1 | Richness Distribution of Cave Bat and Cave Fish

SDMs were successfully developed for 34 cave bat species and 6 cave fish genera. Model evaluation metrics demonstrated robust predictive performance, with mean AUC and TSS values of 0.977 and 0.877 for the cave bat species, and 0.987 and 0.915 for the cave fish genera (Figure S2). These values substantially exceed the commonly accepted thresholds for strong model accuracy (AUC > 0.90; TSS > 0.75; Yang et al. 2022). Mean variable importance analysis revealed distinct drivers of habitat suitability for each taxon. For cave bats, annual precipitation (BIO12) contributed most strongly (40.2%), followed by annual mean temperature (BIO1; 24.9%), temperature seasonality (BIO4; 13.7%), precipitation seasonality (BIO15; 10.9%), land cover (LC; 5.6%), and karst landscape (KRT; 4.8%). In contrast, cave fish distributions were predominantly influenced by bat species richness (BSR; 43.8%) and karst landscape (KRT; 23.8%), with lesser contributions from annual precipitation (BIO12; 16.4%) and annual mean temperature (BIO1; 16.0%).

Both cave bat and cave fish are predominantly distributed in southern China, specifically in the south of the Heihe-Tengchong Line, which aligns with a transition in population density, climate, and topography of China (Figure 1a; Figures S3 and S4). Regions with high cave fish genera richness (FGR) (FGR > 3) occur exclusively within areas of high cave bat species richness (BSR) (BSR > 10), spanning a total area of 846.43 km^2. Areas with exceptionally high fish richness (FGR > 4) are almost entirely restricted to regions where BSR exceeds 20, covering a total area of 213.27 km^2 and representing 98.7% of all FGR > 4 regions. Both taxa exhibit a strong preference for discontinuous karst landscapes (D-Karst; Figure S1). Within D-Karst regions, the mean richness values for cave fish (FGR = 2.95) and bats (BSR = 15.43) are significantly higher than those in non-karst landscapes (N-Karst; mean FGR = 0.63, mean BSR = 6.26) and continuous karst landscapes (C-Karst; mean FGR = 1.22, mean BSR = 7.76; Figure 1b,c).

3.2 | Richness Shifts of Cave Bat Species

Compared to the historical baseline (2010; Figure S3), the species richness center (centroid weighted by species richness) of cave bat is projected to shift northwestward in future periods (Figure 2). Under the SSP5-8.5 scenario, the southeastern regions will experience a severe richness decline (Richness change; RC) (RC < –3) expanding dramatically from 43.05 km^2 in 2050 to 242.21 km^2 by 2090. In contrast, northwestern areas with significant richness gains (RC > 3) expand under both SSP1-2.6 and SSP5-8.5 scenarios, increasing by 482.29 km^2 and 2972.51 km^2 in 2090 compared to 2050, respectively. Notably, extreme richness increases (RC > 9) emerge exclusively under SSP5-8.5 2090, covering 49.83 km^2, while all other scenarios combined show negligible coverage (< 1 km^2) above this increasing threshold.

3.3 | Loss of Cave Fish Genera Richness Intensified by Bat Migration

Climate change is projected to reduce cave fish genera richness, but this decline is dramatically amplified when accounting for concurrent cave bat range shifts (SSP5-8.5—Figure 3; SSP1-2.6—Figure S5). Under climate-only scenarios, the area experiencing substantial richness loss (RL) of cave fish (RL > 0.6) grows with escalating severity of climate change ranging from 0.46 km^2 (SSP5-8.5 in 2050s) to 6.00 km^2 (SSP5-8.5 in 2090s). However, when predicting with combined impacts of climate change and climate-induced bat migration, the area with RL > 0.6 expands dramatically by factors of 12.04 (SSP1-2.6 in 2050s), 17.11 (SSP1-2.6 in 2090s), 47.61 (SSP5-8.5 in 2050s), and 40.02 (SSP5-8.5 in 2090s) compared to the climate-only projections. For instance, under SSP5-8.5 in 2090s, incorporating bat migration increases the RL > 0.6 area from 6.00 km^2 to 246.28 km^2. A similar trend of marked expansion of richness loss occurs for areas with RL > 0.4 (Table 1).

4 | Discussion

Cave bat and cave fish are keystone faunal groups in subterranean ecosystems, playing distinct yet complementary ecological

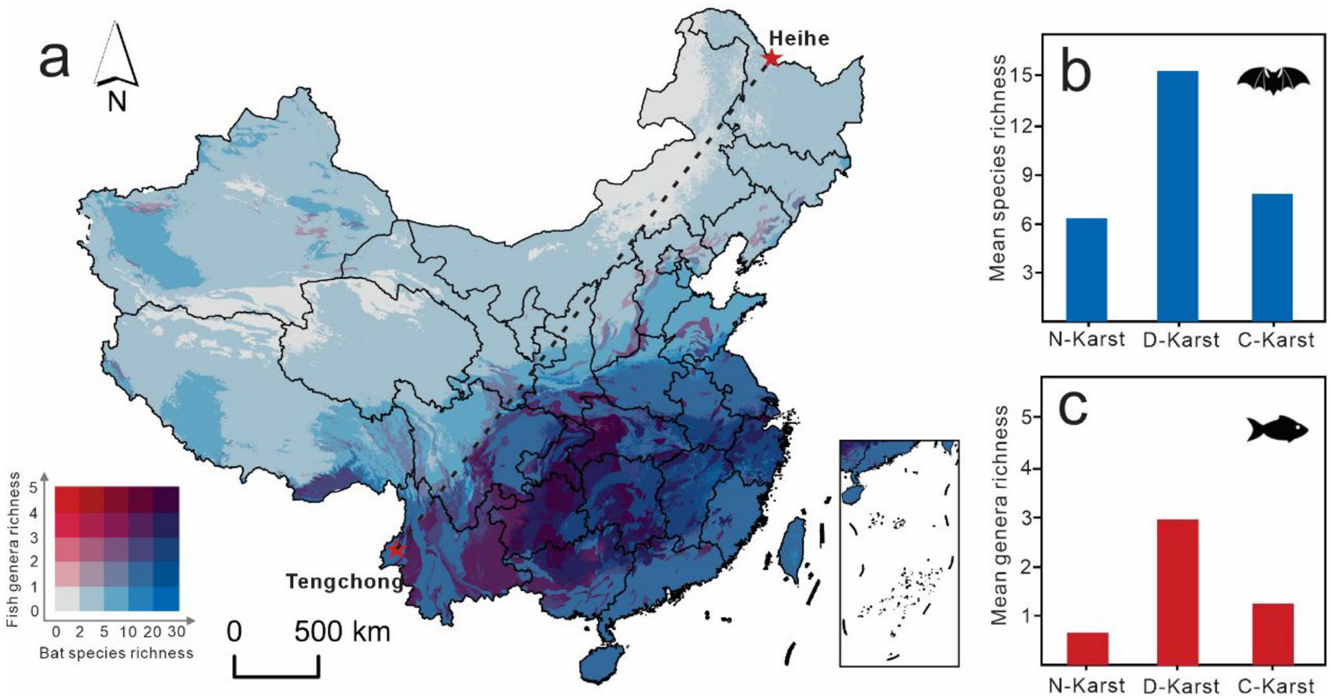

FIGURE 1 | Predicting richness distribution and mean richness of cave bat and fish taxa in different karst rock types. (a) Bivariate map showing the spatial pattern of cave bat species richness and cave fish genera richness from 2001 to 2020; (b and c) Mean cave bat species richness and mean cave fish genera richness in different karst rock types. N-Karst means non-karst landscapes; D-Karst means discontinuous karst rocks; and C-Karst means karst rocks.

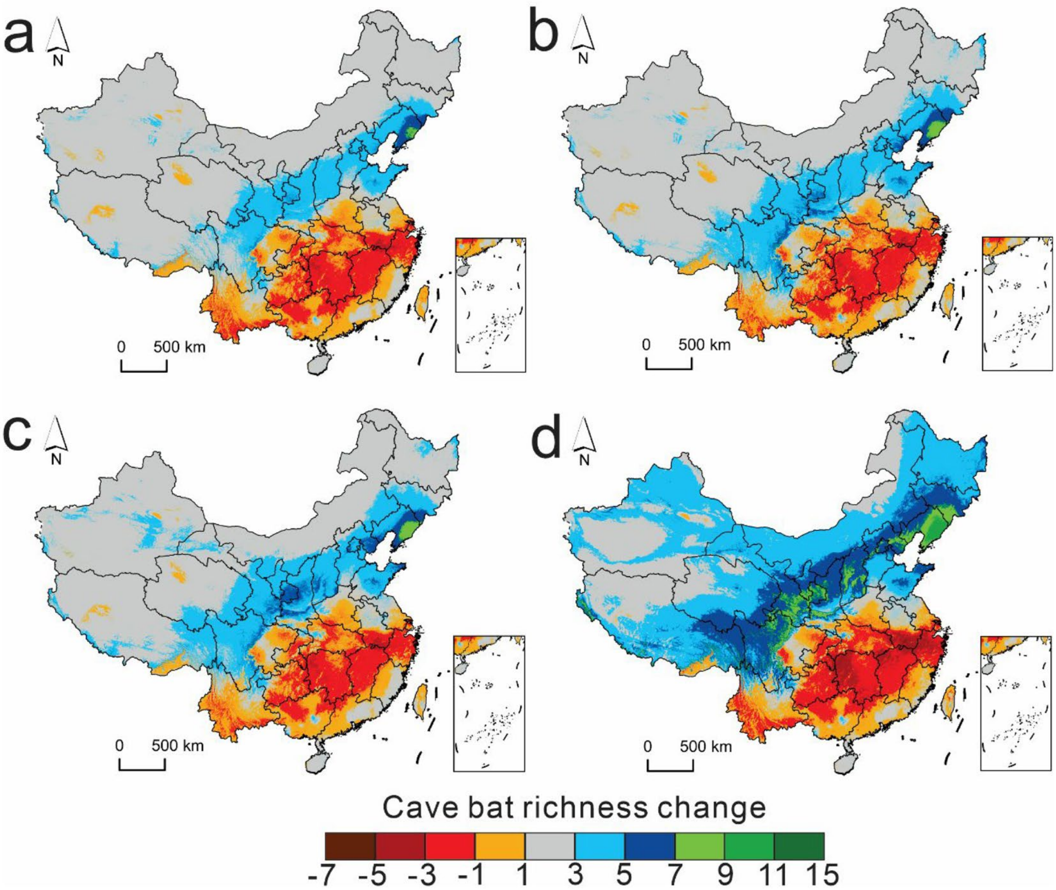

FIGURE 2 | Future richness change of cave bat species under (a) SSP1-2.6 2050, (b) SSP1-2.6 2090, (c) SSP5-8.5 2050, and (d) SSP5-8.5 2090. SSP1-2.6 represents an optimistic scenario for sustainable development, while SSP5-8.5 reflects a pessimistic scenario driven by fossil fuel development.

roles. Cave bats act as critical vectors for nutrient and energy transfer between surface and subsurface environments (Ferreira and Martins 1999; Ferreira 2019; Culver and Pipan 2019), while cave fish represent the most diverse and largest-bodied vertebrate taxa inhabiting these habitats (Zhao et al. 2011). Using collected occurrence data from 2001 to 2020, we developed SDMs for 34 cave bat species and six cave fish genera across China. These models enabled us to assess projected range shifts in cave bats and their cascading effects on cave fish richness. Our findings provide new insights into biodiversity loss under global change, highlighting that the indirect ecological consequences of climate change—mediated through disrupted species interactions—may outweigh its direct physiological impacts on individual taxa.

Our model revealed climatic variables dominated cave bat distribution, with annual precipitation contributing the most (40.2%), followed by annual mean temperature (24.9%), aligning with known climatic sensitivities in bats (Festa et al. 2023). Increased rainfall may elevate flight energy costs and suppress emergence behaviour (Voigt et al. 2011; Xiu et al. 2020), while also altering cave microclimates. Similarly, temperature is critical for roost selection in temperate bats (Arita and Vargas 1995; Vonhof and Barclay 1996; Callahan et al. 1997), a factor likely extending to subtropical and tropical species (Grytnes and McCain 2007). For cavefish genera, bat species richness emerged as the strongest predictor (43.8%), underscoring a symbiotic linkage between these taxa. Spatially, both groups concentrate in southern China (south of the Heihe-Tengchong Line; Figures 1a and S1), with high cave fish genera richness area (e.g., FGR > 3) nested entirely within high bat richness zones. This spatial overlap reflects shared preferences for discontinuous karst microhabitats and highlights cave bat's role in shaping the habitat suitability of cave fish. For instance, bat guano forms the primary diet of *A. mexicanus* (Kasumyan and Marusov 2015), while its accumulation and decomposition can release acidic compounds that modulate inorganic nutrient (e.g., phosphorus, nitrogen) and pH in cave sediments and waters, thereby restructuring cave microenvironment (Shahack-Gross et al. 2004).

Under future climate scenario, the richness center of Chinese cave bat is projected to shift northwestward, with more pronounced shifts under the high-emissions scenario (SSP5-8.5) compared to the low-emissions pathway (SSP1-2.6; Figure 2). This redistribution likely results from the combined influence of multiple drivers. Under SSP5-8.5, rising temperature and altered precipitation regimes are projected to degrade habitat suitability in southeastern China, while northwestern regions may develop more favourable microclimates—characterised by moderate thermal regimes and stable humidity—creating new refugia for cave bats (Ke et al. 2025). This aligns with global trends of species shifting toward higher latitudes or elevations to track suitable climates (Franco et al. 2006; Rödder et al. 2021). Meanwhile, although land cover (LC) contributed modestly to our models (5.6%), its role remains ecologically significant. The reason for the lower importance of LC here is likely that the

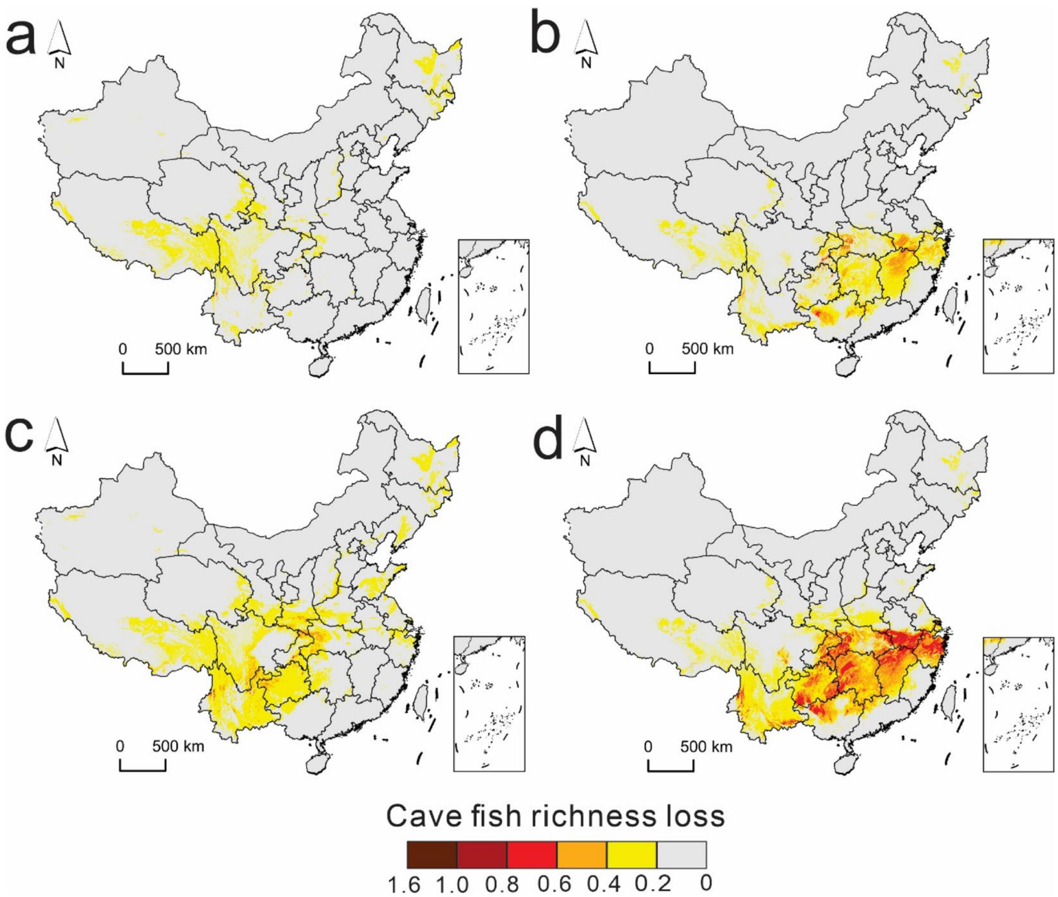

FIGURE 3 | Future richness loss of cave fish genera under SSP5-8.5 2050 considering (a) only climate change and (b) both climate change and bat migration; SSP5-8.5 2090 considering (c) only climate change and (d) both climate change and bat migration.

TABLE 1 | Area of cave fish genera richness loss under C (Climate change) and C + B (Climate change and Bat migration) unit: km^2.

	SSP1-2.6 2050s		SSP1-2.6 2090s		SSP5-8.5 2050s		SSP5-8.5 2090s	
	C	C + B	C	C + B	C	C + B	C	C + B
< −1	0.00	0.08	0.00	0.10	0.00	0.03	0.00	0.40
−1 to −0.8	0.04	0.82	0.16	2.09	0.00	0.20	0.17	28.17
−0.8 to −0.6	2.06	26.54	4.24	77.49	0.46	21.90	5.83	217.71
−0.6 to −0.4	42.08	271.36	52.72	346.79	9.09	174.17	108.39	536.84
−0.4 to −0.2	1092.54	1185.30	1157.94	1219.73	607.73	734.86	1447.41	960.17
−0.2 to 0	8337.31	7989.94	8258.99	7827.84	8856.77	8542.88	7912.25	7730.76

relationship between LC and bat habitats is indirect, with other factors such as habitat structure and food availability playing a more significant role. Cave bats rely on specific LC types, such as intact forests for foraging, rendering them vulnerable to landscape fragmentation (Razgour et al. 2016; Bandara et al. 2022). Thus, even localised LC changes in key habitats could compound climate-driven range shifts (Ke et al. 2025). Furthermore, although our model did not consider specific anthropogenic pressures, such pressures could exacerbate the impact of LC changes on cave bat habitats. For example, forest fragmentation (land-cover change) might force bats to travel longer distances for foraging, thereby increasing their exposure to roads (and the risk of mortality) (Fensome and Mathews 2016; Kerth and Melber 2009). The road network itself is also a key driver of landscape fragmentation (van Strien and Grêt-Regamey 2025). This cascading effect makes the impacts of multiple stresses synergistic, and their total effect is often greater than the sum of the individual factors, a concept that has been confirmed by research (Stone et al. 2015).

Climate change directly threatens biodiversity by altering temperature and precipitation regimes, driving species toward extinction (Urban 2024; Sayer et al. 2025). However, its indirect impacts—mediated through symbiotic relationships—are frequently overlooked, leading to significant underestimations of extinction risks. While localised cave fish genus loss under extreme scenarios rarely exceeds one genus (maximum impacted area: 0.5 km^2), a richness loss greater than 0.6 could signal complete loss of habitats supporting multiple genera. This could equate to the extinction of over 20 cave fish species, given the exceptional diversity of studied genera like *Sinocyclocheilus* (84 species) and *Triplophysa* (41 species) (Table S3; Appendix S1). Critically, projected losses from climate-only models change alone are dwarfed by those incorporating bat migration (Figure 3; Figure S5). When bat redistribution is considered, the affected area expands by tens of times, revealing that extinction risks may be severely underestimated if critical food web linkages are ignored. Specifically, changes in bat abundance could reduce guano-derived organic inputs, leading to food scarcity for cave fish and thereby amplifying extinction risks. Such indirect trophic cascades likely imperil other taxa in subterranean and surface ecosystems, highlighting the urgent need to integrate species symbiosis into global extinction risk assessments—a critical step toward holistic conservation planning under global change.

To account for fundamental biological differences between cave bat and cave fish, we applied distinct modelling assumptions for their future richness projections. Cave bat richness was modelled under unrestricted dispersal because of their capability of long-distance movements, while cave fish richness was calculated under strict dispersal limitation, unable to colonise new habitats or recolonize lost ones (Bai, Zhang, Gan, Brosse, et al. 2025). As highly mobile migrants, bats are among Earth's fastest-flying vertebrates, reaching speeds of up to 160 km/h (McCracken et al. 2016). For example, Mexican free-tailed bats (*Tadarida brasiliensis*) can forage up to 50 km nightly from roosts (Williams et al. 1973), enabling rapid range adjustments to track shifting climates. In contrast, although the exact dispersal ability of cave fish remains poorly understood, long-distance movement is likely implausible for these species, making persistence in situ their only viable response to environmental change (Mammola et al. 2019). Their survival is further constrained by thermal specialisation: adaptations to stable cave microclimates leave them vulnerable to minor temperature fluctuations (Novak et al. 2014; Raschmanová et al. 2018), which can be lethal due to absent thermoregulatory mechanisms (Mermillod-Blondin et al. 2013). Habitat recovery is also severely limited, as their physiology and life history are finely tuned to static subterranean conditions.

While our study incorporated the dispersal ability of cave fish into richness projections, several methodological limitations need further consideration. Our modelling at genus-level may overlook critical behavioural and ecological variation among species within the same genus. Additionally, we did not differentiate Stygobionts (obligate cave dwellers) and Stygophiles (facultative cave users), even though the latter often exhibit broader distributions and greater dispersal capacity (Figures S6 and S7). These limitations arise largely from data scarcity: sampling cave fish requires accessing remote, hazardous caves often in deep systems with great security challenges, and using labor-intensive methods like netting or trapping (as indicated in our cave survey work shown in Figure S8). These limitations also reflect funding constraints, which restricted our field surveys primarily to Guizhou Province. However, we recognise that core karst regions in southern China (e.g., Guangxi, Yunnan, Chongqing) are likewise important habitats for cave fishes (Zhao et al. 2011), and future field efforts should be expanded to these regions. Furthermore, uncertainties inherent in projecting climate change impacts on species distribution (Lobo 2016) compound the accuracy of our predictions. Cave ecosystems host unique microclimatic variations, microevolutionary processes, and biological interactions that are poorly quantified in macro-scale models. A lack of understanding of these factors within the caves would limit the accuracy and reliability of long-term climate change predictions (Hoffmann and Sgrò 2011; Maclean et al. 2015; Merlin et al. 2018). To improve predictive accuracy, future studies should integrate cave-specific microhabitat variables (e.g., sediment chemistry, hydrological stability) into distribution models, bridging the gap between macroclimate projections and subterranean ecological reality. Stygophiles and Stygobionts differ in their tolerance to cave environments: the former may occur in surface waters or have surface congeners (Tobler et al. 2006), whereas the latter are restricted to caves and thus more vulnerable. Their differences and connections warrant further investigation.

In terms of model construction, while our ensemble modelling approach produced stable richness estimates with no evidence of overfitting (Figure S2), the predictive performance of individual species models can be sensitive to the sampling of pseudo-absence (PA) points, especially when presence records are few (Barbet-Massin et al. 2012). Using only around 10 points (five presence points + five PA points) to predict species distributions across the entirety of China is unlikely to adequately capture the environmental heterogeneity at the national scale. We therefore recommend that future studies consider using a PA number at least ten times the number of presence records, or even more (Bai, Zhang, Xiong, Yang, et al. 2025; Zhou et al. 2025). Additionally, there are many other statistics that can be used to evaluate the generalisation capacity of SDMs, such as AUC, Kappa, and True Skill Statistic (TSS). For instance, TSS > 0.7 is also used as a threshold for filtering and weighting models (Liu et al. 2024). However, AUC is threshold-independent, while TSS is not (Franklin and Miller 2009). This means that AUC is more objective and reliable than TSS. Additionally, evidence suggests that TSS is significantly correlated with AUC to some extent (Allouche et al. 2006). Based on these points, we chose AUC in both our previous and current studies (Bai et al. 2024; Bai, Zhang, Xiong, Yang, et al. 2025).

Author Contributions

X.B.: conceptualization, methodology, validation, formal analysis, data curation, writing – original draft, writing – review and editing, visualisation. P.Z.: conceptualization, project administration, funding acquisition, writing – review and editing. B.R.S., T.J., G.S.: writing – review and editing. Y.Z.: data curation. X.D.: formal analysis, data curation, project administration, writing – review and editing.

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).

Funding

This work was supported by the National Natural Science Foundation of China, No. 52179142; Basic Project of Guizhou University, No. [2023]14.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

R code used to conduct this study is available at https://zenodo.org/records/17777787. All information about cave bat is available at https://doi.org/10.1038/s41597-022-01234-4. BIO1 (annual mean temperature), BIO4 (temperature seasonality), BIO12 (annual precipitation), and BIO15 (precipitation seasonality) data are available at https://www.worldclim.org/data/worldclim21.html. LC (Land cover) data are available at Lin et al. 2023. KRT (karst landscape) data are available at https://www.whymap.org/whymap/EN/Maps_Data/Wokam/wokam_node_en.html.

References

Agosta, S. J., D. Morton, B. D. Marsh, and K. M. Kuhn. 2005. "Nightly, Seasonal, and Yearly Patterns of Bat Activity at Night Roosts in the Central Appalachians." *Journal of Mammalogy* 86, no. 6: 1210–1219.

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.

Algar, A. C., H. M. Kharouba, E. R. Young, and J. T. Kerr. 2009. "Predicting the Future of Species Diversity: Macroecological Theory, Climate Change, and Direct Tests of Alternative Forecasting Methods." *Ecography* 32, no. 1: 22–33.

Allouche, O., A. Tsoar, and R. Kadmon. 2006. "Assessing the Accuracy of Species Distribution Models: Prevalence, Kappa and the True Skill Statistic (TSS)." *Journal of Applied Ecology* 43, no. 6: 1223–1232.

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.

Araújo, M. B., and M. New. 2007. "Ensemble Forecasting of Species Distributions." *Trends in Ecology & Evolution* 22, no. 1: 42–47.

Arita, H. T., and J. A. Vargas. 1995. "Natural History, Interspecific Association, and Incidence of the Cave Bats of Yucatan, Mexico." *Southwestern Naturalist* 40: 29–37.

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. Gan, et al. 2025. "Global Diversity Patterns and Threats of Cave Fish." *Global Ecology and Biogeography* 34, no. 11: e70160.

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.

Bai, X., P. Zhang, Z. Yang, et al. 2025. "Terrestrial Protected Areas Stabilize the Inland Habitats of Diadromous Fishes Under Climate Change." *Preprint available at SSRN* 5450322.

Bai, X., P. Zhang, Z. Yang, et al. 2025. "Impacts of Dams on Fish Habitat Connectivity Greatly Outweigh Climate Change in the Jinsha River Basin, China." *Journal of Hydrology* 660: 133411.

Bandara, A. M. J., B. D. Madurapperuma, G. Edirisinghe, D. Gabadage, M. Botejue, and T. D. Surasinghe. 2022. "Bioclimatic Envelopes for Two Bat Species From a Tropical Island: Insights on Current and Future Distribution From Ecological Niche Modeling." *Diversity* 14, no. 7: 506.

Barbet-Massin, M., F. Jiguet, C. H. Albert, and W. Thuiller. 2012. "Selecting Pseudo-Absences for Species Distribution Models: How, Where and How Many?" *Methods in Ecology and Evolution* 3, no. 2: 327–338.

Biancolini, D., M. Pacifici, M. Falaschi, et al. 2024. "Global Distribution of Alien Mammals Under Climate Change." *Global Change Biology* 30, no. 11: e17560.

Booth, T. H., H. A. Nix, J. R. Busby, and M. F. Hutchinson. 2014. "BIOCLIM: The First Species Distribution Modelling Package, Its Early Applications and Relevance to Most Current MAXENT Studies." *Diversity and Distributions* 20, no. 1: 1–9.

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.

Breiman, L. 2001. "Random Forests." *Machine Learning* 45: 5–32.

Buisson, L., W. Thuiller, N. Casajus, S. Lek, and G. Grenouillet. 2010. "Uncertainty in Ensemble Forecasting of Species Distribution." *Global Change Biology* 16, no. 4: 1145–1157.

Calabrese, J. M., G. Certain, C. Kraan, and C. F. Dormann. 2014. "Stacking Species Distribution Models and Adjusting Bias by Linking Them to Macroecological Models." *Global Ecology and Biogeography* 23, no. 1: 99–112.

Callahan, E. V., R. D. Drobney, and R. L. Clawson. 1997. "Selection of Summer Roosting Sites by Indiana Bats (*Myotis sodalis*) in Missouri." *Journal of Mammalogy* 78, no. 3: 818–825.

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.

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

Da Mata, R. A., R. Tidon, G. De Oliveira, et al. 2017. "Stacked Species Distribution and Macroecological Models Provide Incongruent Predictions of Species Richness for Drosophilidae in the Brazilian Savanna." *Insect Conservation and Diversity* 10, no. 5: 415–424.

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.

Deharveng, L. 2005. "Diversity Patterns in the Tropics." In *Encyclopedia of Caves*, edited by D. C. Culver and W. B. White, 166–170. Elsevier/Academic Press.

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.

Dubuis, A., J. Pottier, V. Rion, L. Pellissier, J. P. Theurillat, and A. Guisan. 2011. "Predicting Spatial Patterns of Plant Species Richness: A Comparison of Direct Macroecological and Species Stacking Modelling Approaches." *Diversity and Distributions* 17, no. 6: 1122–1131.

Elith, J., H. Graham, P. Anderson, et al. 2006. "Novel Methods Improve Prediction of Species' Distributions From Occurrence Data." *Ecography* 29, no. 2: 129–151.

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.

Fensome, A. G., and F. Mathews. 2016. "Roads and Bats: A Meta-Analysis and Review of the Evidence on Vehicle Collisions and Barrier Effects." *Mammal Review* 46, no. 4: 311–323.

Ferreira, R. L. 2019. "Guano communities." In *Encyclopedia of Caves*, 474–484. Elsevier.

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.

Festa, F., L. Ancillotto, L. Santini, et al. 2023. "Bat Responses to Climate Change: A Systematic Review." *Biological Reviews* 98, no. 1: 19–33.

Franco, A. M., J. K. Hill, C. Kitschke, et al. 2006. "Impacts of Climate Warming and Habitat Loss on Extinctions at Species' Low-Latitude Range Boundaries." *Global Change Biology* 12, no. 8: 1545–1553.

Franklin, J., and J. A. Miller. 2009. *Mapping Species Distributions: Spatial Inference and Prediction*. Cambridge University Press.

Friedman, J. H. 1991. "Multivariate Adaptive Regression Splines." *Annals of Statistics* 19, no. 1: 1–67.

Friedman, J. H., and B. E. Popescu. 2008. *Predictive Learning via Rule Ensembles*. Vol. 2. Stanford University.

Furey, N. M., and P. A. Racey. 2016. "Conservation Ecology of Cave Bats." In *Bats in the Anthropocene: Conservation of Bats in a Changing World*, edited by V. Christian and K. Tigga, 463–500. Springer.

Gatenby, R. A., R. J. Gillies, and J. S. Brown. 2011. "Of Cancer and Cave Fish." *Nature Reviews Cancer* 11, no. 4: 237–238.

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. 2014. *Methods in Karst Hydrogeology: IAH: International Contributions to Hydrogeology, 26*. Crc Press.

Grytnes, J.-A., and C. M. McCain. 2007. "Elevational Trends in Biodiversity." *Encyclopedia of Biodiversity* 2: 1–8.

Guisan, A., and C. Rahbek. 2011. "SESAM–a New Framework Integrating Macroecological and Species Distribution Models for Predicting Spatio-Temporal Patterns of Species Assemblages." *Journal of Biogeography* 38, no. 8: 1433–1444.

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.

Gunn, J. 2004. *Encyclopedia of Caves and Karst Science*. Routledge.

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.

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.

Hoffmann, A. A., and C. M. Sgrò. 2011. "Climate Change and Evolutionary Adaptation." *Nature* 470, no. 7335: 479–485.

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.

Huang, J., and C. X. Ling. 2005. "Using AUC and Accuracy in Evaluating Learning Algorithms." *IEEE Transactions on Knowledge and Data Engineering* 17, no. 3: 299–310.

Iskali, G., and Y. Zhang. 2015. "Guano Subsidy and the Invertebrate Community in Bracken Cave: The World's Largest Colony of Bats." *Journal of Cave & Karst Studies* 77, no. 1: 28–36.

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.

Kasumyan, A., and E. Marusov. 2015. "Chemoorientation in the Feeding Behavior of the Blind Mexican Cavefish *Astyanax fasciatus* (Characidae, Teleostei)." *Russian Journal of Ecology* 46: 559–563.

Ke, C., L. X. Gong, Y. Geng, et al. 2025. "Patterns and Correlates of Potential Range Shifts of Bat Species in China in the Context of Climate Change." *Conservation Biology* 39, no. 1: e14310.

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

Kerth, G., and M. Melber. 2009. "Species-Specific Barrier Effects of a Motorway on the Habitat Use of Two Threatened Forest-Living Bat Species." *Biological Conservation* 142, no. 2: 270–279.

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.

Lin, X., X. Jiao, Z. Tian, et al. 2023. "Projecting Diversity Conflicts of Future Land System Pathways in China Under Anthropogenic and Climate Forcing." *Earth's Future* 11, no. 10: e2022EF003406.

Liu, M., X. Li, L. Yang, et al. 2024. "Prediction of the Potential Distribution and Conservation Strategies of the Endangered Plant Tapiscia Sinensis." *Forests* 15, no. 9: 1677.

Lobo, J. M. 2016. "The Use of Occurrence Data to Predict the Effects of Climate Change on Insects." *Current Opinion in Insect Science* 17: 62–68.

Luo, J., T. Jiang, G. Lu, L. Wang, J. Wang, and J. Feng. 2013. "Bat Conservation in China: Should Protection of Subterranean Habitats Be a Priority?" *Oryx* 47, no. 4: 526–531.

Maclean, I. M., J. J. Hopkins, J. Bennie, C. R. Lawson, and R. J. Wilson. 2015. "Microclimates Buffer the Responses of Plant Communities to Climate Change." *Global Ecology and Biogeography* 24, no. 11: 1340–1350.

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.

Marmion, M., M. Parviainen, M. Luoto, R. K. Heikkinen, and W. Thuiller. 2009. "Evaluation of Consensus Methods in Predictive Species Distribution Modelling." *Diversity and Distributions* 15, no. 1: 59–69.

Mateo, R. G., Á. M. Felicísimo, J. Pottier, A. Guisan, and J. Munoz. 2012. "Do Stacked Species Distribution Models Reflect Altitudinal Diversity Patterns?" *PLoS One* 7, no. 3: e32586.

McCracken, G. F., K. Safi, T. H. Kunz, D. K. Dechmann, S. M. Swartz, and M. Wikelski. 2016. "Airplane Tracking Documents the Fastest Flight Speeds Recorded for Bats." *Royal Society Open Science* 3, no. 11: 160398.

McCullagh, P. 2019. *Generalized Linear Models*. Routledge.

Medellin, R. A., R. Wiederholt, and L. Lopez-Hoffman. 2017. "Conservation Relevance of Bat Caves for Biodiversity and Ecosystem Services." *Biological Conservation* 211: 45–50.

Meierhofer, M. B., J. S. Johnson, J. Perez-Jimenez, et al. 2024. "Effective Conservation of Subterranean-Roosting Bats." *Conservation Biology* 38, no. 1: e14157.

Merlin, M., A. Duputié, and I. Chuine. 2018. "Limited Validation of Forecasted Northward Range Shift in Ten European Tree Species From a Common Garden Experiment." *Forest Ecology and Management* 410: 144–156.

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.

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

Novak, T., Š. Nina, and A. Estera. 2014. "Cold Tolerance in Terrestrial Invertebrates Inhabiting Subterranean Habitats." *International Journal of Speleology (Edizione Italiana)* 43: 265–272.

O'Neill, B. C., E. Kriegler, K. L. Ebi, et al. 2017. "The Roads Ahead: Narratives for Shared Socioeconomic Pathways Describing World Futures in the 21st Century." *Global Environmental Change* 42: 169–180.

Pearson, R. G., C. J. Raxworthy, M. Nakamura, and A. Townsend Peterson. 2007. "Predicting Species Distributions From Small Numbers of Occurrence Records: A Test Case Using Cryptic Geckos in Madagascar." *Journal of Biogeography* 34, no. 1: 102–117.

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.

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.

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.

Ramanantsalama, R. V., O. S. Noroalintseheno Lalarivoniaina, A. P. Raselimanana, and S. M. Goodman. 2019. "Seasonal Variation in Diurnal Cave-Roosting Behavior of a Malagasy Fruit Bat (*Rousettus madagascariensis*, Chiroptera: Pteropodidae)." *Acta Chiropterologica* 21, no. 1: 115–127.

Raschmanová, N., V. Šustr, Ľ. Kováč, A. Parimuchová, and M. Devetter. 2018. "Testing the Climatic Variability Hypothesis in Edaphic and Subterranean Collembola (Hexapoda)." *Journal of Thermal Biology* 78: 391–400.

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.

Riddle, M. R., A. C. Aspiras, K. Gaudenz, et al. 2018. "Insulin Resistance in Cavefish as an Adaptation to a Nutrient-Limited Environment." *Nature* 555, no. 7698: 647–651.

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.

Rödder, D., T. Schmitt, P. Gros, W. Ulrich, and J. C. Habel. 2021. "Climate Change Drives Mountain Butterflies Towards the Summits." *Scientific Reports* 11, no. 1: 14382.

Sayer, C. A., E. Fernando, R. R. Jimenez, et al. 2025. "One-Quarter of Freshwater Fauna Threatened With Extinction." *Nature* 368: 138–145.

Senay, S. D., S. P. Worner, and T. Ikeda. 2013. "Novel Three-Step Pseudo-Absence Selection Technique for Improved Species Distribution Modelling." *PLoS One* 8, no. 8: e71218.

Seni, G., and J. Elder. 2010. *Ensemble Methods in Data Mining: Improving Accuracy Through Combining Predictions*. Morgan & Claypool Publishers.

Shahack-Gross, R., F. Berna, P. Karkanas, and S. Weiner. 2004. "Bat Guano and Preservation of Archaeological Remains in Cave Sites." *Journal of Archaeological Science* 31, no. 9: 1259–1272.

Sillero, N., S. Arenas-Castro, U. Enriquez-Urzelai, et al. 2021. "Want to Model a Species Niche? A Step-By-Step Guideline on Correlative Ecological Niche Modelling." *Ecological Modelling* 456: 109671.

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.

Stone, E. L., S. Harris, and G. Jones. 2015. "Impacts of Artificial Lighting on Bats: A Review of Challenges and Solutions." *Mammalian Biology* 80, no. 3: 213–219.

Tanalgo, K. C., J. A. G. Tabora, H. F. M. de Oliveira, et al. 2022. "DarkCideS 1.0, a Global Database for Bats in Karsts and Caves." *Scientific Data* 9, no. 1: 155.

Thuiller, W., D. Georges, R. Engler, F. Breiner, M. D. Georges, and C. W. Thuiller. 2016. "Package 'biomod2'." *Species Distribution Modeling Within an Ensemble Forecasting Framework* 10, no. 1600–0587: 2008.

Thuiller, W., B. Lafourcade, R. Engler, and M. B. Araújo. 2009. "BIOMOD–a Platform for Ensemble Forecasting of Species Distributions." *Ecography* 32, no. 3: 369–373.

Tinglei, J., Z. Huabin, H. Biao, et al. 2020. "Research Progress of Bat Biology and Conservation Strategies in China." *Acta Theriologica Sinica* 40, no. 6: 539.

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.

Townsend Peterson, A., 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.

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

van Strien, M. J., and A. Grêt-Regamey. 2025. "Global Expansion of the Ecological Impact of Extra-Urban Road Traffic." *Nature Sustainability* 8: 1294–1303.

Voigt, C. C., K. Schneeberger, S. L. Voigt-Heucke, and D. Lewanzik. 2011. "Rain Increases the Energy Cost of Bat Flight." *Biology Letters* 7, no. 5: 793–795.

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.

Vonhof, M. J., and R. M. Barclay. 1996. "Roost-Site Selection and Roosting Ecology of Forest-Dwelling Bats in Southern British Columbia." *Canadian Journal of Zoology* 74, no. 10: 1797–1805.

Wang, K., C. Zhang, H. Chen, et al. 2019. "Karst Landscapes of China: Patterns, Ecosystem Processes and Services." *Landscape Ecology* 34, no. 12: 2743–2763.

Wen, H., E. Liu, S. Yan, J. Chang, N. Xiao, and J. Zhou. 2022. "Conserving Karst Cavefish Diversity in Southwest China." *Biological Conservation* 273: 109680.

Whitaker, J., Jr., and L. Rissler. 1992. "Seasonal Activity of Bats at Copperhead Cave." *Proceedings of the Indiana Academy of Sciences* 101: 127–134.

Williams, T. C., L. C. Ireland, and J. M. Williams. 1973. "High Altitude Flights of the Free-Tailed Bat, *Tadarida brasiliensis*, Observed With Radar." *Journal of Mammalogy* 54, no. 4: 807–821.

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

Xiu, W., L. Bo, W. Weiwei, et al. 2020. "The Effect of Rain Noise on Emergence Behavior in Least Horseshoe Bats." *Acta Theriologica Sinica* 40, no. 2: 129.

Yang, M., H. Zhao, X. Xian, et al. 2022. "Potential Global Geographical Distribution of *Lolium temulentum* L. Under Climate Change." *Frontiers in Plant Science* 13: 1024635.

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

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. H., and C. G. Zhang. 2009. "Endemic Fishes of Sinocyclocheilus (Cypriniformes: Cyprinidae) in China." In *Species Diversity, Cave Adaptation, Systematics and Zoogeography*. 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.

Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1:** Distribution of karst landscape and occurrence points of cave fish and bat. **Figure S2:** AUC and TSS of SDMs for 34 cave bat species and six cave fish genera. **Figure S3:** Species richness distribution of cave bats in the historical period (2010). **Figure S4:** Richness distribution of cave fish genera in the historical period (2010). **Figure S5:** Future richness loss of cave bat genera under SSP126 2050 considering (a) only climate change and (b) both climate change and bat migration, SSP126 2090 considering (c) only climate change and (d) both climate change and bat migration. **Figure S6:** Distribution of karst landscape and occurrence points of stygobionts and stygophiles. **Figure S7:** Habitat suitability of stygobionts and stygophiles in historical period (2010). **Figure S8:** Entering caves to fish using angling and nets. **Table S1:** Variance inflation factor (VIF) of modelling factors for cave bats and fishes. **Table S2:** GCMs and Institution for BIO [1]. **Table S3:** Genus names of cave fish and the number of species within each genus. **Appendix S1:** Detailed information on cave fish species, including occurrence records, IUCN Red List classifications, taxonomy, and associated references.