

Conservation priorities for global marine biodiversity across multiple dimensions

Huizhong Fan^{1,2*}, Mingpan Huang^{2*}, Youhua Chen^{3*}, Wenliang Zhou¹, Yibo Hu^{2,4},
Fuwen Wei^{1,2,4#}

¹Southern Marine Science and Engineering Guangdong Laboratory (Guangzhou),
Guangdong, 511458, China.

²CAS Key Laboratory of Animal Ecology and Conservation Biology, Institute of
Zoology, Chinese Academy of Sciences, Beijing, 100101, China.

³Chengdu Institute of Biology, Chinese Academy of Sciences, Chengdu, 610041,
China.

⁴University of Chinese Academy of Sciences, Beijing, 100049, China.

*These authors contributed equally to this work.

#Correspondence should be addressed to Fuwen Wei (weifw@ioz.ac.cn).

Abstract

Marine biodiversity plays important roles in ocean ecosystem services and has substantial economic value. Species diversity (SR), genetic diversity (GD) and phylogenetic diversity (PD), which reflect the number, evolutionary potential and evolutionary history of species in ecosystem functioning, are three important dimensions of biodiversity. Marine protected areas (MPAs) have been demonstrated as an effective area-based tool for protecting marine biodiversity, but only 2.8% of the ocean has been fully protected. It is urgent to identify global conservation priority areas and percentage of the ocean across multiple dimensions of biodiversity based on Post-2020 Global Biodiversity Framework. Here, we investigate the spatial distribution of marine genetic and phylogenetic diversity using 80,075 mitochondrial DNA barcode sequences from 4,316 species and a newly constructed phylogenetic tree of 8,166 species. We identify that the Central Indo-Pacific Ocean, Central Pacific Ocean and Western Indian Ocean harbour high levels of biodiversity across three dimensions of biodiversity, which could be designated as conservation priority areas. We also find that strategically protecting approximately 22% of the ocean would allow us to reach the target of conserving approximately 95% of currently known taxonomic, genetic and phylogenetic diversity. Our study provides insights into the spatial distribution pattern of multiple marine diversities and the findings would help to design comprehensive conservation schemes for global marine biodiversity.

Key words: Marine biodiversity, genetic diversity, phylogenetic diversity, conservation priority areas, multiple dimensions.

Introduction

Biodiversity is the foundation of life on Earth. It provides essential ecological support and services for human survival and development [1]. Species richness (SR), genetic diversity (GD) and phylogenetic diversity (PD) are three important dimensions of biodiversity. SR and GD are two fundamental dimensions of biodiversity, PD is increasingly recognized for its unique values in assessing evolutionary histories of species. Specifically, SR refers to the variety of species or taxonomic groups in a given community or area [2], and enhances the ecosystem functioning [3,4]. GD represents the amount of genetic variability among individuals within a species. It provides the basis for the phenotypic variation and reflects the species' evolutionary potential and ability to respond to the changing environment [5]. PD is defined as the sum of phylogenetic branch lengths for all of the species in an area [6]. It is used as a biodiversity index to measure the time scale of species evolution, identify regions with ancient evolutionary history and predict ecosystem functions and ecosystem diversity [7,8]. Therefore, SR, GD and PD, which reflect the number, evolutionary potential and evolutionary history of species in ecosystem functioning, are three main indices to be measured for biodiversity.

The ocean, comprising the majority of our planet's hydrosphere, is a natural

treasure trove of biodiversity [9]. The richness of marine biodiversity plays important roles in maintaining the stability of ocean ecological services [10] and mitigating climate change by promoting carbon sequestration and storage [11]. Moreover, marine biodiversity also has considerable economic value. It feeds millions of people and supports industries that contribute billions of dollars to the global economy [12,13]. Although the spatial distribution of marine species richness [14,15] and genetic diversity patterns for marine fishes [16] have been investigated, the distribution pattern of phylogenetic diversity for global marine animals remain largely unknown.

Human impacts on ocean, particularly overfishing and pollution, are causing the loss of marine biodiversity [17]. Thus, marine-protected areas (MPAs) have been established to conserve the biodiversity and ecosystem of oceans [18]. The MPAs have been confirmed as an effective area-based tool to protect marine biodiversity [19]. However, up to January 2022, only 7.7% of the ocean had been designated as MPAs, of which 2.8% was fully and highly protected [20]. Based on the Post-2020 Global Biodiversity Framework under the Convention on Biological Diversity (CBD) (<https://www.cbd.int/>), it is urgent to identify new priority areas with high conservation value that are not included in MPAs [21]. Previous efforts to identify global conservation priorities mainly focused on one dimension of marine biodiversity-taxonomic diversity such as species richness, endemism and vulnerability [22-24], other dimensions such as genetic diversity and phylogenetic diversity are usually neglected [25]. Therefore, there is clearly a need to identify priority areas

accounting for multiple dimensions of biodiversity to guarantee that the selected areas have broad biological meaning [26]. Moreover, how much of the sea requires full protection to safeguard marine biodiversity remains challenging. Although earlier studies proposed a quite different percentage of ocean range from 21% to 40% [24,27], these numbers are mainly quantified to conserve marine taxonomic diversity. Therefore, it is necessary to quantify this number from the perspective of protecting multifaceted biodiversity to safeguard more components of marine biodiversity.

Herein, from a macro-genetic perspective, we surveyed the genetic diversity and phylogenetic diversity of global marine taxa using mitochondrial gene data. We aim (i) to reveal the global distribution patterns of marine phylogenetic diversity, (ii) to identify the conservation priority areas across multiple dimensions of marine biodiversity and (iii) to quantitatively evaluate the percentage of ocean areas that needs to be fully protected to safeguard multiple dimensions of marine biodiversity. Our findings would help to design comprehensive conservation schemes for global marine biodiversity and provide a new perspective for the CBD Post-2020 Global Biodiversity Framework.

Results

Global distribution of marine genetic diversity

Taking advantage of publicly available marine sequencing data from the NCBI and BOLD repositories, we obtained a total of 80,075 high-quality mitochondrial

cytochrome oxidase subunit I (COI) sequences from a total of 4,316 marine species (Fig. 1a). Using these mitochondrial sequences, we performed species-specific sequence alignment and calculated nucleotide diversity (π) through pairwise comparisons of aligned sequences. To obtain the global distribution map of marine genetic diversity, we divided the world ocean map into 385.9 km \times 385.9 km grid cells and estimated the mean genetic diversity of each cell by averaging the genetic diversity of species located in the cell. The results showed that the Indo-West Pacific and Western Indian Ocean harboured higher genetic diversity, while the regions with low genetic diversity were located in the North Atlantic Ocean, Arctic Ocean and Antarctica Ocean (Fig. 1b). We demonstrated that these patterns are robust to variation in the least number of sequences for each species (Supplement Notes), as indicated by the spatial correlation analysis (Fig. S1). Moreover, we also proved that the unevenly distributed marine species (Fig. S2), different resolution of grid cell size (Fig. S3) and marine species that travel long-distance (Fig. S4) did not bring substantial bias for the estimation of global marine genetic diversity distribution pattern.

Global distribution of marine phylogenetic diversity

The species-level phylogenetic diversity of global marine species was surveyed based on a newly constructed phylogenetic tree using coding sequences of four mitochondrial genes (*Cytb*, *Co1*, *Nd1* and *12S rRNA*). A total of 8,166 marine species

were assessed for phylogenetic diversity with at least one mitochondrial gene sequence. The robustly constructed phylogenetic tree showed that Porifera were sister group to all other animals, followed by Cnidaria, the Arthropoda formed a clade with Mollusca, Echinodermata and Chordata formed another sister group (Fig. 2a). These results are consistent with the previously published animal tree of life [28]. The distribution map of marine phylogenetic diversity was obtained by calculating the phylogenetic diversity of marine species within each cell. The results showed that the Central Indo-Pacific Ocean, Western Indian Ocean and Central Pacific Ocean harboured high phylogenetic diversity, while the South Indian Ocean, Atlantic Ocean, Eastern Pacific Ocean, Arctic Ocean and Antarctica Ocean showed low levels of phylogenetic diversity (Fig. 2b). Additionally, considering that species richness is positively correlated with phylogenetic diversity in this study (Fig. S5) and in many other published studies [29-31], we also calculated the standard effective size of marine phylogenetic diversity (SES-PD) to control for the confounding effect of species richness on phylogenetic diversity [32]. In this study, the SES-PD was estimated as the difference in the observed phylogenetic diversity and the mean expected diversity, divided by the standard deviation of the expected PD in 1,000 randomizations of the taxa labels. The regions with high SES-PD values means that they still have high phylogenetic diversity after excluding the effect of taxonomic richness, indicating that a higher proportion of distantly related and anciently diverged taxa could be identified in these regions. The regions with low SES-PD values imply

that they have low phylogenetic diversity after excluding the effect of taxonomic richness, indicating that they were the center of recent speciation events and contained recent lineages. The results showed that the areas with the top 10% SES-PD scores were mainly located in the central Indo-Pacific Ocean and South Pacific Ocean, suggesting that these regions were home to ancestral lineages. In contrast, the areas with 10% lowest SES-PD values were located in North Atlantic Ocean (Fig. 2c), indicating that these areas are the centres of recent marine speciation events.

Relationship between sea-surface temperature and marine biodiversity

To evaluate the relationship between sea-surface temperature and marine biodiversity, we performed spatial analysis between sea-surface temperature and marine species richness, genetic diversity and phylogenetic diversity using a modified t test accounting for spatial autocorrelation. The results showed that sea-surface temperature was significantly correlated with marine species richness, genetic diversity and phylogenetic diversity, indicating that the sea-surface temperature has a positive impact on marine biodiversity (Fig. S6).

Conservation priority areas across three dimensions of marine biodiversity

The priority areas for global marine biodiversity conservation were identified and compared across three key dimensions of biodiversity. Specifically, based on the normalized value of marine species richness (Fig. S7), genetic diversity (Fig. 1b) and

SES-PD (Fig. 2b), the grid cells were first clustered into six groups (Fig. S8). Then the mean values of three dimensions of marine biodiversity were compared for each cluster and the grid cells in the top three clusters as the conservation priority areas were selected as priority areas (Fig. 3a). We calculated the coverage of each cluster and found that the priority protection areas covered 22.23% of the global ocean surface (Fig. 3b). We mapped the grid cells from the priority areas onto the global world map and found that the areas were mainly located in the Central Indo-Pacific Ocean, Central Pacific Ocean and Western Indian Ocean. In particular, the Indo-Australian Archipelago Ocean and Madagascar island ocean were consistently identified as the largest conservation priority regions (Fig. 3c), indicating that more conservation efforts should be concentrated in these regions.

Conservation efficiency of currently MPAs and priority areas

We developed a new framework to assess the efficiency of current fully protected areas and priority protection areas in conserving multifaceted biodiversity components. The results showed that current fully protected areas perform poorly in terms of protecting multiple dimensions of marine biodiversity. In detail, the fully protected areas conserved only 34%, 63% and 54% of currently known taxonomic, genetic and phylogenetic diversity, significantly lower than the percentages protected by randomly selected areas (Fig. S9). In contrast, the priority areas that we identified could conserve 95%, 99% and 97% of taxonomic, genetic and phylogenetic diversity,

respectively (Fig. 3d-3f), significantly higher than the percentages obtained by randomly selected areas (Fig. S10). These results could help to quantify the exact percentage of global marine areas that needs to be fully and highly protected. Specifically, we could conserve 95% of currently inventoried multidimensional biodiversity (taxonomic, genetic and phylogenetic) by strategically protecting approximately 22% of the global ocean (Fig. 3d-3f).

Discussion

This is the first multiple survey of species, genetic and phylogenetic diversities for global marine species, and the results reveal that the regions located in the Indo-West Pacific harboured the higher marine taxonomic (Fig. S7), genetic (Fig. 1b) and phylogenetic diversity (Fig. 2b), supporting previous studies which revealed that this region was a species richness hotspot for marine animals and plants [15,33]. Previous studies have proposed four hypotheses to explain the high level of species biodiversity in this region: centres of origin [34], centres of accumulation [35], centres of overlap [36] and centres of survival [37]. A study revealed that tropical reef biodiversity hotspots have changed from the Western Tethys to Indo-Pacific areas since the Eocene, supporting the centres of survival hypothesis [38]. In this study, we found that the Indo-West Pacific has high SES-PD, indicating that ancestral lineages can survive and thrive in this region (Fig. 2c). This provides strong evidence for the centres of survival hypothesis, which suggests that this region is a refuge shelter for many ancestral

species.

MPAs have been demonstrated to be one of the most effective tools for restoring marine biodiversity and ecosystem services [18]. The requirement to increase the coverage of MPAs has been already recognised in CBD post-2020 global biodiversity framework. Previous studies focused on the areas featuring high marine taxonomic diversity [22-24], which might neglect the conservation of areas containing species with high evolutionary potential and older evolutionary histories. In this study, we capture the priority areas for marine animals across three dimensions of biodiversity—taxonomic, genetic and phylogenetic. The results revealed that the conservation priority areas are mainly located in the Central Indo-Pacific Ocean, Central Pacific Ocean and Western Indian Ocean (Fig. 3c), suggesting that these regions should receive special conservation attention.

The percentage of ocean that requires to maximally protecting marine biodiversity is a main CBD target. During the recent 15th meeting of the Conference of the Parties (COP15) held in Kunming, the CBD declared that at least 30% of global sea areas should be protected by 2030 [39]. In this study, from the perspective of protecting multifaceted biodiversity components, our results showed that strategically protecting approximately 22% of the global ocean would allow us to reach the target of conserving approximately 95% of currently known taxonomic, genetic and phylogenetic diversity (Fig. 3c-3e). These results may provide an insight in the context of setting global marine biodiversity conservation targets. Of course,

science-based expansion of MPAs should not only consider the conservation of biodiversity, other important factors such as food provision and carbon storage should also take into consideration in the future [27]. In addition, although phylogenetic diversity has potential to identify and prioritize species in need of protection, and improve the spatial planning of conservation areas, it may not be able to forecast functional diversity (FD) of species because it still depends on many assumptions, uncertainties and varying messages [40]. To better conserve biodiversity, FD which reflects the ecological, morphological and physiological strategies of species [41] should also be taken into consideration. Therefore, to design effective conservation planning, multiple dimensions of biodiversity including taxonomic, genetic, phylogenetic and functional diversities should be incorporated to ensure the biodiversity persistence in a changing world.

Methods

Estimation of marine genetic diversity

The mitochondrial COI coding sequences for marine species were retrieved from GenBank (www.ncbi.nlm.nih.gov/genbank) and the BOLD database (www.boldsystems.org). For each marine species, we selected the corresponding sequences from the database and performed sequence alignment analysis using MUSCLE software with default parameters [42]. Only the pairwise alignments whose sequence overlaps were greater than 60% and sequence differences were less than 10%

were used to calculate genetic diversity. The genetic diversity of each species was defined and calculated following Mirado *et al.* [43].

To obtain the distribution pattern of global marine genetic diversity at a finer scale, we divided the world ocean map into 385.9 km × 385.9 km grids representing a 148,953 km² area. Grid cells including coastal habitat in which ocean area accounted for less than 50% of the total area were excluded from the analysis. The genetic diversity of each cell was calculated by averaging Π across all the species located in the cell, which was mathematically defined by

$$GD = \frac{1}{S} \sum_{p=1}^S \Pi$$

where S is the number of species in the cell.

Estimation of marine phylogenetic diversity

We constructed the phylogenetic tree of global marine species based on four mitochondrial genes (*Cytb*, *Co1*, *12S-rRNA* and *Nd1*). We first aligned the coding sequences of each gene using MAFFT software with default parameters [44] and trimmed the poorly aligned sites at the start and end of the sequence. Then, we imported the aligned results of four genes into SequenceMatrix software [45] and constructed a supermatrix with gaps regarded as missing data. Finally, we constructed a phylogenetic tree of global marine species using RAxML 8.2.12 [46] with the ASC_GTRGAMMA model and 1,000 bootstrap replicates. The species *Oscarella*

Microlobata and *Pseudocorticiium Jarrei* from *Homoscleromorpha* were used as the outgroups. We calculated Faith's phylogenetic diversity [6] and SES-PD [32] using the "picante" package [47] in R software.

Collection of global marine species distribution, sea-surface temperature and MPA data

We directly derived the distribution data of global marine species in vectorized shapefile format from the IUCN spatial database (www.iucnredlist.org/resources/spatial-data-download). The global map was from China Ministry of Natural Resources (<http://bzdt.ch.mnr.gov.cn/index.html>). The sea-surface temperature data were collected from MARSPEC database [48]. The spatial information on global MPAs was collected from the World Database on Protected Areas (WDPA) available at <http://protectedplanet.net/>.

Identification of priority areas for marine biodiversity conservation

In this study, priority areas were selected based on three important dimensions of marine biodiversity: species richness, genetic diversity and phylogenetic diversity. To obtain the regions with highest levels of biodiversity across multiple dimensions, we introduced a k-means clustering method [49] to classify the grid cells. In detail, the species richness, genetic diversity and SES-PD values of each grid cell were first normalized from zero to one using the min-max normalization method. Then, the

optimal number of clusters was determined using the `fviz_nbclust` function implemented in the `factoextra` R package. Finally, the k-means method was used to cluster the grid cells, and the priority areas for marine conservation were selected based on the normalized marine biodiversity values.

Assessing the effectiveness of conserving multifaceted biodiversity components

To assess the effectiveness of the proposed priority areas in protecting multifaceted biodiversity components, we used a biodiversity preservation cumulative curve with 95% confidence interval, which is to randomly sample an increasing number of grid cells from all the available grid cells with 1,000 replicates. This randomized biodiversity-preservation curve is applied to the assessments of conservation effectiveness of species richness, genetic diversity and phylogenetic diversity in fully protected areas versus proposed priority areas. The detail steps to obtain species preservation cumulative curves were displayed in supplement notes.

Supplemental Information

Supplemental Information includes all data and can be found with this article online.

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Author contributions

F.W. conceived and supervised the project. H.F., M.H., Y.C., W.Z. and Y.H. performed the data collection and analysis. H.F., Y.C. wrote the manuscript with input from F.W.

Competing interests

The authors declare that they have no competing interests.

Data and code accessibility

All data and code reported in this paper have been deposited in Github database (<https://github.com/fanhuizhong>).

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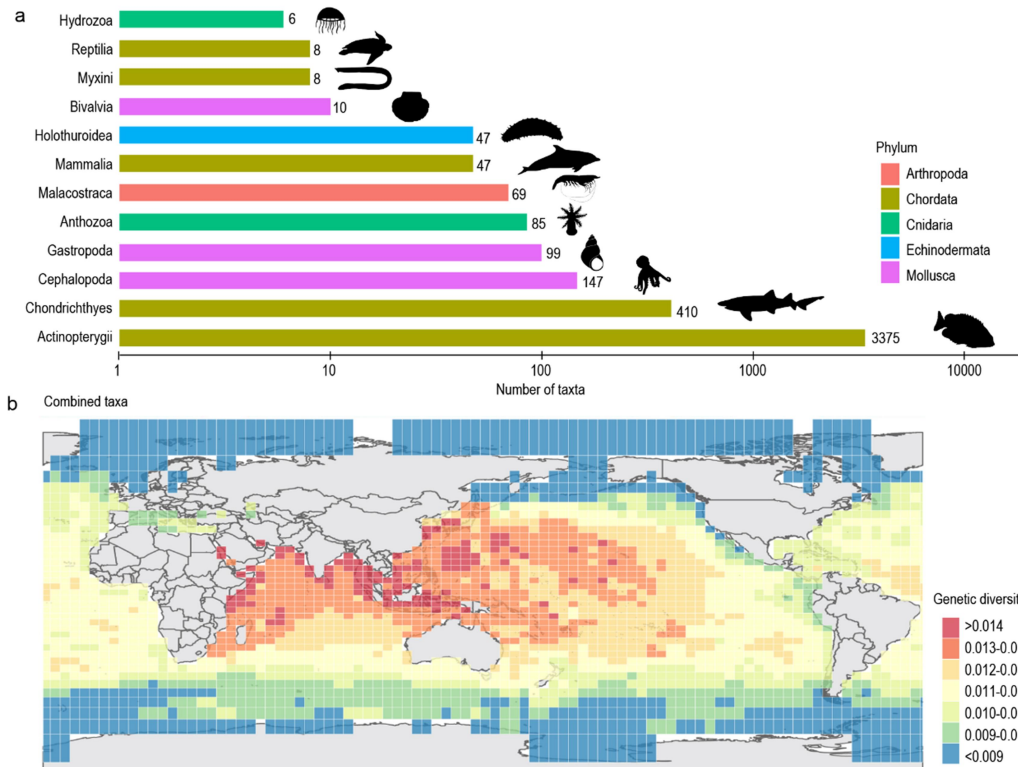


Fig. 1. Number of marine taxa used for genetic diversity assessment and global distribution pattern of marine genetic diversity. (a) The number of marine taxa used for genetic diversity assessment. The taxonomic classes are shown from least (top) to the most (bottom). Only taxonomic classes with more than five species are displayed. (b) The spatial pattern of *COI*-based genetic diversity for global marine species. Credit: the silhouette of species was downloaded under a Creative Commons license CC BY 4.0.

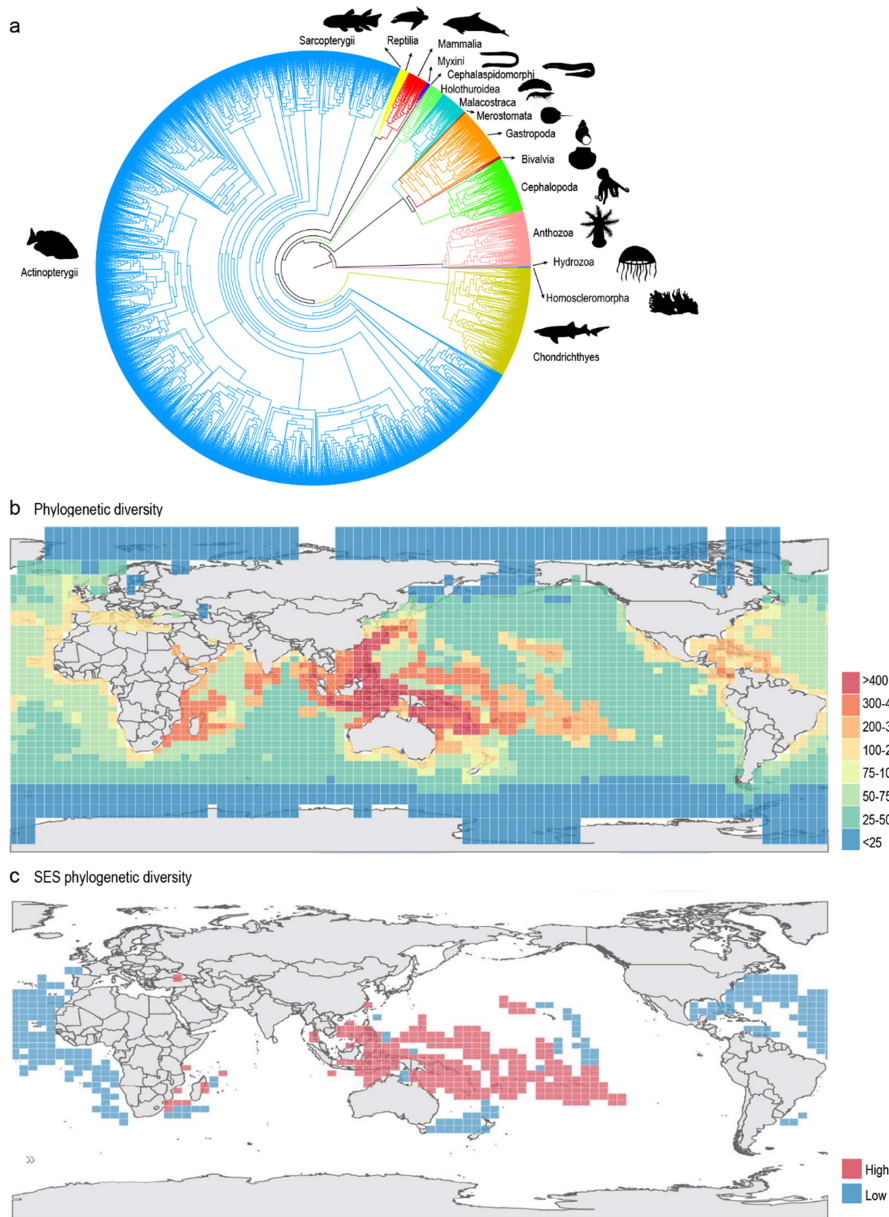


Fig. 2. Phylogenetic tree for global marine species and the global distribution patterns of marine phylogenetic diversity. (a) phylogenetic tree of global marine species based on four mitochondrial genes (*Cytb*, *Co1*, *12S-rRNA* and *Nd1*). (b) Global spatial pattern of marine phylogenetic diversity. (c) The grid cells with the 10% highest (red) and 10% lowest SES-PD value (blue). Credit: the silhouette of species was downloaded under a Creative Commons license CC BY 4.0.

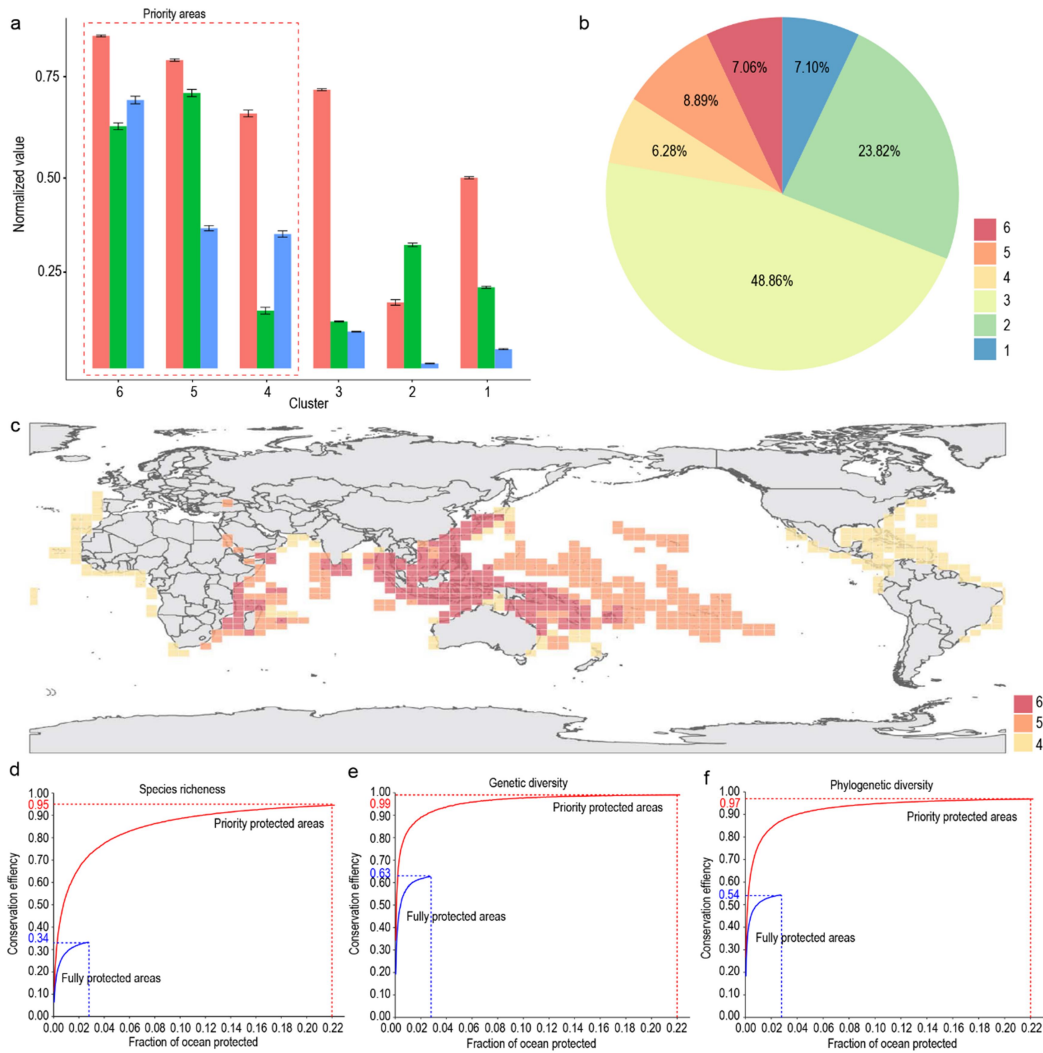


Fig. 3. The identification and distribution of priority for conservation across three dimensions of marine biodiversity. (a) The mean values of SR, GD and PD of each cluster. (b) The percentage of world-wide ocean surface covered by each cluster. (c) The spatial distribution of grid cells within priority protected areas, different colors represent different clusters. (d-f) The efficiency of fully protected areas and the priority protected areas in conserving marine (d) species richness (e) genetic diversity and (f) phylogenetic diversity.