

RESEARCH ARTICLE OPEN ACCESS

Global Patterns, Drivers and Conservation Gaps of Freshwater Crabs: From Species Richness to Phylogenetic Diversity

Wanna Wu¹ | Bing Wang¹ | Zhaomin Zhu¹ | Ruxiao Wang¹  | Boyang Shi¹  | Zhen Wang² | Hongying Sun¹  | Da Pan¹ 

¹Jiangsu Key Laboratory for Biodiversity and Biotechnology, College of Life Sciences, Nanjing Normal University, Nanjing, China | ²National Laboratory of Solid State Microstructures and Department of Materials Science and Engineering, Nanjing University, Nanjing, China

Correspondence: Hongying Sun (sunhongying@njnu.edu.cn) | Da Pan (dapan@njnu.edu.cn)

Received: 19 June 2026 | **Revised:** 31 August 2026 | **Accepted:** 10 September 2026

Editor: April M. H. Blakeslee

Keywords: conservation gaps | freshwater crabs | hotspots | phylogenetic diversity | species distribution modelling | species richness

ABSTRACT

Aim: Freshwater crabs are ecologically vital benthic macroinvertebrates that sustain freshwater ecosystem functions, yet their limited dispersal and fragmented habitats make them vulnerable to human disturbance. Current conservation assessments for freshwater crabs remain incomplete, as most studies focus on species richness while neglecting phylogenetic diversity and conservation gaps. This study aimed to characterize the spatial patterns of freshwater crab species richness (SR) and phylogenetic diversity (PD), identify their key driving factors, and evaluate existing conservation coverage to identify priority areas for targeted freshwater biodiversity protection.

Location: Global.

Methods: We integrated global occurrence data, phylogenetic sequences, and multi-dimensional environmental and anthropogenic datasets. The distribution data covered 95.83% of genera and 82.86% of species. Using an ensemble species distribution model, we predicted potential species distributions and mapped global patterns of SR and PD. Spatial generalized linear mixed models were applied to quantify the driving factors. We further identified biodiversity hotspots, evaluated conservation gaps and pinpointed priority areas.

Results: Freshwater crab biodiversity exhibited a clear low-latitude aggregation pattern, with major SR and PD hotspots concentrated in tropical and subtropical regions. Mountain topography and stable hydrothermal conditions promoted crab diversity, whereas strong precipitation seasonality inhibited species accumulation. Large conservation gaps were identified across core hotspot regions, and current protected areas poorly cover freshwater crab diversity. Moderate spatial optimization of protected areas could greatly enhance conservation coverage under global protection targets.

Main Conclusions: Global freshwater crab biodiversity patterns are shaped by coupled environmental and anthropogenic factors, with SR and PD showing heterogeneous spatial responses. Existing terrestrial-oriented protected areas cannot effectively conserve freshwater crab biodiversity. Optimizing protected area spatial layout based on both SR and PD delivers more efficient conservation outcomes. This study demonstrates the importance of integrating evolutionary information into freshwater conservation planning and provides spatial priorities for filling global freshwater biodiversity conservation gaps.

Wanna Wu and Bing Wang contributed equally to this study.

This is an open access article under the terms of the [Creative Commons Attribution](https://creativecommons.org/licenses/by/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2026 The Author(s). *Diversity and Distributions* published by John Wiley & Sons Ltd.

1 | Introduction

Freshwater accounts for only 0.01% of global water but harbours at least 100,000 species (Balian et al. 2008). Yet freshwater biodiversity decline exceeds that of most terrestrial systems (Albert et al. 2021). Since the Anthropocene, multiple emerging threats such as climate change, invasive species and contaminants have driven functional degradation of freshwater ecosystems (Reid et al. 2019). Understanding their functional interactions is essential for sustainable conservation (Geist 2011). Benthic macroinvertebrates perform key roles via bioturbation, maintaining self-sustaining systems (Chakraborty et al. 2022), but their conservation has been overlooked (Collier et al. 2016; Dudgeon and Strayer 2025).

Freshwater crabs belong to the phylum Arthropoda, class Malacostraca, order Decapoda and infraorder Brachyura. They complete their life cycle in freshwater without a planktonic larval stage, resulting in limited dispersal and highly fragmented distributions (Yeo et al. 2008; Cumberlidge et al. 2009). As primary consumers, they contribute to nutrient cycling, sediment mixing and energy transfer (Costa et al. 2016). International Union for Conservation of Nature (IUCN) assessments show about 48.6% of species are Data Deficient, reflecting a severe lack of distributional information (Figure S1; Cumberlidge et al. 2009). Moreover, existing protected areas designed primarily for terrestrial ecosystems inadequately cover freshwater crab distributions (Shi et al. 2025; Abell et al. 2007).

Species distribution models (SDMs) are essential for predicting potential ranges and supporting conservation (Elith and Leathwick 2009; Guisan et al. 2013; Zurell et al. 2020). In freshwater systems, distributions are constrained by catchment structure, hydrological connectivity, and topographic isolation. SDMs help identify conservation gaps (Reid et al. 2019; Hermoso et al. 2015a). Recent regional SDMs studies on freshwater crabs reveal that protected areas don't adequately cover hotspots (Shi et al. 2025; Yousefi et al. 2022), while global scale systematic studies are lacking.

Beyond species richness (SR), phylogenetic diversity (PD) is increasingly recognized as a key dimension of biodiversity (Reed and Frankham 2003). Within the framework of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES), PD serves as an indicator for NCP18 (maintenance of options), capturing the 'option value' of biodiversity (Faith 2021). PD has three distinct facets: lineage diversification, character divergence, and survival time, each related to different evolutionary processes, exhibiting different spatial patterns, and tied to different goals for conserving biodiversity (Kling et al. 2019). Therefore, integrating multiple SR and PD into a unified conservation framework is essential for comprehensively assessing freshwater crab biodiversity and optimizing conservation strategies.

Despite the recognized ecological importance of freshwater crabs and the growing body of research on this group, comprehensive assessments that simultaneously integrate SR and PD at the global scale remain scarce. To address this gap, we integrated global distribution data and phylogenetic relationships of freshwater crabs and employed ensemble species distribution models combined with spatial analyses. Our objectives were to: (1) characterize the global spatial patterns of SR and PD of

freshwater crabs; (2) reveal the underlying drivers of freshwater crab diversity; (3) evaluate the extent to which the current global protected area network covers these different dimensions of freshwater crab diversity. Through these analyses, we aim to provide a scientific basis for identifying conservation priorities for freshwater crabs and non-flagship freshwater taxa in the context of increasing human pressures.

2 | Materials and Methods

2.1 | Data Compilation and Clean

We compiled global distribution data of freshwater crabs from three sources: the Global Biodiversity Information Facility (GBIF) (for DOIs see Data Availability Statement), the IUCN Red List of Threatened Species on February 2026 (IUCN 2026), and our own long-term field surveys, which provided a substantial number of occurrence records. Because species occurrence data often contain errors and missing fields, we applied the following criteria to filter the GBIF data before subsequent analyses. First, we verified the taxonomic validity of species names against the WoRMS database on 11 June 2026 (WoRMS 2026) and retained only records of accepted species, removing subspecies and variety-level entries. Second, we excluded records lacking latitude and longitude information. Third, we removed obviously erroneous records. After removing these unreliable records, we supplemented distribution data by consulting the relevant literature to fill gaps in the database. For records with coarse geographic descriptions, we used the administrative centre as the representative location. The cleaned locality names were converted to geographic coordinates using the Baidu Geocoding API via the REmap package in R (<https://github.com/lchiffon/REmap>).

We merged the cleaned records from both databases and removed duplicates. To further ensure data reliability, we manually checked and corrected the taxonomic information for all freshwater crab records. This process yielded a total of 13,974 valid occurrence records for subsequent analysis, representing 1465 species across seven families and 299 genera. The coverage was 100% at the family level, 95.83% at the genus level and 82.86% at the species level. Because sample size affects the accuracy of species distribution models (Wisz et al. 2010), we only used species with more than five occurrence records for model building. For species with few records or failed model predictions, we first supplemented their distributions using range maps provided by the IUCN. When such maps were unavailable, we generated a 50-km buffer around each known occurrence point to approximate the potential distribution range.

2.2 | Acquisition and Selection of Environmental Variables

Climate data at 2.5 arc-minute spatial resolution were obtained from the WorldClim v2.1 database (Fick and Hijmans 2017). We initially acquired 19 bioclimatic variables, which primarily capture annual trends and extreme conditions of temperature and precipitation. To avoid multicollinearity among variables, we calculated Pearson correlation coefficients for each pair of

variables. When $|r|$ exceeded 0.8, we retained only one variable. This procedure yielded five climatic variables: mean annual temperature (MAT), temperature seasonality (ISO), temperature annual range (TAR), mean annual precipitation (MAP) and precipitation seasonality (PS). Topographic variables included elevation (ALT), slope (SLP) and aspect (AST), all of which were obtained from the Geospatial Data Cloud site, Computer Network Information Center, Chinese Academy of Sciences (<http://www.gscloud.cn>). Slope was transformed using the sine function, and aspect was converted by subtracting 180° and taking the absolute value.

Vegetation cover was quantified using the GIMMS Normalized Difference Vegetation Index (PKU GIMMS NDVI; Li et al. 2023), which has a spatial resolution of 0.05° and reflects global terrestrial vegetation dynamics from 2011 to 2022. For each grid cell in the study area, we extracted the mean NDVI value as an indicator of vegetation cover.

Human activity variables included land use, human footprint (HFP), road density and river network density. Land use data were derived from the ESA CCI Land Cover Map (ESA 2017). The original 37 land cover classes were reclassified into eight categories: cropland, forest, shrubland, grassland, sparse vegetation, wetland, urban and water bodies. The HFP index was obtained from a global annual terrestrial HFP dataset (2000–2018) developed by Mu et al. (2022), with a spatial resolution of approximately 1 km. This dataset integrates eight indicators of human activity, including nighttime lights, population density, land use and transportation networks, and serves as a proxy for human activity intensity. Road density data were sourced from the Global Roads Inventory Project v4 (Meijer et al. 2018) at a resolution of about 10 km. Based on the total road density raster, we calculated the mean road density per grid cell to represent regional road accessibility. River network data were obtained from HydroRIVERS v1.0 (Lehner and Grill 2013) at a resolution of approximately 15 s. River network density was calculated as the ratio of total river length to land area within each grid cell. This continuous variable effectively captures the availability and spatial configuration of freshwater habitats, allowing the model to weight the importance of river systems when predicting diversity patterns, rather than imposing a strict binary mask (i.e., presence/absence of rivers) that might oversimplify habitat suitability at coarse spatial scales.

Global protected area data were obtained from the World Database on Protected Areas (WDPA, <https://www.protectedplanet.net/en>). We extracted terrestrial portions and standardized them to the WGS84 coordinate system to ensure compatibility with other environmental variables. Subsequently, at a 0.5° grid cell resolution, we calculated the proportion of protected area coverage (protected area divided by total grid area) to assess conservation gaps and the effectiveness of biodiversity conservation.

2.3 | Species Distribution Modelling

We used the R (R Core Team 2019) package SSDM v0.2.11 (Schmitt et al. 2017) to predict potential distribution ranges via an ensemble of five algorithms: GLM (McCullagh and Nelder 1989),

MARS (Friedman 1991), RF (Breiman 2001), MaxEnt (Phillips et al. 2006), and CTA (De'ath and Fabricius 2000). To avoid multicollinearity, we performed VIF screening using the `vifstep` function in the R package `usdm` v2.1.7 and removed variables with $VIF > 5$ (Naimi et al. 2014). For each species, we generated 1000 pseudo-absence points (repeated five times) and used five-fold random cross-validation (80% training / 20% testing). Model performance was evaluated using AUC and TSS, and single models with $AUC < 0.8$ were excluded. We then used the ensemble function of `biomod2` v4.3.4.6 (Guéguen et al. 2026) to calculate an unweighted mean of well-performing single models ($AUC > 0.8$). The continuous probability map was binarized using the optimal TSS threshold ($suitable = 1$, $unsuitable = 0$) and masked to a 50-km buffer around the species' minimum convex polygon. Finally, we projected the maps onto a $2^\circ \times 2^\circ$ global grid to calculate species richness per grid cell. Detailed analyses of species distribution modelling are provided in Appendix S1. Since the present study has included a great number of occurrence records based on our long-term field surveys in China, we conducted an incidence-based rarefaction analysis (Fan et al. 2024) to account for biases from heterogeneous sampling intensity. Rarefaction curves were generated for China and the rest of the world across a continuous range of sampling levels ($q = 1$ to the minimum regional total grid count). To quantify regional differences, we compared the expected species richness $E(S_q)$ at three representative sampling levels ($q = 10, 20, 50$).

2.4 | Phylogenetic Diversity Analysis

We downloaded all available mitochondrial 16S rRNA gene sequences from GenBank using valid scientific names from WoRMS (WoRMS 2026), including both individual fragments and those from complete mitochondrial genomes. Short sequences (< 300 bp) were removed, and alignment was performed using MAFFT v7.526 (Katoh and Standley 2013). Full-length sequences were aligned with '—globalpair' mode, followed by addition of remaining fragments using '—addfragments' mode (Katoh and Frith 2012). In BEAUti v2.5, we set the GTR substitution model and an uncorrelated lognormal relaxed clock (Bouckaert et al. 2019; Drummond et al. 2006). The Yule tree prior was used with three fossil calibrations: *Eriocheir japonica* (5.3–3.6 Ma; Zhang et al. 2015), *Scylla costata* (28.4–23.0 Ma; Rathbun 1919), and *Acanthopotamon martensi* (~2.6 Ma; Klaus et al. 2017). MCMC ran for 5×10^8 generations (sampling every 1000). Convergence was checked in Tracer v1.7.2 (Rambaut et al. 2018). TreeAnnotator discarded 10% burn-in and generated the MCC tree.

Species occurrence points were overlaid onto a 2° equal-area grid, retaining only species present in the phylogenetic tree. Faith's PD and SR were calculated per grid cell using `picante` v1.8.2 (Kembel et al. 2010). SES.PD was computed with the same package (null model = 'taxa.labels', 999 randomizations), excluding cells with $SR < 2$. $SES.PD = (\text{observed PD} - \text{mean random PD}) / \text{SD random PD}$, where positive values indicate phylogenetic overdispersion and negative values indicate clustering. SR, PD and SES.PD were integrated into the grid attribute table. All global maps used the equal-area Behrmann projection, producing final maps of SR, PD, their bivariate distribution, and SES.PD. Detailed analyses of phylogenetic diversity analysis are provided in Appendix S2.

Also, to mitigate potential bias from uneven 16S sequence availability across regions, we performed incidence-based PD rarefaction. This approach standardizes sampling effort across regions to the same grid sampling intensity (q) and calculates the expected phylogenetic diversity $E(PD_q)$ as follows: Fan et al. (2024).

2.5 | EDGE2 Analysis

To complement grid-based PD assessments with species-level evolutionary distinctiveness and extinction risk, we calculated the Evolutionarily Distinct and Globally Endangered 2 index (EDGE2) for all freshwater crab species in our phylogeny. This metric combines a species' evolutionary distinctiveness 2 (ED2) with its global endangerment 2 (GE2). GE2 is a species-specific extinction risk weight derived from IUCN Red List categories (IUCN 2026), following the standardized EDGE2 framework (Gumbs et al. 2023): Critically Endangered (CR)=0.97, Endangered (EN)=0.485, Vulnerable (VU)=0.2425, Near Threatened (NT)=0.12125, Least Concern (LC)=0.060625. For Data Deficient (DD) and Not Evaluated (NE) species, we assigned a conservative GE2 weight of 0.2425 (equivalent to VU), following Pipins et al. (2026).

Based on the global distribution of EDGE2 scores, we confirmed EDGE2 species with EDGE2 scores above the global median and threatened IUCN status (VU, EN, or CR). These represent the highest-priority species for immediate conservation action, as they combine high evolutionary distinctiveness with elevated extinction risk.

2.6 | Drivers of Diversity Distribution Patterns

To investigate the effects of environmental factors on the spatial patterns of diversity, we used SR and PD as response variables in spatial generalized linear mixed models (spaGLMMs). First, we log-transformed and standardized SR and PD separately. For each variable, we extracted the value at the centroid of the corresponding grid cell. All environmental variables were also standardized. We then performed correlation and multicollinearity tests, retaining only variables with a correlation coefficient $|r| < 0.75$ and $VIF < 5$ for model inclusion. Subsequently, we constructed spatial mixed models with SR or PD as response variables using the R package spaMM v4.6.65 (Rousset and Ferdy 2014). A Matern spatial correlation structure based on latitude and longitude was incorporated to account for spatial autocorrelation. Model outputs were used to evaluate the fixed effects and significance of each environmental variable, with 95% confidence intervals estimated. Finally, calculated marginal R^2 values to measure the explanatory power of the models for spatial variation in SR and PD.

2.7 | Identification of Diversity Hotspots

Using ArcGIS v10.5 (ESRI 2011), we overlaid the binarized (0/1) raster layers of potential distributions for each species on a pixel-by-pixel basis and calculated the potential species richness

(PSR) within each raster cell. While preserving the spatial resolution and numeric attributes, we then converted the PSR raster layer into a vector layer, where each polygon corresponded to a unique PSR value. In spatial analysis, biodiversity hotspots are identified by the spatial clustering of metrics such as PSR, determining whether they exhibit concentrated distributions within local areas (Ye et al. 2020; Gary et al. 2019). We calculated the global Moran's I index to test the spatial autocorrelation of SR and assessed its significance to determine whether it shows significant spatial clustering, thereby providing a basis for biodiversity hotspot analysis.

Using the Optimized Hot Spot Analysis tool in ArcGIS, we calculated the local Getis-Ord G_i^* statistic for each grid cell and standardized it to a G_iZ score to identify high-value hotspots. According to the standard normal distribution thresholds, values of $1.65 < G_iZ \text{ score} < 1.96$, $1.96 < G_iZ \text{ score} < 2.58$ and $G_iZ \text{ score} > 2.58$ correspond to confidence levels of 90%, 95% and 99%, respectively (Gary et al. 2019; Ye et al. 2020). These thresholds were used to identify areas of significant spatial clustering of potential SR, thereby showing the spatial distribution patterns of diversity hotspots of freshwater crabs.

2.8 | Identification of Conservation Gaps and Priority Areas

Based on biodiversity hotspots (>90% confidence), we defined planning priority hotspots (Ye et al. 2020). Nature reserve data came from three sources: mainland China (National Earth System Science Data Center; Ministry of Ecology and Environment of the People's Republic of China 2016), Taiwan Island (Taiwan Forestry Bureau), and global data from WDPA (August 2025, <https://www.protectedplanet.net/en>). After spatial registration and format unification, we overlaid hotspots and reserves onto a $0.5^\circ \times 0.5^\circ$ grid. Grid cells within hotspots but outside any reserve were identified as conservation gaps (Burley 1988; Scott et al. 1993; Jennings 2000).

Using the CAZ algorithm in Zonation v5 (Moilanen et al. 2014), we prioritized areas with existing protected area coverage (7.169%) as baseline and set targets of 17% and 30%. High-priority areas were extracted using quantile thresholds. We assigned weights based on median species range (smaller range=1, larger=2), with built-environment pixels receiving negative weights, balancing species diversity features and human footprint (Venter et al. 2016; Moilanen et al. 2014).

From a PD perspective, we calculated PD per 0.5° grid cell as the sum of phylogenetic branch lengths of all species present (Faith 1992). The upper 25th percentile of global PD defined high-PD hotspots (Robuchon et al. 2021). To assess coverage by existing reserves and predict additional priority cells under 17% and 30% targets, we ranked unprotected cells by descending PD value, applied an area weighting factor, and selected cells sequentially until cumulative weighted area reached each target. Detailed analyses of identification of conservation gaps and priority areas are provided in Appendix S3.

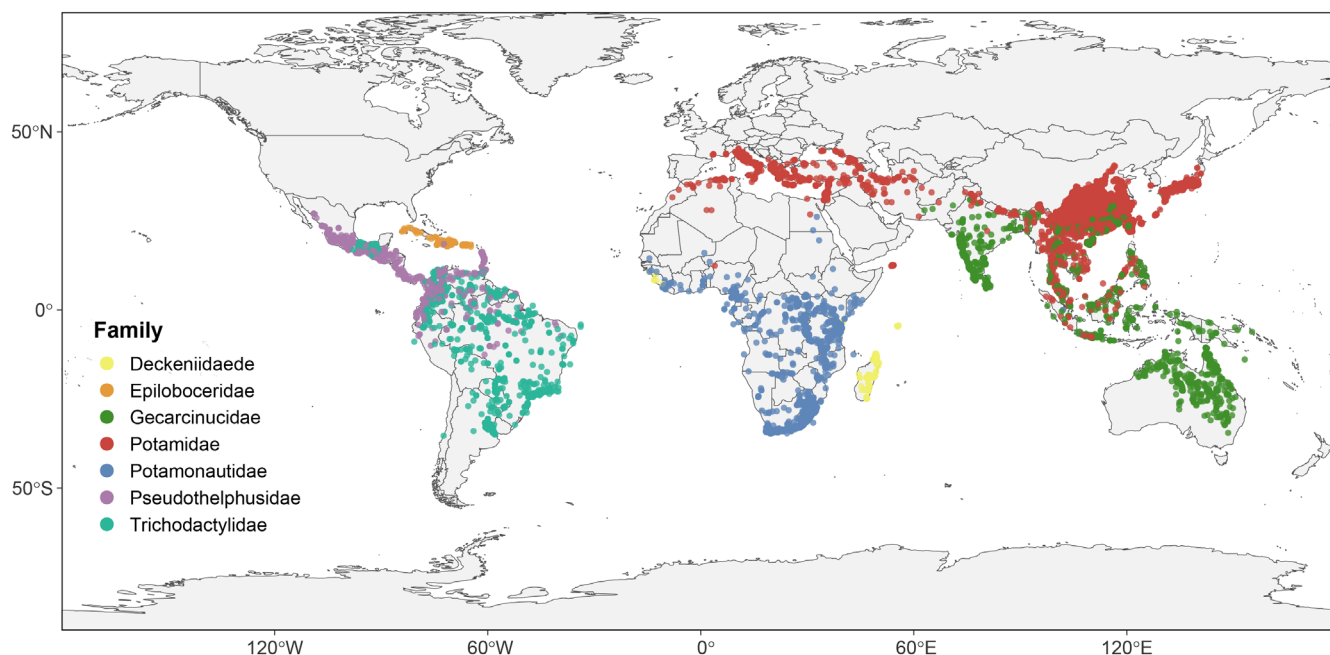


FIGURE 1 | Spatial distribution patterns of freshwater crab families at the global scale.

3 | Results

3.1 | Distribution Patterns of Species Diversity of Freshwater Crabs

A total of 15,893 raw occurrence records of freshwater crabs were obtained. After data correction, coordinate referencing, error filtering and removal of duplicates, 13,797 unique georeferenced records were retained (Figure 1). The global distribution of freshwater crabs showed pronounced spatial unevenness, with concentrations in three major regions: southern China, Southeast Asia and northern South America. In Asia, occurrence records were mainly concentrated in East, Southeast and South Asia, particularly in southern China, the Indochina Peninsula, the Indonesian Archipelago and the Philippines. In Africa, records were widely distributed across central, eastern and southern Africa. In the Americas, the core distribution area extended from northern to central South America, including Panama, Colombia, Ecuador and the Amazon basin. In contrast, records were scarce in arid or temperate regions such as North America, West Asia, Central Asia and inland Australia.

The rarefaction analysis revealed consistently higher expected species richness in China than in other regions across all sampling levels (Figure S2A). At $q = 10, 20$ and 50 , the expected species richness in China was 53.15, 86.81 and 150.17, respectively, compared with 18.09, 33.73 and 72.62 in other regions. The non-overlapping confidence intervals at all three levels indicate that the higher diversity in China is not an artefact of sampling effort.

At the global scale, the distribution of freshwater crab families showed clear spatial differentiation (Figure 1). Potamidae were widely distributed across East, Southeast and South Asia, forming a continuous and dense distribution pattern

in southern China, the Indochina Peninsula and the Indian subcontinent. Gecarcinucidae were concentrated in South and Southeast Asia as well as the Indo-Australian region, occurring in the Indian subcontinent, southern Indochina, the Indonesian Archipelago and northern Australia. Potamonautidae were almost entirely restricted to sub-Saharan Africa. Pseudothelphusidae and Trichodactylidae were both distributed in the New World. The former were concentrated in Mesoamerica and northern South America, including southern Mexico, the Central American isthmus and the northern Andes, whereas the latter had their core distribution in the Amazon basin and its surroundings. Epiloboceridae were confined to the Caribbean region. Deckeniidae occurred along the eastern coast of Africa and on Madagascar, exhibiting a relatively scattered pattern. The ranges and distribution patterns of these families differed markedly, reflecting the spatial differentiation of freshwater crabs at the global scale.

Using species with ≥ 5 occurrence records, we predicted potential distributions of global freshwater crabs with ensemble SDMs. Among the resulting species models, 95% achieved $AUC > 0.85$. The predicted SR pattern was generally consistent with observed occurrences but showed greater spatial continuity and more complete range coverage (Figure 2A; Figure S3).

Global SR of freshwater crabs exhibited pronounced spatial heterogeneity, with high-value areas concentrated in tropical and subtropical regions, forming three core areas: (1) East and Southeast Asia, centred on southern China and extending to Vietnam, Thailand, Malaysia and the Indonesian Archipelago, representing the most species-rich hotspot globally; (2) the northern Neotropics, covering Panama, Colombia and the northern Amazon basin, showing significantly high richness; and (3) central and western Africa, including the Congo Basin and the Gulf of Guinea coast, forming a moderate-to-high

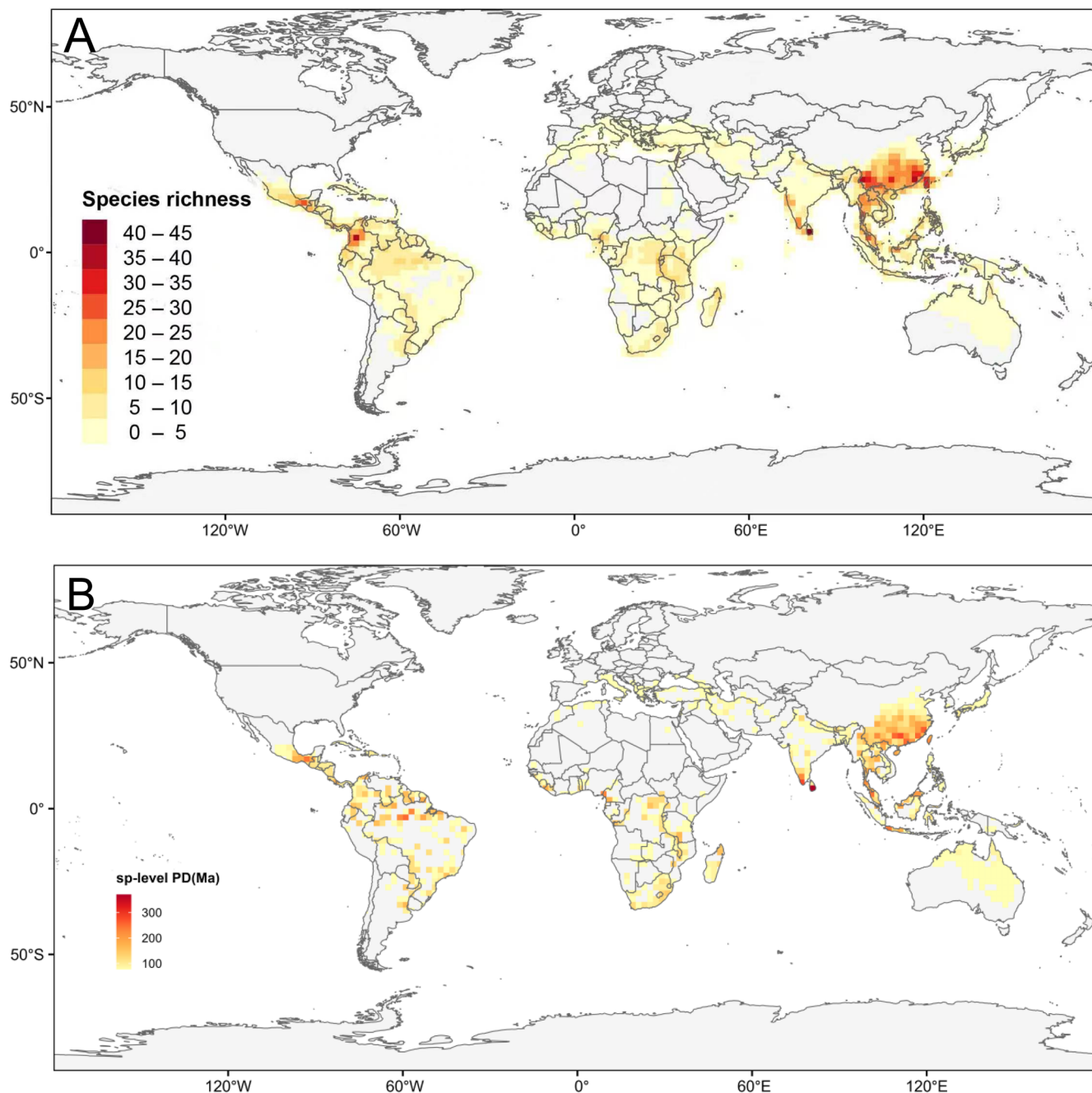


FIGURE 2 | Spatial patterns of diversity in freshwater crab species at the 2° grid level. (A) Potential species richness (PSR); (B) phylogenetic diversity (PD).

diversity core. In addition, Madagascar also displayed high SR. In contrast, the mid-to-high latitudes of North America, West Asia, Central Asia and inland Australia had sparse species records and low richness levels, reflecting a trend of decreasing freshwater crab diversity with increasing latitude.

Genus-level richness patterns were generally consistent with species-level patterns, but high-value areas were more contracted and concentrated (Figure 2A; Figure S3). Overall, at both taxonomic levels, high diversity was confined to tropical-subtropical humid regions, with low diversity in temperate and arid regions.

3.2 | Geographic Patterns of Phylogenetic Diversity of Freshwater Crabs

Using a global 16S rRNA-based phylogeny (660 species), we mapped Faith's PD (Figure 2B). PD showed marked spatial heterogeneity. At the species level, high PD values were concentrated in tropical-subtropical regions, especially East and Southeast Asia (southwestern and southern China, northern Vietnam, Thailand, the Philippines), which are the global PD hotspots. Additional high-PD areas included Sri Lanka, southwestern India (Western Ghats), central and western Africa and the African Great Lakes region, the western Amazon and

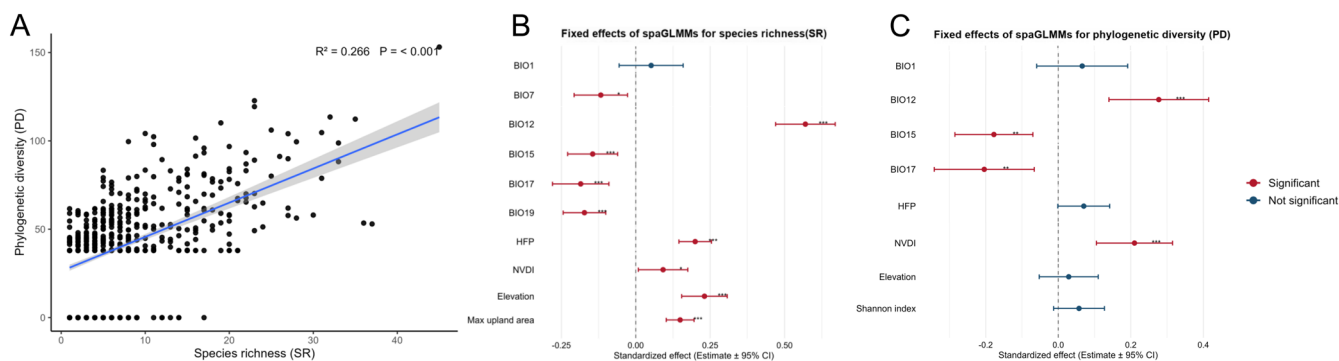


FIGURE 3 | Univariate linear regression of species richness (SR) versus phylogenetic diversity (PD) using $2^\circ \times 2^\circ$ grid cells as operational units (A). Results of spatial generalized linear mixed models (spatial GLMMs) showing the effects of different variables on SR and PD of global freshwater crabs at a grid resolution of $2^\circ \times 2^\circ$. Points represent standardized fixed-effect estimates, and error bars indicate 95% confidence intervals of the estimated coefficients. Red denotes significant effects, and blue denotes non-significant effects. Asterisks indicate significance levels: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$ (B, C).

southeastern Brazil (Figure 2B). At the genus level, high PD was mainly in southern China and Southeast Asia (central Indochina to the Malay Archipelago: Thailand, Vietnam, Malaysia, western Indonesia), plus the Andean region (Peru-Ecuador border). Medium PD occurred in the Congo Basin, West African coast and northeastern India. PD was generally low in North America, Australia, West Asia and Central Asia (Figure S4). Overall, genus-level PD patterns broadly matched species-level patterns, identifying East Asia with southern China as the core and Sri Lanka as global PD hotspots.

After removing grids with $SR < 2$, we calculated SES.PD for 331 grids (Figure S5). Approximately 95% of global freshwater crab populations exhibited $SES.PD \leq 0$, with the majority of grids showing statistical significance ($p < 0.05$). The most pronounced clustering ($SES.PD < -7$) was concentrated in the regions south of the Yangtze River in southern China, where SR was generally high (> 20) and exhibited extremely significant correlations ($p < 0.001$). Moderately clustered grids ($-7 < SES.PD < -3$) covered a broader geographic area, encompassing nearly the entire southern China region as well as Sri Lanka, Southeast Asia, Central America and southern and eastern Africa. In contrast, Australia and South America did not demonstrate clustering patterns. Notably, the grid cell covering the Wanshi Mountain range, Qitianling and the low-altitude valley between them (approx. $113^\circ E$, $25^\circ N$) showed a substantially less negative SES.PD value than the surrounding grid cells.

Globally, freshwater crabs exhibited a clear Old World-New World divergence at the phylogenetic level. Each continent and its surrounding regions could be further divided into several stable biogeographic units, providing a clear spatial and phylogenetic framework for exploring evolutionary history and formation mechanisms.

PD rarefaction analysis showed that the raw total phylogenetic diversity was 2136.997 for Southeast Asia and 3905.393 for the rest of the world while Southeast Asia accounts for only approximately one-sixth of the global distribution range of freshwater crabs. Although the total PD in other regions was approximately twice that of Southeast Asia, after standardizing sampling effort

to the same grid intensity, Southeast Asia exhibited significantly higher expected phylogenetic diversity $E(PD_q)$ than the rest of the world at all standardized levels, with non-overlapping confidence intervals. This confirms that Southeast Asia is a global hotspot of freshwater crab phylogenetic diversity, and that this pattern is not driven by regional heterogeneity in molecular sampling (Figure S2B).

3.3 | Drivers of Diversity Distribution Patterns

The spaMM analysis revealed that multiple environmental variables significantly affected both SR and PD of global freshwater crabs (Figure 3B,C). PD was significantly positively correlated with SR ($R^2 = 0.266$, $p < 0.001$; Figure 3A). For SR (Figure 3B), annual mean precipitation (BIO12), elevation, and HFP index showed significantly positive associations, whereas precipitation of the driest quarter (BIO17), precipitation of the coldest quarter (BIO19), precipitation seasonality (BIO15) and temperature annual range (BIO7) exhibited significantly negative associations. In addition, the normalized difference vegetation index (NDVI) also had a significant positive effect, while annual mean temperature (BIO1) was not significant. For PD (Figure 3C), BIO7, BIO12 and NDVI showed significantly positive associations, whereas BIO17 and BIO15 exhibited significantly negative associations. By contrast, HFP, BIO1, topographic heterogeneity index and elevation did not show significant effects.

Overall, the two types of diversity indices exhibit consistent responses to hydrothermal conditions; BIO12 and NDVI both demonstrate significant positive effects, while BIO15 and BIO17 show significant negative effects. Yet BIO7 exhibits a significant negative effect on SR but a significant positive effect on PD.

3.4 | Analysis of Conservation Priority Areas

Overlay analysis at 0.5° resolution showed that 13.997% of grid cells overlapped with protected areas, while the actual protected area coverage was 7.169%; it was used as baseline in Zonation. In SR hotspot cells, 37.8% were covered by protected

areas, higher than the global coverage, but still leaving most hotspots unprotected. SR exhibited strong positive spatial autocorrelation ($p < 0.001$; Table S1). Among these gaps, southern China and Southeast Asia showed the most prominent conservation gaps. From the eastern margin of the Yunnan-Guizhou Plateau, through northern Guangxi, to the Nanling Mountains, high-hotspot areas were densely distributed but had low overlap with existing protected areas. In South and Southeast Asia, mountainous regions and island chains generally suffered from sparse and insufficient protection coverage. Specifically, the Western Ghats-Sri Lanka region, the mountain belt from Myanmar to Vietnam, the core ecological areas of the Malay Archipelago, and parts of the Philippines all exhibited conservation gaps. Large areas in eastern and south-central New Guinea were almost entirely uncovered by the protected area system. Notable gaps also occurred around the Cameroon Volcanic Line in west-central Africa and on the western side of the East African Rift, as well as in northern South America to the central Amazon basin, and from southern Mexico to northern Central America. Overall, substantial room for improvement exists in southern China, the Southeast Asian island-continent transition zone, the Andean Amazon interface, and the eastern East African Rift.

Currently, protected areas cover only 7.169% of global land, and the average protected proportion of freshwater crab distributions is only about 30% (Figure 4A). Under the 17% target, the average protected proportion rises to about 59%, that is a 9.8% increase roughly doubling coverage. Under the 30% target, the increase slows, indicating diminishing marginal gains (Figure 4B). As the target increases, conservation rates for species (especially narrow-ranged ones) improve markedly (Figure 4C–E).

For PD, current protected areas cover only 28.86% of high-PD hotspots. Expanding to 17% of global land would increase this to 64.68%; at 30%, all high-PD hotspots become fully protected. Overall coverage across the entire distribution would reach 40.31% and 53.32% under the 17% and 30% targets, respectively (Figure S6). Compared with SR, PD-based priorities focus more on unique evolutionary histories; the two hotspot types overlap in some regions but differ in others. Current protected areas insufficiently cover both SR and PD, but an expansion strategy based on priority areas can efficiently enhance protection for both dimensions. PD hotspots can be fully protected under a relatively low target, reflecting higher area efficiency for safeguarding evolutionary history.

In addition, we calculated the EDGE2 index for each species to identify lineages that combine high evolutionary distinctiveness with elevated extinction risk. EDGE2 values ranged from 0.0079 to 15.1421 (average = 1.4942). Using the global median as the threshold, we identified 71 EDGE species (Table S2). The spatial distribution of mean EDGE2 revealed a highly aggregated pattern, with the high values concentrated in Southern India and Sri Lanka (Figure S7). Additional high-value grid cells were sporadically distributed across Southeast Asia, the Greater Antilles, southern Africa and eastern South America, indicating that evolutionarily distinct and threatened lineages are scattered across multiple tropical and subtropical freshwater systems worldwide. In contrast, high-PD regions such as Southeast China exhibited lower EDGE2, indicating that their rich evolutionary history is

not accompanied by immediate high extinction risk at the current stage.

Globally, the newly identified conservation priority areas are unevenly distributed and mainly complement the peripheral zones of existing protected areas. These areas are most dense in tropical and subtropical regions, particularly in Central America, northern South America, tropical Africa and parts of Southeast and East Asia, exhibiting patchy or banded aggregation patterns. In contrast, in temperate and high-latitude regions, they appear as isolated or fragmented patches within or around existing protected areas (Figure 4A). Overall, the existing protected area network is highly uneven, and the newly identified priority areas could significantly expand the coverage of the protected area network for the distribution ranges of freshwater crabs.

4 | Discussion

4.1 | Determinants of Global Biodiversity Hotspots of Freshwater Crabs

Global hotspots of freshwater crab SR are highly aggregated in tropical and subtropical regions, including Central America, northern South America, Southeast Asia, southern China and adjacent island systems (Figure 2A). Our hotspot map generally aligns with that of Alves et al. (2024), who identified northern South America, the Western Ghats-Sri Lanka and southwestern China as global centres of high richness. However, Alves et al. (2024) showed more extensive high-diversity areas in northern South America, likely because their analyses relied on IUCN range maps, which are often coarsely defined and may overestimate species distributions. In China, our study reveals higher SR and a broader geographic range in southwestern China, attributable to the inclusion of more comprehensive distribution data for Chinese freshwater crabs. Nevertheless, we acknowledge that while these additional data greatly improve the representation of species distributions in China, they also potentially introduce geographic imbalances, with sampling unevenly concentrated in certain regions. Additionally, the 16S rRNA gene offers the broadest taxonomic coverage and a suitable evolutionary rate for relaxed-clock estimation among freshwater crabs, making it the pragmatic choice given sparse multi-locus data (Cumberlidge and Daniels 2022; Daniels et al. 2015; Klaus et al. 2014; Schubart 2021). However, single-locus phylogenies are susceptible to gene-tree/species-tree discordance (Maddison 1997) and limited phylogenetic information from short fragments (Chan et al. 2022), which may compromise resolution. These caveats should be considered when interpreting our global-scale results.

SR hotspots don't completely overlap with phylogenetic clustering hotspots (Figure S5). Using $SES.PD < -7$ as the threshold, we identified eight extreme phylogenetic clustering grid cells: four at 27°N (spanning glacial refugia in southern China), two at 31°N (located in a canyon-interlaced topographic transition zone), and two in Taiwan island and surrounding areas (where continental species invaded via land bridges during glacial periods). In contrast, SR hotspots cover a much broader tropical-subtropical region, and only a few grids reach the extreme $SES.PD$ threshold. This spatial inconsistency suggests that the

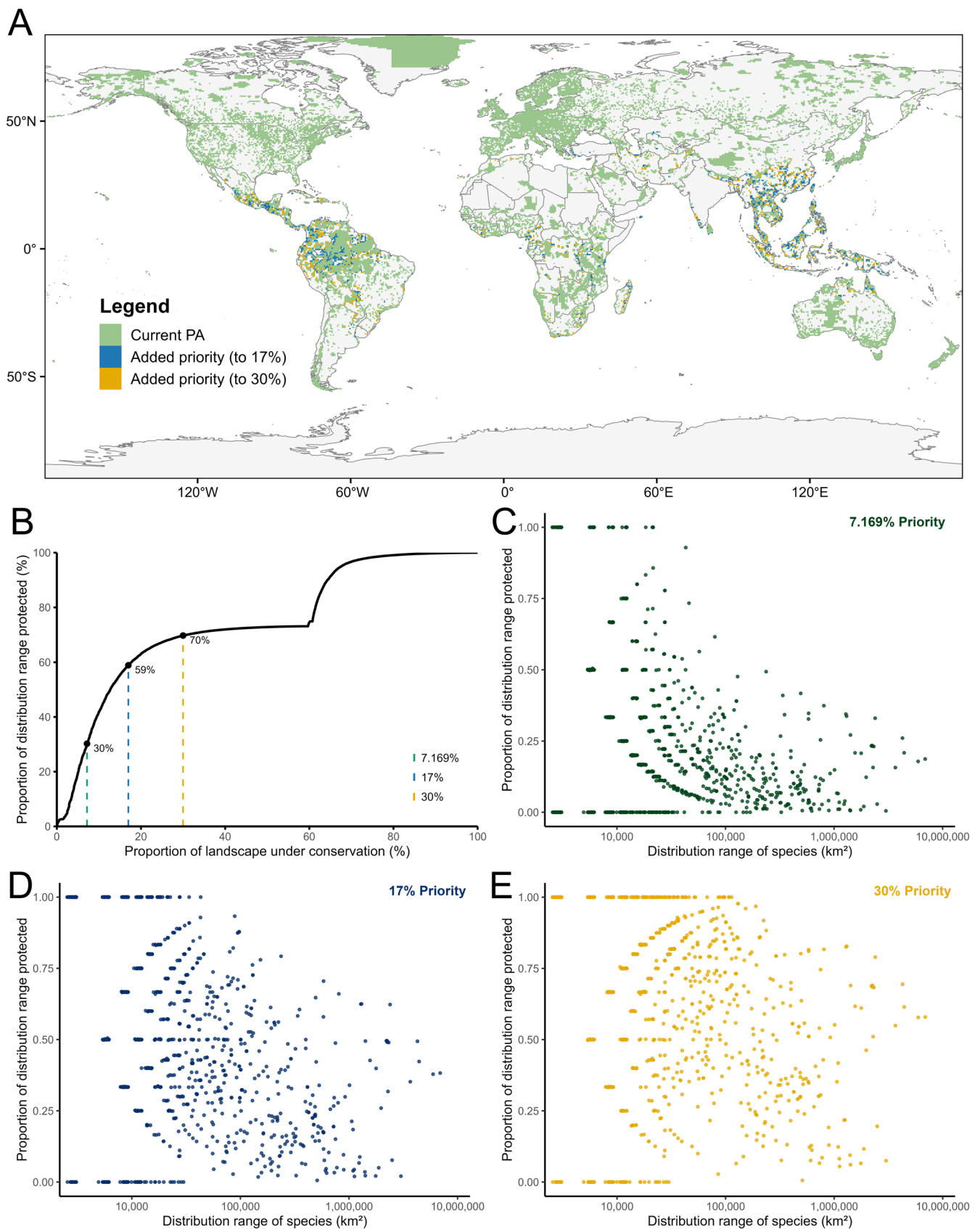


FIGURE 4 | Legend on next page.

intensity of phylogenetic clustering is governed by complex factors rather than simply by species number (Shi et al. 2024; Magneville et al. 2025).

Mountain systems play a crucial role in shaping these patterns. Most hotspots coincide with major mountain ranges characterized by pronounced elevational gradients and complex river

FIGURE 4 | Distribution of protected areas based on spatial priority analysis and coverage performance curves for freshwater crab species. Spatial distribution of existing nature reserves (green) covering 7.169% of the region, 17% conservation target priority areas (blue) covering about 9.8%, and 30% conservation target priority areas (yellow) covering about 13% (A). Coverage performance curves for freshwater crab species under different conservation scenarios, with the x-axis representing the proportion of protected grids and the y-axis representing the mean species coverage range, comparing the effectiveness of the current nature reserve network (7.169%) with that of the 17% and 30% conservation target priority areas (B). Scatter plot showing the distribution ranges of species and the coverage proportion of protected areas under current nature reserves and target priority areas (C–E).

networks. Freshwater crabs have limited dispersal abilities, mountains act as barriers that restrict gene flow and promote in situ diversification (Hughes et al. 2009; Shih and Ng 2011; Shih et al. 2011; Dias et al. 2014). High-elevation habitats isolated by unsuitable low-elevation environments form ‘sky islands’, further enhancing endemism and lineage differentiation (Rahbek et al. 2019). The admixture of lineages that evolved independently on different sky islands (e.g., Wanshi Mountain, Qitianling) can increase mean pairwise phylogenetic distance within communities (Pearse et al. 2013; Hedin et al. 2015). Our spaMM analysis confirms the importance of stable hydrothermal conditions, BIO12 and NDVI have significantly positive effects on both SR and PD, whereas BIO15 and BIO17 show significantly negative effects. Temperate, arid and high-latitude regions exhibit no clear hotspot signals, further indicating that freshwater crab diversity is jointly constrained by geological conditions and hydroclimatic factors (Figure 3B,C).

Approximately 41 Ma, the uplift of the Qinghai-Tibet Plateau and global cooling drove the northward advance of the Asian monsoon (Wu et al. 2022). Since then, the monsoon has dominated a vast area from the Indian subcontinent to Southeast and East Asia (Lu and Ning 2026). In Asia, biodiversity hotspots are mainly concentrated in regions long influenced by this monsoon system and characterized by complex geological histories (Spicer et al. 2025; Shi et al. 2025).

Monsoon intensification provided stable water supply to stream ecosystems. This mechanism is not unique to freshwater crabs: East Asian endemic cyprinid fishes originated during the monsoon period, and their rapid radiation is closely linked to monsoon-driven hydrological connectivity (Feng et al. 2023). Similarly, a phylogeographic study of *Sinopotamon yangtsekiense* found that lineage divergence across the Qinling-Huaihe Line is significantly correlated with Pleistocene monsoon intensity changes (Shi et al. 2021).

Mountains amplify the effects of the monsoon through geographic isolation. The strong orogeny and river valley incision in the Hengduan Mountains have created highly heterogeneous topography and numerous isolated watershed units, promoting lineage differentiation (Clark et al. 2004; Min et al. 2023). Analogous patterns have been observed in other taxa: population differentiation of the mammal *Neotetracus sinensis* in the Hengduan Mountains shows extreme genetic divergence between Gaoligong and Wuliang Mountain populations (Zhou et al. 2026). Our results further show that temperature annual range (BIO7) has a significantly negative effect on SR but a significantly positive effect on PD (Figure 3B,C), suggesting that historical climatic fluctuations promoted phylogenetic divergence while limiting local species accumulation.

Southeast Asia lacks high mountains, Pleistocene sea-level fluctuations created temporary land connections, making its diversity shaped more by repeated colonization and extinction than by long-term in situ diversification (Sholihah et al. 2021). This is consistent with our observation that SES.PD values in Southeast Asia are generally not significantly positive (Figure S5). Similarly, population migration of *Polypedates* between Borneo and the Malay Peninsula has been attributed to successive land connections during mid-Pleistocene fluctuations (Yuan et al. 2021). The significant negative effect of BIO15 on both SR and PD in our analysis further implies that highly seasonal hydrological regimes limit lineage persistence and phylogenetic accumulation in this region.

In the Western Ghats of India, freshwater crab endemism reaches 92%, with 39 gecarcinucid species across 14 genera (Raghavan et al. 2015). This region has experienced species differentiation influenced by both monsoon and geological processes. Sidharthan et al. (2020) found that Miocene southwest monsoon intensification triggered dispersal of endemic mountain *loaches*, and subsequent aridification disrupted river connections, promoting differentiation. Our results show relatively high PD values and moderately clustered SES.PD in the Western Ghats—Sri Lanka, suggesting a history of balanced lineage diversification. The significant negative effect of BIO17 on both SR and PD aligns with the view that seasonal drought fragments stream habitats, thereby enhancing allopatric speciation and endemism.

In the Neotropical realm, extensive hotspots in Central America and northern South America result from complex topography, dense river networks, and long-term humid climates. Highly fragmented watersheds and historical river rearrangements have promoted population isolation, resulting in numerous narrowly distributed endemic lineages (Albert et al. 2011; Dagosta and de Pinna 2017). The two Neotropical families (Pseudothelphusidae and Trichodactylidae) comprise 311 species distributed across almost all Neotropical countries. New species continue to be discovered in the Andean foothills, such as a new *Hypolobocera* species from the Cauca River basin, highlighting the role of topographic complexity in driving speciation (Campos and Alexander 2024).

In the Afrotropical realm, freshwater crab hotspots are scattered, locally high-value areas rather than continuous large-scale hotspots, reflecting watershed scale and river system connectivity (Cumberlidge et al. 2009). Lake Tanganyika harbours at least 1500 freshwater species, yet its diversity distribution remains discontinuous (Marijnissen et al. 2009). Similarly, the three Albertine Rift endemic species described by Cumberlidge and Clark (2018) are each restricted to specific areas. These findings

reveal that in African mountainous regions, where topographic relief is enhanced and watersheds are fragmented, localized isolation processes can promote population differentiation even at relatively small spatial scales.

Overall, Global hotspots show that mountains and stable hydro-thermal conditions promote lineage persistence and speciation in regions with limited dispersal and fragmented habitats. The Asian monsoon shapes Asian biodiversity, while the Neotropics and Afrotropics exhibit different topographic and hydrological combinations. Given that freshwater crabs are characterized by high endemism and restricted distribution ranges (Cumberlidge et al. 2009; Yeo et al. 2008), their strong concentration of diversity in a few hotspot areas has important implications for understanding the evolutionary processes of global freshwater biodiversity and for setting conservation priorities and spatial planning for freshwater taxa.

4.2 | Responses of Diversity to Changes in Biotic and Abiotic Factors

Understanding how freshwater crab diversity responds to climate and human activities is key for conservation decisions (Lu et al. 2020; Bernard et al. 2024; Yang et al. 2024). Stable precipitation ensures year-round stream flow, facilitating gene exchange and regional coexistence. In our research, BIO12 had a significantly positive effect on SR, indicating that water availability strongly influences crab distribution, consistent with high-SR areas being concentrated in humid tropical and subtropical regions (Figure 3B). Alves et al. (2024) did not find a significant effect of annual precipitation in their global model, possibly because they used upstream annual precipitation rather than the grid-extracted BIO12 used here. In contrast, BIO15 and BIO17 showed significantly negative effects on SR (Figure 3B), highly consistent with Alves et al. (2024), who identified precipitation seasonality as the strongest negative predictor ($b = -0.181$, $p < 0.001$). These results suggest that increased intra-annual water fluctuation and dry-season scarcity weaken habitat continuity, hindering stable richness patterns of freshwater crabs at regional scales. Ng et al. (2015) found that acid precipitation reduces SR via stream acidification, showing that water resources affect SR not only through abundance or scarcity but also through physicochemical properties. Changes in precipitation patterns may jointly affect stream flow volume and water quality, potentially exerting a synergistic effect on freshwater crab diversity.

HFP shows a significant positive correlation with SR, likely reflecting spatial overlap between high-biodiversity areas and long-term human settlement rather than a direct promoting effect of human activities (Ellis et al. 2010; Vörösmarty et al. 2010). Alves et al. (2024) globally found that high freshwater crab richness concentrates in heavily impacted regions, consistent with our observation. Similarly, Mecenero et al. (2015) reported a positive correlation between butterfly SR and human density in South Africa, possibly because areas with high SR also have favourable geological and climatic conditions that attract human settlement. However, spatial correlation does not imply causality, and local scales often show different effects (Alves et al. 2024). Guo et al. (2019) found that natural factors such

as precipitation, temperature and surface water dominate fish community composition, but freshwater fish SR is negatively correlated with urbanization. The Colombian endemic crab *Strengeriana fuhrmanni* has lost more than 50% of its original range due to urbanization-driven green space reduction (Rivera-Pérez et al. 2023). These comparisons suggest that aquatic animals exhibit taxon-specific and spatial-scale differences in habitat response, and freshwater crabs may have higher adaptability to certain levels of habitat disturbance.

PD showed significantly positive correlations with BIO12 and NDVI (Figure 3C). Increased precipitation seasonality and dry-season water scarcity were negatively associated with PD, indicating that stable hydrological conditions and high vegetation cover favour high PD. da Silva et al. (2012) found similar humidity effects on amphibian PD in the Brazilian Atlantic Forest. BIO7 had a significantly positive effect on PD (Figure 3C), suggesting that larger temperature fluctuations may promote lineage differentiation or coexistence of lineages with different adaptive strategies. Supporting this, Gunkel and Daniels (2024) showed that climate oscillations drove phylogenetic differentiation in the South African freshwater crab *Potamonautes mariepskopie*, with seasonal precipitation and temperature variation as key drivers. In contrast, PD showed a weak, non-significant response to the HFP index, indicating that at the current analytical scale, recent human activities have not yet translated into detectable changes in phylogenetic structure (Mazel et al. 2020).

In summary, our research demonstrates that freshwater crab diversity is jointly influenced by hydrological conditions, climatic stability, topographic structure, and human activities, with different diversity dimensions having distinct drivers. SR mainly reflects the influence of current ecological conditions and landscape structure, whereas PD is more indicative of long-term environmental stability and evolutionary history. The spatial patterns of SR and PD don't fully overlap. Some regions exhibited high values for both SR and PD, indicating that they are not only important areas for recent species accumulation but also refugia for deep evolutionary lineages. Relying solely on SR may underestimate the importance of phylogenetic structure; therefore, conservation practice should incorporate both SR and PD to more comprehensively reflect regional conservation value.

4.3 | Spatial Conservation Priority Areas

Freshwater crabs have long life cycles and high sensitivity to habitat conditions, making them important indicators of freshwater ecosystem integrity (Cumberlidge et al. 2009; Yeo et al. 2008). Nevertheless, non-flagship taxa like freshwater crabs remain marginalized in conservation planning. Previous studies have assessed their distribution and threat status (Cumberlidge et al. 2009, 2014; Alves et al. 2024), but systematic global analyses of conservation coverage and spatial priorities are still limited. Our research shows that under the current protected area network, the average protected proportion of freshwater crab distribution ranges is less than half (Figure 4), indicating notable deficiencies. Raghavan et al. (2015) found that only seven of 40 conservation priority sites for Western Ghats decapods were within protected areas, and over half of species were Data Deficient. Acreman

et al. (2020) reported that only 51% of protected areas effectively conserve freshwater biodiversity. Sinclair et al. (2025) found no difference in biodiversity change between protected and unprotected upstream sites. Together, these results suggest that protected area systems established primarily for terrestrial ecosystems are insufficient to adequately conserve freshwater taxa that depend on hydrological networks (Abell et al. 2007; Vörösmarty et al. 2010).

Zonation analysis shows that optimizing the spatial configuration of protected areas can significantly improve conservation effectiveness for freshwater crabs. There is a logarithmic relationship between conservation coverage and species coverage gain. Currently, protected areas cover only 30% of freshwater crab distribution ranges. Increasing protected area proportion to 17% would raise species coverage to 59%, roughly doubling it. Further increasing the conservation target to 30% yields only 70% species coverage, with a marked slowdown (Figure 4B). Beyond that, the coverage gain flattens, reflecting the trade-off between species spatial aggregation and protected area expansion efficiency (Venter et al. 2014; Di Marco et al. 2019). Green and Ostling (2003) found that high species aggregation increases extinction risk, illustrating that as protected areas expand, remaining populations are scattered and peripheral, so additional area yields diminishing gains. Hermoso et al. (2015b) argued that by prioritizing areas under different management regimes and considering connectivity requirements, the total area requiring strict protection could be reduced threefold, lowering costs and improving efficiency. This suggests that systematic conservation planning based on species distribution patterns and spatial priorities is more efficient than simply expanding area (Moilanen et al. 2005; Lehtomäki and Moilanen 2013).

EDGE2 analysis indicates that southern India and Sri Lanka need to urge protection. The extreme EDGE2 value of *Perbrinckia cracens* (EDGE2=15.1421) highlights that in some regions, particularly isolated island systems like Sri Lanka, a single species can represent over 15 million years of unique evolutionary history. This underscores the concept of 'Conservation Triage', protecting a single CR species in Sri Lanka may safeguard more irreplaceable evolutionary heritage than protecting hundreds of LC species elsewhere (Marris 2007; Bottrill et al. 2008). A parallel EDGE2 assessment of freshwater crayfish found 10.401% priority species but concentrated in Australia, contrasting with our crab hotspots in southern India and Sri Lanka, suggesting that taxon-specific planning is essential and no single region can represent all freshwater decapod evolutionary priorities (Pipins et al. 2026).

Compared to SR analysis, PD-oriented conservation priority areas show higher marginal efficiency per unit area. Regions with high PD values that are currently not protected are primarily concentrated in Southeast Asia. Also scattered throughout southern North America, northern and eastern South America, and southern Africa. These regions exhibit the strongest mismatch between high PD and low current protection, representing urgent opportunities for expanding protected area networks to safeguard evolutionarily distinct freshwater crab lineages.

Our analysis further demonstrates that PD-based spatial optimization can efficiently capture evolutionary history, with the 17% target alone covering nearly two-thirds of existing high-PD hotspots. With only moderate expansion of protected areas, most high-PD hotspots can be covered, ultimately achieving full protection across 30% of the world's land area (Figure S6). This supports Pollock et al. (2015) in that small but strategically located areas disproportionately preserve evolutionary lineages. PD is highly aggregated in space. Baselga et al. (2025) noted that phylogenetic endemism is the most efficient single criterion to maximize global PD within the smallest land area. Gumbs et al. (2020), studying reptilian PD, found that areas with highest human pressure coincide with highest irreplaceability. Our study based on freshwater crabs further validates the generality of this pattern in freshwater biotic groups.

The newly identified conservation priority areas were mainly concentrated in tropical and subtropical regions, particularly Central America, northern South America, tropical Africa, and parts of Southeast and East Asia. These areas lie on the periphery of existing nature reserves or remain inadequately covered, and they simultaneously exhibit high freshwater crab diversity potential but relatively low conservation investment. In contrast, the distribution of priority areas in temperate and high-latitude regions was relatively scattered and fragmented, reflecting the wider distribution ranges and stronger spatial continuity of freshwater crabs in these regions, as well as the relatively dispersed layout of existing protected areas.

4.4 | Implications for Freshwater Crab Conservation

Under the global biodiversity governance framework, Aichi Target 11 of the Convention on Biological Diversity and the Kunming-Montreal Global Biodiversity Framework set protection targets of at least 17% and 30% for terrestrial and inland water areas, respectively (CBD 2010, 2022). Arneth et al. (2023) questioned simple percentage targets, suggesting that improving protected area effectiveness would help slow biodiversity loss. Pimm et al. (2018) and Mogg et al. (2019) found that even under the highest effectiveness, about half of terrestrial protected areas would not cover all plant or mammal species. Our study shows that simply expanding protection domain doesn't proportionally increase conservation effectiveness. Combining percentage targets with spatial priority identification improves representative coverage of species' ranges (Shi et al. 2025). Whether a protected area network achieves its goals depends on coverage proportion, spatial configuration, and management effectiveness (Watson et al. 2014; Venter et al. 2018). Overall, protective priority areas effectively compensate for insufficient coverage of existing protected areas over freshwater crab distributions, improving ecological representativeness at the global scale. The results show significant spatial differences between diversity dimensions, indicating that single-dimension assessments may not fully reflect conservation value. Future planning should prioritize areas with high PD, especially those without the highest SR but with unique evolutionary histories or genetic structures.

Author Contributions

Wanna Wu: writing – original draft, writing – review and editing, visualization, formal analysis, data curation, investigation. **Bing Wang:** writing – original draft, writing – review and editing, visualization, formal analysis, data curation, investigation. **Zhaomin Zhu:** formal analysis. **Ruxiao Wang:** writing – review and editing, formal analysis. **Boyang Shi:** writing – review and editing, formal analysis. **Zhen Wang:** writing – review and editing, formal analysis. **Hongying Sun:** writing – review and editing, supervision, investigation, conceptualization. **Da Pan:** writing – review and editing, investigation, supervision, methodology, conceptualization.

Acknowledgements

The authors are grateful to everyone who has offered their help and support in the more than 20 years of fieldwork. This work was supported by the National Natural Science Foundation of China (No. 32470460 to D. Pan; 32170454 to H. Sun). Z.W. acknowledges the financial support from the National Lab of Solid State Microstructures, Nanjing University (No. M38067).

Funding

This work was supported by the National Natural Science Foundation of China (32470460, 32170454) and the National Lab of Solid State Microstructures, Nanjing University (M38067).

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Freshwater crab occurrence records were obtained from the Global Biodiversity Information Facility (GBIF, <https://www.gbif.org>) separately for each family (Decapoda: <https://doi.org/10.15468/dl.cr3qb3>; Epilobocera: <https://doi.org/10.15468/dl.fkbc2s>; Gecarcinidae: <https://doi.org/10.15468/dl.4bz83t>; Potamidae: <https://doi.org/10.15468/dl.pgcesk>; Potamonautidae: <https://doi.org/10.15468/dl.yaufj4>; Pseudothelphusidae: <https://doi.org/10.15468/dl.n2wshk>; Trichodactylidae: <https://doi.org/10.15468/dl.8khn3y>), the IUCN Red List of Threatened Species (<https://www.iucnredlist.org>, accessed December 2024), and the authors' own field surveys. The cleaned occurrence datasets are accessible through the Dryad Digital Repository (<https://doi.org/10.5061/dryad.3n5tb2s17>). Climate data were sourced from WorldClim v2.1 (<http://www.worldclim.org>). Topographic data were obtained from the Geospatial Data Cloud platform of the Chinese Academy of Sciences (<http://www.gscloud.cn>). Vegetation cover data were derived from the PKU GIMMS Normalized Difference Vegetation Index (Li et al. 2023). Human activity data were sourced from the ESA CCI Land Cover Map (ESA 2017), the Global Roads Inventory Project (GRIP) v4 (Meijer et al. 2018), HydroRIVERS v1.0 (Lehner and Grill 2013) and a global annual terrestrial human footprint dataset (2000–2018) developed by Mu et al. (2022). Global protected area data were obtained from the World Database on Protected Areas (WDPA, <https://www.protectedplanet.net/en>). Mitochondrial 16S rRNA gene sequences were obtained from GenBank. The resulting sequence alignments have been deposited in the Dryad Digital Repository (<https://doi.org/10.5061/dryad.3n5tb2s17>).

References

- Abell, R., J. D. Allan, and B. Lehner. 2007. "Unlocking the Potential of Protected Areas for Freshwaters." *Biological Conservation* 134: 48–63.
- Acreman, M., K. A. Hughes, A. H. Arthington, D. Tickner, and M. A. Dueñas. 2020. "Protected Areas and Freshwater Biodiversity: A Novel

Systematic Review Distills Eight Lessons for Effective Conservation." *Conservation Letters* 13: e12684.

Albert, J. S., G. Destouni, S. M. Duke-Sylvester, et al. 2021. "Scientists' Warning to Humanity on the Freshwater Biodiversity Crisis." *Ambio* 50: 85–94.

Albert, J. S., P. Petry, and R. E. Reis. 2011. *Major Biogeographic and Phylogenetic Patterns*, 21–57. University of California Press.

Alves, D. F. R., P. A. Martinez, C. Magalhães, S. P. Barros-Alves, A. C. de Almeida, and T. F. Amado. 2024. "Global Patterns and Predictors of Primary Freshwater Crab Richness Across Taxa and Realms." *Hydrobiologia* 851: 4149–4165.

Arneth, A., P. Leadley, J. Claudet, et al. 2023. "Making Protected Areas Effective for Biodiversity, Climate and Food." *Global Change Biology* 29: 3883–3894.

Balian, E. V., H. Segers, C. Lévêque, and K. Martens. 2008. "The Freshwater Animal Diversity Assessment: An Overview of the Results." *Hydrobiologia* 595: 627–637.

Baselga, A., R. Martín-Devasa, and C. Gómez-Rodríguez. 2025. "Areas of High Biodiversity Value Evidenced by the Spatial Scaling of Phylogenetic Uniqueness." *Ecology Letters* 28, no. 7: e70179.

Bernard, A., H. Fritz, A. B. Dufour, J. A. Venter, and C. Guerbois. 2024. "A Local Ecological Knowledge-Based Assessment of Anthropodependence for Large Mammals in Anthropogenic Landscapes." *Biological Conservation* 290: 110450.

Bottrill, M., L. Joseph, J. Carwardine, et al. 2008. "Is Conservation Triage Just Smart Decision Making?" *Trends in Ecology & Evolution* 23: 649–654.

Bouckaert, R., T. G. Vaughan, J. Barido-Sottani, et al. 2019. "BEAST 2.5: An Advanced Software Platform for Bayesian Evolutionary Analysis." *PLoS Computational Biology* 15, no. 4: e1006650.

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

Burley, F. W. 1988. "Monitoring Biological Diversity for Setting Priorities in Conservation." In *Biodiversity*, edited by E. O. Wilson, 227–230. National Academy Press.

Campos, M. R., and M. Alexander. 2024. "A New Species of Freshwater Crab of the Genus *Hypolobocera* ortmann, 1897 From Colombia (Crustacea: Decapoda: Pseudothelphusidae), Including a Key to the Species of the Genus Distributed in Colombia." *Zootaxa* 20, no. 5453: 282–290.

CBD. 2010. *Strategic Plan for Biodiversity 2011–2020 and the Aichi Biodiversity Targets*. Convention on Biological Diversity.

CBD. 2022. *Kunming-Montreal Global Biodiversity Framework*. Convention on Biological Diversity.

Chakraborty, A., G. K. Saha, and G. Aditya. 2022. "Macroinvertebrates as Engineers for Bioturbation in Freshwater Ecosystem." *Environmental Science and Pollution Research* 29: 64447–64468.

Chan, K. O., S. T. Hertwig, D. N. Neokleous, J. M. Flury, and R. M. Brown. 2022. "Widely Used, Short 16S rRNA Mitochondrial Gene Fragments Yield Poor and Erratic Results in Phylogenetic Estimation and Species Delimitation of Amphibians." *BMC Ecology and Evolution* 22: 37.

Clark, M. K., L. M. Schoenbohm, L. H. Royden, et al. 2004. "Surface Uplift, Tectonics, and Erosion of Eastern Tibet." *Geology* 32: 525–528.

Collier, K. J., P. K. Probert, and M. Jeffries. 2016. "Conservation of Aquatic Invertebrates: Concerns, Challenges and Conundrums." *Aquatic Conservation: Marine and Freshwater Ecosystems* 26: 817–837.

Costa, L., W. Kiffer Jr., C. Casotti, et al. 2016. "Influence of *Trichodactylus fluviatilis* on Leaf Breakdown in Streams: Understanding the Role of Freshwater Crabs in Detritus-Based Food Webs." *Zoological Studies* 55: e54.

- Cumberlidge, N., F. Alvarez, and J. L. Villalobos. 2014. "Results of the Global Conservation Assessment of the Freshwater Crabs (Brachyura, Pseudothelphusidae and Trichodactylidae): The Neotropical Region, With an Update on Diversity." *ZooKeys* 457: 133–157.
- Cumberlidge, N., and P. F. Clark. 2018. "Albertine Rift Valley Endemics: Three New Species of Freshwater Crabs (Brachyura: Potamoidea: Potamonautidae) From Uganda, The Democratic Republic of the Congo, and Rwanda." *Journal of Natural History* 52, no. 25–26: 1637–1656.
- Cumberlidge, N., and S. R. Daniels. 2022. "A New Multilocus Phylogeny Reveals Overlooked Diversity in African Freshwater Crabs (Brachyura: Potamoidea): A Major Revision With New Higher Taxa and Genera." *Zoological Journal of the Linnean Society* 194: 1268–1311.
- Cumberlidge, N., P. K. L. Ng, D. C. J. Yeo, et al. 2009. "Freshwater Crabs and the Biodiversity Crisis: Importance, Threats, Status, and Conservation Challenges." *Biological Conservation* 142: 1665–1673.
- da Silva, F. R., M. Almeida-Neto, V. H. M. do Prado, et al. 2012. "Humidity Levels Drive Reproductive Modes and Phylogenetic Diversity of Amphibians in the Brazilian Atlantic Forest." *Journal of Biogeography* 39: 1720–1732.
- Dagosta, F., and M. de Pinna. 2017. "Biogeography of Amazonian Fishes: Deconstructing River Basins as Biogeographic Units." *Neotropical Ichthyology* 15: e170034.
- Daniels, S. R., E. E. Phiri, S. Klaus, C. Albrecht, and N. Cumberlidge. 2015. "Multilocus Phylogeny of the Afrotropical Freshwater Crab Fauna Reveals Historical Drainage Connectivity and Transoceanic Dispersal Since the Eocene." *Systematic Biology* 64: 549–567.
- De'ath, G., and K. E. Fabricius. 2000. "Classification and Regression Trees: A Powerful Yet Simple Technique for Ecological Data Analysis." *Ecology* 81: 3178–3192.
- Di Marco, M., O. Venter, H. P. Possingham, et al. 2019. "Changes in Human Footprint Drive Changes in Species Extinction Risk." *Nature Communications* 10: 4621.
- Dias, M. S., J. F. Cornu, T. Oberdorff, J. F. Cornu, C. A. Lasso, and P. A. Tedesco. 2014. "Natural Fragmentation in River Networks as a Driver of Speciation for Freshwater Fishes." *Ecography* 37: 683–689.
- Drummond, A. J., S. Y. W. Ho, M. J. Phillips, and A. Rambaut. 2006. "Relaxed Phylogenetics and Dating With Confidence." *PLoS Biology* 4, no. 5: e88.
- Dudgeon, D., and D. L. Strayer. 2025. "Bending the Curve of Global Freshwater Biodiversity Loss: What Are the Prospects?" *Biological Reviews* 100: 205–226.
- 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: 677–697.
- Ellis, E. C., K. K. Goldewijk, S. Siebert, et al. 2010. "Anthropogenic Transformation of the Biomes, 1700 to 2000." *Proceedings of the National Academy of Sciences of the United States of America* 107: 12904–12910.
- ESA. 2017. "Land Cover CCI Product User Guide Version 2. Tech. Rep." http://maps.elie.ucl.ac.be/CCI/viewer/download/ESACCI-LC-Ph2-PUGv2_2.0.pdf.
- ESRI. 2011. "ArcGIS Desktop: Release 10. Environmental Systems Research Institute."
- Faith, D. P. 1992. "Conservation Evaluation and Phylogenetic Diversity." *Biological Conservation* 61: 1–10.
- Faith, D. P. 2021. "Valuation and Appreciation of Biodiversity: The 'Maintenance of Options' Provided by the Variety of Life." *Frontiers in Ecology and Evolution* 9: 635670.
- Fan, H., T. Liu, Y. Chen, et al. 2024. "Geographical Patterns and Determinants of Insect Biodiversity in China." *Science China Life Sciences* 67: 1255–1265.
- Feng, C., K. Wang, W. Xu, et al. 2023. "Monsoon Boosted Radiation of the Endemic East Asian Carps." *Science China Life Sciences* 66: 563–578.
- Fick, S. E., and R. J. Hijmans. 2017. "WorldClim 2: New 1km Spatial Resolution Climate Surfaces for Global Land Areas." *International Journal of Climatology* 37: 4302–4315.
- Friedman, J. H. 1991. "Multivariate adaptive regression splines." *Annals of Statistics* 19: 1–67.
- Gary, D., K. Mougey, N. E. McIntyre, et al. 2019. "Identification of Hotspots of At-Risk Terrestrial Vertebrate Species in the South-Central Great Plains of North America: A Tool to Inform and Address Regional-Scale Conservation." *Journal for Nature Conservation* 50: 125684.
- Geist, J. 2011. "Integrative Freshwater Ecology and Biodiversity Conservation." *Ecological Indicators* 11: 1507–1516.
- Green, J. L., and A. Ostling. 2003. "Endemics-Area Relationships: The Influence of Species Dominance and Spatial Aggregation." *Ecology* 84: 3090–3097.
- Guéguen, M., H. Blancheteau, R. Lemaire-Patin, et al. 2026. "biomod2: Ensemble Platform for Species Distribution Modeling."
- Guisan, A., R. Tingley, J. B. Baumgartner, et al. 2013. "Predicting Species Distributions for Conservation Decisions." *Ecology Letters* 16: 1424–1435.
- Gumbs, R., C. L. Gray, M. Böhm, et al. 2020. "Global Priorities for Conservation of Reptilian Phylogenetic Diversity in the Face of Human Impacts." *Nature Communications* 11: 2616.
- Gumbs, R., C. L. Gray, M. Böhm, et al. 2023. "The EDGE2 Protocol: Advancing the Prioritisation of Evolutionarily Distinct and Globally Endangered Species for Practical Conservation Action." *PLoS Biology* 21: e3001991.
- Gunkel, K. G. R., and S. R. Daniels. 2024. "Plio/Pleistocene-Induced Climatic Oscillations Drive Cladogenesis in a High-Altitude Freshwater Crab, *Potamonautes mariepskoppie* (Decapoda: Potamonautidae), in South Africa." *Biological Journal of the Linnean Society* 143, no. 3: bla098.
- Guo, C., Y. Chen, R. E. Gozlan, et al. 2019. "Biogeographic Freshwater Fish Pattern Legacy Revealed Despite Rapid Socio-Economic Changes in China." *Fish and Fisheries* 20: 857–869.
- Hedin, M., D. Carlson, and F. Coyle. 2015. "Sky Island Diversification Meets the Multispecies Coalescent – Divergence in the Spruce-Fir Moss Spider (*Microhexura montivaga*, Araneae, Mygalomorphae) on the Highest Peaks of Southern Appalachia." *Molecular Ecology* 24: 3467–3484.
- Hermoso, V., L. Cattarino, M. J. Kennard, M. Watts, and S. Linke. 2015b. "Catchment Zoning for Freshwater Conservation: Refining Plans to Enhance Action on the Ground." *Journal of Applied Ecology* 52: 940–949.
- Hermoso, V., A. F. Filipe, P. Segurado, and P. Beja. 2015a. "Filling Gaps in a Large Reserve Network to Address Freshwater Conservation Needs." *Journal of Environmental Management* 161: 358–365.
- Hughes, J. M., D. J. Schmidt, and D. S. Finn. 2009. "Genes in Streams: Using DNA to Understand the Movement of Freshwater Fauna and Their Riverine Habitat." *Bioscience* 59: 573–583.
- IUCN. 2026. "The IUCN Red List of Threatened Species." Version 2026-2. <https://www.iucnredlist.org>.
- Jennings, M. D. 2000. "Gap Analysis: Concepts, Methods, and Recent Results." *Landscape Ecology* 15: 5–20.
- Katoh, K., and M. C. Frith. 2012. "Adding Unaligned Sequences Into an Existing Alignment Using MAFFT and LAST." *Bioinformatics* 28: 3144–3146.
- Katoh, K., and D. M. Standley. 2013. "MAFFT Multiple Sequence Alignment Software Version 7: Improvements in Performance and Usability." *Molecular Biology and Evolution* 30: 772–780.

- Kembel, S. W., P. D. Cowan, M. R. Helmus, et al. 2010. "Picante: R Tools for Integrating Phylogenies and Ecology." *Bioinformatics* 26: 1463–1464.
- Klaus, S., K. Fernandez, and D. C. J. Yeo. 2014. "Phylogeny of the Freshwater Crabs of the Western Ghats (Brachyura, Gecarcinucidae)." *Zoologica Scripta* 43: 651–660.
- Klaus, S., B. Singh, L. Hartmann, K. Krishan, A. Ghosh, and R. Patnaik. 2017. "A Fossil Freshwater Crab From the Pliocene Tatrot Formation (Siwalik Group) in Northern India (Crustacea, Brachyura, Potamidae)." *Palaeoworld* 26: 566–571.
- Kling, M. M., B. D. Mishler, A. H. Thornhill, B. G. Baldwin, and D. D. Ackerly. 2019. "Facets of Phylodiversity: Evolutionary Diversification, Divergence and Survival as Conservation Targets." *Philosophical Transactions of the Royal Society, B: Biological Sciences* 374: 20170397.
- Lehner, B., and G. Grill. 2013. "Global River Hydrography and Network Routing: Baseline Data and New Approaches to Study the World's Large River Systems." *Hydrological Processes* 27: 2171–2186.
- Lehtomäki, J., and A. Moilanen. 2013. "Methods and Workflow for Spatial Conservation Prioritization Using Zonation." *Environmental Modelling & Software* 47: 128–137.
- Li, M., S. Cao, Z. Zhu, Z. Wang, R. B. Myneni, and S. Piao. 2023. "Spatiotemporally Consistent Global Dataset of the GIMMS Normalized Difference Vegetation Index (PKU GIMMS NDVI) From 1982 to 2022." *Earth System Science Data* 15: 4181–4203.
- Lu, H., and L. Ning. 2026. "Initiation, Evolution and Variability of the Asian Monsoon Through the Cenozoic Era: Insights From the Successions of the Weihe Basin and Loess Plateau of Central China, and Beyond." *Palaeogeography, Palaeoclimatology, Palaeoecology* 682: 113406.
- Lu, Y., Y. Yang, B. Sun, et al. 2020. "Spatial Variation in Biodiversity Loss Across China Under Multiple Environmental Stressors." *Science Advances* 6: eabd0952.
- Maddison, W. P. 1997. "Gene Trees in Species Trees." *Systematic Biology* 46: 523–536.
- Magneville, C., M. Cartereau, J. A. Hernández-Agüero, et al. 2025. "Echoes of the Past: Long-Term Climate Stability Shapes Functional and Phylogenetic Diversity in Euro-Mediterranean Forests." *Global Ecology and Biogeography* 34: e70177.
- Marijnissen, S. A. E., E. Michel, D. F. R. Cleary, and P. B. McIntyre. 2009. "Ecology and Conservation Status of Endemic Freshwater Crabs in Lake Tanganyika, Africa." *Biodiversity and Conservation* 18: 1555–1573.
- Marris, E. 2007. "Conservation Priorities: What to Let Go." *Nature* 450: 152–155.
- Mazel, F., M. W. Pennell, M. W. Cadotte, et al. 2020. "Prioritizing Phylogenetic Diversity Captures Functional Diversity Unreliably." *Nature Ecology & Evolution* 4: 1477–1486.
- McCullagh, P., and J. A. Nelder. 1989. *Generalized Linear Models*. 2nd ed. Chapman and Hall.
- Mecenero, S., R. Altwegg, J. F. Colville, and C. M. Beale. 2015. "Roles of Spatial Scale and Rarity on the Relationship Between Butterfly Species Richness and Human Density in South Africa." *PLoS One* 10: e0124327.
- Meijer, J. R., M. A. J. Huijbregts, K. C. G. J. Schotten, and A. M. Schipper. 2018. "Global Patterns of Current and Future Road Infrastructure." *Environmental Research Letters* 13: 064006.
- Min, R., Y. Zhao, B. Kang, et al. 2023. "Vicariance and Monsoon as Drivers of Diversification of *Nemacheilid loaches* (Teleostei: Cypriniformes) Around the Hengduan Mountains of China." *Zoological Research* 44: 936–938.
- Ministry of Ecology and Environment of the People's Republic of China. 2016. "China Has 2,740 Nature Reserves." https://english.mee.gov.cn/News_service/media_news/201607/t20160705_357133.shtml.
- Mogg, S., C. Fastre, M. Jung, et al. 2019. "Targeted Expansion of Protected Areas to Maximise the Persistence of Terrestrial Mammals." *bioRxiv: the preprint server for biology*, 608992.
- Moilanen, A., A. M. A. Franco, R. I. Early, R. Fox, B. Wintle, and C. D. Thomas. 2005. "Prioritizing Multiple-Use Landscapes for Conservation: Methods for Large Multi-Species Planning Problems." *Proceedings of the Royal Society B* 272: 1885–1891.
- Moilanen, A., F. M. Pouzols, L. Meller, et al. 2014. *Zonation: Spatial Conservation Planning Methods and Software. Version 4.0. User Manual*. University of Helsinki.
- Mu, H., X. Li, Y. Wen, et al. 2022. "A Global Record of Annual Terrestrial Human Footprint Dataset From 2000 to 2018." *Scientific Data* 9: 176.
- Naimi, B., N. Hamm, T. A. Groen, N. A. S. Hamm, A. K. Skidmore, and A. G. Toxopeus. 2014. "Where Is Positional Uncertainty a Problem for Species Distribution Modelling." *Ecography* 37: 191–203.
- Ng, D. J. J., D. C. J. Yeo, N. Sivasothi, and P. K. L. Ng. 2015. "Conservation Challenges and Action for the Critically Endangered Singapore Freshwater Crab *Johora singaporensis*." *Oryx* 49, no. 2: 345–351.
- Pearse, W. D., F. A. Jones, and A. Purvis. 2013. "Barro Colorado Island's Phylogenetic Assemblage Structure Across Fine Spatial Scales and Among Clades of Different Ages." *Ecology* 94: 2861–2872.
- Phillips, S. J., R. P. Anderson, and R. E. Schapire. 2006. "Maximum Entropy Modeling of Species Geographic Distributions." *Ecological Modelling* 190: 231–259.
- Pimm, S. L., C. N. Jenkins, and B. V. Li. 2018. "How to Protect Half of Earth to Ensure It Protects Sufficient Biodiversity." *Science Advances* 4: eaat2616.
- Pipins, S., M. Böhm, L. Bland, et al. 2026. "Phylogenetically-Informed Crayfish Conservation in the Face of Climate Change." *Animal Conservation* 29: 274–284.
- Pollock, L. J., D. F. Rosauer, A. H. Thornhill, et al. 2015. "Phylogenetic Diversity Meets Conservation Policy: Small Areas Are Key to Preserving Eucalypt Lineages." *Philosophical Transactions of the Royal Society, B: Biological Sciences* 370: 1–10.
- R Core Team. 2019. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing.
- Raghavan, R., N. Dahanukar, S. Philip, et al. 2015. "The Conservation Status of Decapod Crustaceans in the Western Ghats of India: An Exceptional Region of Freshwater Biodiversity." *Aquatic Conservation: Marine and Freshwater Ecosystems* 25: 259–275.
- Rahbek, C., M. K. Borregaard, A. Antonelli, et al. 2019. "Building Mountain Biodiversity: Geological and Evolutionary Processes." *Science* 365: 1114–1119.
- Rambaut, A., A. J. Drummond, D. Xie, et al. 2018. "Posterior Summarisation in Bayesian Phylogenetics Using Tracer 1.7." *Systematic Biology* 67, no. 5: 901–904.
- Rathbun, M. J. 1919. "West Indian Tertiary Decapod Crustaceans." *Carnegie Institution of Washington Publication* 291: 157–184.
- Reed, D. H., and R. Frankham. 2003. "Correlation Between Fitness and Genetic Diversity." *Conservation Biology* 17: 230–237.
- Reid, A. J., A. K. Carlson, I. F. Creed, et al. 2019. "Emerging Threats and Persistent Conservation Challenges for Freshwater Biodiversity." *Biological Reviews of the Cambridge Philosophical Society* 94: 849–873.
- Rivera-Pérez, J. M., L. F. Salazar-Salinas, and C. De-Souza. 2023. "Effects of Green Areas and the Urbanization Process in the Natural Populations of the Endemic Freshwater Crab *Strengeriana fuhrmanni* (Decapoda: Pseudothelphusidae) in Colombia." *Aquatic Ecology* 57: 733–745.
- Robuchon, M., S. Pavoine, S. Véron, et al. 2021. "Revisiting Species and Areas of Interest for Conserving Global Mammalian Phylogenetic Diversity." *Nature Communications* 12: 3694.

- Rousset, F., and J. B. Ferdy. 2014. "Testing Environmental and Genetic Effects in the Presence of Spatial Autocorrelation." *Ecography* 37: 781–790.
- Schmitt, S., R. Pouteau, D. Justeau, F. Boissieu, and P. Birnbaum. 2017. "SSDM: An R Package to Predict Distribution of Species Richness and Composition Based on Stacked Species Distribution Models." *Methods in Ecology and Evolution* 8: 1795–1803.
- Schubart, C. D. 2021. "Recent Mitochondrial Approaches to Decapod Phylogeny [Meeting Abstract S8-1.3]." Society for Integrative & Comparative Biology Annual Meeting.
- Scott, J. M., F. W. Davis, B. Csuti, et al. 1993. "Gap Analysis: A Geographic Approach to Protection of Biological Diversity." *Wildlife Monographs* 123: 3–41.
- Shi, B., X. Hao, R. Wang, et al. 2025. "Underlying Spatial Diversity Patterns of Freshwater Crabs in Southern China, With Recommendations for Conservation of Freshwater Biodiversity." *Ecology and Evolution* 15: e71551.
- Shi, B., D. Pan, Y. Sun, et al. 2021. "Regional Climates Shape the Biogeographic History of a Broadly Distributed Freshwater Crab Species Complex." *Journal of Biogeography* 48: 1432–1447.
- Shi, B., D. Pan, K. Zhang, et al. 2024. "Diversification of Freshwater Crabs on the Sky Islands in the Hengduan Mountains Region, China." *Molecular Phylogenetics and Evolution* 190: 107955.
- Shih, H., and P. K. L. Ng. 2011. "Diversity and Biogeography of Freshwater Crabs (Crustacea: Brachyura: Potamidae, Gecarcinucidae) From East Asia." *Systematics and Biodiversity* 9: 1–16.
- Shih, H. T., X. M. Zhou, G. X. Chen, I. C. Chien, and P. K. L. Ng. 2011. "Recent Vicariant and Dispersal Events Affecting the Phylogeny and Biogeography of East Asian Freshwater Crab Genus *Nanhaipotamon* (Decapoda: Potamidae)." *Molecular Phylogenetics and Evolution* 58: 427–438.
- Sholihah, A., E. Delrieu-Trottin, F. L. Condamine, et al. 2021. "Impact of Pleistocene Eustatic Fluctuations on Evolutionary Dynamics in Southeast Asian Biodiversity Hotspots." *Systematic Biology* 70: 940–960.
- Sidharthan, A., R. Raghavan, V. K. Anoop, S. Philip, and N. Dahanukar. 2020. "Riddle on the Riffle: Miocene Diversification and Biogeography of Endemic Mountain Loaches in the Western Ghats Biodiversity Hotspot." *Journal of Biogeography* 47: 2741–2754.
- Sinclair, J. S., R. Stubbington, E. A. R. Welts, et al. 2025. "Current Protected Areas Provide Limited Benefits for European River Biodiversity." *Nature Communications* 16: 11146.
- Spicer, R. A., A. Farnsworth, T. Su, et al. 2025. "The Progressive Co-Evolutionary Development of the Pan-Tibetan Highlands, the Asian Monsoon System and Asian Biodiversity." *Geological Society, London, Special Publications* 549: 55–112.
- Venter, O., R. A. Fuller, D. B. Segan, et al. 2014. "Targeting Global Protected Area Expansion for Imperiled Biodiversity." *PLoS Biology* 12: e1001891.
- Venter, O., A. Magrach, N. Outram, et al. 2018. "Bias in Protected-Area Location and Its Effects on Long-Term Aspirations of Biodiversity Conventions." *Conservation Biology* 32: 127–134.
- Venter, O., E. W. Sanderson, A. Magrach, et al. 2016. "Sixteen Years of Change in the Global Terrestrial Human Footprint and Implications for Biodiversity Conservation." *Nature Communications* 7, no. 1: 12558.
- Vörösmarty, C. J., P. B. McIntyre, M. O. Gessner, et al. 2010. "Global Threats to Human Water Security and River Biodiversity." *Nature* 467: 555–561.
- Watson, J. E. M., N. Dudley, D. B. Segan, and M. Hockings. 2014. "The Performance and Potential of Protected Areas." *Nature* 515: 67–73.
- Wisz, M. S., R. J. Hijmans, J. Li, et al. 2010. "Effects of Sample Size on the Performance of Species Distribution Models." *Diversity and Distributions* 14: 763–773.
- WoRMS. 2026. "World Register of Marine Species." <https://www.marinespecies.org>.
- Wu, F., X. Fang, Y. Yang, et al. 2022. "Reorganization of Asian Climate in Relation to Tibetan Plateau Uplift." *Nature Reviews Earth & Environment* 3: 684–700.
- Yang, R., X. Dong, S. Xu, et al. 2024. "Fragmentation of Key Biodiversity Areas Highlights Attention to Human Disturbance Patterns." *Biological Conservation* 290: 110428.
- Ye, P., G. Zhang, and J. Wu. 2020. "Hotspots and Conservation Gaps: A Case Study of Key Higher Plant Species From Northwest Yunnan, China." *Global Ecology and Conservation* 23: e01005.
- Yeo, D. C. J., P. K. L. Ng, N. Cumberlidge, C. Magalhães, S. R. Daniels, and M. R. Campos. 2008. "Global Diversity of Crabs (Crustacea: Decapoda: Brachyura) in Freshwater." *Hydrobiologia* 595: 275–286.
- Yousefi, M., R. Naderloo, and A. Keikhsravi. 2022. "Freshwater Crabs of the Near East: Increased Extinction Risk From Climate Change and Underrepresented Within Protected Areas." *Global Ecology and Conservation* 38: e02266.
- Yuan, L., X. Deng, D. Jiang, et al. 2021. "Geographical Range Evolution of the Genus *Polypedates* (Anura: Rhacophoridae) From the Oligocene to Present." *Zoological Research* 42, no. 1: 116–123.
- Zhang, D., G. Ding, B. Ge, H. Zhang, and B. Tang. 2015. "Molecular Dating of a Marine Species, *Eriocheir japonica* (Decapoda: Grapsidae), Corroborates Cenozoic Tectonic Events and Sea Level Fluctuation." *Biochemical Systematics and Ecology* 63: 45–50.
- Zhou, J., N. Chen, W. Dou, et al. 2026. "Genomic Analysis and Population Divergence Driven by Geographic Isolation in *Neotetracus sinensis*." *Ecology and Evolution* 16, no. 4: e73375.
- Zurell, D., B. Schröder, C. F. Dormann, et al. 2020. "A Standard Protocol for Reporting Species Distribution Models." *Ecography* 43: 1261–1277.

Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1:** Proportion of global freshwater crab species by IUCN threat category. **Figure S2:** Rarefaction curves of freshwater crab diversity at the 2° grid level. (A) Species richness rarefaction comparing China vs. other regions; (B) phylogenetic diversity rarefaction comparing Southeast Asia vs. other regions. **Figure S3:** Spatial pattern of potential diversity distribution at the genus level for freshwater crabs based on a 2° grid. **Figure S4:** Spatial patterns of phylogenetic diversity (PD) at the genus level for freshwater crabs based on a 2° grid. **Figure S5:** Spatial patterns of standardized effect size of phylogenetic diversity (SES.PD) in freshwater crab species based on a 2° grid. **Figure S6:** Distribution maps of conservation priority areas based on phylogenetic diversity (PD) under different protection objectives. **Figure S7:** Global spatial distribution of EDGE2 for freshwater crabs based on a 2° grid. **Table S1:** Results of spatial autocorrelation analysis of global freshwater crab SR distribution patterns at a grid resolution of 0.5° × 0.5°. **Table S2:** EDGE2 species list. **Appendix S1:** Detail methods of species distribution modelling. **Appendix S2:** Detail methods of phylogenetic diversity analysis. **Appendix S3:** Detail methods of identification of conservation gaps and priority areas.