Unveiling the Suitable Habitats and Conservation Gaps of Tridacna maxima in the Indo-Pacific Core Area Based on Species Distribution Model

Shenghao Liu[1], Tingting Li[1], Bailin Cong[1], Leyu Yang[1], Zhaohui Zhang[2], and Linlin Zhao[1]

[1]First Institute of Oceanography Ministry of Natural Resources
[2]First Institute of Oceanography

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Abstract

Tridacna maxima (T. maxima) are widely distributed in shallow areas near coral reefs and hold significant commercial value as a food source and for marine tourism. However, it has been extensively harvested and depleted in many regions, leading to it being listed as endangered species by the International Union for Conservation of Nature (IUCN). While marine protected areas (MPAs) are considered effective conservation tools, it remains uncertain whether existing MPAs adequately protect these vulnerable giant clams. Here, we employed a Species Distribution Models (SDMs) approach, combining occurrence records of T. maxima with environmental variables, to predict their distribution and capture spatiotemporal changes. The findings revealed the importance of land distance and light at bottom in determining the distribution of T. maxima, with suitable habitats predominantly found in shallow coastal waters rather than deep sea areas. Furthermore, we modeled potential distribution areas for T. maxima in 2050 and 2100 under different climate change scenarios, highlighting varying impacts on suitable habitats across different model predictions. To evaluate current conservation gaps, we conducted an analysis by overlaying suitable areas with existing protected areas. The results showed that the potential distribution area of T. maxima is 1,519,764.73 km2, accounting for only 16.10% of the total protected areas. It became evident that the existing protected areas are insufficiently large or well-connected, suggesting their ineffectiveness in safeguarding giant clams. Therefore, management efforts should focus on establishing a network of MPAs along the coastlines of West Pacific-Indonesia, matching the dispersal capability of giant clams. These findings provide valuable insights for the conservation of endangered giant clams, offering a scientific foundation for designing MPA networks in the Indo-Pacific region.

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Shenghao Liu[1,2,3], Tingting Li[1], Bailin Cong[1,3], Leyu Yang[1,3], Zhaohui Zhang[1,2], Linlin Zhao[1,2,3]*

[1]Key Laboratory of Marine Ecology and Environment Science, First Institute of Oceanography, Ministry of Natural Resources, Qingdao, 266061, China; [2] Marine Ecology and Environmental Science Laboratory, Pilot National Laboratory for Marine Science and Technology, Qingdao 266237, China; [3] School of Advanced Manufacturing, Fuzhou University, Jinjiang 362200, China

*Correspondence: Linlin Zhao, Email: zhaolinlin@fio.org.cn

Abstract

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depleted in many regions, leading to it being listed as endangered species by the International Union for Conservation of Nature (IUCN). While marine protected areas (MPAs) are considered effective conservation tools, it remains uncertain whether existing MPAs adequately protect these vulnerable giant clams. Here, we employed a Species Distribution Models (SDMs) approach, combining occurrence records of *T. maxima* with environmental variables, to predict their distribution and capture spatiotemporal changes. The findings revealed the importance of land distance and light at bottom in determining the distribution of *T.maxima* , with suitable habitats predominantly found in shallow coastal waters rather than deep sea areas. Furthermore, we modeled potential distribution areas for *T. maxima* in 2050 and 2100 under different climate change scenarios, highlighting varying impacts on suitable habitats across different model predictions. To evaluate current conservation gaps, we conducted an analysis by overlaying suitable areas with existing protected areas. The results showed that the potential distribution area of *T. maxima* is 1,519,764.73 km^2, accounting for only 16.10% of the total protected areas. It became evident that the existing protected areas are insufficiently large or well-connected, suggesting their ineffectiveness in safeguarding giant clams. Therefore, management efforts should focus on establishing a network of MPAs along the coastlines of West Pacific-Indonesia, matching the dispersal capability of giant clams. These findings provide valuable insights for the conservation of endangered giant clams, offering a scientific foundation for designing MPA networks in the Indo-Pacific region.

Keywords: Giant clams, *Tridacna maxima,*Species distribution models, Habitat suitability, Potential distribution area, Marine protected areas

Introduction

Geographical environmental factors exert constraints on the growth, development, and geographic migration of species. The flourishing and reproductive success of marine organisms hinge upon their reliance on distinct ecological niches. Unfortunately, climate change and human activities have triggered a series of alterations within the marine environment, including elevated water temperatures, diminished primary productivity, ocean acidification, and hypoxia (Cheung et al., 2013; Lumpkin et al., 2020; Monllor-Hurtado et al., 2017). These alterations have the potential to surpass physiological and ecological thresholds, leading to habitat loss and even the extinction of numerous species (Duncan et al., 2023; Penn & Deutsch, 2022). In comparison to terrestrial communities, marine communities are more susceptible to environmental changes induced by climate change (Sorte et al., 2010a; Sorte et al., 2010b). As a species occupies a specific ecological niche, modifications in the attached environmental conditions can disrupt the distribution of that species (Faleiro et al., 2018; Fu et al., 2021). Given these circumstances, comprehending the impact of future climate change on species distribution is vital for effective species conservation.

Giant clams, belonging to the *Tridacna* genus, hold significant importance as coral reef inhabitants in the Indian and Pacific Oceans. Their massive colored shells and vibrant mantle tissue make them easily recognizable (Huelsken et al., 2013). *Tridacna* species are crucial for coral reef ecosystems, serving as ecologically valuable reef-builders with protective functions. They provide habitat, breeding grounds, and shelter for other reef organisms, thus playing a crucial role in marine environments, particularly coral reef ecosystems. The feeding mechanism of *Tridacna* is one of its unique biological characteristics. It involves symbiotic zooxanthellae living in its mantle tissue, utilizing inorganic nutrients from seawater through photosynthesis for growth and respiration (Jantzen et al., 2008; Lucas, 2014; Todd et al., 2009). This symbiosis holds both ecological and morphological significance for *Tridacna* . It is estimated that approximately 66% of the energy source for *Tridacna* comes from the photosynthetic activity of zooxanthellae (Klumpp et al., 1992; Norton et al., 1992). Over the past two decades, *Tridacna*populations have suffered substantial damage due to human activities and global environmental changes, leading to critical endangerment for most species (Andréfouët et al., 2013; Cabaitan et al., 2008; Neo et al., 2015). *T. maxima* , a giant clam species, has been classified as an endangered species in the ”China Red List,” listed under Appendix II of CITES, categorized as a species of least concern in the IUCN Red List, and listed as a Class II protected wild animal in the ”National Key Protected Wildlife List”. It exhibits wide distribution in the western Indian Ocean and the Red Sea, spanning from the Indo-Malayan archipelago to the Socotra archipelago in the central Pacific (Andréfouët et al., 2014;

Gilbert et al., 2007).

Species Distribution Models (SDMs) are currently valuable tools for predicting potential species distribution (Anibaba et al., 2022; Capinha et al., 2011; Guisan et al., 2017). The underlying principle of SDMs involves using existing species distribution data and environmental variables to establish ecological requirements based on the species' niche. This approach explores the non-random relationship between environmental characteristics in known distribution areas and potential distribution areas (Araújo et al., 2019). It allows for the prediction of current and future species distribution under varying climatic conditions (Booth et al., 2014; Guisan & Thuiller, 2005). However, most contemporary studies only use SDMs at the species level, neglecting intraspecific species variation (Zhang et al., 2021). Local adaptation and intraspecific variation can influence how a species responds to environmental changes (Li et al., 2022). Therefore, species-level SDMs often overpredict a species' future distribution (Hu et al., 2021; Pack et al., 2022). Consequently, incorporating intraspecific genetic differences into SDMs can result in better and more accurate predictions, providing valuable information for marine biodiversity conservation efforts (Hu et al., 2021).

The convergence zone between the Indian and Pacific Oceans, a tropical region, represents a biogeographic hotspot characterized by exceptionally high species diversity in shallow marine ecosystems. This hotspot is predominantly centered around the Indo-Malay Archipelago (Hoeksema, 2007; Nuryanto & Kochzius, 2009). The Indo-Pacific core region provides unprecedented opportunities for scientific investigations into the origin, maintenance, and conservation of biodiversity. Literature has documented significant levels of biodiversity in the Central Indian Ocean-Pacific, Western Indian Ocean, and Central Pacific regions across various dimensions, designating them as priority areas for conservation (Fan et al., 2023). Current research efforts in this area predominantly focus on unraveling the ecological and evolutionary processes that shape marine biodiversity. However, human activities, notably overfishing and pollution, have contributed to the loss of marine biodiversity (Halpern et al., 2008). In response, marine protected areas (MPAs) have been established to preserve the marine environment and its biodiversity (Sala & Giakoumi, 2018). MPAs have proven effective as area-based conservation techniques for protecting marine biodiversity (Grorud-Colvert et al., 2021). Despite these efforts, few studies have assessed the effectiveness of existing protected areas in protecting threatened *Tridacna* species under future climate conditions and ongoing human activities.

Based on geographical and genetic variations, the *T. maxima*population in the Indo-Pacific core region is primarily divided into two evolutionary lineages: East Indian Ocean-South China Sea (EIOS) and West Pacific-Indonesia (WPI) (Hui et al., 2016; Nuryanto & Kochzius, 2009). Although the degree of distribution overlap and genetic exchange between populations remains uncertain, these two populations have inhabited distinct ecological environments throughout their extensive evolutionary history, potentially leading to local adaptations. This study aims to assess the distribution patterns of species richness between these two populations and identify priority conservation areas as well as conservation gaps of the current protected areas network. Our study will provide scientific support for the Post-2020 Global Biodiversity Framework and aid in the development of comprehensive conservation plans for the marine biodiversity of the Indo-Pacific core region.

Materials and Methods

2.1 Study area and species occurrence data collection

T. maxima is mainly distributed in the Indian Ocean and the Western Pacific. The Indo-West Pacific region, centered around the Indo-Malay Archipelago, exhibits the highest species diversity in shallow waters of the ocean. Our study focuses on a limited area of 90˜140°E, 11°S˜15°N, based on the known distribution ranges of the two populations. We obtained occurrence records of *T. maxima* (27091 records) from online public databases such as the Global Biodiversity Information Facility (GBIF, https://www.gbif.org/), iNaturalist (https://www.inaturalist.org/), and the Ocean Biogeographic Information System (OBIS, https://obis.org/). To minimize sampling bias and avoid the representation of conditions in densely sampled areas, we employed the R software package spThin for spatial refinement of the distribution data. Each 5×5 arc-minute grid was assigned one occurrence point, resulting in a spatial resolution of 9.2×9.2 km, consistent with the environmental predictors' resolution. After data cleansing, we retrieved 213 records within our study area. According to the genetic population structure (Hui et al., 2016), the EIOS clade was assigned 113 occurrence records, and the WPI clade had 100 occurrence records (Fig. 1).

2.2 Environmental variables acquisition and filtering

The spatial distribution of species can be significantly influenced by the surrounding habitat environment (Zhao et al., 2023). In this study, we obtained raster data of variable projections from the comprehensive dataset Bio-ORACLE (http://www.bio-oracle.org) and Global Marine Environment Datasets (http://gmed.aucklan-d.ac.nz), considering their biological relevance and data availability. To assess collinearity among candidate predictor variables, scatter collinearity analysis, Pearson's correlation coefficients, and the variation inflation factor (VIF) were employed (Zuur et al., 2010). Variables with correlation values below 0.8 and VIF values below 10 were retained. Nine predictors were considered based on the collinearity analysis, including mean current velocity, mean salinity, mean temperature, temperature range, mean dissolved oxygen, light at bottom, phytoplankton, water depth, and land distance (Table 1, Fig. 2).

Bio-ORACLE provides future environmental projections for two time periods (2040-2025, 2090-2100) using three atmospheric-ocean general circulation models (AOGCMs: CCSM4, HadGEM2-ES and MIROC5) under four Representative Concentration Pathways (RCPs) emission scenarios: RCP 2.6, RCP 4.5, RCP 6.0 and RCP8.5 (Assis et al., 2018). To reduce uncertainty in environmental projections, we averaged the predictions from the three AOGCMs to represent future climate conditions. RCP 2.6 indicates an optimistic emission level with well-controlled greenhouse gas concentration, while RCP 4.5 and RCP 6.0 represent moderate emission levels. RCP8.5 represents a pessimistic scenario without controlled emissions (Moss et al., 2010). For comparability, we used two RCPs (RCP 2.6 and RCP 8.5) to predict future distributions for the 2050s (2040–2050) and 2100s (2090–2100). Future environmental factors, including current velocity, mean salinity, mean temperature, temperature range, are downloaded from Bio-ORACLE, while the other factors were assumed to remain unchanged in the future (Zhang et al., 2021).

2.3 Model construction and assessment

The modeling program used in this study is SDM based on the biomod2 package in the R platform (Thuiller et al., 2020). The package includes ten modeling algorithms: maximum entropy (Maxent), random forest (RF), surface extent envelope (SRE), multiple adaptive regression splines (MARS), artificial neural network (Moss et al.), flexible discriminant analysis (FDA), classification tree analysis (CTA), generalized boosting model (GBM), generalized linear model (GLM), and generalized additive model (GAM). Species distribution modeling and prediction rely on existing/pseudo-missing records and current environmental data. Due to limited actual sampling point data for most species, pseudo-distribution data is used as a substitute to overcome this limitation (Barbet-Massin et al., 2012). The pseudo-absences function in the R package MOPA is employed to randomly simulate an equal number of pseudo-absent records and compare them with the conditions of actual presence points, thereby improving the model's predictive performance (Guisan et al., 2017). To evaluate the accuracy of the model predictions, a five-fold cross-validation method with 10 replicates was used (Fu et al., 2021). In this methodology, 80% of the dataset is randomly selected for model calibration and testing, while the remaining 20% is reserved for assessing model predictions.

Two model evaluation indices embedded in biomod2, namely true skill statistics (TSS) and the area under the receiver operating characteristic curve (AUC), are calculated to estimate predictive accuracy. Given the potential diversity in outcomes generated by the ten models, an ensemble projecting approach is adopted to reduce uncertainty and enhance reliability (Buisson et al., 2010; Morato et al., 2020). To improve the accuracy of ensemble models, only models with an AUC greater than 0.8 and a TSS greater than 0.7 are retained, indicating high predicted accuracy and low uncertainty (Allouche et al., 2010; Mei et al., 2017).

Species-level and population-level modeling analyses are conducted, drawing species response curves for each environmental variable using the generated SDMs to visualize the variation in species occurrence probability along the environmental gradient. The significance of each predictor is estimated using a randomly permuted method (Guisan et al., 2017). The potential distributions of the entire species and the two populations (EIOS and WPI) under present and future climate scenarios (2050s, 2100s) for RCP 2.6 and RCP 8.5, respectively, were predicted using the ensemble models at both species and population levels. Continuous habitat suitability maps are created based on the direct outputs from the ensemble models. Using automatically derived thresholds that maximize the TSS values of the ensemble model, we translated the continuous prediction into binary values for a clearer comprehension of habitat appropriateness (Liu et al., 2013).

2.4 Niche differentiation comparison

The ecological niche space occupied by a population, which depends on environmental variables influencing population occurrence, can be estimated using the n-dimensional ecological hypervolume (Lê et al., 2008). Using the R package hypervolume, we then estimated the four-dimensional hypervolumes for the EIOS and WPI populations based on the selected principal components. The size of the population's niche space can be quantified by the values of hypervolume, a unitless measure. We used the R package BAT to calculate the niche differentiation between the EIOS and WPI populations. Total niche differentiation (βTotal) represents the degree of overlap or separation between two hypervolumes. It can be further divided into two parts: niche contraction/expansion, which indicates the net variations in how much space each hypervolume encompasses, and niche shift, which represents the replacement of the space between the hypervolumes inhabited by two populations (Carvalho & Cardoso, 2020; Mammola & Cardoso, 2020).

2.5 Identifying the conservation gaps

For subsequent analysis, the binary maps were utilized to calculate the extent of suitable habitat and retrieve information on all marine protected areas within the Indo-Pacific core area, Data online from the world's protected areas (http://www.protectedplanet.net, WDPA) in June 2023. ArcGIS was employed to conduct an overlay analysis by combining the distribution data of these protected areas with the potential distribution range of *T. maxima* . This analysis aimed to assess current protection gaps and identify areas lacking protection for the *T. maxima* species in the Indo-Pacific core area. Furthermore, to evaluate the effectiveness of the existing protected area system for *T. maxima* in the Indo-Pacific core area, we also calculated the ratio between the species' distribution area within the established protected areas and its potential distribution area. This ratio serves as a measure to determine the level of effective protection provided to the species.

Results

3.1 Niche differentiation among the two populations

To minimize the dimensionality of the niche space, we initially conducted a principal component analysis (PCA) on environmental variables. The top four principal components were retained as they collectively explained 81.7% of the total variance (Fig. 3A). The EIOS (1992.44) had a larger four-dimensional hypervolume than the WPI (1588.38). There was a modest level of niche differentiation between the two populations (βTotal = 0.465), primarily driven by niche shift (0.180), which accounted for 49.32% of the observed difference, and niche contraction/expansion (0.184), which accounted for 50.41% of the difference. Analyzing the niche centroids for the two population comparisons revealed that PCA1 played a crucial role in explaining the distinct niches of the EIOS and WPI populations (Fig. 3B). This difference was mainly attributed to variations in mean temperature, mean dissolved oxygen, phytoplankton abundance, and mean salinity (Fig. 3C).

3.2 Model training fitting and environmental variable assessment

To improve model performance, a 10-replicate five-fold cross-validation procedure was employed. During simulation, 20% of the known species distribution data was used for model validation, while the remaining 80% was used for training. The predictive performance of the 10 modeling algorithms varied, as indicated by different TSS and AUC values. The modeling technique with the highest predictive performance, determined by TSS and AUC values, was selected. Eight out of the ten single models (excluding MAXENT and SRE) were chosen to create weighted ensemble models at both the species and population levels (Fig. 4A, 3B). Overall, the ensemble models demonstrated good accuracy for most species, with AUC values above 0.80

and TSS values above 0.70. The high AUC and TSS values across all three ensemble models indicated strong predictive performance (Table 2).

The habitat suitability models developed in this study incorporated nine different predictors, each contributing differently to the modeled species (Fig. 4C). In general, land distance and light at bottom emerged as the most important predictors for *T. maxima* , contrasting with ocean depth, current velocity, dissolved oxygen, salinity, mean temperature, and phytoplankton (Fig. 4C). The species-level model revealed that the distribution of *T. maxima* was primarily influenced by land distance and light at bottom. The model predicted that *T. maxima* tends to prefer environments with land distances between 0 and 30 km (Fig. 5A1) and light at bottom between 5 and 45 (Fig. 5A2). At the population level, land distance and mean temperature were the most significant predictors for the distribution of EIOS, while light at bottom and land distance played key roles in predicting the distribution of WPI. For the EIOS population, occurrence probability decreased with increasing distance from land and was highest when the mean temperature ranged from 10 to 30 °C (Fig. 5B1, 4B2). As for the WPI population, preferred habitats exhibited light at bottom above 20 and were located near the coast within approximately 100 m (Fig. 5C1, 4C2).

3.3 Habitat suitability in scenarios of the current and future climatic conditions

The modeling analyses were conducted at both the species level (species model) and population level (EIOS model and WPI model). Under present conditions, potential habitat for *T. maxima* exhibited higher suitability indices in the Indo-Pacific core area. In terms of distribution ranges, the predictions from the species-level and population-level models frequently demonstrated good agreement (Fig. 6A). *T. maxima* 's preferred habitats occurred primarily in shallow coastal waters, with little of it in deep ocean regions. Notably, the species-level prediction showed the largest suitable habitat area (1,519,764.73 km^2), while the two population-level predictions indicated the areas of 1,326,478.08 km^{2}and 1,204,511.84 km^2, respectively. Despite limited ecological niche differentiation, certain variations in the projected results were identified between two populations that were predicted by EIOS model and WPI model (Fig. 6B and C). Moreover, distinct differences are observed in certain regions. For instance, in the South China Sea, the species-level model predicts the smallest suitable habitat area for *T. maxima* , whereas the WPI population-level model predicts the largest area. In the Strait of Malacca, the EIOS model predicts a larger suitable zone compared to the species-level and WPI models.

The extent of habitat change depends on the scenario of climate change. Under the pessimistic scenario of uncontrolled greenhouse gas emissions (RCP 8.5), significant changes in the suitable range are projected (Table 3, Fig. 7). The species-level and population-level models predict different impacts of climate change on potential suitable habitats. The species-level model presents a more pessimistic outcome with greater loss of potential suitable habitats for *T. maxima* in the Nansha Islands, Strait of Malacca, and Java Sea regions under RCP 8.5 scenarios. The EIOS model predicted moderate loss of suitable areas for *T. maxima* among the Indo-Pacific core area, while the WPI model forecasted substantial loss of suitable areas in shallow waters surrounding the Philippine Islands, Sumatra Island, and Java Island. Unlike the species-level and WPI models, the EIOS model predicted a gain (approximately 2.43%) of spotted suitable habitats in coastal waters of the Nansha Islands, Mindoro Island, Eastern and Southern Indonesia under RCP 8.5 scenarios.

3.4 Identifying the conservation gaps in the Indo-Pacific core area

The distribution of potential suitable habitats was predicted by SDMs. Areas far from the coast were identified as less critical for conservation, while the most important areas tended to be coastal. From the distribution of existing protected areas (Fig. 8), it can be seen that they are scattered in different directions and present a "point-like" pattern, greatly weakening their protective role for habitat. According to the gap analysis, the potential distribution area of *T. maxima* within natural protected areas is 244730.58 km^2, with a protection ratio of only 16.10%, which does not match the status of the study area as a biodiversity center. Most of the potential areas for the *T. maxima* have not yet been protected, indicating an urgent need to expand and optimize the protected area system in the Indo-Pacific core region, moving from a "point-like" pattern towards a "grid-like" one, to comprehensively improve the effectiveness of species protection.

Discussion

4.1 Ecological niche differentiation in SDMs

The use of species distribution models (SDMs) in biodiversity assessments primarily focuses on estimating habitat suitability at the species level (Collart et al., 2021; Elith et al., 2010; Elith & Leathwick, 2009). These species-level SDMs assume "ecological niche conservatism" and overlook within-species phylogenetic or functional heterogeneity. However, recent studies have highlighted the importance of considering population-level differences in sustainable management systems, as they reveal variations in climate predictor responses within species (Benito Garzón et al., 2019; Collart et al., 2021; Nielsen et al., 2021; Song & Li, 2023). Using the Japanese crayfish (*Cambaroides japonicus*) as an example, researchers demonstrated that by accounting for local adaptations in distinct populations, SDMs with resolutions below the species level can more reliably forecast changes in biodiversity (Zhang et al., 2021).

Our findings indicate intermediate niche differences (0.465) between the EIOS and WPI lineages of *T. maxima* , suggesting the need for population-level SDMs for this species (Fig. 1-2). While all our models exhibited strong predictive performance and good model transferability (Table 2), the species-level model projected larger range contractions due to climate change compared to the lineage-level models (Table 3). Incorporating possible local adaptations, population-level SDMs yield different predictions regarding the effects of climate change. Therefore, our distribution predictions were less pessimistic when using lineage-level models, aligning with earlier research suggesting that intraspecific variation may mitigate the impact of climate change on species distribution (Chardon et al., 2020; Razgour et al., 2019).

4.2 Effects of environment factors on the distribution of *T. maxima*

Land distance and light at bottom were important variables of habitat suitability for *T. maxima*(Fig. 5), consistent with studies on species distributions of *Acropora tenuis* in the Great Barrier Reef (Strahl et al., 2019) and *T. maxima* in the Central Red Sea (Rossbach et al., 2019). The most unique biological feature of *T. maxima* is its nutritional relationship with *Zooxanthellae* , whereby the majority of their required nutrients and energy are obtained through photosynthesis (Lucas, 2014; Yonge, 1975). This symbiotic relationship has significant ecological and morphological significance for *T. maxima* . On the one hand, the distribution of *T. maxima* is limited by their symbiotic dinoflagellates, which require sufficient light for photosynthesis. Land distance is generally shallow with high transparency and ample sunshine, meeting the basic conditions for maintaining the symbiotic relationship. In addition, *T. maxima* attach themselves to coral reefs or live freely. Their habitat is mainly in the low tide zone near coral reefs in tropical waters or in shallower reefs, making them an important component of coral reef ecosystems. Giant clams support overall reef biodiversity and functionality, making them flagship taxa for coral reef conservation efforts (Killam et al., 2023; Lee et al., 2022). A significant decline in the number of *T. maxima* in a particular area indicates damage to the coral reef ecosystem. Conversely, a relatively stable population size and species composition of *T. maxima* indicate good health of the coral reef ecosystem (Dewiyanti et al., 2021). Interestingly, the distribution range of coral reefs highly coincides with that of *T. maxima* , as shown in the Allen Coral Atlas (Lyons et al., 2020), further explaining why *T. maxima* are found at a close land distance and verifying the accuracy of species distribution models in predicting their distribution. We speculate that coevolution of these species in this shared environment has led to similar response patterns among associated species in the face of climate change (Chen et al., 2023). This also provides an ideal system for studying how each species in *Tridacninae* , corals, and *Zooxanthellae* utilizes local climate adaptation, dispersal, and other strategies to mitigate the risks of climate change in the future. In addition, light directly or indirectly affects *Tridacninae* physiological activities, such as growth and energy metabolism (Ip et al., 2006). Studies have shown that the oxygen production rate in *T. crocea* gradually increases with rising light intensity within an experimental range. Light intensity significantly impacts the metabolic synthesis of *T. crocea* and other symbiotic dinoflagellates, promoting their photosynthetic activity and growth (Liu et al., 2018; Liu et al., 2021).

4.3 Giant clam protection and adaptative management

SDMs establish relationships between species occurrence records and environmental factors using species coordinates and environmental data, enabling the prediction of suitable habitats and distribution patterns (Guisan et al., 2017; Hällfors et al., 2016). As field surveys have limited coverage, SDM predictions play a crucial role as supplements in marine biodiversity conservation efforts. In recent years, numerous studies have utilized SDMs to identify distribution characteristics of diverse marine taxonomic groups, providing a vital foundation for the development of scientifically sound conservation plans (Hu et al., 2022; Wang et al., 2023). Notably, there is increasing momentum under the Post-2020 Global Biodiversity Framework to raise protection targets to 30% of the ocean by 2030 (Brito-Morales et al., 2022). Our study revealed that the potential distribution area of *T. maxima* is 1,519,764.73 km^2, while only 244,730.58 km^2 falls within protected areas, constituting 16.10% of the total (Fig. 8). These findings contradict the Indo-Pacific region's reputation as the world's richest in terms of marine species. Although a certain number of marine protected areas have been established here (with a total area of approximately 459,711.65 km^2), they inadequately cover the suggested priority conservation areas identified in this study due to their scattered distributions. The existing protected areas are not sufficiently large or well-connected, suggesting that they may not be effective for protecting giant clams. Therefore, management efforts should include establishing a MPA network along the coastlines of West Pacific-Indonesia to match the dispersal capability of giant clams.

It has been demonstrated that under future climate scenarios, global marine species distributions are shifting at rates of tens to hundreds of kilometers per decade (Stuart-Smith et al., 2017). In the present study, the projected future potential distribution area of *T. maxima* is 1,285,800.49 km^2, with 208,080.73 km^2 falling within protected areas, accounting for 16.18% (Fig. 8). Considering the impact of climate change on habitats, it is crucial to assess whether existing protected areas can still fulfill their original conservation functions. Additionally, management efforts should address the effects of future climate change on habitats in order to maintain population connectivity and adaptability in separated regions. This requires constructing appropriate models to understand the distribution patterns of numerous threatened species under climate change, identifying species richness hotspots in the Indo-Pacific core region, and evaluating the effectiveness of individual and networked marine protected areas. Such endeavors hold significant importance in formulating adaptive and forward-looking conservation policies.

4.4 Model performance and verification

Habitat suitability modeling techniques have inherent limitations, but we have taken several measures to ensure the accuracy of our research findings. We employed ensemble modeling to reduce uncertainties associated with SDMs. However, it is important to acknowledge that SDM modeling algorithms still have their own limitations. Previous studies have emphasized the presence of uncertainties in SDMs, which can be minimized through a combination modeling approach (Guisan et al., 2017; Thuiller et al., 2019; Zhang et al., 2019). By integrating multiple models, we can address variable importance and capture habitat changes resulting from different factors, thereby advancing the study of species' spatial distribution more efficiently and accurately (Fig. 3-4). Furthermore, during model validation, techniques for validating presence/absence models are well-developed and offer higher interpretability of prediction results (Palialexis et al., 2011). Therefore, this study utilized presence/absence data for habitat analysis. Moreover, existing evidence suggests that *T. maxima*exhibits two evolutionary branches within our study area's spatial scale (Nuryanto & Kochzius 2009; Hui et al. 2016). However, a more detailed classification would likely lead to more accurate predictions. Future research can explore this hypothesis by conducting further genetic studies on *T. maxima* .

Conclusion

Post-2020, biodiversity conservation has become a shared concern among all parties to the Convention on Biological Diversity. Giant clams hold significant economic and ecological importance as coral reef species. In the present study, we employed SDMs with a dataset comprising 213 occurrence records and nine environmental variables to assess the potential distribution of *T. maxima* , a giant clam species, in the Indo-Pacific core region. We identified that land distance and light intensity are the dominate factors influencing the distribution of*T. maxima* . Our analysis encompassed both current and future climate scenarios. Our study revealed that the potential distribution area of T. maxima is 1,519,764.73 km2, constituting 16.10% of the total protected areas. Additionally, through an overlay analysis, we evaluated the alignment between potential suitable areas and existing protected areas, enabling us to identify gaps in conservation efforts. Our findings provide insight into the spatial distribution patterns of*T. maxima* , offering scientific guidance for effective conservation management and recommendations for the establishment of future protected areas.

Data availability statement

The raw data used in this study are available through the following links: the Global Biodiversity Information Facility (GBIF, https://www.gbif.org/), iNaturalist (https://www.inaturalist.org/), and the Ocean Biogeographic Information System (OBIS, https://obis.org/). Bio-ORACLE (https://bio-oracle.org/downloads-to-email.php) and Global Marine Environment Datasets (GMED, https://gmed.auckland.ac.nz/download.html). If the manuscript is accepted, then the code for the analysis will be available at datadryad.org.

Author contributions

Shenghao Liu: Conceptualization; Formal analysis; Funding acquisition; Writing – original draft. Tingting Li: Data curation; Formal analysis; Methodology; Visualization. Bailin Cong: Data curation; Formal analysis; Methodology. Leyu Yang: Data curation; Formal analysis. Zhaohui Zhang: Conceptualization; Supervision; Project administration. Linlin Zhao: Conceptualization; Funding acquisition; Writing – review & editing.

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Conflict of Interest

The authors declare that they have no conflicts of interest regarding this research.

Figure Captions

Figure 1 The global distribution map of Tridacna maxima (A) and the study area map (B). The red dots represent existing occurrence records of the T. maxima worldwide, while the yellow and blue dots represent occurrence records of the East Indian Ocean-South China Sea population (EIOS) and the West Pacific-Indonesian population (WPI), respectively.

Figure 2 Results of collinearity analysis of nine predictors. Scatter collinearity analysis (A), Pearson's correlation analysis (B), and variance inflation factor analysis (C) results for nine predictor variables. Depth - ocean depth; LandD - land distance; Cv - current velocity; Do - dissolved oxygen; Sal - salinity; Tmean – temperature mean; Trange – temperature mean; Lb - Light at bottom; Pp - Phytoplankton.

Figure 3 Ecological niche differentiation. (A) Percentage of explained variance of each principal component of principal component analysis for the nine selected predictors. (B) The niches of the two populations of*Tridacna maxima* quantified via four-dimensional hypervolumes. To visualize the shape and boundary of the hypervolumes in two dimensions, a random selection of 20,000 stochastic points for each hypervolume was used. The large blue and orange points indicate the mean niche position (niche centroid) of EIOS and WPI, respectively. (C) Contribution of environmental predictors to each principal component (PC). The number in the bar indicates the contribution rate (%) of each predictor to PC axes, and only values>15% are shown. Depth - ocean depth; LandD - land distance; Cv - current velocity; Do - dissolved oxygen; Sal - salinity; Tmean – temperature mean; Trange – temperature mean; Lb - Light at bottom; Pp - Phytoplankton.

Figure 4 Model evaluation and importance of environmental factors. Predictive abilities of the ten modeling algorithms in projecting the distribution of*Tridacna maxima* at the population and species levels. (A) the True Skill Statistics (TSS) value; (B) the Area Under the receiver operating characteristic Curve (AUC) value. The black horizontal lines indicate the cutoff values of the AUC (0.8) and TSS (0.7) of the single model used to build the ensemble model. (C) Relative importance of the nine predictor variables in the three ensemble models built at population and species levels. Data are expressed as mean ± standard error. Depth - ocean depth; LandD - land distance; Cv - current velocity; Do - dissolved oxygen; Sal - salinity; Tmean – temperature mean; Trange – temperature mean; Lb - Light at bottom; Pp - Phytoplankton.

Figure 5 The response curves of *Tridacna maxima* occurrence probability against the two most important driving factors based on the population-level (A1, A2) and species-level model (including the Eastern Indian Ocean – South Sea population (B1, B2) and the Western Pacific – Indonesia population (C1, C2)). LandD - land distance; Tmean – temperature mean; Lb - Light at bottom.

Figure 6 Habitat suitability maps of *Tridacna maxima* predicted by species and population level integrated models under current climate scenarios. Panels (A1, A2) show the corresponding continuous and binary maps for the species; panels (B1, B2) show the corresponding maps for EIOS; panels (C1, C2) show the corresponding maps for WPI.

Figure7 Future predictions and changes. Habitat suitability maps of*Tridacna maxima* predicted by an integrated model established at both species and population levels under future climate scenarios. Panels (A1, B1, C1) are binary maps for each species, and panels (A2, B2, C2) show the predicted changes in suitable habitats for the 2100s under RCP 8.5 (0085). The category “loss” represents areas projected to be suitable under current climatic conditions but unsuitable under future climatic conditions; “stable” represents areas projected to be suitable under both current and future climatic conditions; “gain” represents areas projected to be unsuitable under current climatic conditions but suitable under future climatic conditions; and “unsuitable” represents areas projected to be unsuitable under current and future climatic conditions.

Figure 8 Analysis of Marine Protected Area (MPA) Gaps. (A) Analysis of suitable habitats for *Tridacna maxima* in the current climate scenario and existing MPA gaps. (B) Analysis of suitable habitats for *Tridacna maxima* in the 2100s under the RCP 8.5 climate scenario and existing MPA gaps.

Table 1 The nine environmental variables selected for this study

Environment variable	**Unit**	**Source**	**Data for the future**
Current velocity	m·S^{-1}	*http://www.bio-oracle.org*	Downloaded from Bio-oracle
Salinity	PSS	*http://www.bio-oracle.org*	Downloaded from Bio-oracle
Temperature Mean		*http://www.bio-oracle.org*	Downloaded from Bio-oracle
Temperature Range		*http://www.bio-oracle.org*	Downloaded from Bio-oracle
Depth	m	*http://www.bio-oracle.org*	Remain unchanged
Land Distance	km	*http://gmed.auckland.ac.nz*	Remain unchanged
Dissolved oxygen	mol·m^{-3}	*http://gmed.auckland.ac.nz*	Remain unchanged
Light at bottom	/	*http://www.bio-oracle.org*	Remain unchanged
Phytoplankton	µmol·m^{-3}	*http://www.bio-oracle.org*	Remain unchanged

Table 2 Mean values of the true skill statistics (TSS) and the area under the receiver operating characteristic curve (AUC) for the ensemble models built at the species level (species model) and populations level (EIOS model and WPI model).

Ensemble models	**TSS**	AUC
Species model	0.753	0.892
EIOS model	0.822	0.928
WPI model	0.773	0.886

EIOS, East Indian Ocean-South China Sea; WPI, West Pacific-Indonesia.

Table 3 Size of predicted changes (%) in species range based on population-level and species-level models for the middle (2050s) and end (2100s) of the 21st century under RCPs 2.6 and 8.5.

Year RCP	EIOS	EIOS	WPI	WPI	SPECIES	SPECIES
	2050s	2100s	2050s	2100s	2050s	2100s
RCP 2.6	4.17	4.15	-8.60	-8.43	-10.72	-15.13
RCP 8.5	3.87	2.43	-10.11	-17.79	-18.49	-25.86

References

Allouche, O., Tsoar, A. & Kadmon, R. (2010) Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). Journal of Applied Ecology 43, 1223-1232.*https://doi.org/10.1111/j.1365-2664.2006.01214.x*

Andréfouët, S., Van Wynsberge, S., Fauvelot, C., Bruckner, A. & Remoissenet, G. (2014) Significance of new records of *Tridacna squamosa* Lamarck, 1819, in the Tuamotu and Gambier Archipelagos (French Polynesia). Molluscan Research 34, 277-284.*https://doi.org/10.1080/13235818.2014.940662*

Andréfouët, S., Van Wynsberge, S., Gaertner-Mazouni, N., Menkes, C., Gilbert, A. & Remoissenet, G. (2013) Climate variability and massive mortalities challenge giant clam conservation and management efforts in French Polynesia atolls. Biological Conservation 160, 190-199.*https://doi.org/10.1016/j.biocon.2013.01.017*

Anibaba, Q.A., Dyderski, M.K. & Jagodziński, A.M. (2022) Predicted range shifts of invasive giant hogweed (*Heracleum mantegazzianum*) in Europe. Sci Total Environ 825, 154053.*https://doi.org/10.1016/j.scitotenv.2022.154053*

Araújo, M.B., Anderson, R.P., Márcia Barbosa, A., Beale, C.M., Dormann, C.F., Early, R., Garcia, R.A., Guisan, A., Maiorano, L., Naimi, B., O'Hara, R.B., Zimmermann, N.E. & Rahbek, C. (2019) Standards for distribution models in biodiversity assessments. Science Advances 5, eaat4858.*https://doi.org/10.1126/sciadv.aat4858*

Assis, J., Tyberghein, L., Bosch, S., Verbruggen, H., Serrão, E.A. & De Clerck, O. (2018) Bio-ORACLE v2.0: Extending marine data layers for bioclimatic modelling. Global Ecology and Biogeography 27, 277-284.*https://doi.org/10.1111/geb.12693*

Barbet-Massin, M., Jiguet, F., Albert, C.H. & Thuiller, W. (2012) Selecting pseudo-absences for species distribution models: how, where and how many? Methods in Ecology and Evolution 3, 327-338.*https://doi.org/10.1111/j.2041-210X.2011.00172.x*

Benito Garzón, M., Robson, T.M. & Hampe, A. (2019) ΔTraitSDMs: species distribution models that account for local adaptation and phenotypic plasticity. New Phytologist 222, 1757-1765.*https://doi.org/10.1111/nph.15716*

Booth, T.H., Nix, H.A., Busby, J.R. & Hutchinson, M.F. (2014) bioclim: the first species distribution modelling package, its early applications and relevance to most current MaxEnt studies. Diversity and Distributions 20, 1-9.*https://doi.org/10.1111/ddi.12144*

Brito-Morales, I., Schoeman, D.S., Everett, J.D., Klein, C.J., Dunn, D.C., García Molinos, J., Burrows, M.T., Buenafe, K.C.V., Dominguez, R.M., Possingham, H.P. & Richardson, A.J. (2022) Towards climate-smart, three-dimensional protected areas for biodiversity conservation in the high seas. Nature Climate Change 12, 402-407.*https://doi.org/10.1038/s41558-022-01323-7*

Buisson, L., Thuiller, W., Casajus, N., Lek, S. & Grenouillet, G. (2010) Uncertainty in ensemble forecasting of species distribution. Glob Chang Biol 16, 1145-1157.*https://doi.org/10.1111/j.1365-2486.2009.02000.x*

Cabaitan, P.C., Gomez, E.D. & Aliño, P.M. (2008) Effects of coral transplantation and giant clam restocking on the structure of fish communities on degraded patch reefs. Journal of Experimental Marine Biology and Ecology 357, 85-98.*https://doi.org/10.1016/j.jembe.2008.01.001*

Capinha, C., Leung, B. & Anastácio, P. (2011) Predicting worldwide invasiveness for four major problematic decapods: an evaluation of using different calibration sets. Ecography 34, 448-459.*https://doi.org/10.1111/j.1600-0587.2010.06369.x*

Carvalho, J.C. & Cardoso, P. (2020) Decomposing the Causes for Niche Differentiation Between Species Using Hypervolumes. Frontiers in Ecology and Evolution 8.*https://doi.org/10.3389/fevo.2020.00243*

Chardon, N.I., Pironon, S., Peterson, M.L. & Doak, D.F. (2020) Incorporating intraspecific variation into species distribution models improves distribution predictions, but cannot predict species traits for a wide-spread plant species. Ecography 43, 60-74.*https://doi.org/10.1111/ecog.04630*

Chen, Y., Ge, D., Ericson, P.G.P., Song, G., Wen, Z., Luo, X., Yang, Q., Lei, F. & Qu, Y. (2023) Alpine burrow-sharing mammals and birds show similar population-level climate change risks. Nature Climate Change.*https://doi.org/10.1038/s41558-023-01772-8*

Cheung, W.W., Watson, R. & Pauly, D. (2013) Signature of ocean warming in global fisheries catch. Nature 497, 365-368.*https://doi.org/10.1038/nature12156*

Collart, F., Hedenäs, L., Broennimann, O., Guisan, A. & Vanderpoorten, A. (2021) Intraspecific differentiation: Implications for niche and distribution modelling. Journal of Biogeography 48, 415-426.*https://doi.org/10.1111/jbi.14009*

Dewiyanti, I., Mulyadi, M., Ulfa, M., Haridhi, H.A.J.I.C.S.E. & Science, E. (2021) Biodiversity of megabenthos and coral reef condition in Tuan Island, Aceh Besar.*https://doi.org/10.1088/1755-1315/869/1/012041*

Duncan, M.I., Micheli, F., Boag, T.H., Marquez, J.A., Deres, H., Deutsch, C.A. & Sperling, E.A. (2023) Oxygen availability and body mass modulate ectotherm responses to ocean warming. Nat Commun 14, 3811.*https://doi.org/10.1038/s41467-023-39438-w*

Elith, J., Kearney, M. & Phillips, S. (2010) The art of modelling range-shifting species. Methods in Ecology and Evolution 1, 330-342.*https://doi.org/10.1111/j.2041-210X.2010.00036.x*

Elith, J. & Leathwick, J.R. (2009) Species Distribution Models: Ecological Explanation and Prediction Across Space and Time. Annual Review of Ecology, Evolution, and Systematics 40, 677-697.*https://doi.org/10.1146/annurev.ecolsys.110308.120159*

Faleiro, F.V., Nemésio, A. & Loyola, R. (2018) Climate change likely to reduce orchid bee abundance even in climatic suitable sites. Glob Chang Biol 24, 2272-2283.*https://doi.org/10.1111/gcb.14112*

Fan, H., Huang, M., Chen, Y., Zhou, W., Hu, Y. & Wei, F. (2023) Conservation priorities for global marine biodiversity across multiple dimensions. Natl Sci Rev 10, nwac241.*https://doi.org/10.1093/nsr/nwac241*

Fu, J., Zhao, L., Liu, C. & Sun, B. (2021) Estimating the impact of climate change on the potential distribution of Indo-Pacific humpback dolphins with species distribution model. PeerJ 9, e12001.*https://doi.org/10.7717/peerj.12001*

Gilbert, A., Planes, S., Andréfouët, S., Friedman, K. & Remoissenet, G. (2007) First observation of the giant clam Tridacna squamosa in French Polynesia: a species range extension. Coral Reefs 26, 229-229.*https://doi.org/10.1007/s00338-007-0218-x*

Grorud-Colvert, K., Sullivan-Stack, J., Roberts, C., Constant, V., Horta, E.C.B., Pike, E.P., Kingston, N., Laffoley, D., Sala, E., Claudet, J., Friedlander, A.M., Gill, D.A., Lester, S.E., Day, J.C., Gonçalves, E.J., Ahmadia, G.N., Rand, M., Villagomez, A., Ban, N.C., Gurney, G.G., Spalding, A.K., Bennett, N.J., Briggs, J., Morgan, L.E., Moffitt, R., Deguignet, M., Pikitch, E.K., Darling, E.S., Jessen, S., Hameed, S.O., Di Carlo, G., Guidetti, P., Harris, J.M., Torre, J., Kizilkaya, Z., Agardy, T., Cury, P., Shah, N.J., Sack, K., Cao, L., Fernandez, M. & Lubchenco, J. (2021) The MPA Guide: A framework to achieve global goals for the ocean. Science 373, eabf0861.*https://doi.org/10.1126/science.abf0861*

Guisan, A. & Thuiller, W. (2005) Predicting species distribution: offering more than simple habitat models. Ecology Letters 8, 993-1009.*https://doi.org/10.1111/j.1461-0248.2005.00792.x*

Guisan, A., Thuiller, W. & Zimmermann, N.E. (2017) Habitat Suitability and Distribution Models: With Applications in R. Cambridge University Press, Cambridge.

Hällfors, M.H., Aikio, S., Fronzek, S., Hellmann, J.J., Ryttäri, T. & Heikkinen, R.K. (2016) Assessing the need and potential of assisted migration using species distribution models. Biological Conservation 196, 60-68.*https://doi.org/10.1016/j.biocon.2016.01.031*

Halpern, B.S., Walbridge, S., Selkoe, K.A., Kappel, C.V., Micheli, F., D'Agrosa, C., Bruno, J.F., Casey, K.S., Ebert, C., Fox, H.E., Fujita, R., Heinemann, D., Lenihan, H.S., Madin, E.M., Perry, M.T., Selig, E.R., Spalding, M., Steneck, R. & Watson, R. (2008) A global map of human impact on marine ecosystems. Science 319, 948-952.*https://doi.org/10.1126/science.1149345*

Hoeksema, B.W., (2007) Delineation of the Indo-Malayan centre of maximum marine biodiversity: the Coral Triangle, Biogeography, time, and place: distributions, barriers, and islands. Springer, pp. 117-178.

Hu, W., Zheng, X., Li, Y., Du, J., Lv, Y., Su, S., Xiao, B., Ye, X., Jiang, Q., Tan, H., Liao, B. & Chen, B. (2022) High vulnerability and a big conservation gap: Mapping the vulnerability of coastal scleractinian corals in South China. Sci Total Environ 847, 157363.*https://doi.org/10.1016/j.scitotenv.2022.157363*

Hu, Z.-M., Zhang, Q.-S., Zhang, J., Kass, J.M., Mammola, S., Fresia, P., Draisma, S.G.A., Assis, J., Jueterbock, A., Yokota, M. & Zhang, Z. (2021) Intraspecific genetic variation matters when predicting seagrass distribution under climate change. Molecular Ecology 30, 3840-3855.*https://doi.org/10.1111/mec.15996*

Huelsken, T., Keyse, J., Liggins, L., Penny, S., Treml, E.A. & Riginos, C. (2013) A novel widespread cryptic species and phylogeographic patterns within several giant clam species (Cardiidae: *Tridacna*) from the Indo-Pacific Ocean. PLoS One 8, e80858.*https://doi.org/10.1371/journal.pone.0080858*

Hui, M., Kraemer, W.E., Seidel, C., Nuryanto, A., Joshi, A. & Kochzius, M. (2016) Comparative genetic population structure of three endangered giant clams (Cardiidae:*Tridacna* species) throughout the Indo-West Pacific: implications for divergence, connectivity and conservation. Journal of Molluscan Studies 82, 403-414.*https://doi.org/10.1093/mollus/eyw001*

Ip, Y.K., Loong, A.M., Hiong, K.C., Wong, W.P., Chew, S.F., Reddy, K., Sivaloganathan, B. & Ballantyne, J.S. (2006) Light induces an increase in the pH of and a decrease in the ammonia concentration in the extrapallial fluid of the giant clam Tridacna squamosa. Physiol Biochem Zool 79, 656-664.*https://doi.org/10.1086/501061*

Jantzen, C., Wild, C., El-Zibdah, M., Roa-Quiaoit, H.A., Haacke, C. & Richter, C. (2008) Photosynthetic performance of giant clams, Tridacna maxima and T. squamosa, Red Sea. Marine Biology 155, 211-221.*https://doi.org/10.1007/s00227-008-1019-7*

Killam, D., Thompson, D., Morgan, K. & Russell, M. (2023) Giant clams as open-source, scalable reef environmental biomonitors. PLoS One 18, e0278752.*https://doi.org/10.1371/journal.pone.0278752*

Klumpp, D.W., Bayne, B.L. & Hawkins, A.J.S. (1992) Nutrition of the giant clam *Tridacna gigas* (L.) I. Contribution of filter feeding and photosynthates to respiration and growth. Journal of Experimental Marine Biology and Ecology 155, 105-122.*https://doi.org/10.1016/0022-0981(92)90030-E*

Lê, S., Josse, J. & Husson, F. (2008) FactoMineR: An R Package for Multivariate Analysis. Journal of Statistical Software 25, 1 - 18.*https://doi.org/10.18637/jss.v025.i01*

Lee, L.K., Neo, M.L., Lim, Z.F., Hii, K.S., Lim, H.C., Chan, A.A., Gu, H.F., Lim, P.T. & Leaw, C.P. (2022) Population status and genetic diversity of two endangered giant clams (*Tridacna squamosa* and *Tridacna maxima*) on the fringing reefs of Perhentian Islands, Malaysia. AQUATIC CONSERVATION-MARINE AND FRESHWATER ECOSYSTEMS 32, 1005-1021.*https://doi.org/10.1002/aqc.3807*

Li, L., Zhao, L., Fu, J., Sun, B. & Liu, C. (2022) Predicting the habitat suitability for populations of Pacific cod under different climate change scenarios considering intraspecific genetic variation. Ecological Indicators 142.*https://doi.org/10.1016/j.ecolind.2022.109248*

Liu, C., Liu, X., Wang, H., Wang, A. & Gu, Z. (2018) Effects of light intensity and spectra on metabolism of ammonia, active phosphates, and oxygen consumption in *Tridacna Crocea* . Oceanologia et Limnologia Sinica 49, 313-318.*http://doi.org/10.11693/hyhz20170700183*

Liu, C., White, M., Newell, G. & Pearson, R. (2013) Selecting thresholds for the prediction of species occurrence with presence-only data. Journal of Biogeography 40, 778-789.*https://doi.org/10.1111/jbi.12058*

Liu, E., He, Y., Gu, Z., Shi, Y., Wang, A. & Liu, C. (2021) Effect of light intensity on the change in mantle color of the boring giant clam *Tridacna crocea* . Marine Sciences 45, 70-75.*https://doi.org/10.11759/hykx20200424002*

Lucas, J.S. (2014) Giant clams. Curr Biol 24, R183-184.*https://doi.org/10.1016/j.cub.2013.11.062*

Lumpkin, R., Baringer, M., Bif, M.B., Boyer, T., Bushinsky, S.M., Carter, B.R., Cetinić, I., Chambers, D.P., Cheng, L., Chiba, S., Dai, M., Domingues, C.M., Dong, S., Fassbender, A.J., Feely, R.A., Frajka-Williams, E., Franz, B.A., Gilson, J., Goni, G., Hamlington, B.D., Hu, Z.-Z., Huang, B., Ishii, M., Jevrejeva, S., Johns, W.E., Johnson, G.C., Johnson, K.S., Kennedy, J., Kersalé, M., Killick, R.E., Landschützer, P., Lankhorst, M., Lee, T., Leuliette, E., Li, F., Lindstrom, E., Locarnini, R., Lozier, S., Lyman, J.M., Marra, J.J., Meinen, C.S., Merrifield, M.A., Mitchum, G.T., Moat, B., Monselesan, D., Nerem, R.S., Perez, R.C., Purkey, S.G., Rayner, D., Reagan, J., Rome, N., Sanchez-Franks, A., Schmid, C., Scott, J.P., Send, U., Siegel, D.A., Smeed, D.A., Speich, S., Stackhouse, P.W., Sweet, W., Takeshita, Y., Thompson, P.R., Triñanes, J.A., Visbeck, M., Volkov, D.L., Wanninkhof, R., Weller, R.A., Westberry, T.K., Widlansky, M.J., Wijffels, S.E., Wilber, A.C., Yu, L., Yu, W. & Zhang, H.-M. (2020) Global Oceans. Bulletin of the American Meteorological Society 101, S129-S184.*https://doi.org/10.1175/bams-d-20-0105.1*

Lyons, M.B., Roelfsema, C.M., Kennedy, E.V., Kovacs, E.M., Borrego-Acevedo, R., Markey, K., Roe, M., Yuwono, D.M., Harris, D.L., Phinn, S.R., Asner, G.P., Li, J.W., Knapp, D.E., Fabina, N.S., Larsen, K., Traganos, D. & Murray, N.J. (2020) Mapping the world's coral reefs using a global multiscale earth observation framework. REMOTE SENSING IN ECOLOGY AND CONSERVATION 6, 557-568.*https://doi.org/10.1002/rse2.157*

Mammola, S. & Cardoso, P. (2020) Functional diversity metrics using kernel density n-dimensional hypervolumes. Methods in Ecology and Evolution 11, 986-995.*https://doi.org/10.1111/2041-210X.13424*

Mei, Luo, Hao, Wang, Zhi & Lyu (2017) Evaluating the performance of species distribution models Biomod2 and MaxEnt using the giant panda distribution data. The Journal of Applied Ecology.*https://doi.org/10.13287/j.1001-9332.201712.011*

Monllor-Hurtado, A., Pennino, M.G. & Sanchez-Lizaso, J.L. (2017) Shift in tuna catches due to ocean warming. PLoS One 12, e0178196.*https://doi.org/10.1371/journal.pone.0178196*

Morato, T., González-Irusta, J.M., Dominguez-Carrió, C., Wei, C.L., Davies, A., Sweetman, A.K., Taranto, G.H., Beazley, L., García-Alegre, A., Grehan, A., Laffargue, P., Murillo, F.J., Sacau, M., Vaz, S., Kenchington, E., Arnaud-Haond, S., Callery, O., Chimienti, G., Cordes, E., Egilsdottir, H., Freiwald, A., Gasbarro, R., Gutiérrez-Zárate, C., Gianni, M., Gilkinson, K., Wareham Hayes, V.E., Hebbeln, D., Hedges, K., Henry, L.A., Johnson, D., Koen-Alonso, M., Lirette, C., Mastrototaro, F., Menot, L., Molodtsova, T., Durán Muñoz, P., Orejas, C., Pennino, M.G., Puerta, P., Ragnarsson, S., Ramiro-Sánchez, B., Rice, J., Rivera, J., Roberts, J.M., Ross, S.W., Rueda, J.L., Sampaio, Í., Snelgrove, P., Stirling, D., Treble, M.A., Urra, J., Vad, J., van

Oevelen, D., Watling, L., Walkusz, W., Wienberg, C., Woillez, M., Levin, L.A. & Carreiro-Silva, M. (2020) Climate-induced changes in the suitable habitat of cold-water corals and commercially important deep-sea fishes in the North Atlantic. Glob Chang Biol 26, 2181-2202.*https://doi.org/10.1111/gcb.14996*

Moss, R.H., Edmonds, J.A., Hibbard, K.A., Manning, M.R., Rose, S.K., van Vuuren, D.P., Carter, T.R., Emori, S., Kainuma, M., Kram, T., Meehl, G.A., Mitchell, J.F.B., Nakicenovic, N., Riahi, K., Smith, S.J., Stouffer, R.J., Thomson, A.M., Weyant, J.P. & Wilbanks, T.J. (2010) The next generation of scenarios for climate change research and assessment. Nature 463, 747-756.*https://doi.org/10.1038/nature08823*

Neo, M.L., Eckman, W., Vicentuan, K., Teo, S.L.M. & Todd, P.A. (2015) The ecological significance of giant clams in coral reef ecosystems. Biological Conservation 181, 111-123.*https://doi.org/10.1016/j.biocon.2014.11.004*

Nielsen, E.S., Henriques, R., Beger, M. & von der Heyden, S. (2021) Distinct interspecific and intraspecific vulnerability of coastal species to global change. Glob Chang Biol 27, 3415-3431.*https://doi.org/10.1111/gcb.15651*

Norton, J.H., Shepherd, M.A., Long, H.M. & Fitt, W.K. (1992) The Zooxanthellal Tubular System in the Giant Clam. Biol Bull 183, 503-506.*https://doi.org/10.2307/1542028*

Nuryanto, A. & Kochzius, M. (2009) Highly restricted gene flow and deep evolutionary lineages in the giant clam *Tridacna maxima* . Coral Reefs 28, 607-619.*https://doi.org/10.1007/s00338-009-0483-y*

Pack, K.E., Mieszkowska, N. & Rius, M. (2022) Rapid niche shifts as drivers for the spread of a non-indigenous species under novel environmental conditions. Diversity and Distributions 28, 596-610.*https://doi.org/10.1111/ddi.13471*

Palialexis, A., Georgakarakos, S., Karakassis, I., Lika, K. & Valavanis, V.D. (2011) Prediction of marine species distribution from presence–absence acoustic data: comparing the fitting efficiency and the predictive capacity of conventional and novel distribution models. Hydrobiologia 670, 241-266.*https://doi.org/10.1007/s10750-011-0673-9*

Penn, J.L. & Deutsch, C. (2022) Avoiding ocean mass extinction from climate warming. Science 376, 524-526.*https://doi.org/10.1126/science.abe9039*

Razgour, O., Forester, B., Taggart, J.B., Bekaert, M., Juste, J., Ibáñez, C., Puechmaille, S.J., Novella-Fernandez, R., Alberdi, A. & Manel, S. (2019) Considering adaptive genetic variation in climate change vulnerability assessment reduces species range loss projections. Proceedings of the National Academy of Sciences 116, 10418-10423.*https://doi.org/10.1073/pnas.1820663116*

Rossbach, S., Saderne, V., Anton, A. & Duarte, C.M. (2019) Light-dependent calcification in Red Sea giant clam *Tridacna maxima* . BIOGEOSCIENCES 16, 2635-2650.*https://doi.org/10.5194/bg-16-2635-2019*

Sala, E. & Giakoumi, S.J.I.J.o.M.S. (2018) No-take marine reserves are the most effective protected areas in the ocean. 75, 1166-1168.*https://doi.org/10.1093/icesjms/fsx059*

Song, W.H. & Li, J.J. (2023) The effects of intraspecific variation on forecasts of species range shifts under climate change. Sci Total Environ 857, 159513.*https://doi.org/10.1016/j.scitotenv.2022.159513*

Sorte, C.J.B., Williams, S.L. & Carlton, J.T. (2010a) Marine range shifts and species introductions: comparative spread rates and community impacts. Global Ecology and Biogeography 19, 303-316.*https://doi.org/10.1111/j.1466-8238.2009.00519.x*

Sorte, C.J.B., Williams, S.L. & Zerebecki, R.A. (2010b) Ocean warming increases threat of invasive species in a marine fouling community. Ecology 91, 2198-2204.*https://doi.org/10.1890/10-0238.1*

Strahl, J., Rocker, M.M. & Fabricius, K.E. (2019) Contrasting responses of the coral Acropora tenuis to moderate and strong light limitation in coastal waters. Mar Environ Res 147, 80-89.*https://doi.org/10.1016/j.marenvres.2019.04.003*

Stuart-Smith, R.D., Edgar, G.J. & Bates, A.E. (2017) Thermal limits to the geographic distributions of shallow-water marine species. Nature Ecology & Evolution 1, 1846-1852.*https://doi.org/10.1038/s41559-017-0353-x*

Thuiller, W., Georges, D. & R., E. (2020) Biomod2: ensemble platform for species distribution modeling. R Package Version 3 (4), 6.*https://doi.org/10.1111/j.1600-0587.2008.05742.x*

Thuiller, W., Guéguen, M., Renaud, J., Karger, D.N. & Zimmermann, N.E. (2019) Uncertainty in ensembles of global biodiversity scenarios. Nat Commun 10, 1446.*https://doi.org/10.1038/s41467-019-09519-w*

Todd, P.A., Lee, J.H. & Chou, L.M. (2009) Polymorphism and crypsis in the boring giant clam (*Tridacna crocea*): potential strategies against visual predators. Hydrobiologia 635, 37-43.*https://doi.org/10.1007/s10750-009-9859-9*

Wang, Z., Zeng, C. & Cao, L. (2023) Mapping the biodiversity conservation gaps in the East China sea. J Environ Manage 336, 117667.*https://doi.org/10.1016/j.jenvman.2023.117667*

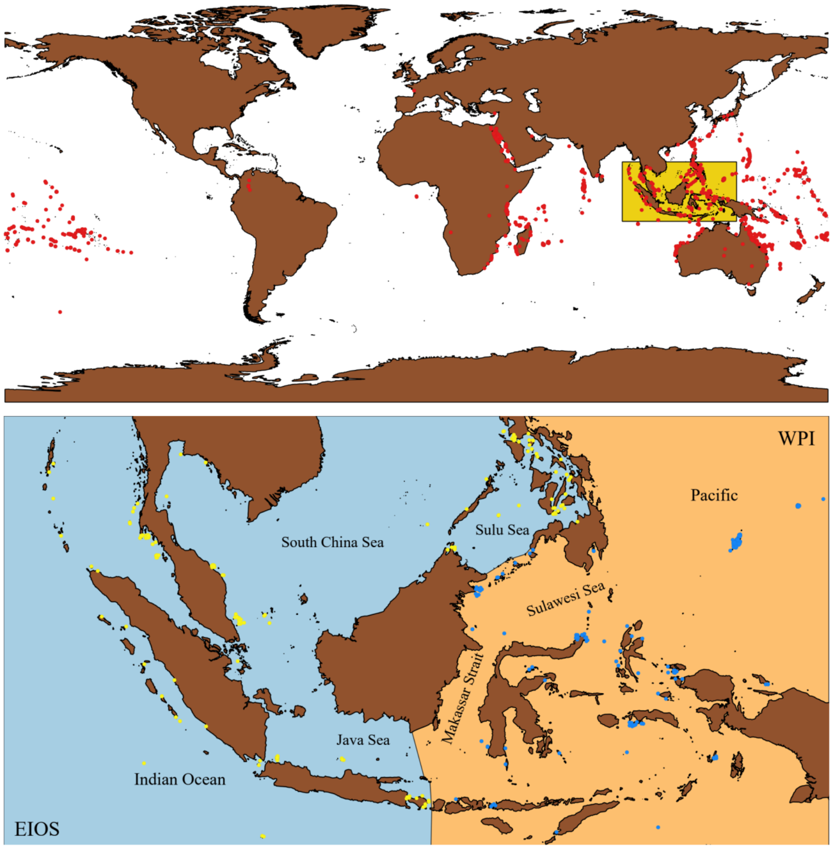
Yonge, C.M. (1975) Giant clams. Sci Am 232, 96-105.*https://doi.org/10.1038/scientificamerican0475-96*

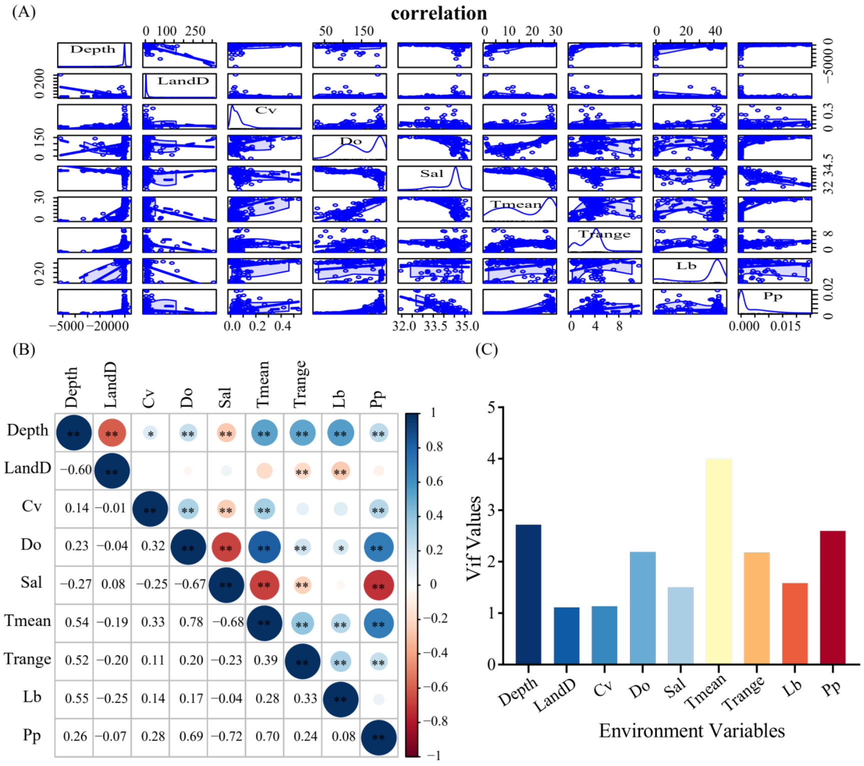
Zhang, Z., Capinha, C., Weterings, R., McLay, C.L., Xi, D., Lü, H. & Yu, L. (2019) Ensemble forecasting of the global potential distribution of the invasive Chinese mitten crab, Eriocheir sinensis. Hydrobiologia 826, 367-377.*https://doi.org/10.1007/s10750-018-3749-y*

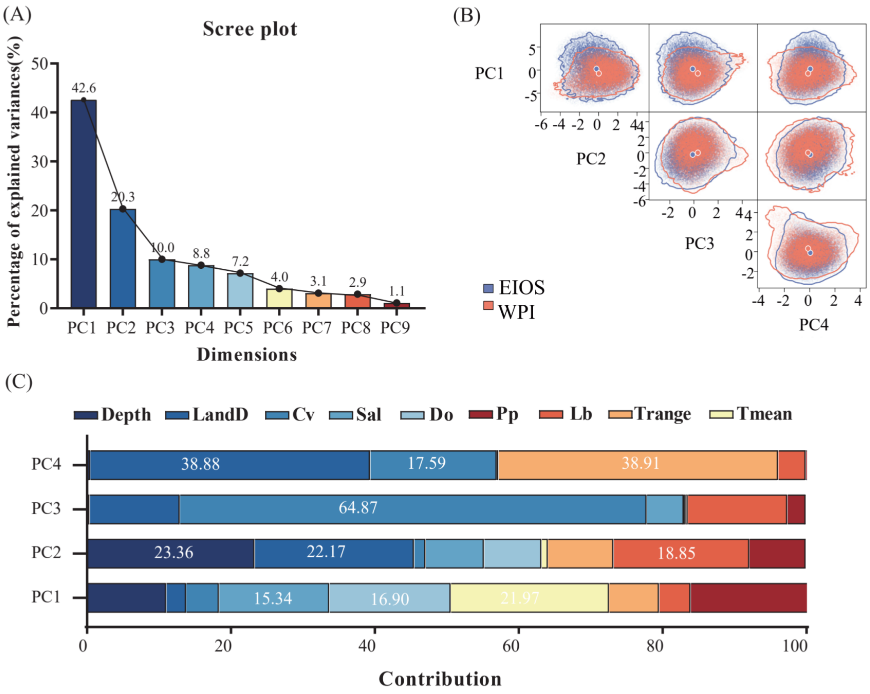
Zhang, Z., Kass, J.M., Mammola, S., Koizumi, I., Li, X., Tanaka, K., Ikeda, K., Suzuki, T., Yokota, M., Usio, N. & Real, R. (2021) Lineage-level distribution models lead to more realistic climate change predictions for a threatened crayfish. Diversity and Distributions 27, 684-695.*https://doi.org/10.1111/ddi.13225*

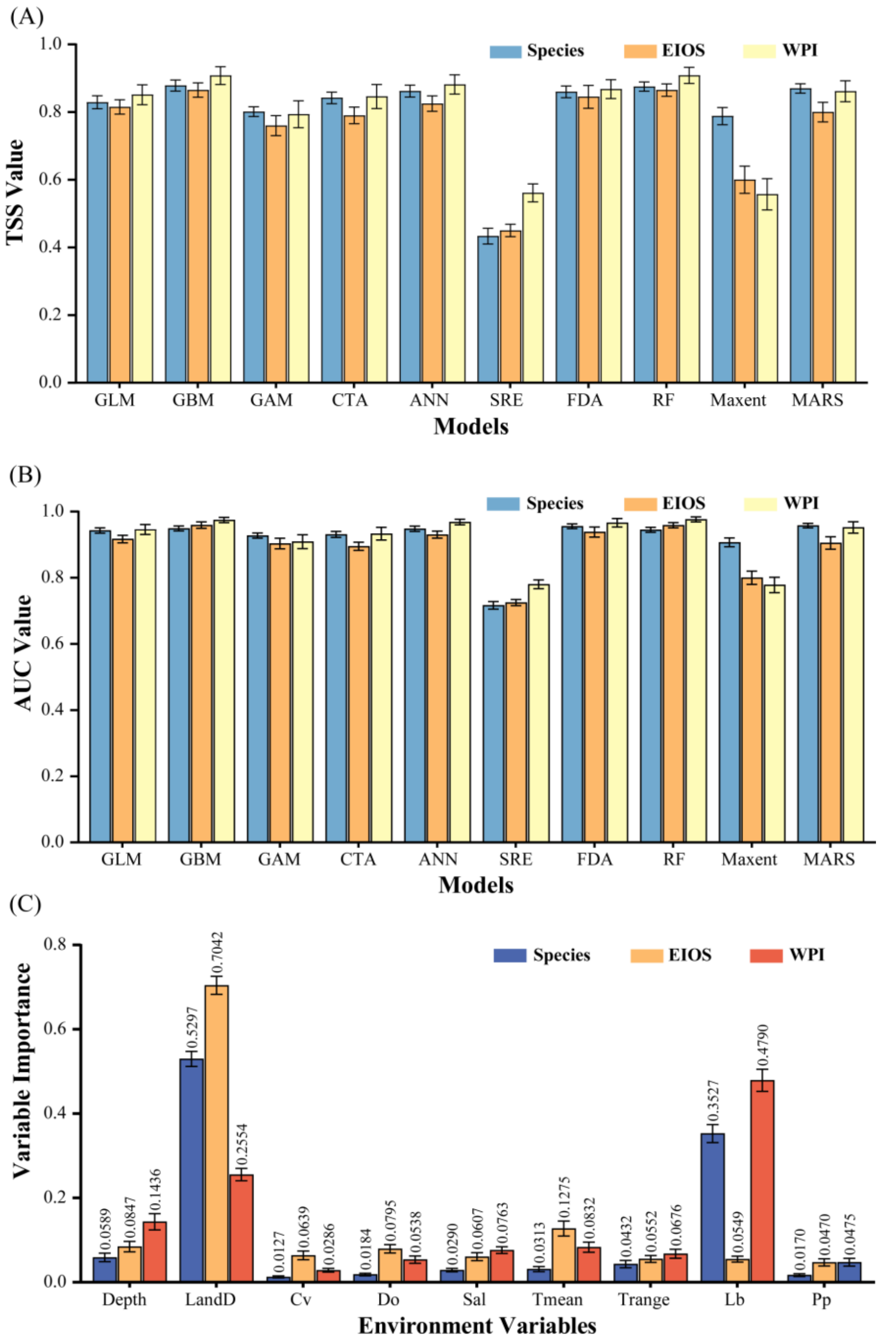
Zhao, L., Gao, R., Liu, J., Liu, L., Li, R., Men, L. & Zhang, Z. (2023) Effects of Environmental Factors on the Spatial Distribution Pattern and Diversity of Insect Communities along Altitude Gradients in Guandi Mountain, China. Insects 14, 224.*https://doi.org/10.3390/insects14030224*

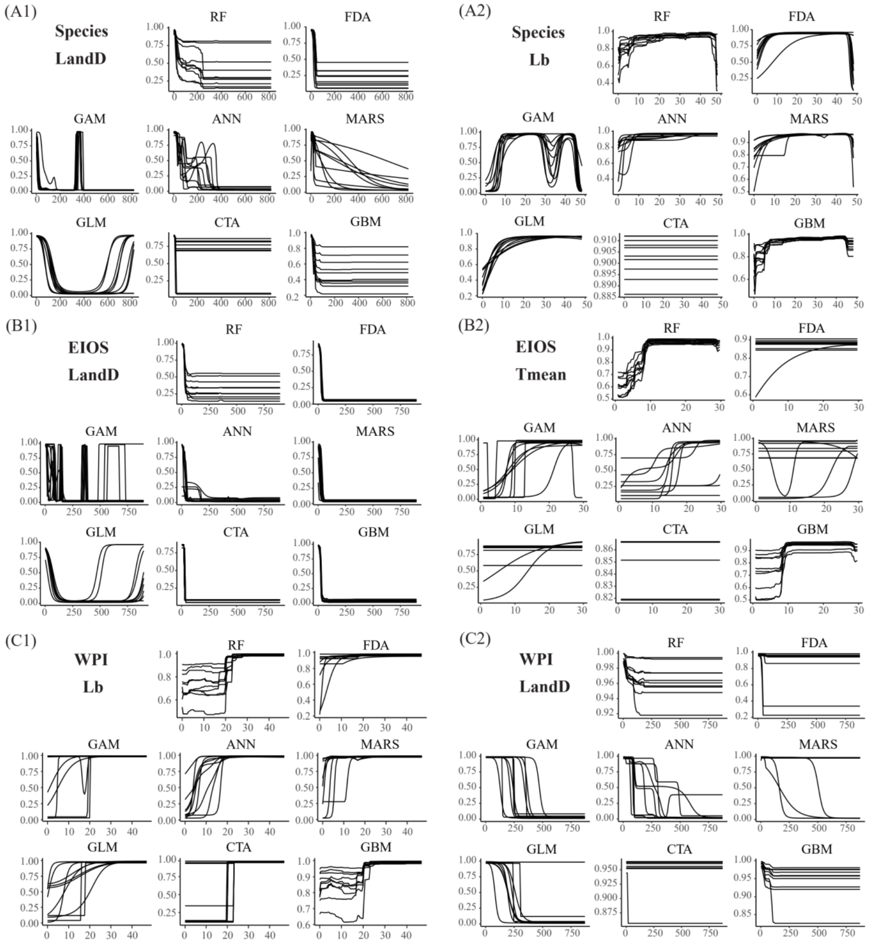
Zuur, A.F., Ieno, E.N. & Elphick, C.S. (2010) A protocol for data exploration to avoid common statistical problems. Methods in Ecology and Evolution 1, 3-14.*https://doi.org/10.1111/j.2041-210X.2009.00001.x*

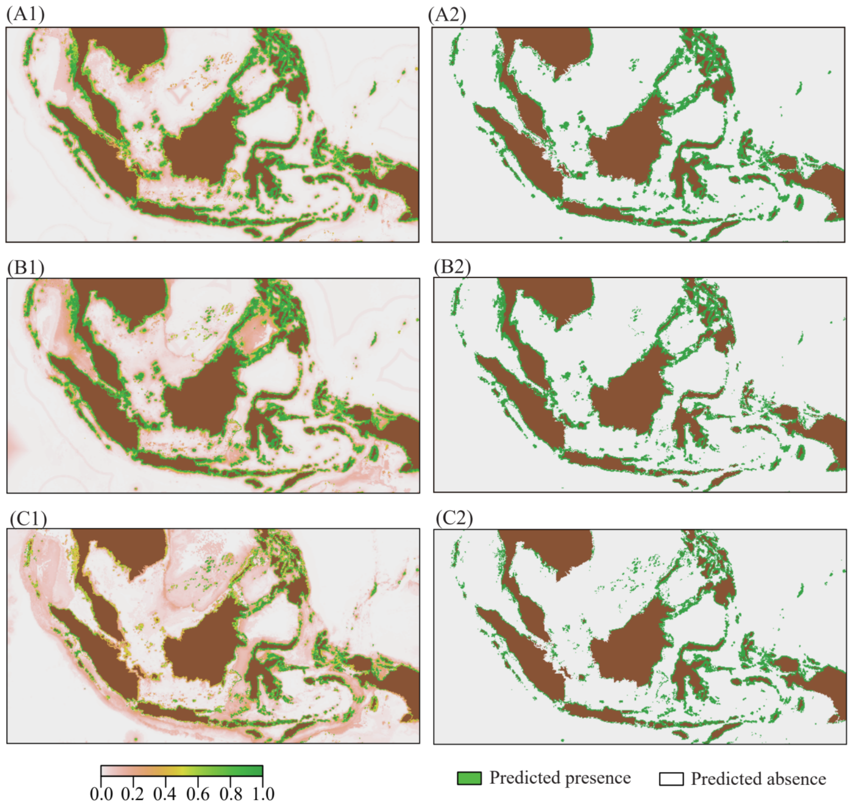

WPI
Pacific
South China Sea
Sulu Sea
Sulawesi Sea
Makassar Strait
Java Sea
Indian Ocean
EIOS

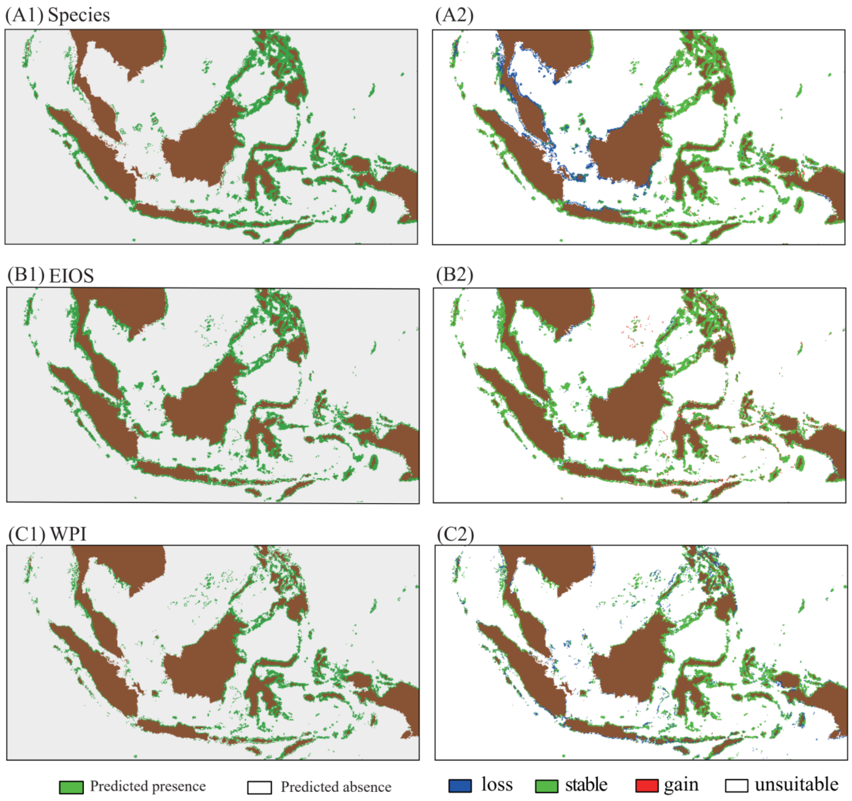

(A)
correlation
Depth
LandD
Cv
Do
Sal
Tmean
Trange
Lb
Pp
(B)
Depth LandD Cv Do Sal Tmean Trange Lb Pp
LandD −0.60
Cv 0.14 −0.01
Do 0.23 −0.04 0.32
Sal −0.27 0.08 −0.25 −0.67
Tmean 0.54 −0.19 0.33 0.78 −0.68
Trange 0.52 −0.20 0.11 0.20 −0.23 0.39
Lb 0.55 −0.25 0.14 0.17 −0.04 0.28 0.33
Pp 0.26 −0.07 0.28 0.69 −0.72 0.70 0.24 0.08
1 0.8 0.6 0.4 0.2 0 −0.2 −0.4 −0.6 −0.8 −1
(C)
Vif Values
Environment Variables
Depth LandD Cv Do Sal Tmean Trange Lb Pp
0 1 2 3 4 5

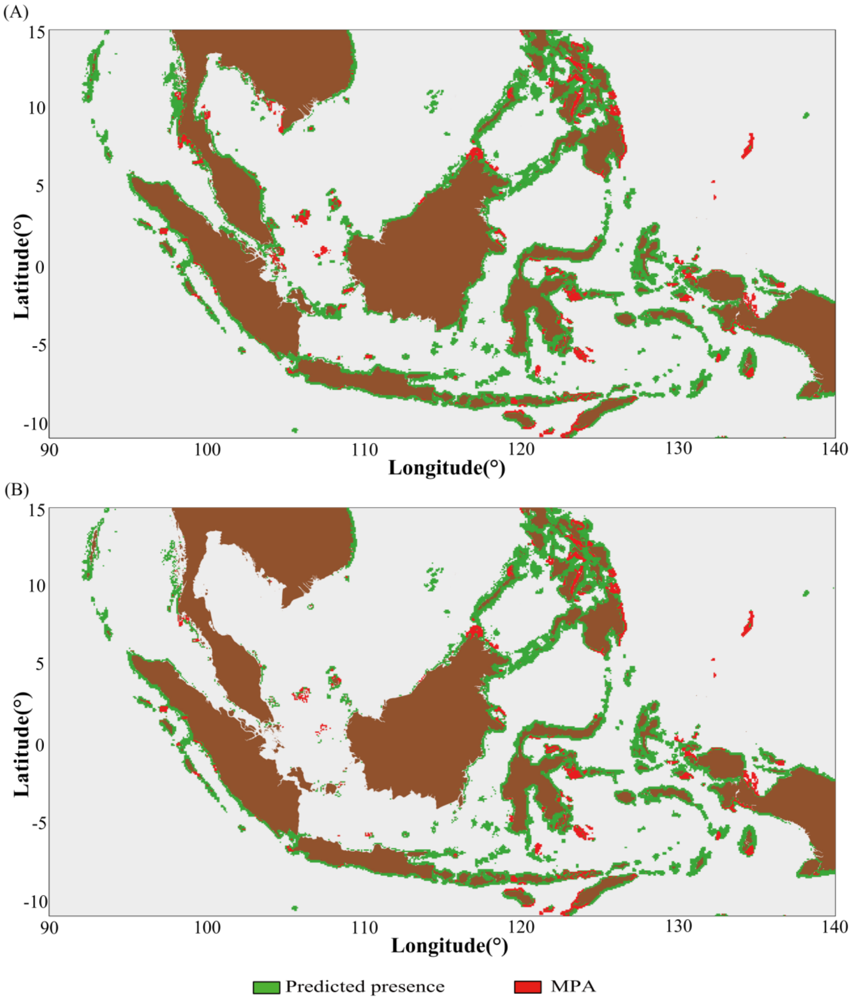

(A)
Scree plot
Percentage of explained variances(%)
Dimensions
PC1 42.6
PC2 20.3
PC3 10.0
PC4 8.8
PC5 7.2
PC6 4.0
PC7 3.1
PC8 2.9
PC9 1.1
(B)
PC1
PC2
PC3
PC4
EIOS
WPI
(C)
Depth LandD Cv Sal Do Pp Lb Trange Tmean
PC4 38.88 17.59 38.91
PC3 64.87
PC2 23.36 22.17 18.85
PC1 15.34 16.90 21.97
0 20 40 60 80 100
Contribution


(A)
Species
EIOS
WPI
TSS Value
1.0
0.8
0.6
0.4
0.2
0.0
GLM
GBM
GAM
CTA
ANN
SRE
FDA
RF
Maxent
MARS
Models
(B)
Species
EIOS
WPI
AUC Value
1.0
0.8
0.6
0.4
0.2
0.0
GLM
GBM
GAM
CTA
ANN
SRE
FDA
RF
Maxent
MARS
Models
(C)
Species
EIOS
WPI
Variable Importance
0.8
0.6
0.4
0.2
0.0
0.0589
0.0847
0.1436
0.5297
0.7042
0.2554
0.0127
0.0639
0.0286
0.0184
0.0795
0.0538
0.0290
0.0607
0.0763
0.0313
0.1275
0.0832
0.0432
0.0552
0.0676
0.3527
0.0549
0.4790
0.0170
0.0470
0.0475
Depth
LandD
Cv
Do
Sal
Tmean
Trange
Lb
Pp
Environment Variables


(A1)
Species
LandD
RF
FDA
GAM
ANN
MARS
GLM
CTA
GBM
(A2)
Species
Lb
RF
FDA
GAM
ANN
MARS
GLM
CTA
GBM
(B1)
EIOS
LandD
RF
FDA
GAM
ANN
MARS
GLM
CTA
GBM
(B2)
EIOS
Tmean
RF
FDA
GAM
ANN
MARS
GLM
CTA
GBM
(C1)
WPI
Lb
RF
FDA
GAM
ANN
MARS
GLM
CTA
GBM
(C2)
WPI
LandD
RF
FDA
GAM
ANN
MARS
GLM
CTA
GBM


(A1)
(A2)
(B1)
(B2)
(C1)
(C2)
0.0 0.2 0.4 0.6 0.8 1.0
🟩 Predicted presence
☐ Predicted absence


(A1) Species
(A2)
(B1) EIOS
(B2)
(C1) WPI
(C2)
Predicted presence
Predicted absence
loss
stable
gain
unsuitable



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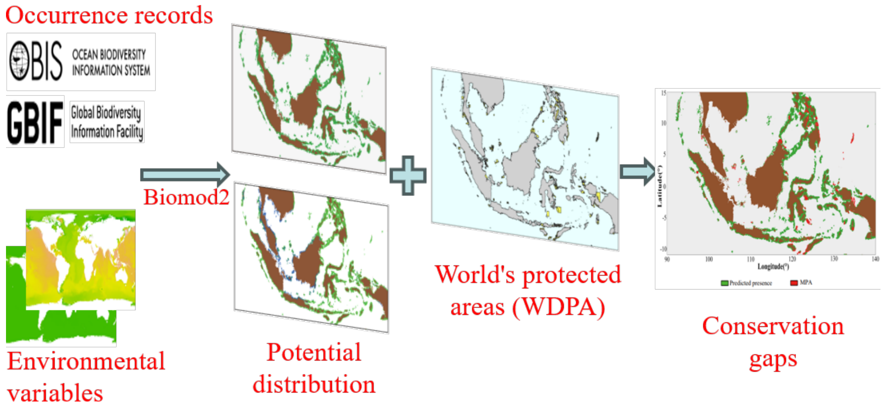
Occurrence records
OBIS OCEAN BIODIVERSITY INFORMATION SYSTEM
GBIF Global Biodiversity Information Facility
Biomod2
Environmental variables
Potential distribution
World's protected areas (WDPA)
Conservation gaps
Latitude(°)
15
10
5
0
-5
-10
90
100
110
120
130
140
Longitude(°)
Predicted presence
MPA