Where marine protected areas would best represent 30% of ocean biodiversity

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Where Marine Protected Areas would best represent 30% of ocean biodiversity

Abstract

The IUCN (the International Union for Conservation of Nature) World Conservation Congress called for the full protection of 30% of each marine habitat globally and at least 30% of all the ocean. Thus, we quantitatively prioritized the top 30% areas for Marine Protected Areas (MPA) globally using global scale measures of biodiversity from the species to ecosystem level. The analysis used (a) Ecosystems mapped based on 20 environmental variables, (b) four Biomes (seagrass, kelp, mangrove, and shallow water coral reefs) plus seabed rugosity as a proxy for habitat, and (c) species richness within each biogeographic Realm (indicating areas of species endemicity), so as to maximise representivity of biodiversity overall.

We found that the 30% prioritized areas were mainly on continental coasts, island arcs, oceanic islands, the southwest Indian Ridge, the northern Mid-Atlantic Ridge, the Coral Triangle, Caribbean Sea, and Arctic Archipelago. They generally covered 30% of the Ecosystems and over 80% of the Biomes. Although 58% of the areas were within countries Exclusive Economic *Zones* (EEZ), only 10% were in MPAs, and < 1% in no-take MPAs (IUCN category Ia). These prioritised areas indicate where it would be optimal to locate MPA for recovery of marine biodiversity within and outside country's EEZ. The countries Canada, Australia, United States of America, Greenland, Indonesia, Russia, and New Zealand have the largest EEZ*s* within the prioritized areas. For the areas outside EEZ, countries could most easily agree to designate prioritised areas that are also wilderness as these already have the least human disturbance and conflict with economic activities. Our results thus provide a map that will aid both national and international planning of where to protect marine biodiversity as a whole.

1 Introduction

The 2016 IUCN (the International Union for Conservation of Nature) World Conservation Congress called for the protection of at least 30% of each marine habitat globally and at least 30% of all the ocean for worldwide effective marine biodiversity conservation by 2030 (IUCN, 2016). According to the IUCN annual report (2018a), the overall ocean coverage of MPAs was almost 7% at the end of 2017, whereas it was 1.6% in 2012 (IUCN, 2013). However, although the number of MPAs has been increasing, most are ineffective because they do not aim to prevent fishing from altering food webs, and fully protected areas which are no-take (hereafter called marine reserves) only cover 2% of the ocean (Costello & Ballantine, 2015; Marine Conservation Institute, 2019).

Conservation aims to protect species from extinction by protecting their populations, habitats and ecosystems from human impacts. The CBD defines biodiversity as including variation within and between species and of ecosystems (United Nations, 1992). A world network of protected areas would therefore need to encompass replicated populations of species, habitats and ecosystems that are representative of biodiversity as a whole (Convention on Biological Diversity, 2010). As the environmental conditions of marine ecosystems affect species' growth, reproduction, and their abundance (for example, such as temperature influencing biological metabolism and growth), understanding the distribution of ecosystems is desirable for conservation planning (Zhao & Costello, 2019a). In addition, an economical way to select protected areas would be to identify regions of high species endemicity (i.e., realms) and/or richness that would be a priority for conservation. Analogous to biomes in the terrestrial domain, marine vegetation can be divided into large geographical areas called marine biomes (Woodward et al., 2004). Marine biomes are formed by species of seagrass, kelp, mangroves and shallow water coral reefs as they provide three-dimensional habitat for other species and are primary producers. Although animals, the shallow water coral reefs are considered biomes because they host photosynthetic algae (zooxanthellae) and provide complex habitat structure. Thus, these biomes form part of the species composition, habitat and ecosystem components of biodiversity. Asaad et al. (2018) found a strong positive correlation between biomes and overall marine species richness and fish endemicity in the 'Coral Triangle'. At a local scale, these biomes are composed of particular species and termed habitats. Non-vegetated seabed habitats can be defined based on their sediments, rock substrata and exposure to water movement (Costello & Emblow, 2005). In the absence of a global seabed substrata map, the distribution of erosional and depositional habitat can be predicted using topographic variability, also called benthic rugosity, which is an indicator measure of seabed habitat heterogeneity (Asaad et al., 2018). Rugosity is derived from variations of depth and slope (Walbridge et al., 2018).

Previous marine conservation area prioritization planning has been based on qualitative methods (e.g. Lourie & Vincent, 2004; Martin et al., 2015; Olson & Dinerstein, 2002), targeting specific species (e.g., Klein et al., 2010; Wallace et al., 2010), and at regional scales (Abdulla et al., 2008; e.g., Ban et al., 2009; Leathwick et al., 2008). However, to date, only Selig et al. (2014), Klein et al. (2015) and Jenkins and Van Houtan (2016) provided a global scale analysis of where MPAs should be located. Selig et al. (2014) used species richness and two indicators of endemism based on modelled distribution data for 12,500 species produced by AquaMaps (Kaschner et al., 2010) as well as considering human impacts. Klein et al. (2015) analysed the overlap between modelled distributions of 17,348 marine species, using a further expanded AquaMaps dataset (Kaschner et al., 2013) and MPAs. Jenkins and Van Houtan (2016) developed an index to prioritize areas based on 4,352 marine species, considering species vulnerability, coverage by MPAs, and human impacts. However, none of these analyses specifically distinguished and/or incorporated areas of different species composition, such as areas of high species endemicity (Jefferson & Costello, 2019), nor ecosystems, biomes or habitats.

When proposing a global MPA network it may be useful to know how it compares to the distribution of existing MPAs (Klein et al., 2015), which areas are inside and outside national jurisdiction, and current states of human impact or 'pristineness'. IUCN classified protected areas into seven categories (Ia, Ib, II, III, IV, V, VI) based on specific management aims (Lausche, 2011). Only the category of IUCN Ia is no-take, and effective for marine conservation (Costello & Ballantine, 2015). Some MPAs have been established outside Exclusive Economic Zones (EEZ), i.e., in 'High Seas', also called 'Areas Beyond National Jurisdiction' (ABNJ), notably the Ross Sea MPA (CCAMLR, 2019). Another consideration may be how pristine an area is. A recent study mapped "marine wilderness", and defined it as those areas with the 10% lowest effects of 19 human impacts (Jones et al., 2018).

Our paper reports a spatial prioritization analysis based on ecosystems, biomes, realms of species endemicity, and species richness. The prioritization mapped the optimal locations to maximise representivity of all facets of biodiversity in an MPA network covering 30% of the ocean using the decision support software Zonation (Moilanen, 2007; Moilanen et al., 2005). The prioritized areas were compared with all MPAs, marine reserves, the EEZs and ABNJ, and the marine wilderness areas.

2 Methods

The prioritization analysis used data layers representing the variation between species and of ecosystems at a global scale. These were world maps of Ecosystems defined by environmental variables, Biomes defined by habitat forming species, seabed topographic variation (Benthic Rugosity), and the level of species richness in regions of species endemicity (Within-Realm Species Richness). By including richness, endemicity and biogenic habitats, we have also included multiple levels of genetic variability.

2.1 The data layers

Ecosystems

We used the classification of marine Ecosystems (Zhao et al., 2019) in the Zonation analysis (Figure 1, Table S1). The Ecosystems were identified by an unsupervised cluster analysis of 20 physical, biochemical, and nutrient variables. Some areas belonging to the same Ecosystem were geographically divided by continents but distributed at similar latitudes and symmetrically on both sides of the equator. Most of the coastal regions belonged to Ecosystem 3, excluding the polar coastal regions. The distribution of Ecosystems showed good correspondence with Ecological Marine Units (Sayre et al., 2017), biogeographic realms (Costello et al., 2017), and biogeochemical provinces (Longhurst, 2007). Each of the Ecosystems were represented by presence-absence layer in the prioritization analysis, so that there were seven layers in total and none of them overlapped each other.

Biomes

(i) Seagrass

The three-dimensional structure of the seagrass meadows provides feeding, breeding and nesting habitat for a variety of associated fauna (Jayathilake & Costello, 2019a). Because of its conservation importance, maps have been developed to understand its global distribution (Green et al., 2003; Jayathilake & Costello, 2018). We used the most recent and comprehensive global seagrass biome raster layer (Figure 2). The seagrass biome distribution was made using MaxEnt distribution modelling of 43,037 species occurrence records and 13 abiotic layers (Jayathilake & Costello, 2018).

(ii) Kelp

Kelp species, defined as seaweeds of the Order Laminariales, provide feeding, breeding, and nesting habitats for associated fauna and flora including fish, urchins, crustaceans, molluscs, polychaetes, and mammals (Jayathilake & Costello, 2019b). We used a new global composite kelp species map generated by MaxEnt distribution modelling of 44,265 records from 93 different laminarian kelp species and abiotic layers (Jayathilake & Costello, 2019c) (Figure 2).

(iii) Mangrove

Mangroves provide nursery habitats for juvenile coastal fish and crustaceans (Rönnbäck, 1999). The global mangrove distribution was created using field records and remote sensing data from the Global Land Survey (GLS) and Landsat archive during the years 1997-2000 by a hybrid of supervised and unsupervised digital image classification techniques (Giri et al., 2011) (Figure 2).

(iv) Shallow-water Coral Reefs

Shallow-water zooxanthellate coral reef ecosystems contain about one third of all marine species (Costello, 2015). Their world map was acquired from UNEP-WCMC et al., (2010) (Figure 2). Of the data sources, 85% were from the Millennium Coral Reef Mapping Project at a consistent 30m resolution (Andrefouet et al., 2006).

Rugosity

Rugosity, or surface roughness, is an index based on the differences in the depths of neighbouring cells. The level of rugosity is positively associated with species richness and used as an indicator of habitat complexity (Asaad et al., 2018; Baker & Harris, 2012; Ziegler et al., 2017). Shallow waters have more wave action and stronger currents (Costello et al., 2018) which increase erosion and rugosity. Offshore environments have less deposition of sediments from land and relatively soft sediments derived from deposition of plankton (Somme et al., 2011). While a global database of seabed composition is not available, the occurrence of erosional and depositional conditions can be approximated by the benthic rugosity index which maps topographic features including canyons, seamounts, abyssal hills and ridges. We calculated the rugosity index by applying the Benthic Terrain Modeller (BTM) 3.0 (Walbridge et al., 2018) with a neighbourhood size of seven in ArcGIS 10.5.1 with depth data acquired from GMED that had a resolution of 5 arcmin (9.2 × 9.2 km at equator) (Basher et al., 2014) (Figure 3a). Because the calculation of rugosity requires the variation of the depth among neighbouring cells, some cells at coasts and polar regions did not have adequate neighbouring cells to calculate rugosity and were thus excluded from the analysis (the white cells in Figure 3a).

Within-Realm Species Richness

i) Global Species Richness

AquaMaps is an online atlas containing maps of the probability of species occurrence based on models using species occurrence records and environmental variables (Kaschner et al., 2016) (Figure S1). Species specific environmental envelopes with respect to temperature, salinity, primary production, and sea ice concentration were derived from occurrence point data that had been verified to fall within a species' known distribution as recorded in the literature. The AquaMaps data set included 24,904 species, of which 2,925 species ranges have been validated by experts (Kesner-Reyes et al., 2016). Following Selig et al. (2014), we used the probability threshold of >0.00 to define species presence in a cell.

AquaMaps represents 10% of all named marine species (Horton et al., 2019) (Table 1). Half of the species are fish, and 58% of fish species are included. The dataset represents more than half of the marine species within Chordata, Actinopterygii, Elasmobranchii, and Mammalia, and near half (>45%) of Sipuncula and Scaphopoda. In contrast, the dataset covers < 4% of Annelida and Bryozoa. The most species-rich taxa had the biggest influence on the species richness map, and comprised Actinopterygii (bony fish), Crustacea Malacostraca (crabs, lobsters, shrimps, etc.), Anthozoa (corals, sea anemones, etc.), Echinodermata (sea stars, sea urchins, sea cucumbers, etc.), Bivalvia (clams, oysters, cockles, etc.), and Gastropoda (sea snails, slugs, etc.) (Table 1). The majority of the species in the dataset were benthic, as is the case for marine species overall (Costello & Chaudhary, 2017). There were more than 600 species from the order Scleractina, including the deep-sea reef-constructing corals *Lophelia pertusa, Oculina varicosa,* and *Madrepora oculata*. There were also more than 400 species from the phylum Porifera, including the deep-sea benthic sponges *Geodia macandrewi, Euchelipluma pristina,* and *Rosella racovitzae.* Therefore, our data include both coastal and deep-sea habitats formed by benthic animals and plants.

ii) The Within-Realms Species Richness

To only use species richness as an indicator of where MPA should be located might overlook regions which have few but unique (endemic) species. For example, almost half the marine species around New Zealand and Antarctica are endemic to these areas (Costello et al., 2010). Here, we used a 30 realms classification to provide an indication of areas of contrasting marine species endemicity (Costello et al., 2017) (Figure S2). We combined this with the estimate of species richness based on species ranges from AquaMaps (Kaschner et al., 2016) to generate a layer of 'Within-Realm Species Richness' (Figure 3b). This indicated the species rich locations in each Realm. We respectively normalized the species richness numbers of the cells belonging to each Realm, using the Z score method with all the same settings to let the normalized data in each Realm have their mean as 0 and their standard deviation as 1.

2.2 The preparation of data layers

The decision-support software *Zonation* was used to quantitatively prioritise areas for protection (Lehtomäki & Moilanen, 2013; Moilanen et al., 2011; Moilanen & Arponen, 2011; Moilanen et al., 2005). *Zonation* iteratively removes geographic cells, starting with cells with the fewest biodiversity attributes (e.g., Biomes absence, low Rugosity, few species). Thus it retains the cells that most parsimoniously occupied 30% of the ocean and collectively included at least 30% of (a) each of the seven Ecosystems and four Biomes, (b) of cells with highest rugosity, and (c) of cells with the highest species richness per realm of endemicity.

All the global data layers were converted to a 182 × 402 grid-cell raster file with 52,093 marine cells at a resolution of ~10,000 km^2 near the equator (~0.9˚). The layers ranged from 84.5°N to 78.7°S and covered all longitudes. All the terrestrial cells and the areas with missing data (representing only 2 % of the ocean) in each layer were given the value of -9999 in all layers. In the seven Ecosystem and four Biome layers, their presence was represented by '1' whilst the other marine cells were represented by '0'. The numbers in the layers of the Rugosity and the Within-Realms Species Richness were continuous numbers from low to high, indicating the complexity of rugosity and the level of species richness within each Realm respectively. The pre-treatment of raw data was done with MATLAB (2017b), and the results of pre-treatment were exported in geotiff format by ArcGIS (10.5.1).

The raster layers used for the prioritization were projected by equal degrees so that the cells at high latitudes were smaller than those at equator. This does not affect the analysis of presence-layers (Ecosystems, Biomes) but might affect apparent species richness as larger cells may contain more species. However, the effect of varying cell size was reduced by the fact that the Realms were divided across latitudes, meaning that cell sizes were similar within Realms. Because the sizes of each cell in each Realm at high latitudes were equally distorted, this would not affect the normalization of species richness within each Realm. Therefore, the distortion of cell sizes in high latitudes could not significantly affect the prioritization analyses.

2.3 Prioritization

The *Zonation* analysis used the Target Based Function (Moilanen, 2007) cell-removal method to prioritize 30% of the global ocean for protection and cover 30% of each Biome and Ecosystem. The Target Based Function prioritizes the cells which contain more features (e.g., seagrass biome, rugosity) from multiple layers rather than the cells which only have high importance from a single layer (Moilanen, 2007). In addition, during the process of iterative cell-removal, once the proportion of the remaining cells in a layer achieves a pre-set number (i.e., the target), the prioritizing would then remove the cells which were prioritized as low in other layers rather than further removing the cells in the layer that had achieved the 30% target. In this work, the seven Ecosystems and four Biomes were presence-absence layers and were targeted to include 30% of the presence cells in each layer. Meanwhile the Rugosity and Within Realm Species Richness were continuous data layers and were targeted to include the 30% highest value geographic cells.

Hereafter we name the main output of this work, the 30% highest prioritized areas, as 'the Prioritized Area'. To evaluate how well the Prioritized Areas satisfied the goal of protecting 30% of each habitat and 30% of all the ocean surface, they were compared with each layer to assess the proportion covered by the Prioritized Areas. To evaluate how well the Prioritized Areas covered the two continuous data layers (i.e., species richness and rugosity), we respectively identified the 30% highest areas of Rugosity (Figure S3a) and Within-Realm Species Richness (Figure S3b) for comparison with the Prioritized Area. If the areas completely coincided with each other (which means the proportion achieves 1.0), the Prioritized Area would have completely covered the two layers so that the prioritization perfectly protected the 30% most significant areas indicated by Rugosity and Within-Realm Species Richness.

In addition to the chosen cell removal rule (Target Based Function), two other basic cell removal rules in Zonation are the Core-Area Zonation (Moilanen et al., 2005) and the Additive Benefit Function (Arponen et al., 2005). All the three rules remove cells iteratively. Opposite to Target Based Function, Core-Area Zonation prioritizes the cells which only have high importance from a single layer rather than the cells which contain more features from multiple layers. As we wished to retain a range of features but not a single feature, the Core-Area Zonation not as suitable for the present analysis as the Target Based Function. Additive Benefit Function allows weights to be applied on data layers prior to prioritization. The Additive Benefit Function with (a) equal weights, and (b) weights adjusted by the areas of the Ecosystems, were compared with the Prioritized Area using Target Based Function. Because the Additive Benefit Function tends to prioritize the small areas first (Arponen et al., 2005), our trial down-weighted the small Ecosystems in proportion to their geographic area to better balance prioritisation across all Ecosystems. Thus, the weights of Ecosystems 1 to 7 were set as ‘1.3’, ‘2.4’, ‘1.0’, ‘3.4’, ‘1.4’, ‘3.1’, ‘1.7’, respectively. Weights of Biomes, Rugosity, and Within-Realms Species richness were ‘1.0’. However, because the Additive Benefit Function method is unable to keep a specific proportion from particular layers during the cell removal process, it was not as suitable as the Target Based Function either. Nevertheless, we found that the distribution of the prioritized areas in the Target Based Function map was generally the same as the map by the Additive Benefit Function without weight (81% coincided), and with the weights by area size (76% coincided), except for a few differences at regional scales (Figure S4). Specifically, the Target Based Function gave higher priority to the Arctic and the southern Caribbean Sea and less to the offshore South China Sea and the offshore regions of the eastern Pacific. The Target Based Function also prioritized more coastal areas, especially the ones along the coasts of Europe and the northern Indian Ocean. These trials validated the suitability of the Target Based Function, as there were not large differences between alternative prioritizations algorithms. Only results for Target Based Function analysis are presented in the main body of this paper.

2.4 Comparison with MPA, EEZ, and Wilderness areas

The current MPA data, including all the IUCN protected area categories (Ia, Ib, II, III, IV, V, VI), were obtained from UNEP-WCMC and IUCN (2018), the EEZs and the ABNJ were retrieved from Flanders Marine Institute (2014), and the marine wilderness from Jones et al. (2018). Each was converted to the same geographical format as the layers for prioritization as described previously. All the converted marine areas were 182 × 402 grid-cell raster files with a resolution of ~100 × 100 km (10,000 km^2) near the equator (~0.9˚), ranging from 84.5°N to 78.7°S and covering all longitudes. Because the raw resolution of marine wilderness is much finer (~1.2 km^2 at equator), the converted cells contained both wilderness and non-wilderness areas. If the converted cell contained the non-wilderness areas more than the wilderness, it was judged as a non-wilderness cell. Thus, some of the thin non-wilderness areas (mainly along the shipping routes at the eastern Pacific) were not in the converted map as they were surrounded by so many non-wilderness areas that the cells there were judged as non-wilderness. The percentage of these management areas and the countries covered by the prioritized areas were compared.

3 Results

3.1 Prioritized areas

The Prioritized Areas were mainly located on the continental coasts, island arcs, oceanic islands, offshore ocean ridges (e.g., the Southwest Indian Ridge, the northern Mid-Atlantic Ridge), southern-most Atlantic, the Coral Triangle, Caribbean Sea, and Arctic Archipelago (Figure 4).

The coverage of the Prioritized Area for Ecosystems (Figure 1) and Biomes (Figure 2) generally achieved the goal of 30% protection (Figure 5). To avoid confusion with the “30%” Prioritised Area, we report overlap between the Prioritised Area and the Ecosystems, Biomes, rugosity, and Richness as a proportion from 0 to 1. The lowest coverage (0.18) was for Ecosystem 6 which was mainly located in the ABNJ at middle latitudes (Figure 1f). The Biomes of seagrass, kelp, mangrove and coastal coral were very well covered (>0.86) by the Prioritized Areas along coastal regions and oceanic islands.

The Prioritized Area overlapped with the top 30% areas in Rugosity (Figure S3a) and Within Realm Species Richness (Figure S3b) also showed a good match (0.59 for Rugosity and 0.68 for Within Realm Species Richness) (Figure 5). The Prioritized Area differed from the top 30% areas of Rugosity in the areas along coasts and the Arctic, where there was high prioritization but low Rugosity. Likewise, the Prioritized Area was different from the top 30% areas of Within Realm Species Richness in the offshore regions at high latitudes (low prioritization but high richness) and the mid-ocean ridge (high prioritization but low richness).

3.2 MPAs, EEZs, ABNJ and Marine Wilderness

All the present MPAs (IUCN Ia, Ib, II, III, IV, V, VI) covered only 10% of the Prioritized Areas and the no-take MPAs (IUCN Ia, marine reserves) covered even less (<1%) (Figure 6a, b). The coverage was mainly located to the north-west of Hawaii (the Papahanaumokuakea MPA), the protected areas along the Aleutian Islands, the Habitat Protection Zone and National Park at the Coral Sea, and the coastal regions of some oceanic islands.

The EEZs overlapped 58% of the Prioritized Areas and the ABNJ 42% (Figure 6c, d, Table 2). In the Coral Triangle, the EEZs of Indonesia, Philippines, Malaysia, Timor-Leste, Brunei, and Singapore covered >69% of the Prioritized Areas. The Prioritised Areas also covered >67% of the EEZs of Thailand, Vietnam, and Cambodia. Likewise, great parts (>74%) of the EEZs around the Caribbean Sea (Colombia, Venezuela, Cuba, Honduras, Jamaica, Nicaragua, Haiti, Dominican Republic, Cayman Islands, Belize, St. Lucia, St. Vincent & Grenadines, and St. Kitts & Nevis) were distributed in the Prioritized Area. The EEZs of U.K., Ireland, and France were also well- covered (>69%). Several littoral countries of the Baltic Sea (Sweden, Denmark, Latvia, and Estonia) had a >71% overlap of their EEZs and the Prioritized Areas. Similarly, some countries around the Black Sea (Georgia, Ukraine, Romania and Bulgaria) had over 78% overlap of Prioritised Areas. The Prioritized Areas covered most of the Red Sea and the Persian Gulf, and thus strongly (>76%) overlapped the EEZs of the countries there (Saudi Arabia, Jordan, Sudan, Eritrea, Qatar, Bahrain, and Iraq). There were also oceanic EEZs (e.g., Fiji, French Polynesia and Bouvet Island) well-covered (>74%) by the Prioritized Areas.

While the proportion of an EEZ that was prioritised is important from a national viewpoint, what is important for global conservation is which countries can protect the largest areas. The countries where over 1.9 million km^2 was prioritised comprised Canada, Australia, United States of America, Greenland, Indonesia, Russia, and New Zealand (Table 2, full list in Table S2). These countries can thus do most to protect marine biodiversity through MPA.

A significant proportion, 35%, of the Prioritized Areas, were in the places classified as Marine Wilderness (Figures 6e). These were mainly in the Arctic and Southern Ocean, but also in the mid-Pacific and mid-south Atlantic.

4 Discussion

4.1 The current and previous prioritizations

The Prioritized Areas identified the 30% of the global oceans that was representative of the breadth of biodiversity, including ecosystems, biomes, benthic habitats and topography, species richness and endemicity (Figures 5). Compared to previous prioritizations, this paper not only involved extra ecological factors (ecosystems, biomes, and species endemicity), but also advanced the prioritization methodology for marine biodiversity conservation by using decision-support software.

We advanced marine conservation planning by including a wider range of biodiversity measures than previous studies (Jenkins & Van Houtan, 2016; Klein et al., 2015; Selig et al., 2014). In a review of international conservation initiatives that prioritised areas for protection, Asaad et al., (2017) concluded that eight ecological criteria have been most widely used, namely: unique and rare habitats, fragile and sensitive habitats, ecological integrity, representativeness, conservation concern, restricted range, biological diversity, and important for life history stages. In our study, the criteria *unique and rare habitats* and *fragile and sensitive habitats* were approximated by the four biomes (sea grass, kelp, mangrove, shallow water coral reefs) and Rugosity. The latter includes regions of topographic heterogeneity, including canyons, seamounts, abyssal hills and areas with hydrothermal vents (e.g., Uejima et al., 2017). The Ecosystems, Realms, and species richness satisfy the criteria of *representativeness* and *endemicity*. Future studies could consider data on human impacts to address *ecological integrity*. Perhaps the greatest gap in our analysis is consideration of species threatened with extinction, including areas important for their breeding and growth (i.e. life-history stages) (IUCN Red List, 2018b). Because threatened species distributions may not always coincide with areas of high species endemicity or richness, such as found for sea turtles (Asaad et al. 2018a), their conservation requires species-specific analyses. MPA, particularly the ones in IUCN Ia category, may be only one of several measures necessary to aid their recovery.

Other conservation planning exercises prioritised areas of highest human impacts, particularly in terrestrial ecosystems (Buchanan et al., 2011; e.g., Wala et al., 2012). Alternatively, such areas could be avoided at the risk of biasing prioritization to ‘residual’ areas which may not be optimal for conservation (e.g., Jones et al., 2018). In contrast to the situation on much of the land, human impacts have been less severe in the ocean (Costello, 2015; McCauley et al., 2015), so identifying the most important areas for biodiversity will be a first step in allowing their recovery if impacted. Based on this research, additional analyses could be conducted using extra data layers and various weightings depending on particular management objectives and scenarios. Considering monsoon and/or other seasonal factors the seasonal Ecosystems layers (Zhao & Costello, 2019b) could be added in prioritization analysis. Another option would be to use the ‘administrative units’ analysis in Zonation (Moilanen & Arponen, 2011) on national EEZs to evaluate the alternative prioritizations within the EEZs of particular countries, as conducted by Asaad et al. (2018b) for countries in the Coral Triangle.

4.2. MPA planning

Some prioritized areas overlapped and/or were adjacent to already protected areas. For example, the areas bordering the Atlantic and the Southern Oceans could be an expansion of the MPAs of South Georgia and South Sandwich Islands (Figure 6a). Furthermore, the most highly prioritized areas (e.g., the darkest red cells in Figure 4, such as the Coral Triangle) should most urgently receive full protection as marine reserves (IUCN category Ia). The regional implementation of new MPAs should also consider local factors to evaluate how the designation of MPAs may allow recovery and/or reduce loss of biodiversity. For example, Assad et al. (2018) used a similar approach and Zonation to map where MPA would be best located in the Coral Triangle, and in the EEZs of its constituent countries of Indonesia, Malaysia, Papua New Guinea, the Philippines, Solomon Islands, Timor-Leste, Brunei Darussalam and Singapore. Such considerations would guide the actual boundaries of new MPAs, and are best decided at a national level in consultation with local communities (Costello, 2014).

Our analysis prioritized areas in all major seas and oceans, both coastal and offshore. Most (58%) of the prioritized areas were within EEZs and can thus be protected by their responsible countries (Table S2). Especially, Canada, Australia, United States of America, Greenland, Indonesia, Russia, and New Zealand respectively have the largest Prioritized Areas within EEZs over 1.9 million km^2 (Table 2). As the proportion of the Prioritized Areas covered by MPAs are very low (Figures 6a, b), these countries need to establish more and/or expand MPAs. There were also marine regions where the EEZs were almost entirely prioritized, such as the Coral Triangle, and Caribbean Sea. This means these countries have a special responsibility for marine conservation. The governments of these countries could upgrade the protection level of their MPAs which are below the Ia category to marine reserves within the Prioritized areas.

While the Baltic and Black Seas were included with the Prioritized Areas, this was because they had been classified as a distinct realm because each contains both marine and freshwater species which distinguish it from fully marine realms (Costello et al. 2017). Thus, regional scale analyses are recommended in these and other 'seas' that recognize their unique aquatic environments and species distributions.

Within EEZs, the current fragmented and small MPAs could be aggregated to be larger and increase connectivity of MPAs for greater effectiveness. This may also be more cost efficient for management (Davies et al., 2017). Biogeographic theory holds that larger areas include relatively more species per unit area than smaller areas, and they are likely to contain a greater variety of habitats (Lomolino et al., 2010). It would thus be more efficient to have larger and fewer MPAs than many small ones. However, conservation can be considered effective if the protected areas are representative of all aspects of biodiversity, from ecosystems to species (Gaston et al., 2006). Within such representative networks as proposed here, individual MPAs should be as large as possible so that they sustain species abundance in the long term and minimise potential boundary fishing effects (Costello & Ballantine, 2015).

The MPAs established and/or expanded within EEZs would meet multiple socio-political challenges (Gleason et al., 2013). Some recreational and commercial fishing organizations and/or individuals might question the need for new and/or expanded MPAs in addition to the already heavily regulated (in their perspective) fisheries management areas. However, such arguments overlook the general failure and unsustainability of past fisheries regulatory practices due to increased fishing pressures (more people), improved fishing technologies, government subsidies that sponsor over-fishing, and enforcement difficulties (e.g., McCauley et al., 2015; Pauly & Zeller, 2016). Rather, sustainable fisheries could be addressed through demonstrating the benefits of marine reserves in restoring fished populations. Increases in fish populations inside a reserve have been demonstrated to lead to increased fish catch outside (Warner & Pomeroy, 2012). A benefit of the methodology used in our study is that preferences of different social groups, including local communities, can be quantitatively compiled as data layers and/or be weighted within the prioritization process. For example, one would consider competition between fisheries and wildlife (e.g., Sydeman et al., 2017). Then the prioritized areas could also reflect local communities' needs and desires.

Nearly half (42%) of the Prioritized Areas were located outside EEZ in the ABNJ. Conservation in ABNJ will require international agreement, such as through the United Nations Convention on the Law of the Sea (UNCLOS) wherein countries have already agreed to protect nature (United Nations, 1982). In this regard, perhaps countries can most easily agree to designate areas that are both wilderness and prioritized because these already have the least human disturbance and associated economic activities.

With less than 1 % of the ocean designated to be fully protected from deliberate human impacts such as fishing, and most coastal countries without any marine reserves, it is clear that marine conservation has not been a priority to date. We also recognize that current databases overestimate protection by including areas not yet legally protected, that many areas are multi-use with only small parts aimed to be fully protected, and others have been misclassified (Costello & Ballantine, 2015; Smallhorn-West & Govan, 2018). Even countries with adequate resources to enforce MPA do not do so, such as in Europe ((Dureuil et al., 2018). Nevertheless, we hope our prioritisation will help discussions nationally and internationally about where to designate MPA and marine reserves most cost-effectively in terms of area covered. Such protection will have long-term benefits in not only protecting biodiversity, but will enable ecosystems and fisheries to recover, provide spill-over benefits to fisheries, promote ecotourism, and resilience to climate change (Bates et al., 2019).

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Table 1. The number of species amongst higher taxa used in the species richness layer, and their percentage of all named species in the taxon.

Higher Taxon	**Number of species**	**% of global**
Acanthocephala	2	0%
Annelida	377	3%
Arthropoda	**3,435**	**6%**
Brachiopoda	51	12%
Bryozoa	146	2%
Chaetognatha	32	24%
Chlorophyta	83	3%
Chordata	**13,228**	**58%**
Cnidaria	**1,258**	**11%**
Ctenophora	6	3%
Cyanobacteria	5	1%
Cycliophora	1	50%
Dinophyta, Dinophyceae	1	0%
Echinodermata	**956**	**13%**
Echiura	3	1%
Foraminifera	17	0%
Gastrotricha	44	9%
Gnathostomulida	3	3%
Haptophyta	1	0%
Hemichordata	6	1%
Kamptozoa, Entoprocta	20	10%
Loricifera	2	7%
Tracheophyta	1	0%
Mollusca	**4,557**	**9%**
Nemertea	8	0%
Ochrophyta	21	0%
Phoronida	7	64%
Platyhelminthes	3	0%
Porifera	440	5%
Priapulida	4	10%
Rhodophyta	97	1%
Rotifera	1	0%
Sagenista	2	3%
Sipuncula	74	47%
Tracheophyta	12	4%
Total	**24,904**	**10%**

	Number of species	**% of global**
Arthropoda		
Malacostraca	2,867	9%
Pycnogonida	332	17%
Hexanauplia	170	1%
Other	66	0%
Chordata		
Actinopterygii	11,472	65%
Elasmobranchii	834	69%
Ascidiacea	638	22%
Mammalia	119	86%
Reptilia	34	29%
Other	131	41%
Cnidaria		
Anthozoa	918	13%
Hydrozoa	321	9%
Other	19	8%
Echinodermata		
Ophiuroidea	281	13%
Asteroidea	279	15%
Echinoidea	186	18%
Holothuroidea	123	7%
Crinoidea	87	13%
Mollusca		
Gastropoda	2,852	7%
Bivalvia	1,018	12%
Cephalopoda	295	36%
Scaphopoda	267	46%
Other	125	10%

Table 2. The countries and/or regions whose Exclusive Economic Zones (EEZ) ($10^4 \times km^2$) overlapped the Prioritized Area, listed by their area (>400,000 km^2). The percentage of each EEZ within the prioritized areas is also shown.

The EEZs	Areas within the Prioritized Areas ($10^4 \times km^2$) greater than 400,000 km^2	% EEZ
Canada	457	35
Australia	393	55
United States	380	36
Greenland	348	47
Indonesia	335	69
Russia	331	17
New Zealand	192	42
South Georgia & the South Sandwich Is.	180	86
Svalbard	166	51
French Polynesia	139	100
Japan	138	37
Philippines	117	77
Brazil	110	35
Papua New Guinea	109	56
French Southern & Antarctic Lands	98	40
United States Minor Outlying Islands	94	31
Chile	92	24
Mexico	85	30
Micronesia	82	34
Norway	81	40
Portugal	75	43
United Kingdom	74	69
Jan Mayen	72	99
Marshall Is.	70	42
Solomon Is.	66	50
Falkland Islands	65	100
Bouvet I.	61	99
South Africa	57	36
Spain	52	51
Ireland	51	90
China	51	62
Saint Helena, Ascension en Tristan da Cunha	49	32
New Caledonia	48	40
Iceland	45	32
Colombia	44	74
Argentina	43	34
Seychelles	42	39
India	42	22
The Bahamas	42	78
Madagascar	42	40

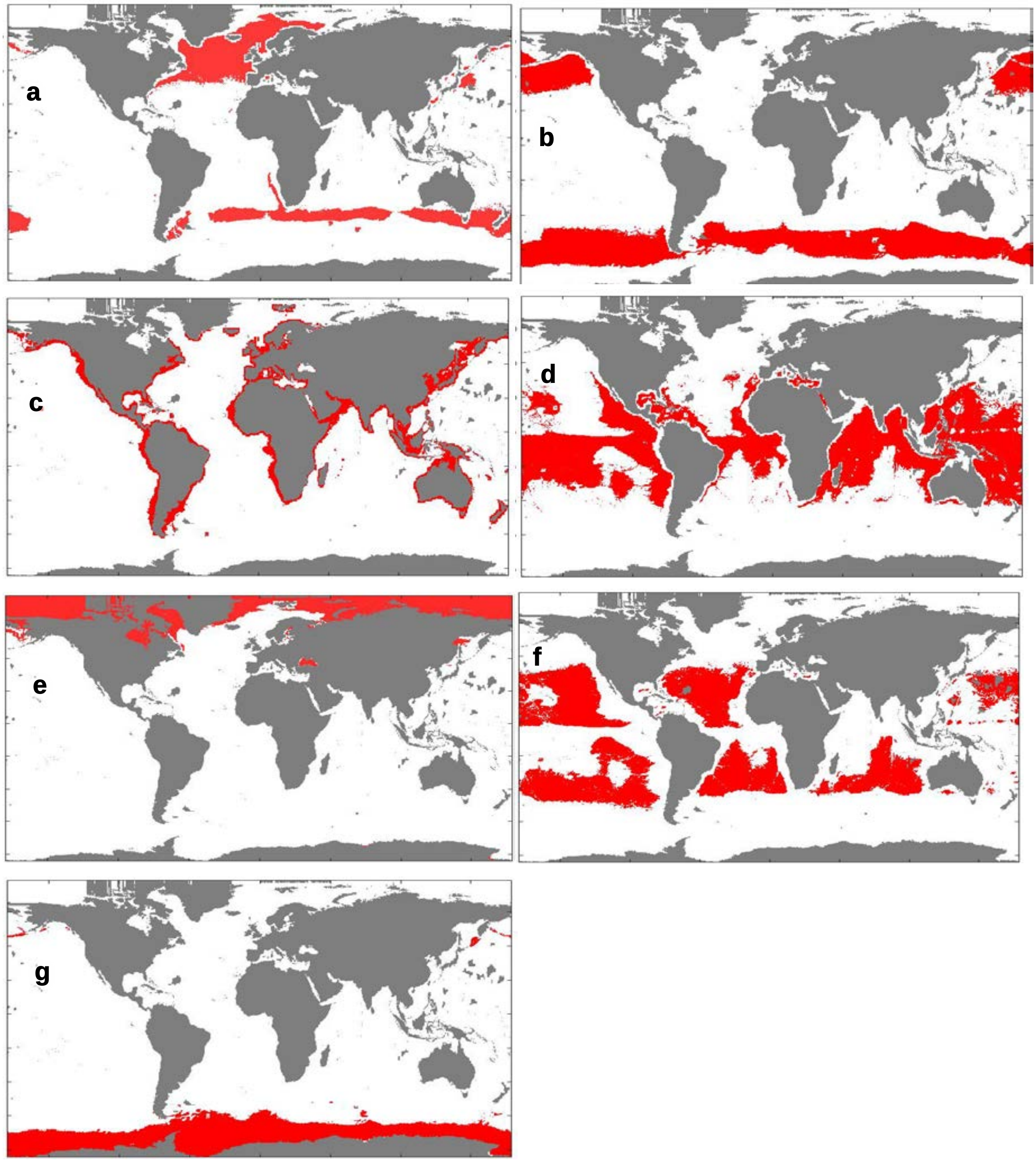


Figure 1. The areas of marine Ecosystems 1 to 7 (in red), (a) to (g) respectively, used in the in the Zonation analysis.

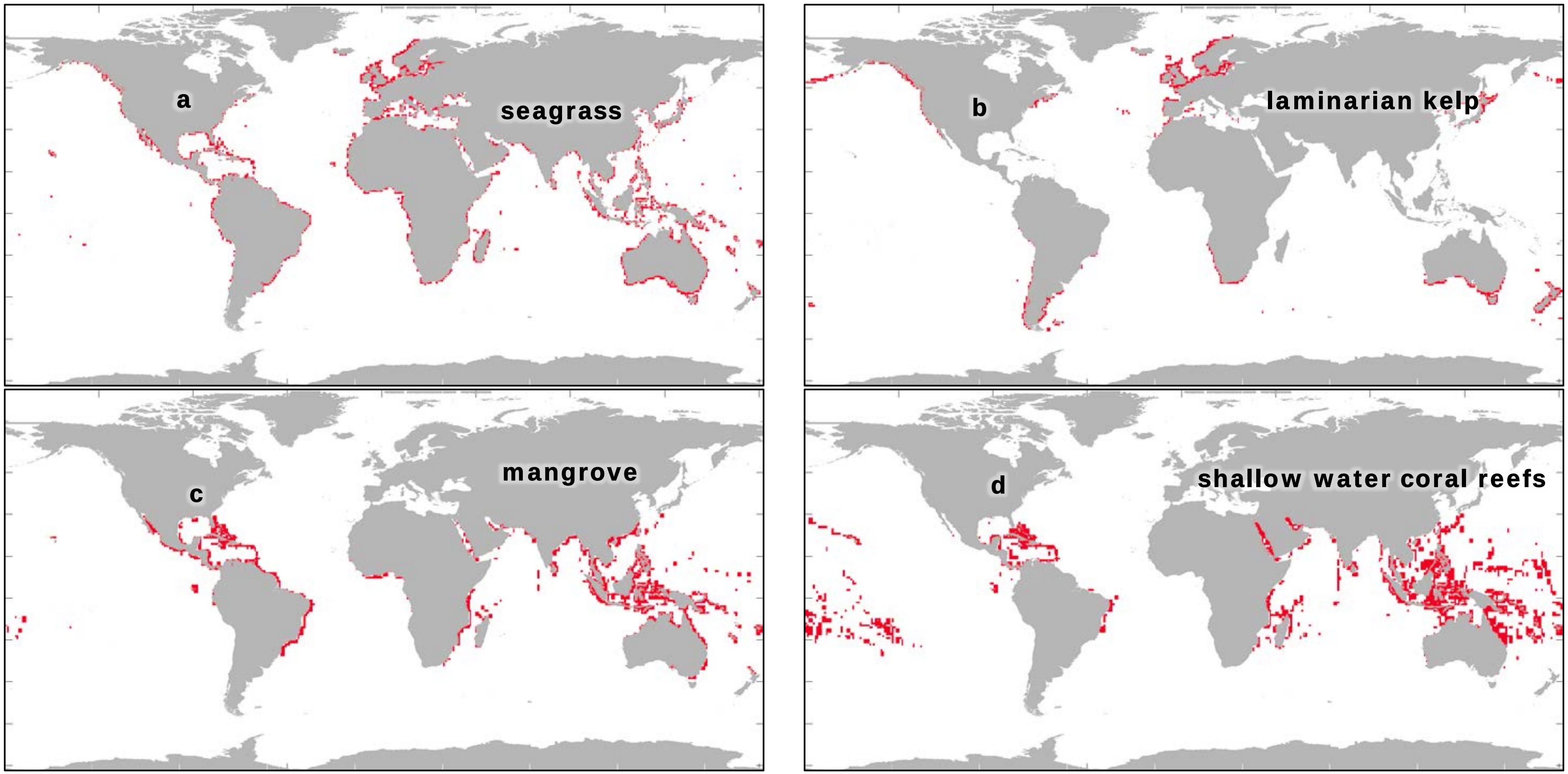


Figure 2. The layers in red of (a) seagrass, (b) laminarian kelp, (c) mangrove, and (d) shallow water coral reefs used in the Zonation analysis.

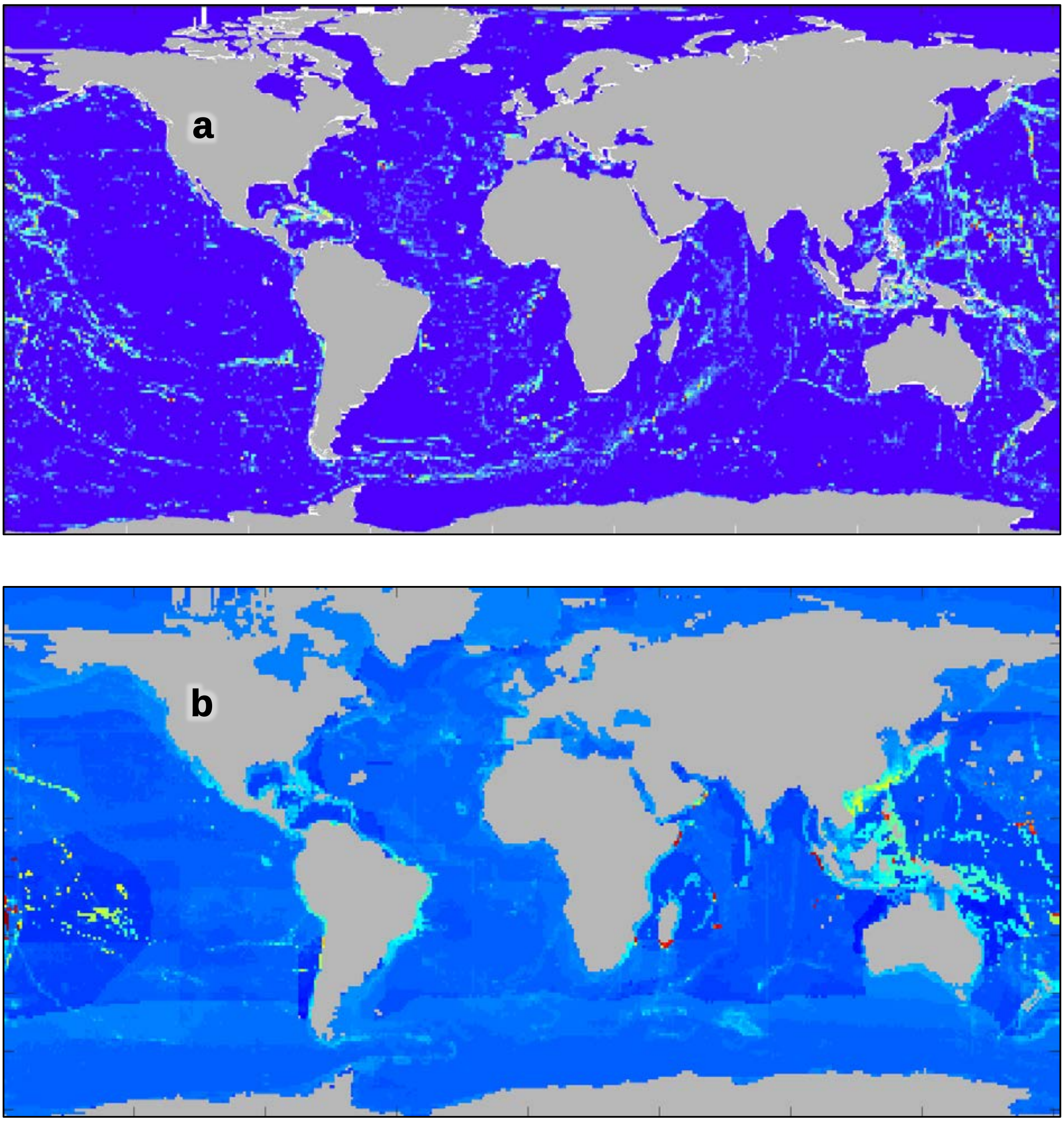


Figure 3. The colours represent the values from low (blue) to high (red) in (a) the benthic rugosity index, and (b) the Within-Realm Species Richness used in the Zonation analysis.

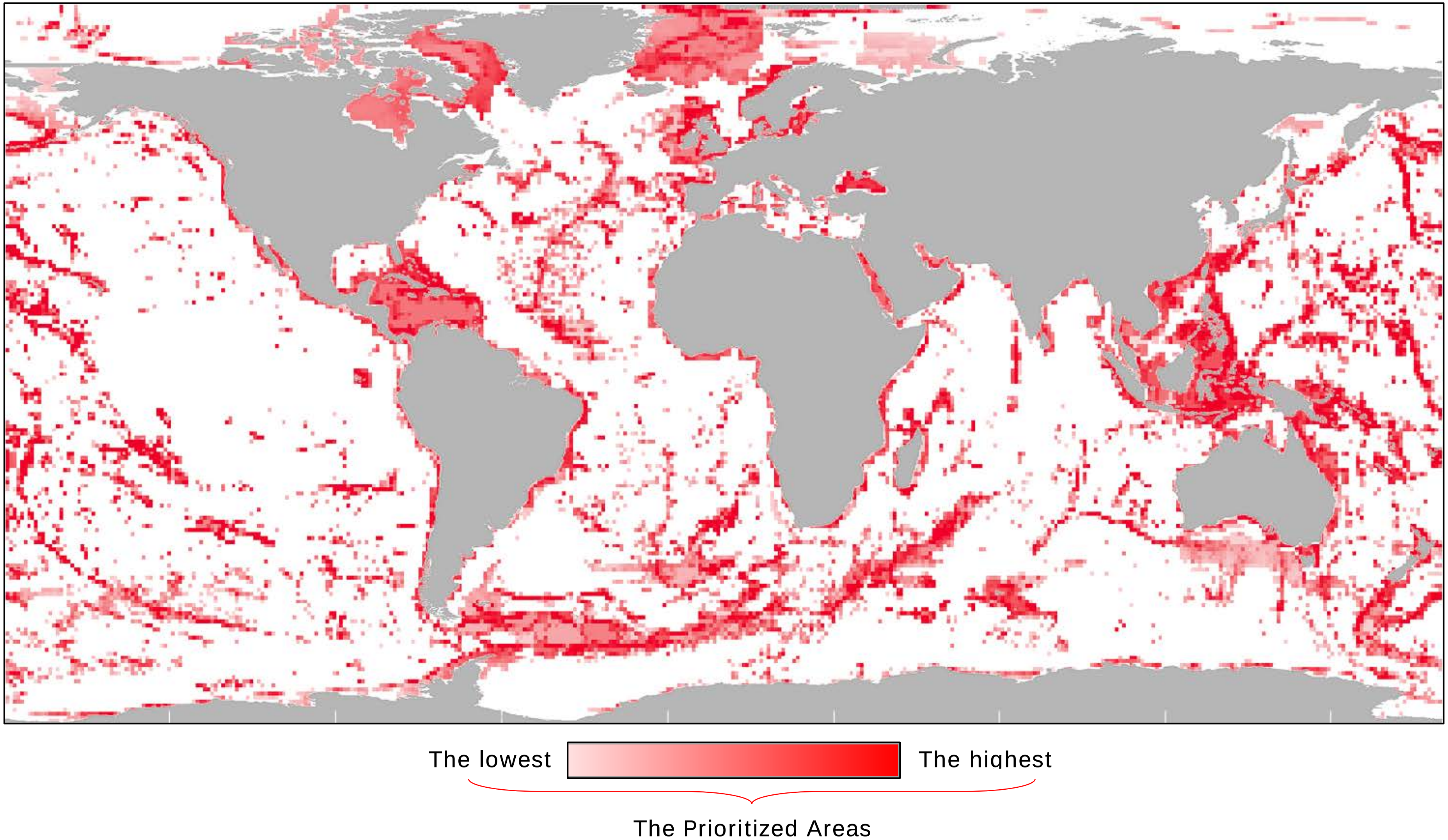


Figure 4. The global distribution of the Prioritized Areas (the 30% highest prioritized areas) for planning a global MPA network based on the layers in Figures 1, 2, and 3. The red colour scale represents the Prioritized Areas from the lowest (light red) to the highest (dark red) within the 30% highest prioritized areas.

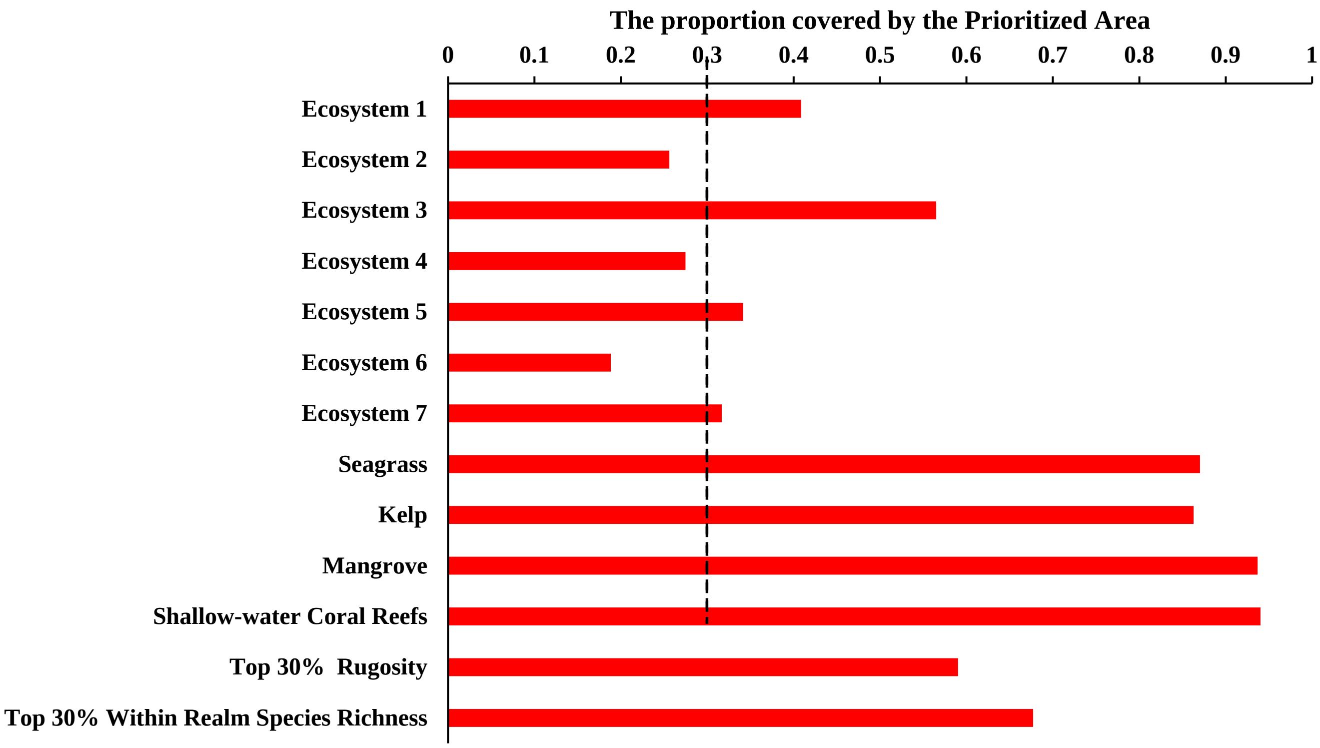
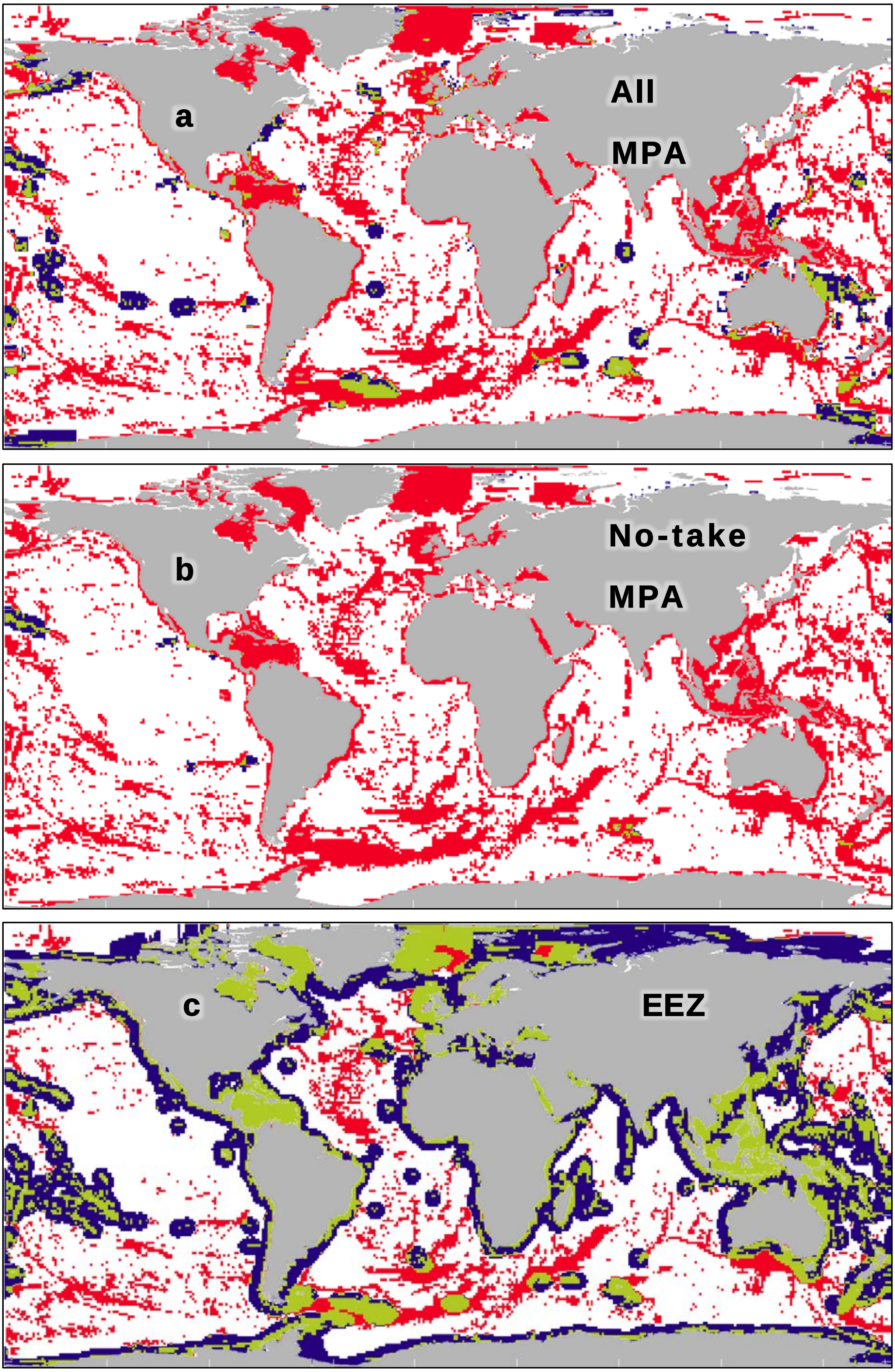


Figure 5. The proportion of the cells in the seven Ecosystems (Figure 1) and four Biomes (Figure 2) covered by the Prioritized Area. The dashed line shows the 0.3 proportion. The proportion of the top 30% cells in the layers of Rugosity and Within-Realm Species Richness (Figure S3a, Figure S3b) are also shown.


a
All
MPA
b
No-take
MPA
c
EEZ

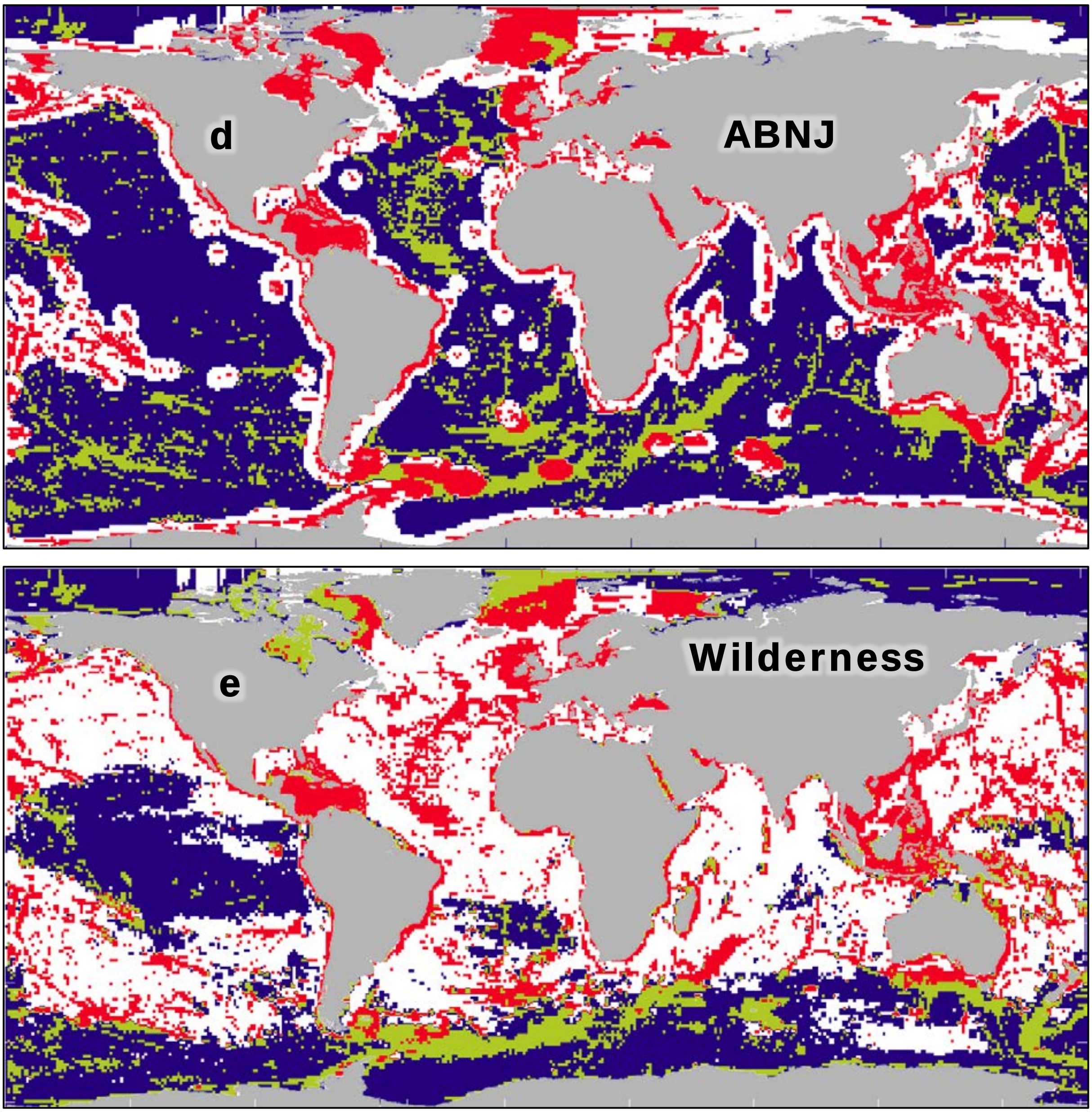


Figure 6. The overlap (green) between the Prioritized Areas (red) with the areas (blue) of: (a) all the MPAs; (b) marine reserves (no-take MPA); (c) the Exclusive Economic Zone (EEZ); (d) the Areas Beyond National Jurisdiction (ABNJ); and (e) the marine wilderness.

Supplementary Material

Table S1. (a) Summary of the seven Ecosystem's characteristics (Figure 1). See Zhao et al. (2019) for details.

Ecosystems	Location	% ocean area	Distinguishing characteristics
1	Offshore Northern Atlantic and edge of the temperate Southern Ocean	9	Cold temperate
2	Offshore middle of Southern Ocean and Northern Pacific	17	Boreal, high nutrients,
3	Coastal Areas excluding Polar regions	7	High and variable chlorophyll and productivity, high wave height
4	Offshore Tropics	24	Tropical and high PAR
5	Arctic Ocean	10	Polar, high ice cover, low wind and salinity
6	Offshore subtropics	22	Subtropical
7	Antarctic shelf	12	Polar, high nutrients and ice cover, lower oxygen

(b) The variables used for mapping the seven Ecosystems (obtained from Basher et al., 2014).

Physical	**Biochemical**	**Nutrients**
Temperature	pH	Saturated Oxygen
Wind Speed	Photosynthetically Active Radiation	Utilized Oxygen
Slope	Chlorophyll-α	Silicate
Land Distance	Primary Productivity	Phosphate
Surface Current		Dissolved Oxygen
Diffuse Attenuation Coefficient		Nitrate
Salinity		Calcite
Wave Height		

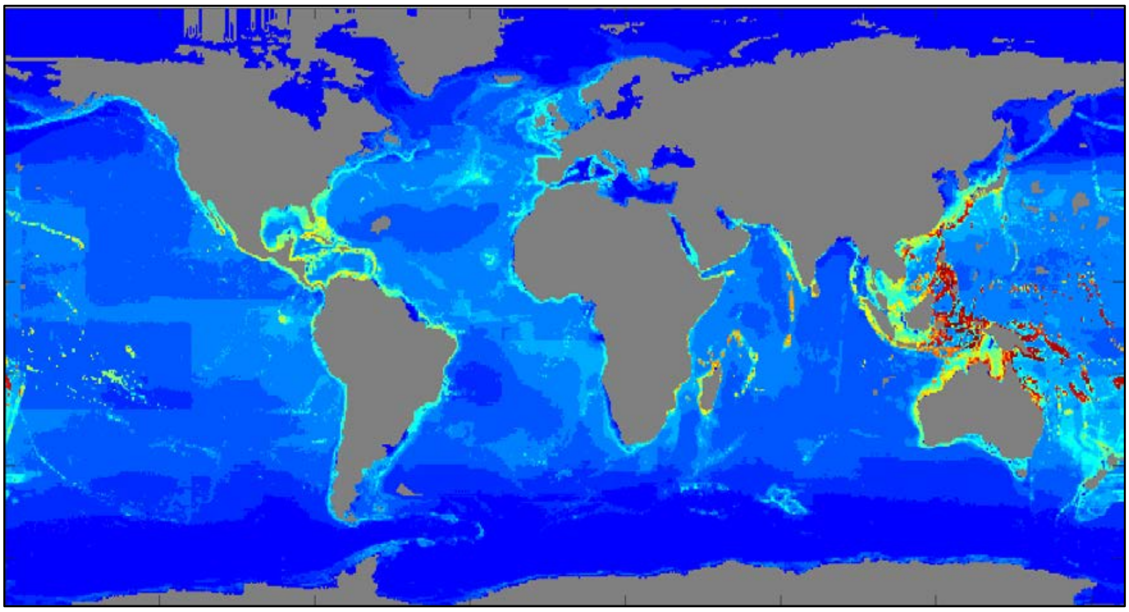


Figure S1. The map of global species richness from AquaMaps (Kaschner et al., 2016). The colours represent the species richness from low (blue) to high (red, up to 8,070 species per cell).

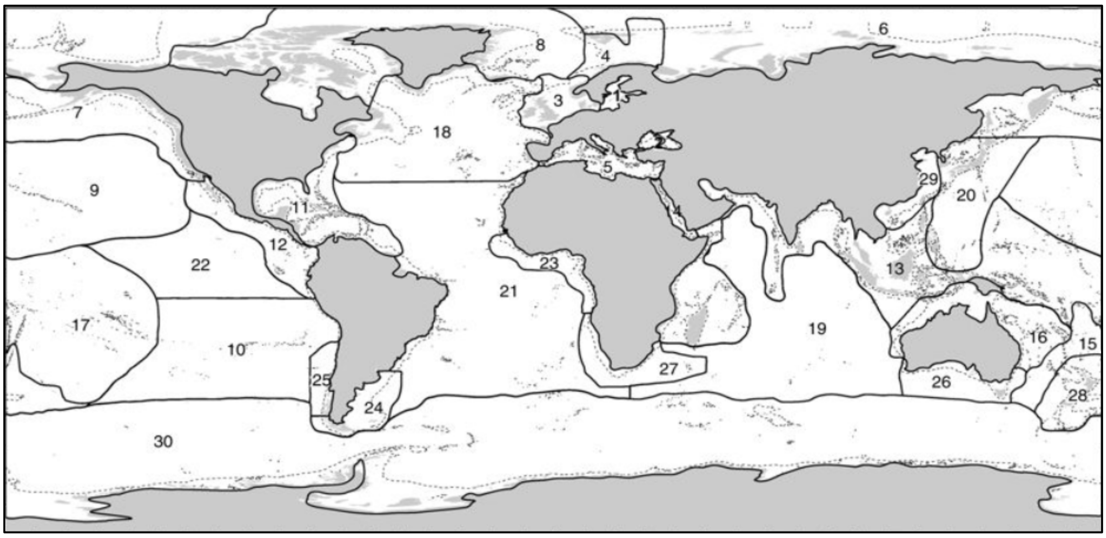


Figure S2. The map of the biogeographic Realms as numbered 1~30 (Costello et al., 2017).

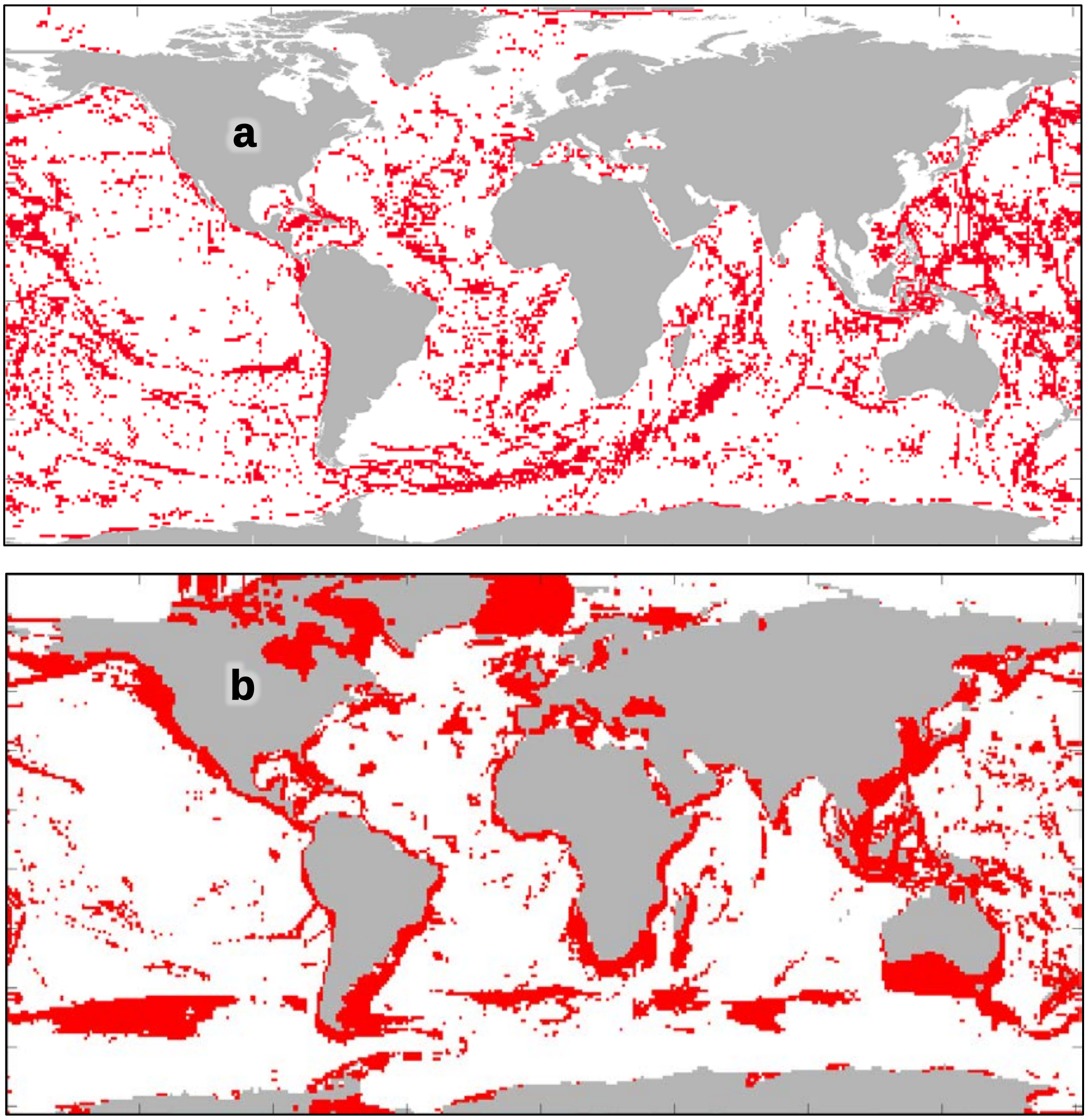


Figure S3. The red areas represent for (a) 30% highest rugosity, (b) 30% highest Within-Realm Species Richness.

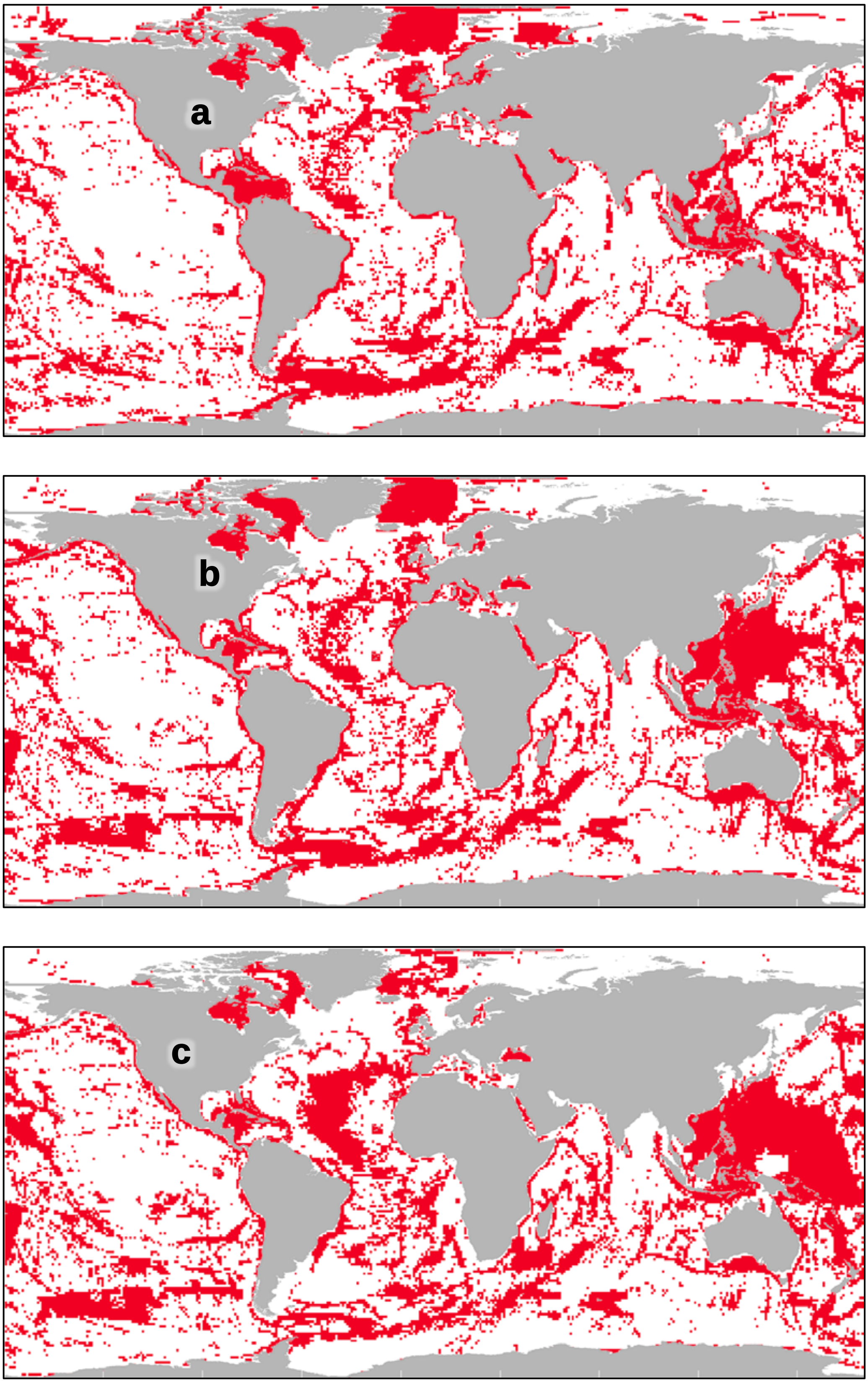


Figure S4. The maps of the 30% highest prioritization respectively by (A) the Target Based Function in Figure 4, (B) the Additive Benefit Function without weighing, and (C) the Additive Benefit Function with the weighing on Ecosystems based on their area size.

Table S2. The countries and/or regions whose Exclusive Economic Zone (The EEZs) areas (10^4×km^2) overlapped the Prioritized Area, listed by the size of their EEZ. The percentage of each EEZ within the prioritized areas is also shown. The high percentages were highlighted in bold.

The EEZs	Area in the Prioritized Areas (10^4×km^2)	% EEZ
Canada	457.3	35
Australia	392.9	55
United States	380.2	36
Greenland	347.9	47
Indonesia	335.0	69
Russia	331.3	17
New Zealand	192.2	42
South Georgia & the South Sandwich Is.	**180.2**	**86**
Svalbard	165.6	51
French Polynesia	**138.6**	**100**
Japan	137.9	37
Philippines	**117.2**	**77**
Brazil	109.6	35
Papua New Guinea	109.1	56
French Southern & Antarctic Lands	97.7	40
United States Minor Outlying Islands	94.3	31
Chile	91.9	24
Mexico	85.1	30
Micronesia	82.3	34
Norway	81.3	40
Portugal	74.7	43
United Kingdom	73.7	69
Jan Mayen	**72.0**	**99**
Marshall Is.	69.6	42
Solomon Is.	66.0	50
Falkland Islands	**64.8**	**100**
Bouvet I.	**60.7**	**99**
South Africa	56.9	36
Spain	51.5	51
Ireland	**51.0**	**90**
China	50.5	62
Saint Helena, Ascension en Tristan da Cunha	48.9	32
New Caledonia	47.6	40
Iceland	44.9	32
Colombia	**44.1**	**74**
Argentina	43.4	34
Seychelles	42.4	39
India	42.2	22
The Bahamas	**41.8**	**78**
Madagascar	41.7	40
Northern Marinana Islands-Guam	36.4	44
Venezuela	**36.3**	**92**
Vietnam	35.8	67
Fiji	**34.7**	**74**
Kiribati	32.4	24
Cook Is.	31.4	19
Cuba	**30.3**	**95**
Tonga	30.1	52
Heard I. & McDonald Is.	27.0	48
Malaysia	**26.6**	**73**
Faroe Is.	25.4	35
Vanuatu	24.6	47
Spratly Islands	23.5	65
Italy	23.4	41
Ecuador	23.2	27
Palau	23.1	47
Dominican Republic	**21.4**	**93**
Jamaica	**20.8**	**100**
Maldives	20.2	27
Mauritius	20.2	19
France	**19.8**	**100**
Thailand	**19.5**	**77**
Sweden	**19.5**	**74**
Saudi Arabia	**17.9**	**92**
Namibia	17.0	34
Yemen	16.8	37
Honduras	**16.7**	**90**
Panama	16.7	61
Nicaragua	**16.0**	**83**
Mozambique	15.9	32
Taiwan	15.6	53
Paracel Islands	15.2	61
Ukraine	**14.6**	**94**
Tuvalu	14.3	23
Myanmar	14.0	32
Peru	13.9	20

Greece	13.7	27
Puerto Rico	**13.3**	**89**
Wallis & Futuna	13.3	62
Somalia	12.3	19
American Samoa	12.2	36
Iran	11.0	53
Libya	10.9	32
Christmas I.	10.7	40
Conflict zone Japan/Russia	10.6	44
Haiti	**10.5**	**100**
Denmark	**10.5**	**71**
Western Sahara	10.4	47
Egypt	10.3	42
Cayman Is.	**10.2**	**100**
Oman	10.1	22
Finland	10.0	9
Sri Lanka	9.5	22
Angola	9.3	23
British Indian Ocean Territory	9.1	17
Turks & Caicos Is.	9.0	66
Tanzania	9.0	38
Morocco	8.6	32
Niue	8.3	31
Cocos Is.	8.2	21
Turkey	7.9	29
Costa Rica	7.9	17
Equatorial Guinea	7.6	30
Norfolk I.	7.6	19
Samoa	7.5	69
Conflict zone China/Japan/Taiwan	**6.6**	**100**
Pitcairn Is.	6.4	9
Guyana	6.3	57
French Guiana	6.3	16
Cape Verde	6.3	9
Senegal	6.1	47
Sudan	**5.7**	**99**
Tokelau	5.7	22
Eritrea	**5.6**	**84**
Germany	5.1	64
Mauritania	4.8	36
Estonia	**4.6**	**83**
Guadeloupe	4.6	60
Comoros	4.6	33
Tunisia	4.4	44
Kenya	4.4	44
Suriname	4.2	40
Cambodia	**4.0**	**100**

Bulgaria	**3.9**	**100**
Virgin Islands, British	3.9	56
Trinidad & Tobago	3.8	62
Netherlands	3.8	44
Bermuda	3.8	9
Antigua & Barbuda	3.6	39
Clipperton Island	3.6	10
Croatia	3.3	53
Anguilla	3.3	41
Latvia	**3.2**	**75**
United States Virgin Islands	**3.1**	**100**
Saint Vincent and the Grenadines	**3.0**	**100**
Romania	**3.0**	**89**
Algeria	3.0	23
Pakistan	3.0	15
Belize	**2.7**	**88**
South Korea	2.7	8
Martinique	2.6	65
Joint regime Japan/Korea	2.6	33
Nigeria	2.6	17
Curaçao	**2.5**	**100**
Timor-Leste	**2.5**	**71**
Poland	2.5	57
Qatar	**2.4**	**84**
Nauru	2.4	10
Gabon	2.3	15
Grenada	**2.2**	**100**
Cote d'Ivoire	2.2	16
Aruba	**2.1**	**100**
United Arab Emirates	2.1	43
Mayotte	2.1	40
Sao Tome & Principe	2.1	19
Barbados	2.0	13
Ghana	2.0	11
Bonaire, Sint-Eustasius, Saba	**1.9**	**100**
Brunei	**1.9**	**90**
Georgia	**1.9**	**78**
Bangladesh	1.9	26
Dominica	**1.8**	**73**
El Salvador	1.8	24
Guinea	1.8	20
Joint regime Colombia/Jamaica	**1.5**	**100**
Area of overlap Australia/Indonesia	1.5	40
Reunion	1.4	5
St. Lucia	**1.3**	**100**
North Korea	1.3	10

Cameroon	**1.2**	**87**
Guernsey	**1.1**	**100**
The Gambia	1.0	53
Guatemala	1.0	11
Uruguay	1.0	7
Liberia	1.0	5
St. Kitts & Nevis	**0.9**	**100**
Congo	0.9	28
Albania	0.8	68
Conflict zone Japan/South Korea	0.8	12
Guinea-Bissau	0.8	9
Joint development area Australia/East Timor	0.7	26
Sierra Leone	0.7	6
Montserrat	**0.6**	**100**
Kuwait	0.6	49
Saint Martin	**0.5**	**100**
Bahrain	**0.5**	**76**
Djibouti	0.4	68
Lebanon	0.4	22
Congo, DRC	0.4	16
Protected zone Australia/Papua New Guinea	**0.3**	**100**
Togo	0.3	27
Benin	0.3	14
Disputed Kenya/Somalia	0.3	7
Cyprus	0.3	4
Netherlands Antilles	**0.2**	**100**
Jersey	0.2	42
Lithuania	0.2	24
Disputed Western Sahara/Mauritania	0.2	5
Singapore	**0.1**	**100**
Iraq	**0.1**	**100**
Sint Maarten	**0.0**	**100**
Gibraltar	**0.0**	**100**
Slovenia	**0.0**	**100**
Jordan	**0.0**	**100**
Monaco	**0.0**	**79**
Syria	0.0	4
Malta	0.0	0
Israel	0.0	0

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