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Climate change will greatly alter multifaceted biodiversity patterns in goatfish species

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Multifaceted biodiversity is crucial for biological conservation and ecosystem sustainability but has been largely neglected in marine biodiversity research. Here we focused on 53 goatfish species of the family Mullidae, developed species distribution models using 34,577 georeferenced occurrence records, and examined redistribution of multifaceted biodiversity patterns under climate change. Our results show that under current climate conditions, the species, phylogenetic, and functional diversity patterns of goatfishes peak in biodiversity hotspots such as the Indo-Pacific convergence zone, Coral Triangle, and Madagascar. These three facets of biodiversity are projected to undergo dramatic changes under climate change, with spatial mismatches observed across different facets. Our results suggest that future climate change might alter the biodiversity patterns of goatfishes and policymakers should account for multifaceted biodiversity when developing conservation strategies.

The loss of biodiversity constitutes a foremost challenge to marine ecosystem sustainability^{1–3}. Although marine biodiversity plays an important and unique role in maintaining the global carbon cycle and ecosystem health^{4,5}, the current rates of marine extinction may be a prelude to a major extinction pulse⁶. Approximately 33% of marine mammals and nearly 30% of reef-forming corals, sharks, and shark relatives are threatened by extinction⁷. The Living Planet Index of marine species, which represents a metric evaluating the state of the world's biodiversity based on population trends of vertebrate species in marine, freshwater, and terrestrial habitats, has dropped by 35%^{7,8}. Climate change is one of the main causes of marine biodiversity loss and may lead to sudden losses of biodiversity^{7,9,10}. Therefore, understanding the intricate relationship between marine biodiversity and climate change is a critical challenge in the ecological and conservation sciences¹¹.

Exploring biodiversity patterns has always been a central theme in biology, particularly in reference to climate change^{12–15}. Multifaceted Biodiversity encompasses all life forms, ecosystems and ecological processes, acknowledging the hierarchy at genetic, taxon and ecosystem levels^{16–18}, and it can be measured as species (taxonomic) diversity (SD), functional diversity (FD), and phylogenetic diversity (PD)^{19–21}. FD refers to the variety and distribution of species' traits or characteristics^{22,23}, and it provides a better explanation of ecosystem functioning than other classical measures of diversity²⁴. PD incorporates species historical evolution or phylogenetic distance between species^{25,26}, and it establishes a promising method of explaining the role of species interactions and biogeographic histories in the structure and composition of communities²⁷. Although SD is a common

measure of biodiversity, different aspects of biodiversity vary in their degree of spatial congruence^{13,28,29}. Therefore, relying on SD alone can compromise our understanding of the mechanisms underlying the spatiotemporal dynamics of biodiversity^{30–32}. Many researchers who focused on biodiversity research and conservation have argued that multidimensional biodiversity indicators covering phylogenetics, traits, and other factors should be considered to compensate for the limitations of single indicators^{33–35}. Multifaceted Biodiversity plays a key role in biological conservation and ecosystem sustainability^{36,37}. However, multifaceted biodiversity has not received sufficient attention and thus has not been widely applied in marine biodiversity research.

Goatfishes are a globally distributed and species-rich marine group (over 100 species)³⁸. As typical reef-dwellings, goatfishes show great variation in morphological traits and must deal with drastic changes in external environments by changing their geographical distributions^{39,40}. Goatfishes are recognized as valuable indicator species in tropical and temperate coastal habitats⁴¹, and their population density and species richness are strongly associated with live hard coral cover^{41–43}. Evidence supported that distribution and diversity of goatfishes were sensitive to environmental changes, making them indicators of temperature and climate change⁴¹. For instance, temperature increase could lead to increased growth rates of *Mullus surmuletus* in the North Sea, and longer warming periods induced it to migrate to higher latitudes^{40,44}. In addition, goatfishes exhibit active foraging behavior and use their barbels and mouths to vigorously stir up sediments^{45,46}. This behavior may provide important ecosystem services,

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including resuspension and formation of mixed-species foraging associations^{47–49}. Although goatfishes exhibit important behavior that contributes to ecosystem functioning, most existing research focuses on documenting species presence⁵⁰, regional diversity⁵¹, or specific ecological traits^{52,53}. To the best of our knowledge, no study has been performed to address the multifaceted biodiversity distribution patterns of goatfishes.

This study used goatfishes (Actinopteri: Syngnathiformes: Mullidae) as marine environmental indicator species to explore the spatial and temporal patterns of multifaceted biodiversity by species distribution models (SDMs). SDMs can estimate the habitat suitability of target species by linking species distribution data to relevant environmental predictors and have been widely used to project species redistributions under climate change^{54,55}. Therefore, we hypothesized that climate change might cause goatfishes to migrate to higher latitudes, and change the biodiversity pattern of species, phylogenetic and functional. Our findings highlight the sensitivity of goatfish species to climate change and have important implications for conservation strategies in an era of climate change.

Results

Model performance and variable contribution

The predictive values of the generalized additive model (GLM), generalized linear model (GAM), and the maximum entropy model (MaxEnt) are greater than the threshold values of the receiver operating characteristics curve (AUC), the true skill statistics (TSS), and the continuous Boyce index (Boyce) (Fig. 1a, c, e), indicating high predictive ability. The AUC mean values vary from 0.714 (± 0.118) to 0.991 (± 0.003), the TSS mean values vary from 0.474 (± 0.153) to 0.934 (± 0.019), the Boyce mean values vary from 0.424 (± 0.316) to 0.986 (± 0.007) (Supporting Information Table S1). These algorithms are selected for ensemble modeling and descriptive analysis. The AUC, TSS, and Boyce mean values of the ensemble model are 0.959 (± 0.029), 0.819 (± 0.686), and 0.957 (± 0.050). In addition, AUC mean values of the null model for GLM, GAM, and MaxEnt algorithms are 0.541 (± 0.046), 0.571 (± 0.067), and 0.532 (± 0.034) (Supporting Information Table S2). All evaluation indicators reflected the predictive ability of the model and credibility of the data.

Our results showed that all three models (GLM, GAM, and MaxEnt) consistently identified water depth as the most influential predictor for goatfishes distribution (Fig. 1b, d, f). With respect to the other predictor variables, their importance varied among modeling algorithms. For instance, the results calculated by GAM for each species showed that maximum pH (0.227 \pm 0.271) contributed the second most, followed by maximum ocean temperature (0.208 \pm 0.258), and distance to shore (0.187 \pm 0.233). GLM results suggested maximum ocean temperature (0.190 \pm 0.240) contributed the second most, followed by maximum salinity (0.164 \pm 0.209), and distance to shore (0.162 \pm 0.237). MaxEnt results highlighted that maximum ocean temperature (0.258 \pm 0.258) contributed the second most, followed by distance to shore (0.216 \pm 0.215), minimum pH (0.190 \pm 0.230), and maximum pH (0.179 \pm 0.253).

Current diversity patterns

Our results showed that high SD was concentrated in the Indo-Pacific convergence zone, Temperate Australasia and Temperate Northern Pacific regions, with notable peaks in the Central Indo-Pacific convergence zone (Fig. 2a–c). With migration towards higher latitudes, SD decreased to its minimum values in polar regions. PD followed a similar pattern as SD but showed more pronounced gradients and peaks in tropical regions (Fig. 2d–f). The highest PD was found in the Central Indo-Pacific convergence zone and Temperate Australasia regions, indicating a high evolutionary history and lineage diversity. Moreover, PD was significantly higher than SD in certain areas, suggesting a high degree of evolutionary distinctiveness. The FD hotspots largely overlapped with those of SD and PD, with significant values in the Central Indo-Pacific convergence zone and Temperate Australasia (Fig. 2g–i). However, FD was relatively higher than SD and PD in certain regions, indicating unique functional traits that were not aligned with species richness or phylogenetic breadth. These

mismatches highlight areas where species contribute uniquely to ecosystem functions (Supporting Information Fig. S1). The congruence among the three diversity facets was the highest in tropical and subtropical regions, particularly in the Indo-Pacific convergence zone, which serve as biodiversity hotspots.

Future potential distributions and diversity patterns

Due to goatfish species have a planktonic stage, which can drift to new suitable habitats within the corresponding calibration area in the future. Therefore, we mainly employed an unlimited dispersal hypothesis (species can freely occupy any suitable habitat as it becomes available, for detailed explanations, please refer to method) when projecting the changes in potentially suitable habitats and biodiversity patterns of goatfishes under two carbon emission scenarios (SSP 2–4.5 and SSP 5–8.5) for 2040–2050 and 2090–2100. SSP 2–4.5 for 2090–2100 is widely used as a benchmark for assessing future climate risks and impacts, as it best reflects the balance between ongoing economic development and moderate climate actions in the real world^{56,57}, therefore, this scenario was used as an example for further description. For the average SD at latitude, a sharp reduction was observed around 40°N, and an increasing trend was observed near the equator and high latitudes (Fig. 3b). For SD at the regional level, the loss of the Red Sea and Gulf of Aden, Somali/Arabian, Sahul Shelf and Northern Australian Shelf were particularly serious and suitable habitats will mainly change to Western Indo-Pacific convergence zone (Fig. 3a), which implied that goatfishes may migrate to high latitudes under future climate change. Compared with the changes in SD, a greater loss of PD and FD was observed. PD and FD in the southern of the Central Indo-Pacific convergence zone and Temperate Australasia lost to varying degrees. With the East China Sea, South China Sea, Andaman, and Java Transitional regions expected to become areas of high functional and phylogenetic diversity in the future (Fig. 3c–f), it suggests these regions might have extremely diverse species' characteristics, ecological roles and historical evolutionary capabilities^{24,58,59}. The change trends in these scenarios (SSP 2–4.5 for 2040–2050, SSP 5–8.5 for 2040–2050, and SSP 5–8.5 for 2090–2100) were relatively similar (Supporting Information Fig. S2–S4).

Discussion

This study aimed to elucidate the environmental determinants of multiple facets of goatfishes diversity, examine the spatial patterns between these different biodiversity facets. Our findings consistently identified water depth as the primary predictor of goatfishes redistribution. The Indo-Pacific convergence zone exhibited high species diversity, functional diversity, and phylogenetic diversity under current climate, which were regarded as biodiversity hotspots. Interestingly, under the SSP 2–4.5 scenario for 2090–2100, species, functional and phylogenetic diversity all significantly declined at hotspots of medium-low latitudes, and goatfishes might migrate to higher latitudes.

This study revealed that all three modeling algorithms consistently identified water depth as the most influential predictor in regulating goatfishes geographical distributions. Several studies showed that water depth is especially important for both benthic and pelagic species, as it shapes habitat structure and influences other variables like light and pressure^{60–62}. Previous studies showed clear depth related patterns in goatfishes distribution^{42,63,64}. Surveys in the Mediterranean and Vietnam seas found the highest goatfishes densities and biomasses in shallower waters, with a marked decrease as depth increases^{64,65}. For example, goatfishes abundance was highest at depths less than 20 m and lowest between 30 and 50 m. Goatfishes also showed preferences for specific bottom types and substrates, but these preferences were closely linked to depth zones, reinforcing the primary role of water depth in their distribution^{42,63,64}. Our results aligned with previous findings by Engle & Summers⁶⁶, who reported similar determinants for estuarine fish assemblages. This study also revealed that maximum temperature was among the top three significant predictors. This finding aligned with the results of previous studies on the role of thermal limits in shaping marine biodiversity patterns⁶⁷. Tittensor et al.⁶⁷ demonstrated that

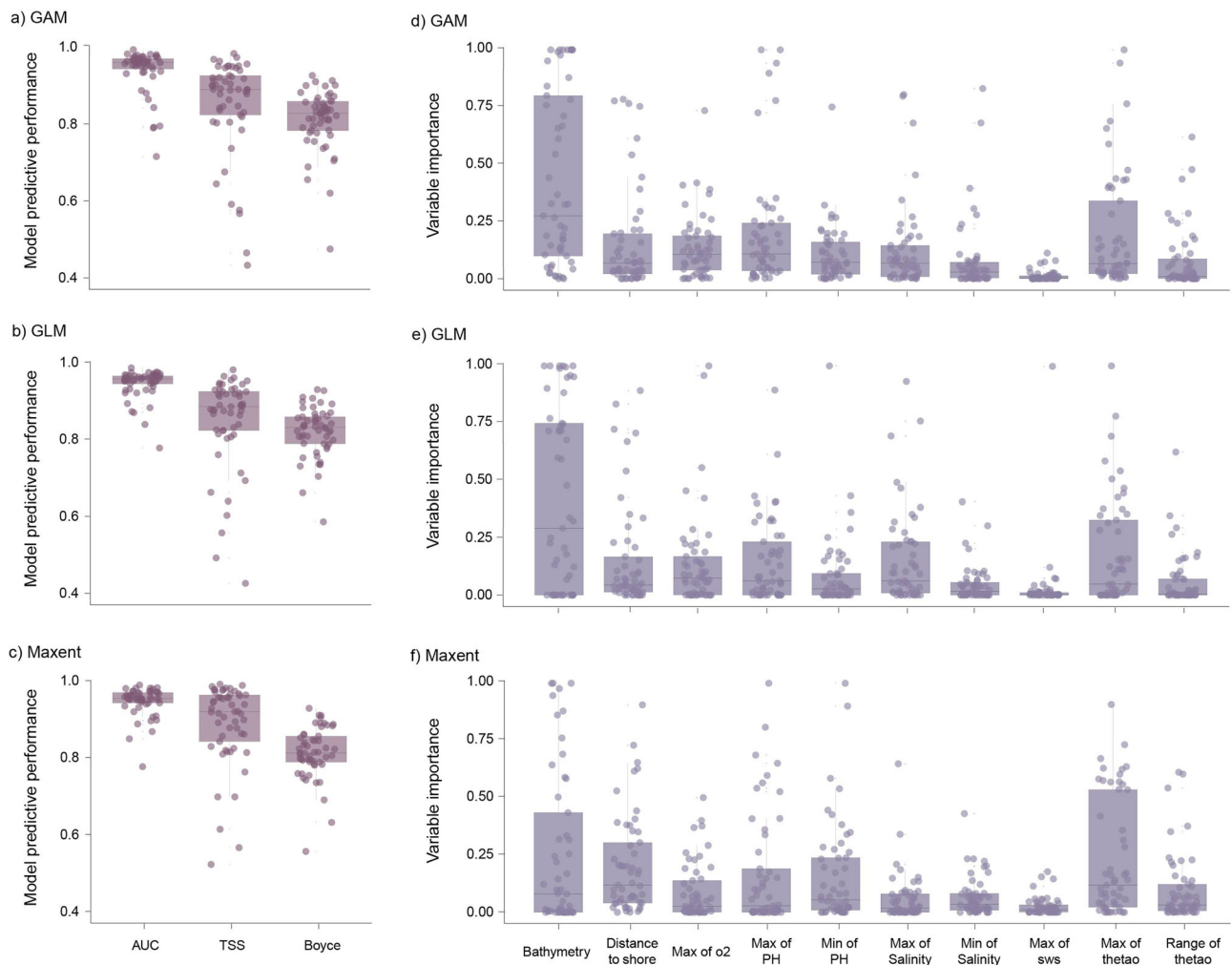


Fig. 1 | Discrimination ability and variable importance of species distribution models. **a** Model predictive performance of GAM. **b** Model predictive performance of GLM. **c** Model predictive performance of MaxEnt. **d** Variable importance of GAM. **e** Variable importance of GLM. **f** Variable importance of MaxEnt.

Discrimination abilities illustrate the predictive performance of the SDMs using GAM, GLM, and MaxEnt algorithms, and variable importance of ten predictors of based on above algorithms predictive results. Multifaceted biodiversity patterns under the present climate scenario.

temperature is a key determinant of species richness in various marine taxa, while Sunday et al.⁶⁸ emphasized the importance of thermal tolerance in the redistribution of marine species under climate change. In addition, Uiblein⁴¹ pointed that as an indicator species, goatfishes were sensitive to the changes of temperature. Increased temperature could push goatfishes beyond their optimal range, and migrate to cooler areas or higher latitudes. For example, warming seas have led to the northward migration of goatfish species such as the *Mullus surmuletus* into previously cooler regions like the North Sea^{40,44}. All of this reflects the significant impact of temperature on the redistribution of goatfishes.

In addition to water depth and temperature, distance to shore was important predictors. These factors are essential for defining suitable habitats for marine species and influence nutrient availability, habitat complexity, and predation pressure^{69,70}. Salinity also plays an important role in shaping the distribution of marine species, particularly in regions with significant freshwater input⁷¹. This is consistent with the results of Courrat et al.⁷², who found that salinity gradients significantly affected the distribution of juvenile fish in estuarine systems. Notably, the mean current velocity ranges presented minimal contributions to the model predictions. This finding suggests that although these variables may influence other aspects of marine ecosystems, they are less critical for goatfishes distribution. For example, current velocity has a greater effect on larval dispersal and nutrient transport than adult fish distribution^{73,74}.

However, our results suggested that the three algorithms predicted the variable contributions of the same factor differently. Smith & Santos⁷⁵ showed different algorithms can yield varying assessments. This variation arose from differences in algorithm structure, assumptions, and sensitivity to data characteristics⁷⁶. In addition, the clustering results analyzed by the K-Means algorithm⁷⁷ and the Silhouette Score⁷⁸ showed that the differences in the contributions of the same factors across different goatfish species highlighted species-specific response to environmental conditions (Supporting Information Tables S3, and S4), for instance, the living depth range of Cluster 5 in GLM and Cluster 6 in MaxEnt are relatively large, which may indicate that these species can survive in a wider range of water depths; Cluster 3 in GLM and Cluster 6 in MaxEnt prefer higher temperatures, which may indicate that these species are adapted to tropical or subtropical environments; Cluster 2 and Cluster 5 in GLM as well as Cluster 3 and Cluster 6 in GAM prefer reef-related habitats, which may indicate that these species rely on coral reefs or similar-structured habitats.

This variability underscored the need for tailored conservation and management strategies that considered the unique ecological requirements of each species⁷⁹. This complexity in species-specific responses was echoed by the findings of Rocchini et al.⁸⁰, who stressed the importance of incorporating species-specific ecological niches into biodiversity conservation models. The consistency of trends across GLM and GAM models, despite slight differences in contribution values, reinforced the robustness of our

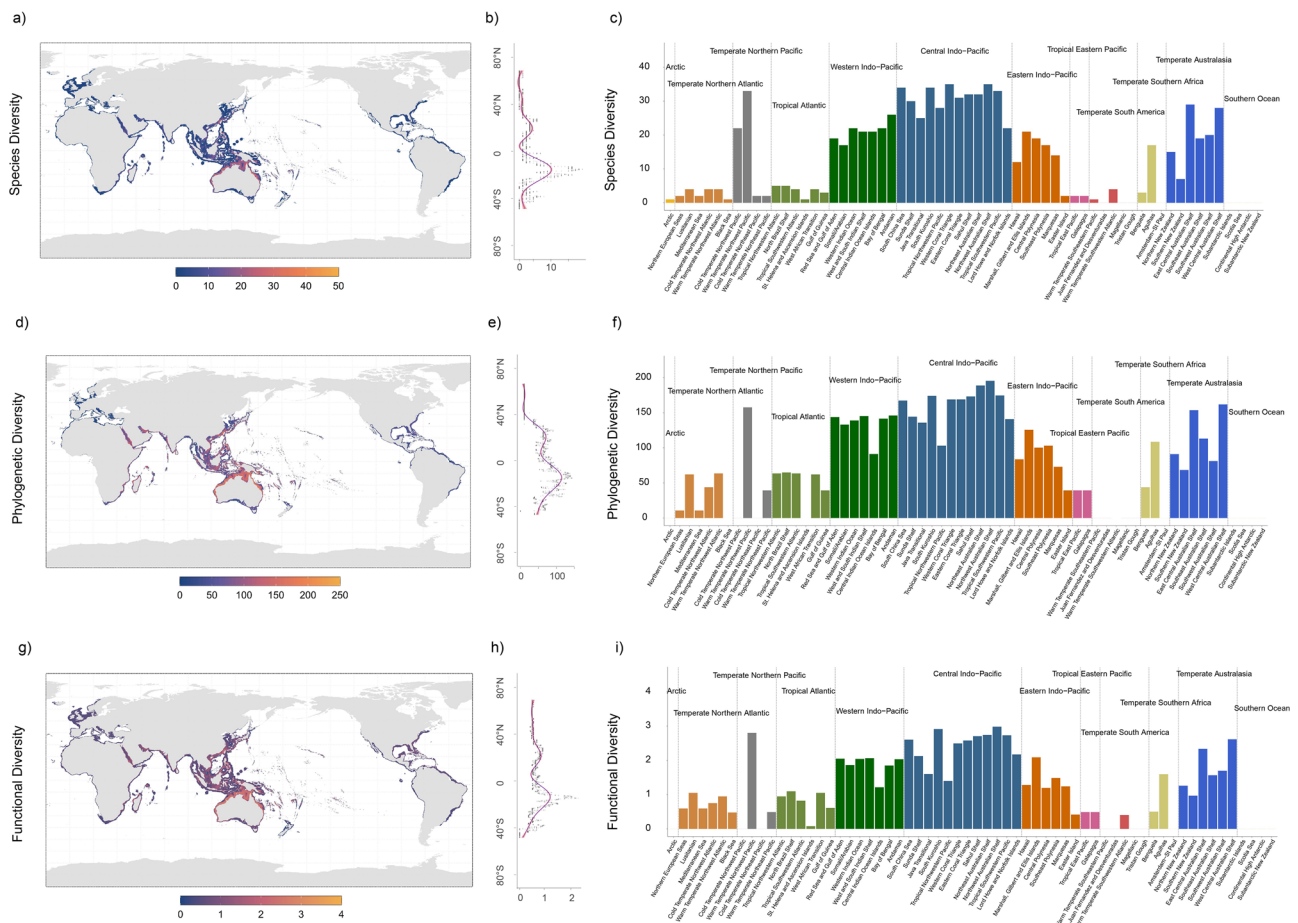


Fig. 2 | Spatial, latitudinal, and local region patterns of species diversity, phylogenetic diversity, and functional diversity for goatfishes predicted by species distribution models under the present climate scenario. a Spatial patterns of species diversity. **b** Latitudinal patterns of species diversity. **c** Local region patterns of species diversity. **d** Spatial patterns of phylogenetic diversity. **e** Latitudinal patterns of phylogenetic diversity. **f** Local region patterns of phylogenetic diversity. **g** Spatial patterns of functional diversity. **h** Latitudinal patterns of functional diversity. **i** Local region patterns of functional diversity. **a**, **d**, and **g** are based on the prediction results of ensemble models to calculate species, functional, and phylogenetic diversity on a

global scale, which can precisely reflect the diversity indicators in each grid. The more orange the color is, the higher the diversity; **b**, **e**, and **h** are based on the results of **a**, **d**, **g**, and use the Generalized Linear Model (GAM) to calculate the median of each diversity at latitude. The larger the value on the X-axis, the higher the diversity; **c**, **f**, and **i** is to calculate these three diversity indicators of each province in the marine ecoregion based on the prediction results of the ensemble model, which is helpful for visually presenting the diversity results at the local scale; Multifaceted biodiversity patterns under the SSP 2–4.5 for 2090–2100 climate scenario.

findings. Moreover, this result was similar to the observations of Guisan & Zimmermann⁸¹, who noted the reliability of ensemble modeling approaches in ecological predictions.

Despite the importance of our findings, we acknowledge that our models can be improved in different ways. For instance, sea-level rise associated with climate change will have some effects on geographical predictors (i.e., water depth and distance to shore) considered in our study, we encourage future studies to account for these effects in models. Moreover, apart from abiotic predictors, species distributions can be influenced by additional processes, including biotic interactions, which should be incorporated when data becomes available.

This study revealed the spatial distributions of three facets of marine biodiversity under current climate conditions. The highest SD was concentrated in the Central Indo-Pacific convergence zone regions, followed by Western Indo-Pacific convergence zone, Temperate Australasia and Eastern Indo-Pacific convergence zone. This pattern aligns with the results of previous studies, indicating that tropical and subtropical regions harbor the richest marine biodiversity owing to their favorable environmental conditions and historical biogeographical events^{69,82}. As latitude increases, SD decreases, with minimal values reached in polar regions, which is consistent with the well-documented latitudinal diversity gradient^{83,84}. PD mirrors SD

but shows more pronounced gradients and peaks in tropical regions, particularly the Central Indo-Pacific convergence zone and Western Indo-Pacific convergence zone, suggesting the high evolutionary history and lineage diversity of these regions. This finding is in line with previous research highlighting the tropics as cradles of marine biodiversity where evolutionary rates are accelerated, and ancient lineages are preserved⁸⁵. Areas, where PD was significantly higher than SD, suggest regions of high evolutionary diversity, underscoring the importance of these areas for conservation because of their unique evolutionary history⁸⁶. FD hotspots largely overlapped with those of SD and PD, particularly in the Central Indo-Pacific convergence zone, Western Indo-Pacific convergence zone, and Temperate Australasia. However, some regions exhibited relatively higher FD than SD or PD, indicating unique functional traits that were not aligned with species richness or phylogenetic breadth. This mismatch highlights areas where species uniquely contribute to ecosystem functions, which is critical for understanding ecosystem resilience and functionality⁸⁷. Previous studies have emphasized that FD can reveal hidden aspects of biodiversity that SD and PD cannot, thereby underscoring the fact that FD provides a more comprehensive picture of ecosystem health and stability²³.

Future projections indicate that under SSP 2–4.5 for 2090–2100, regions currently exhibiting high SD will experience a greater degree of

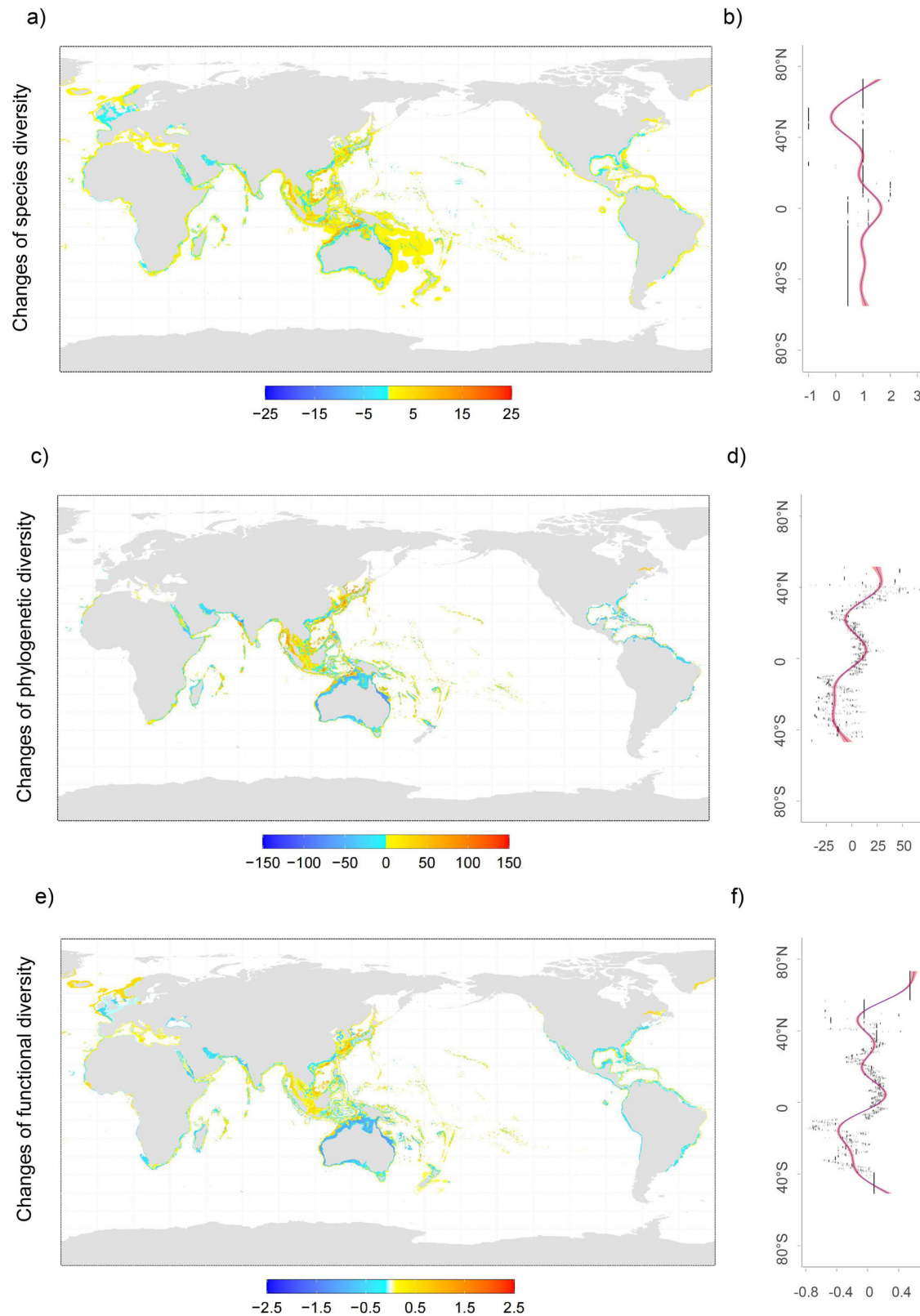


Fig. 3 | Spatial and latitudinal patterns of species diversity changes, phylogenetic diversity changes and functional diversity changes for goatfishes projected by species distribution models under the SSP 2-4.5 for 2090–2100 climate scenario. **a** Spatial patterns of species diversity changes. **b** Latitudinal patterns of species diversity changes. **c** Spatial patterns of phylogenetic diversity changes. **d** Latitudinal patterns of phylogenetic diversity changes. **e** Spatial patterns of functional diversity changes. **f** Latitudinal patterns of functional diversity changes. For other SSP and time period combinations please refer to Figs. S2–S4. **a**, **c**, and **e** are based on the

prediction results of ensemble models to calculate the changes of species, functional, and phylogenetic diversity on a global scale, which can precisely reflect the diversity indicators in each grid. The more blue the color is, the greater the loss of diversity. The more red the color is, the greater the increased of diversity; **b**, **d**, and **f** are based on the results of **a**, **c**, **e**, and use the Generalized Linear Model (GAM) to calculate the median of each diversity at latitude. The larger the value on the X-axis, the higher the diversity.

decline, such as Sahul Shelf, Australian Shelf, South China Sea and Sunda Shelf et al., while an increasing trend of SD is also observed at higher latitudes. This change suggests that goatfishes may migrate to higher latitudes under future climate change, thus reflecting a common trend in marine species as they track their thermal niches poleward^{88,89}. The significant loss of biodiversity in the most regions of Central Indo-Pacific convergence zone underscores the vulnerability of these biodiversity hotspots to climate change⁹⁰. The research by Penn & Deutsch⁹¹ also showed that regions such as the Central Indo-Pacific convergence zone and the Tropical Eastern Pacific were high extinction risks and were considered areas of vulnerable biodiversity. However, interesting to note SD decreasing in the Southern Atlantic and Australia may be influenced by the lack of suitable reef environments for species to migrate. Previous studies showed that, in these area, coral and reef-associated species face a “cul-de-sac” due to rising ocean temperature, coral bleaching and limited of habitats^{92–94}. In addition, the narrow and limited continental shelf further south limits habitat continuity, causing taxonomic and functional diversity to plummet in the southernmost reefs⁹⁵. This spatial constraint increases species' local extinction vulnerability, yet it's often overlooked in broader discussions, underscoring the need for targeted conservation strategies addressing these geographic barriers.

The loss of PD and FD is projected to be greater than that of SD. This pattern is concerning because it implies that the evolutionary and functional aspects of biodiversity, which are critical for ecosystem resilience and adaptive capacity, are disproportionately affected by climate change^{11,96}. Our results align with those of studies showing that climate change can erode the evolutionary heritage of regions by disproportionately affecting lineages with narrow climatic niches⁹⁷. Regions such as the Yellow Sea, southern Australia, and southern Africa are projected to become refuges for goatfish species under future climate change scenarios. These areas may provide critical habitats capable of supporting the persistence of evolutionary and functional traits, which are essential for maintaining ecosystem functions in the face of changing environmental conditions⁹⁸.

Methods

Species distribution data and marine predictors

Following the latest taxonomy by Nash et al.³⁸ and Eschmeyer's Catalog of Fishes⁹⁹, we generated a list of 102 goatfish species (Supporting Information Table S5). A total of 371,698 occurrence records for goatfish species were obtained from field surveys in the South China Sea between 2016 and 2021, online repositories such as the Ocean Biodiversity Information System (<https://obis.org>) and Global Biodiversity Information Facility (<https://doi.org/10.15468/dl.g6g7vp>)¹⁰⁰, and a literature review (Supporting Information Table S6). High-quality occurrence records are necessary to obtain reliable species-environment associations. To guarantee the reliability of species occurrence records, we first determined geographical ranges of each goatfish species based on information from the FishBase database (<https://www.fishbase.org>) and removed records outside species native geographical ranges, then removed records located on land and those with invalid coordinates (e.g., zero coordinates) using the CoordinateCleaner R package version 2.0.20¹⁰¹. It has been demonstrated that sampling biases are pervasive in biodiversity data, which should be reduced in SDMs studies¹⁰². To reduce sampling bias, just one record was obtained for each 3 arcmin. Considering the crucial impact of sample size on model predictive performance¹⁰³, we considered species with over 10 filtered records in our subsequent analyses^{98,104}. After data cleaning, a total of 69 species satisfied this criterion with average (\pm standard deviation) number of filtered occurrences of 501 (\pm 663) records per species (Supporting Information Fig. S5; Supporting Information Table S7).

Considering the ecological importance of marine predictors, this study initially considered 28 predictors, including 2 geographical predictors and 26 marine environmental predictors (Supporting Information Fig. S6; Supporting Information Table S8). Environmental and geographical predictors were sourced from the Bio-ORACLE v3.0 dataset (<https://www.bio-oracle.org>)¹⁰⁵ and global marine environmental dataset ([\[auckland.ac.nz\]\(http://auckland.ac.nz\)\)¹⁰⁶. The Bio-ORACLE database provides marine surface and benthic layers, we considered benthic layers \(average depth\) given the fact that goatfishes are benthic species. We considered future projections of marine layers across two future time periods \(average of 2040–2050 and average of 2090–2100\) and under SSP 2–4.5 and SSP 5–8.5 scenarios. Following previous studies¹⁰⁷, we hypothesized that water depth and distance to shore remain unchanged in the future. All marine predictors had a spatial resolution of 3 arcmin. Goatfish species mainly inhabit coastal waters⁴², as a result, we restricted our analyses within coastal and shelf areas determined by the Marine Ecoregions of the World¹⁰⁸.](https://gmed.</p>
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Collinearity of variables may affect model prediction performance^{109,110}; therefore, we checked for collinearity among the 28 predictor variables within the Marine Ecoregion of the World by calculating pairwise Pearson's correlations (r) (Supporting Information Fig. S6) and excluded collinear predictors ($|r| > 0.7$)⁵⁷. Based on the ecophysiological relevance of the predictors and collinearity results^{110,111}, ten predictors were retained for subsequent analyses, including maximum ocean temperature, range ocean temperature, maximum pH, minimum pH, minimum salinity, maximum salinity, maximum dissolved molecular oxygen, maximum sea water speed, water depth, and distance to shore.

Distribution model development

Redistribution of species under climate change is closely associated with species dispersal capacity to track changing climates¹¹². Since goatfish species possess a planktonic stage that can drift to new suitable habitats within the corresponding calibration area in the future, we focused on the unlimited dispersal scenario. The unlimited dispersal assumption assumes species can colonize all newly suitable areas in the future. We used three algorithms (GAM, GLM, MaxEnt) to build the SDMs under the unlimited dispersal scenario. These algorithms are commonly applied in biodiversity research and exhibit relatively good predictive capabilities^{113–115}. It is important to properly define the study extent¹¹⁶ in SDMs. As with previous marine SDMs studies^{60,117,118}, we delineated calibration area by creating a 1000 km buffer using R package sf version 1.0-4 around species' occurrence records. To explore the robustness of our findings, we additionally performed a sensitivity analysis by considering a 2000 km buffer and our main findings remain unchanged (Supporting Information Fig. S7). We then randomly selected 50,000 points within the species calibration area as the background data^{119,120}. Model complexity is known to influence model performance and predictions; therefore, the default settings of the modeling algorithms should be avoided^{121,122}. Following the guidelines of Sillero et al.¹²³, we fitted GAM and GLM with intermediate parameterization complexity. For MaxEnt, we optimized the model parameters (i.e., feature class and regularization multiplier) using the R package ENMeval version 2.0.2¹²⁴. To identify the optimal parameter combination for each algorithm, 50,000 pseudo-distribution points were selected as background data in the 1000 km buffer zone, and the observed presence points were used as input data, with 80% used for training and the remaining 20% used for validation. We first filtered the top 10% of the models according to their omission rates (for a detailed explanation, see Kass et al.¹²⁴) and then selected the best model from these candidates based on the validation area under the receiver operating characteristics curve (AUC)^{124,125}. The fivefold random cross-validation with 10 replicates was then used to predict the performance of the three modeling algorithms⁵⁰. AUC calculated by R package pROC version 1.18.2, TSS and Boyce calculated by R package ecospat version 3.2 were used to evaluate the predictive ability of the model, where the threshold of AUC was 0.7 and that of TSS and Boyce was 0.4^{126–128}. The higher the value in its range, the better the predictive performance.

To ensure the accuracy of our prediction results, following the approach proposed by Raes & ter Steege²⁹, for each species, we developed SDMs based on presence and background data, and calculated the empirical AUC value. Then we randomly sampled the same number of points as species presences from presence-background data, developed a null model based on pseudo-presence data, and calculated the null AUC value. We repeated this step 999 times. We checked whether the empirical AUC value

is higher than the upper limit of the 95% confidence interval for the null distribution.

The model capabilities of the 53 species were sufficient for the final model prediction (Supporting Information Table S1). For the SDMs predictions, GAM and GLM used the R package raster version 3.5.21 and biomod2 version 3.5.1 to fit the distribution data and environmental variables, while MaxEnt used the R package ENMeval version 2.0.2 to fit and obtain the occurrence probability of each site. To reduce the uncertainty associated with a single modeling algorithm, the probability of occurrence for each site was determined using Boyce weighted ensemble modeling^{130,131}. The AUC, TSS, and Boyce index were used to evaluate the predictive ability of the models for the overall data. We also assessed the relative importance of each variable in predicting the species distributions using the R package biomod2 version 3.5.1¹³². To understand whether the responses of different goatfish to environmental factors are similar, we run a cluster using the K-Means algorithm analysis⁷⁷ with species association coefficients to have an indicative of possible groups of species that may show similar response. The Silhouette Score⁷⁸ was used to evaluate the clustering effect and determine the optimal number of clusters. Then, we combined the trait characteristic of each species to conduct a feature analysis to understand the characteristics of each cluster.

Functional traits and biodiversity mapping

We used the 10th percentile omission rate as threshold to convert continuous habitat suitability maps into binary. This threshold has been widely utilized in the literature^{133,134}. The total number of species distributed in each 3 arcmin cell was counted to estimate SD. To estimate the FD, we selected seven traits associated with ecological functions^{135,136}, namely, climate vulnerability, habitat type, living depth range, maximum length at first maturity, mean preferred temperature, resilience, and trophic level (Supporting Information Table S9). Climate vulnerability indicates the sensitivity of a species to climate change, which influences its survival and reproductive success⁹⁷. Habitat type represents the specific environment in which a species lives, which influences its adaptability and survival strategies¹³⁷, and has been applied to understand species distribution patterns and community structures, thereby contributing to biodiversity conservation and ecosystem management^{24,138}. Living depth range reflects the vertical distribution of marine species, which affects their exposure to light, pressure, and predation risk¹³⁹. This trait is essential for predicting species responses to environmental changes, such as ocean warming and habitat alteration^{140,141}. The maximum length at first maturity represents the size at which a species first reproduces, which affects population dynamics and resilience¹⁴². The mean preferred temperature represents the average temperature range within which a species thrives, which influences the species' metabolic rate and distribution⁶⁸. Resilience reflects a species' ability to recover from disturbances, such as environmental changes and human impacts¹⁴³. The trophic level indicates the position of a species in the food web, which reflects its role in energy transfer and ecosystem functioning¹⁴⁴ (for a detailed explanation, please see the Supporting Information Table S10). Trait records were extracted from the FishBase database (<https://www.fishbase.org/>). Missing values were filled using the R package missForest version 1.5, which iteratively uses random forests if the missing values of functional traits were greater than 20% of the total¹⁴⁵.

We used the R package BAT version 2.9.2 to calculate the Gower distance using the neighbor-joining (NJ) method to generate a trait tree¹⁴⁶, and FD was calculated using the default parameters of the R package BAT version 2.9.2. To estimate PD, we used the phylogenetic tree dated by Nash et al.³⁸ and calculated PD using the default parameters of the R package BAT version 2.9.2.

Data availability

Data presented in this article are available on Figshare Repository (<https://figshare.com/s/44625f9b457f3b45326d>).

Code availability

R scripts used to develop species distribution models are available in Figshare Repository (<https://figshare.com/s/44625f9b457f3b45326d>).

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Author contributions

Q.L., Z.Z., and G.Q. conceived and supervised the study; H.H. collected the distribution data and environmental data; H.H. performed data analyses with suggestions from Z.Z.; H.H. wrote the original manuscript, and H.H. prepared figures 1–3; H.H., Z.Z., and Q.L. revised the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

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