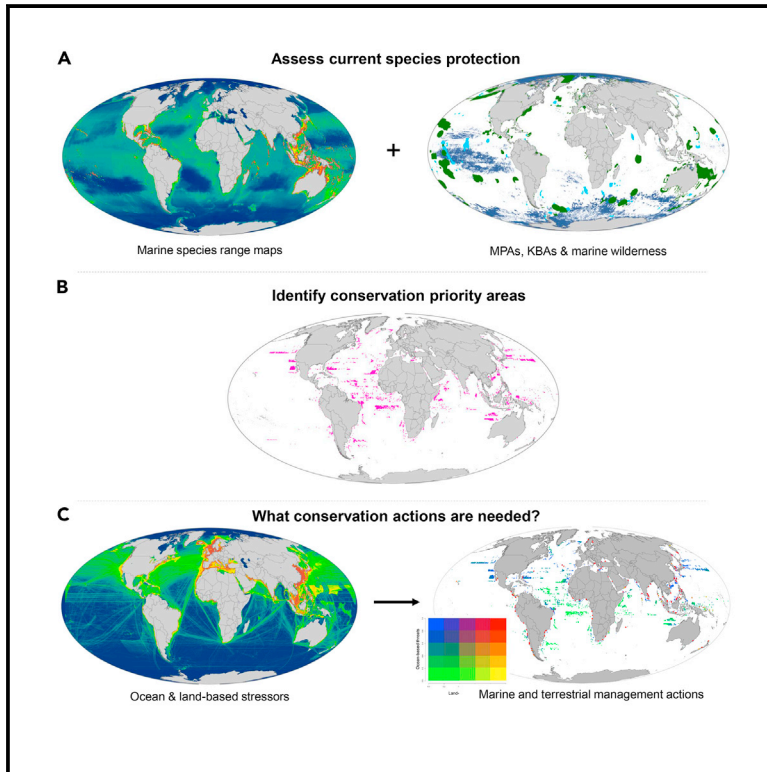


Area Requirements to Safeguard Earth's Marine Species

Graphical Abstract



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In Brief

Marine biodiversity is in rapid decline, and the international community recognizes the need for increased conservation efforts. We identify 8.5 million km² of new conservation priority areas and show that at least 26% of the ocean needs effective conservation to preserve marine biodiversity. With a post-2020 global biodiversity agreement currently under development, our analysis demonstrates the overall scale of conservation action required and helps identify areas on which local and regional conservation efforts should focus.

Highlights

- We identify 8.5 million km² of the marine realm that needs conservation attention
- At least 26% of the ocean needs conservation to preserve marine biodiversity
- Suitable conservation actions range from protected areas to broad-scale policies
- We demonstrate the scale of action required in future global conservation frameworks



Area Requirements to Safeguard Earth's Marine Species

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SCIENCE FOR SOCIETY Despite substantial biodiversity conservation efforts over the past two decades, Earth's biodiversity is rapidly declining. We identify global priorities for the expansion of marine conservation efforts, aiming to conserve at least 10% of the range of all 22,885 mapped marine species. We found that a minimum of 8.5 million km² (2.5% of the ocean) of new conservation areas are required, and show that, in total, at least 26% of the ocean needs effective conservation to preserve marine biodiversity. For each priority area, we recommend broad conservation responses—ranging from marine protected areas to large-scale policy approaches (e.g., fisheries regulations)—best suited to mitigate threats to biodiversity in that area. With a post-2020 global biodiversity agreement currently under development, our analysis provides insights into the scale of conservation action required across the marine realm and identifies new areas that clearly warrant conservation attention.

SUMMARY

Despite global policy commitments to preserve Earth's marine biodiversity, many species are in a state of decline. Using data on 22,885 marine species, we identify 8.5 million km² of priority areas that complement existing areas of conservation and biodiversity importance. New conservation priorities are found in over half (56%) of all coastal nations, including key priority regions in the northwest Pacific Ocean and Atlantic Ocean. We identify where different conservation actions, ranging from marine protected areas to broader policy approaches, might best overcome anthropogenic threats to these areas. This analysis shows 26%–41% of the ocean (depending on targets used for species representation) needs to be effectively managed and conserved through a combination of site-based actions and broad policy responses to achieve global conservation and sustainable development agendas.

INTRODUCTION

Biodiversity loss is one of the biggest environmental issues of our time.¹ Human activities associated with agriculture, urbanization, and natural resource extraction have led to large-scale habitat destruction and degradation, causing not only species declines and extinctions^{2,3} but also the rapid erosion of intact ecosystems on land and in the sea.^{4,5} The disparity between increasing conservation efforts, including a doubling of the protected area (PA) estate in just two decades,⁶ and persistent biodiversity decline has led to a number of calls for more ambitious, science-based plans to halt biodiversity loss.^{7–10}

There is clear evidence showing that effectively conserving biodiversity will require substantial increases in area-based conservation efforts.^{11–13} The need for such increases is already recognized in a draft post-2020 global biodiversity framework,¹⁴ the final form of which will likely require not only the growth of strict, well-funded, and well-managed PAs, but also other effective area-based conservation measures (OECMs)¹⁵ and policy responses that have objectives and/or outcomes relevant to conservation.^{7,16} It is now crucial that baseline analyses provide the necessary detail on the scale and geography of conservation

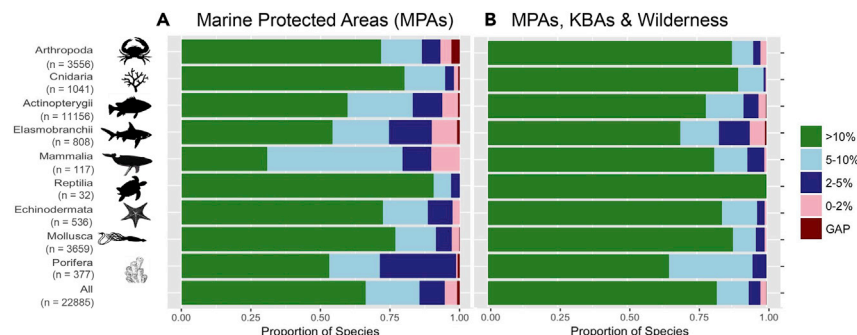


Figure 1. Protection Levels across Marine Taxa

Percentage of marine species with 0% (dark red), 0%–2% (pink), 2%–5% (dark blue), 5%–10% (light blue), and >10% (green) of their range overlapping with (A) marine protected areas (MPAs) and (B) MPAs, key biodiversity areas (KBAs), and marine wilderness areas. Data are shown for all species (bottom) and species in the six largest phyla where the largest phyla (Chordata) is split into its four largest classes (Actinopterygii, Chondrichthyes, Mammalia, Reptilia).

actions needed to safeguard biodiversity. This is especially true in the ocean, because existing conservation efforts are insufficient for the majority of marine species,¹⁷ and an agreement to address sustainable use of marine biodiversity in areas beyond national jurisdictions is currently being negotiated by the United Nations.¹⁸

Here, we identify global priorities for the expansion of conservation efforts, encompassing both site-based conservation action (including formal PAs and other area-based approaches) and broad-scale policy responses (e.g., addressing fisheries management) to secure marine species. We first evaluate how well ~23,000 marine species (fishes, mammals, and invertebrates) are represented within current marine protected areas (MPAs), key biodiversity areas (KBAs),¹⁹ and the ocean's remaining wilderness areas.⁴ We chose MPAs, KBAs, and marine wilderness areas as the conservation baseline because all three currently play an essential role in safeguarding marine life, although only MPAs, as a governance structure, are defined as being actively managed. Well-placed and resourced MPAs are critically important in stabilizing or increasing species populations²⁰ and maintaining coral cover,²¹ and generally have higher biomass than unprotected areas.²² Similarly, marine KBAs are sites of significance for the global persistence of biodiversity, supporting threatened or geographically restricted species/ecosystems, intact ecological communities, and important biological processes (e.g., breeding aggregations), as well as having high irreplaceability.¹⁹ Marine wilderness areas are, by definition, the least anthropogenically affected areas of the ocean, and so are mostly free of threats to biodiversity, at least for now.⁴ Wilderness areas, although not necessarily highly biodiverse, also often contain high genetic diversity, unique functional traits and endemic species, and much higher biomass than more anthropogenically affected areas, so safeguarding them is critical in a time of human-forced climate change.^{4,23} Some KBAs and marine wilderness areas are contained within MPAs, or are seen as core priorities for future MPA expansion,^{4,19} whereas others are covered by OECMs¹⁵ or are best conserved through sectoral approaches and policy responses (e.g., fisheries restrictions). We hereafter refer to these areas (MPAs, KBAs, and marine wilderness) as “areas of conservation or biodiversity importance,” as all offer accepted conservation benefits through direct protection (i.e., MPAs) or as areas of documented biodiversity importance (e.g., KBAs and marine wilderness).

Our analysis identifies species that have none of their range contained within areas of existing conservation or biodiversity importance, as well as those that do not meet various represen-

tation targets (we focus on the minimum target of 10% of total range covered, although other targets were explored). We then use an algorithm for solving integer linear programming problems²⁴ to identify additional conservation priorities to achieve coverage targets for each species while minimizing the total area required. To assess broadly the actions that might be needed to conserve species within these areas, we then map the intensity of 15 damaging human activities across them, using the most comprehensive database of human stressors to the ocean.²⁵ We distinguish between ocean-based stressors (e.g., fishing)—which can be managed with MPAs, OECMs, or other regulations concerning ocean activities—and land-based stressors (e.g., nutrient runoff), which require terrestrial management. We ignore stressors where local actions have limited benefit (e.g., climate change). In this way, we present an ecologically relevant plan to inform the development of future international marine conservation frameworks. Down-scaling our results to inform regional and national conservation efforts will require incorporating local biodiversity data along with information on existing planning efforts and ocean uses, but our analysis can act as a flexible template to follow when doing so.

RESULTS

Current Species Coverage

Using data on the global distribution of MPAs, we find that two-thirds of species ($n = 15,149$) meet a target of >10% range coverage by PAs (10% is the total ocean area that nations have committed to protecting under the Convention on Biological Diversity; Figure 1A).²⁶ Coverage levels vary considerably across marine taxa (Table S1). Reptiles ($n = 32$) are the most well-covered group, with >90% of species meeting the 10% threshold, and all species having >2% of their range within MPAs (Figure 1A). In contrast, 3% of 3,556 arthropod species have none of their range covered by PAs, and only one-third of 117 mammal species reach the 10% threshold (Figure 1A). In total, 7,736 species (33%) have <10% of their range covered by current MPAs. Around half of these species have under 5% of their range covered, and 216 species (~1%) have no part of their range within MPAs (Figure 1A).

We repeated this analysis to include all areas of conservation or biodiversity importance (MPAs, KBAs, and marine wilderness areas) and found that species representation improved, with 82% of all species ($n = 18,804$) having >10% of their range inside MPAs, KBAs, or marine wilderness (Figure 1B). Despite

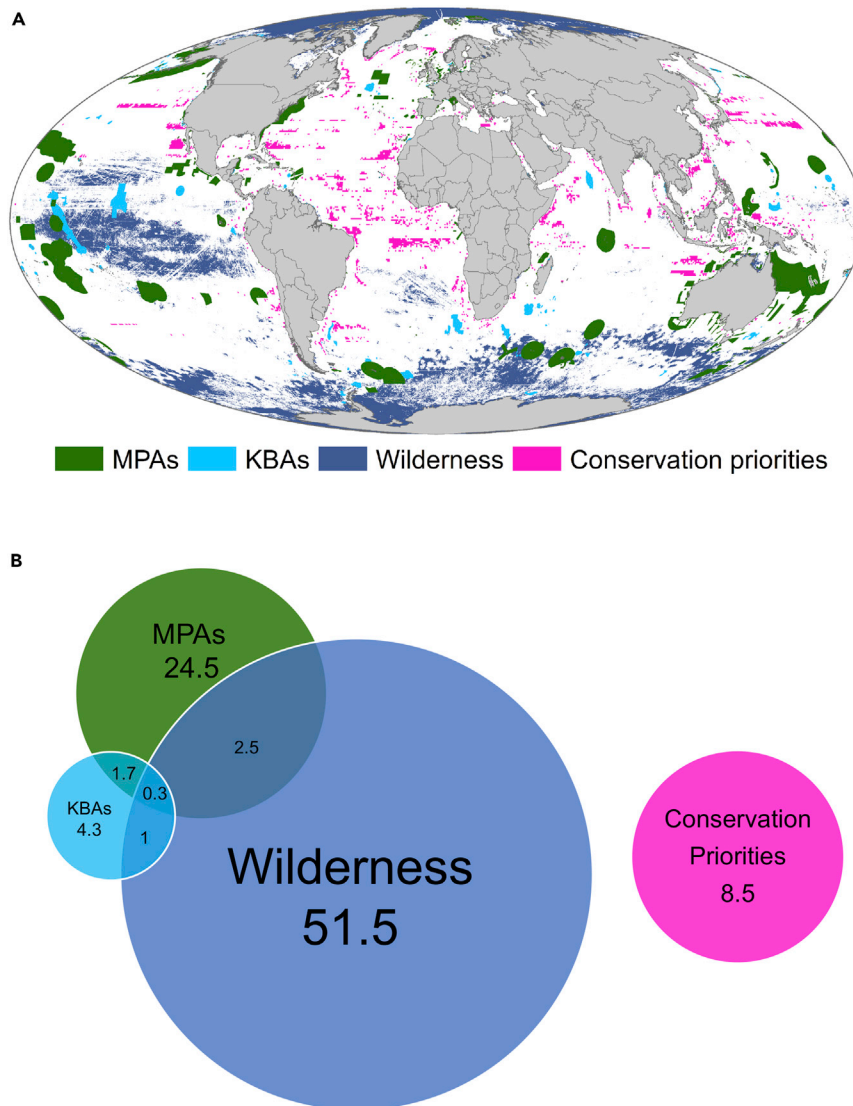


Figure 2. Location and Size of Conservation Priorities

(A) Minimum area required for conservation action to reach 10% coverage for approximately 23,000 marine species with known distributions, while accounting for existing marine protected areas (MPAs), key biodiversity areas (KBAs), and marine wilderness areas.

(B) Area of each mapped zone and their overlaps, in millions of km².

targets for all species in the minimum total area. Because neither Aichi target 11 of the UN Convention on Biological Diversity (CBD) nor the UN Sustainable Development Goals (SDG) set specific targets for protecting individual marine species ranges, we set a minimum target of 10% of each species' range (because both mechanisms aim to conserve at least 10% of the ocean, especially "areas of particular importance for biodiversity").^{26,27} However, we also explored two other scenarios, one that used a 20% target for all species and one that set high targets (100%) for small-ranged species, lower targets (10%) for large-ranged species, and linearly scaled targets between these values for medium-ranged species (see [Experimental Procedures](#)). We used a uniform proxy for cost data (area of conservation zones), rather than socioeconomic data (e.g., fishing effort) to avoid inaccuracies and errors in socioeconomic data biasing the selection of planning units.²⁸

Representing 10% of all mapped species ranges would require 8.5 million km² (~2.5% of the ocean) of new conservation

priority areas in total, with just over half (55.4%, 4.7 million km²) located inside Exclusive Economic Zones (EEZs; [Figures 2 and S2](#)). Combined with existing MPAs, KBAs, and marine wilderness, these areas cover 94.3 million km² (26%) of the ocean ([Figure 2](#)). In comparison, expanding priority areas to meet species range size-based targets, which vary from 10% for large-ranged species to 100% for small-ranged species,²⁹ would require 66 million km² of new conservation priorities. When combined with existing areas of conservation and biodiversity importance, these expanded priorities would cover 152 million km² (41%) of the ocean ([Figure S3](#)).

only 33 species (<0.1%) having no part of their range covered, there are still 4,081 (18%) species with <10% coverage and 500 (2%) species with <2% coverage ([Figure 1B](#)). Low-coverage species (<2% coverage) are mostly found in the Atlantic Ocean, especially between Africa and South America, and also in the Pacific near China and Japan ([Figure S1](#)). Elasmobranchs (sharks and rays) and Porifera (sponges) are the least well covered phyla overall, with one-third of species having <10% coverage ([Figure 1B](#)). Under range-size-based targets, 25.8% of species are adequately represented when considering only MPAs, and 66.1% of species are adequately represented when considering all areas of conservation or biodiversity importance.

Global Conservation Priorities

We mapped global marine conservation priorities using integer linear programming²⁴ to identify where additional conservation responses, beyond effective conservation of MPAs, KBAs, and marine wilderness areas, are needed to meet the representation

targets for all species in the minimum total area. Because neither Aichi target 11 of the UN Convention on Biological Diversity (CBD) nor the UN Sustainable Development Goals (SDG) set specific targets for protecting individual marine species ranges, we set a minimum target of 10% of each species' range (because both mechanisms aim to conserve at least 10% of the ocean, especially "areas of particular importance for biodiversity").^{26,27} However, we also explored two other scenarios, one that used a 20% target for all species and one that set high targets (100%) for small-ranged species, lower targets (10%) for large-ranged species, and linearly scaled targets between these values for medium-ranged species (see [Experimental Procedures](#)). We used a uniform proxy for cost data (area of conservation zones), rather than socioeconomic data (e.g., fishing effort) to avoid inaccuracies and errors in socioeconomic data biasing the selection of planning units.²⁸

Representing 10% of all mapped species ranges would require 8.5 million km² (~2.5% of the ocean) of new conservation priority areas in total, with just over half (55.4%, 4.7 million km²) located inside Exclusive Economic Zones (EEZs; [Figures 2 and S2](#)). Combined with existing MPAs, KBAs, and marine wilderness, these areas cover 94.3 million km² (26%) of the ocean ([Figure 2](#)). In comparison, expanding priority areas to meet species range size-based targets, which vary from 10% for large-ranged species to 100% for small-ranged species,²⁹ would require 66 million km² of new conservation priorities. When combined with existing areas of conservation and biodiversity importance, these expanded priorities would cover 152 million km² (41%) of the ocean ([Figure S3](#)).

New conservation priorities based on the 10% range target scenario are primarily located in places where there are few existing areas of conservation or biodiversity importance, and high concentrations of species with low coverage in existing areas of conservation and biodiversity importance. Key regions for these priority areas include the Northern Pacific Ocean near China and Japan and the Atlantic Ocean between West Africa and the Americas ([Figure S1](#)).

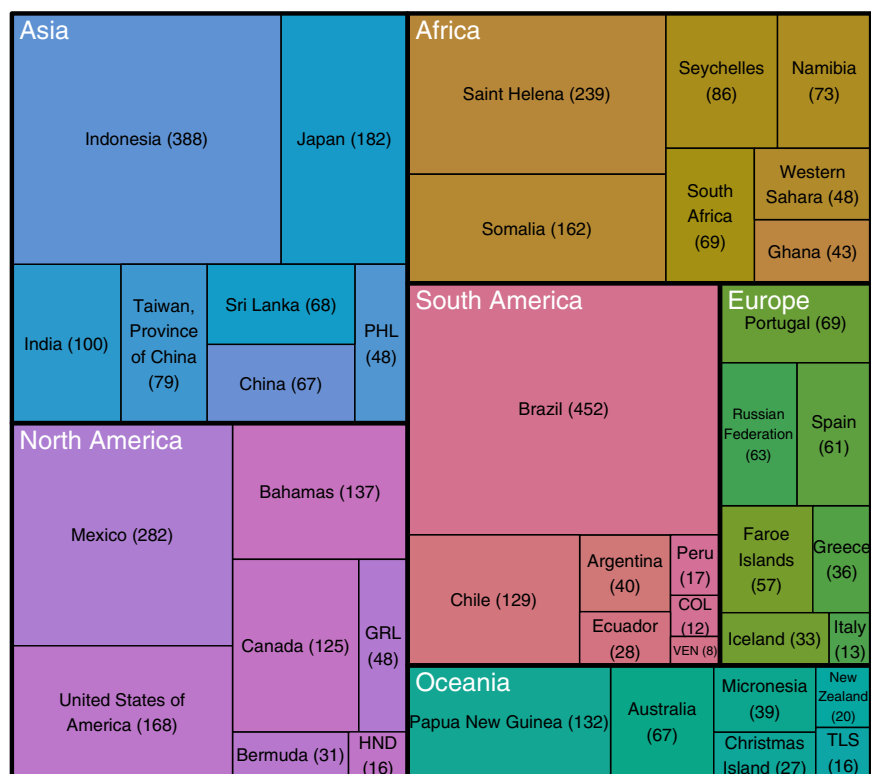


Figure 3. Size of Conservation Priority Areas per Continent

Area (thousands of km²) of new conservation priorities (under the 10% range target scenario) within Exclusive Economic Zones of the seven countries within each continent that contain the largest area of new conservation priorities. The size of each section is proportional to the area of conservation priorities within each continent and country. Antarctica is excluded because it is the territory of multiple nations. COL, Colombia; GRL, Greenland; HND, Honduras; PHL, Philippines; TLS, Timor-Leste; VEN, Venezuela.

well our conservation priority areas overlap with seabird ranges. We found that priority areas overlap with 67.4% ($n = 247$) of all seabird ranges (data from BirdLife International and *Handbook of the Birds of the World* 2018) and cover 12.2% of individual species' distributions on average, and >10% of the range of 42.8% ($n = 157$) species.

Assessing Threats to Priority Areas

To assess threats to species across new conservation priority areas, we used the most comprehensive, globally consistent

We did not include ecologically or biologically significant marine areas (EBSAs) because many are mapped at such large spatial scales that they are not useful as targets for area-based conservation without further refinement. However, our new and existing priority areas (under the 10% range target scenario) overlap with 89% of individual EBSAs and cover 22% of total EBSA area (Figure S4). For individual EBSAs that are smaller than global mean MPA size (~2,000 km²), our new and existing priority areas overlap with 40% of their extent on average.

Just over half (56%) of all coastal nations contain new priority areas (under the 10% range target scenario), although the amount within each country varies considerably (Figure 3). Of the new conservation priorities within EEZs, almost half are found in Asian and North American countries (Figure 3). Brazil has the largest area of new conservation priorities (452,000 km²), 64,000 km² more than that of the next highest nation, Indonesia (388,000 km²; Figure 3). Some nations with very large MPA estates still contain a substantial extent of new priority areas. For example, the United States has the largest MPA estate in the world,⁶ but the nation contains 168,000 km² of new conservation priority areas (Figure 3), in part because it has the largest EEZ in the world, spanning three oceans. Timor-Leste, The Bahamas, and Taiwan have the largest area of conservation priorities relative to EEZ size, all having >20% of their EEZ covered by new priority areas (Figure S3). Under a scenario using range-size-based species representation targets, priority areas are found in almost all coastal regions throughout the Atlantic Ocean and in the West Pacific Ocean (Figure S3).

Given the omission of seabirds—a prominent marine group—from the species distribution data we used, we assessed how

database on 19 human stressors to the marine environment.²⁵

We excluded four climate stressors because they can only be effectively addressed through global action to reduce emissions, whereas here we focus on conservation actions that can be taken at the local to national scale. We classified the 15 remaining stressors on the basis of whether they are ocean based (e.g., fishing, commercial shipping) and can thus be managed with strict MPAs or other spatial regulations, or are land based (e.g., nutrient runoff) and will require terrestrial actions such as land-use management to reduce runoff (Table S2).

Most new conservation priority areas (under the 10% range target scenario) are affected primarily by ocean-based threats because the footprint of land-based pressures is constrained to near-coastal areas (Table S3). Key areas of ocean-based threats to new conservation priorities include the East China Sea and the North Sea off the Norwegian coast, which are both areas of intense industrial fishing activity (Figure 4 [blue colors] and Table S3).³⁰ Ocean-based threats are generally lower in high-seas areas than near-shore priority areas, especially in the South Atlantic Ocean (Figure 4 and Table S3). Although some coastal priority areas show very low levels of ocean-based threats, this might be partly due to a lack of data, as there are obvious geographical gaps in global fishing activity datasets.³⁰ Such data gaps can result in substantial underestimation of fishing activity. For example, in Somalia it is estimated that illegal, unregulated, and unreported fishing catch is almost three times higher than official estimates.³¹

A small number of new conservation priority areas (under the 10% range target scenario) are affected by high levels of both ocean- and land-based threats (Figure 4 [red colors] and Table S3). These impacts are highest in areas where high fishing

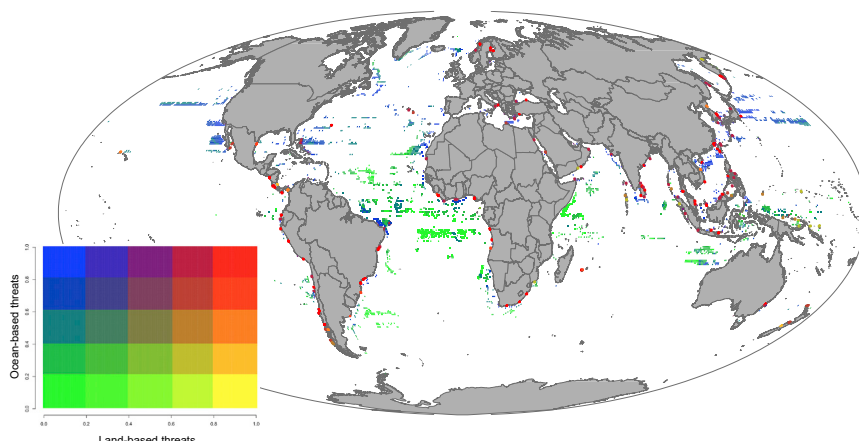


Figure 4. Threats to New Priority Areas for Conservation

Spatial relationship between ocean-based threats (e.g., fishing, shipping; blue areas) and land-based threats (e.g., pollution runoff, nutrient runoff; yellow areas) across global priority areas for conservation (under the 10% range target scenario). Areas with high levels of ocean-based and land-based threats are shown in red, and those with low levels of ocean-based and land-based threats are shown in green. Boundaries of areas within the top two quintiles of land-based threat level (orange/red colors) have been enlarged to increase visibility.

activity coincides with high levels of agriculture and livestock grazing in very large nearby drainage basins, such as the Gulf of Mexico and the South China Sea. Many of these areas, such as the Indus river in Pakistan, have been previously identified as threat hotspots where coordinated management of land- and ocean-based impacts is vital.³² However, in some cases effects might be so high that reducing them becomes virtually impossible, and conservation resources can be better utilized in areas where reducing human impacts is more feasible. The exception to this occurs in places where a single site holds the last population of a species, and thus is crucial to conserve regardless of the impact level.³³ There are few new priority areas that are affected primarily by high levels of land-based threats, but exceptions include southern Chile and parts of Indonesia (Figure 4, yellow colors).

A substantial proportion of new conservation priorities (under the 10% range target scenario) are currently facing relatively low overall threat (Figure 4, green colors). It is crucial to prevent threats from expanding into these areas, as low-pressure habitat holds levels of biodiversity unparalleled in areas of higher impact.³⁴ Monitoring is essential in these areas, but as they are often remote and located beyond national jurisdiction, this can be difficult. However, with advances in remote vessel monitoring technology, such as Global Fishing Watch,³⁰ it is becoming increasingly possible.

DISCUSSION

Future global strategies to address biodiversity loss will require rapid action to secure imperiled species and ecosystems, combined with long-term approaches to sustainably manage the ocean in its entirety.⁸ We show that effective conservation of an additional 8.5 million km²—alongside improved management of existing MPAs, and proactive conservation of KBAs and marine wilderness (which cover ~60 million km²)—could achieve a minimum representation target of 10% for all mapped marine species. If species range size-based targets are used, an additional 15% of the ocean (~57 million km²) would require conservation. Regardless of the target used, our findings echo previous analyses showing that meeting global conservation targets for all mapped terrestrial species ranges will require large increases in the total area under conservation.³⁵

Our findings, showing that at least 26%–41% of the ocean needs to be conserved, are similar to recent calls from CBD parties and observers for a post-2020 conservation framework that ensures at least 30% of Earth is covered by effectively managed PAs and OECMs.^{36,37} However, we are unable to quantify the proportion of priority areas that require conserving through site-based approaches (i.e., PAs and OECMs) versus broad-scale policy responses (which might be particularly relevant for some areas of extensive marine wilderness). Indeed, it is important to note that our results do not represent an actionable conservation plan, but instead serve to demonstrate the overall scale of conservation action required and highlight important areas on which regional and local conservation efforts could focus. More detailed analyses that incorporate local-scale data on biodiversity, human activities, and the cost of management activities will be crucial for designing and implementing specific conservation actions.

Our estimate that 26%–41% of the ocean requires effective conservation should be regarded as a bare minimum. Beyond the fact that the lower value was based on a minimal 10% species representation target, our species data notably excludes all marine birds and represents a tiny fraction all marine species.³⁸ Moreover, we do not consider the fact that species are changing their distributions in response to climate change,³⁹ and assume that conservation of all areas within a species' range contribute equally toward its conservation, ignoring areas important for different life-history stages (e.g., breeding grounds, feeding areas, and migration routes). However, KBAs often capture these important areas, and given that recently adopted KBA criteria¹⁹ have yet to be applied to many taxa and ecosystems, the marine KBA network will increase in the near future. EBSAs also often capture areas of special importance for life-history stages and so could be considered for conservation action, especially given that 89% of them overlap with the conservation priorities we identify here (Figure S3). Because EBSAs vary substantially in size, appropriate conservation responses could range from formal PAs for smaller EBSAs to broad-scale policy approaches for very large EBSAs.

The benefits of marine conservation actions (e.g., MPAs, OECMs) are clearly commensurate with good design, adequate resourcing, fair governance, and equitable management, which are lacking in many countries.⁴⁰ However, our results assume

that all MPAs are effective in stopping threats to biodiversity, likely vastly overestimating their conservation impact.⁴¹ For effective conservation, MPAs should conform to the International Union for Conservation of Nature's global standards for conservation success,³⁶ and as such it is timely to consider revising the status of some areas currently considered MPAs (e.g., removing areas that are managed for fishing and have little or no conservation benefit). Furthermore, it is crucial to recognize that well-managed MPAs are only part of a suite of management options necessary to maintain ocean health,³⁶ and that they must be combined with OECMs, land-based actions, and broad-scale approaches leading to improved management of the ocean beyond the PA estate (e.g., catch documentation schemes, mandatory environmental impact assessments). These broad-scale policy approaches will often be better suited for wilderness conservation than MPAs given the size and remoteness of many wilderness areas. In all cases it will be key to incorporate local-scale data on threats to biodiversity when designing conservation interventions, as global data are inevitably limited in accuracy and comprehensiveness. It is also important to consider the costs of various conservation actions, as these costs are highly dependent on human uses of the ocean (e.g., fishing), and can substantially change conservation priorities.⁴²

Although addressing land- and ocean-based threats is important in the immediate term, conservation strategies must also look forward to assess the future risk posed by human-forced climate change.⁴³ Local conservation actions are unable to stop or reverse the impacts of climate change, but there are many actions that can increase the ability of biodiversity to adapt to a changing climate. For example, there is mixed evidence for MPAs enhancing recovery and resilience of degraded coral reefs,⁴⁴ and reducing land-based stressors might increase reef resilience to climate change.⁴⁵ However, as most studies on how conservation efforts influence climate-change resilience focus on coral reef ecosystems, further research on other coastal ecosystems (e.g., seagrass, kelp forests) and pelagic systems is vital. It is also important to recognize and plan for the impacts of human responses to climate change, which include shifting fishing efforts to track fish stocks or building sea-walls to prevent sea-level rise.⁴³

Because over 46% of priority areas are located in the high seas, developing and implementing conservation actions in these areas will be crucial for future conservation agreements. Conservation action in the high seas is legally challenging and has so far been limited, with only 1.18% currently protected.⁶ However, an international legally binding agreement to address sustainable use of marine biodiversity in areas beyond national jurisdictions is currently being negotiated under the United Nations Convention on the Law of the Sea.⁴⁶ Legal options for conservation and sustainable use of marine biodiversity under such an agreement are still being debated, but it will likely provide an opportunity to increase the use of area-based management tools to advance protection and ecosystem-based management measures.⁴⁶ Given that this high seas conservation agreement is being developed concurrently with the CBD post-2020 biodiversity framework, it is crucial that the definitions, standards, and criteria used in both are consistent and can be effectively applied across all jurisdictions (e.g., within and

beyond EEZs). Internationally agreed definitions on MPAs and OECMs, for example, would allow for accurate assessments of the area under conservation at both national and global scales.

With the 2020 deadline for achieving global conservation targets under the CBD fast approaching, this work highlights new priorities for conservation action to fulfill current targets. Our work shows that effective conservation of at least an additional 8.5 million km²—alongside improved management of existing MPAs and proactive conservation of KBAs and marine wilderness—could secure 10% of all mapped marine species ranges. This effort would lead to considerable progress toward the Life Below Water Goal (SDG 14) of the UN Sustainable Development Goals.²⁷ Our analysis demonstrates the overall scale of conservation action required in a post-2020 biodiversity framework, and if combined with an agenda focused on improved management of the ocean in its entirety, these results represent the start of a bold plan for the conservation and sustainable use of marine biodiversity.

EXPERIMENTAL PROCEDURES

All spatial data described were processed using ESRI ArcGIS v10.5 in Mollweide equal-area projection. All prioritization analyses were conducted using R statistical software 3.3.

Gap Analysis

Data on the global distribution of PAs were obtained from the November 2017 World Database on Protected Areas.⁴⁷ Following similar global PA studies,⁴⁸ we extracted PAs from the WDPA database by selecting those areas that had a status of “designated,” “inscribed,” or “established,” and were not designated as UNESCO Man and Biosphere Reserves. We included only PAs with detailed geographic information in the database, excluding those represented as a point only. We then used a layer delineating global coastline to identify MPAs by clipping PA polygons to only include those which have some overlap with marine area (<http://datadryad.org/resource/doi:10.5061/dryad.6gb90.2>). EBSA data were taken from <https://www.cbd.int/ebsa/ebsas>.

Data on KBAs were obtained from the 2016 release of the World Database of Key Biodiversity Areas (<http://www.keybiodiversityareas.org/>). We used a layer of terrestrial country boundaries to clip KBA polygons to only include those which overlap with marine area (<http://datadryad.org/resource/doi:10.5061/dryad.6gb90.2>). We used previously identified data on marine wilderness areas,^{4,5} which were mapped by identifying areas that have both little to no impact across 15 human stressors to the marine environment (excluding four climate stressors), and also a low combined impact from 19 human stressors including climate-change stressors. To avoid double-counting areas that are covered by MPAs, KBAs, and marine wilderness, we merged these three layers and dissolved areas where they overlapped.

2015 data on marine biodiversity was obtained from AquaMaps,³⁶ a species distribution modeling tool that correlates known species occurrence points with environmental data (e.g., temperature, salinity) to produce standardized global range maps for 22,885 aquatic species. This is the most comprehensive and highest resolution data available on the distribution of marine biodiversity globally, and includes Animalia (fishes, marine mammals, and invertebrates), Plantae (fleshy algae, seagrass), Chromista (calcifying algae), and Protozoa. The species distribution maps predict relative probabilities of species occurrence (ranging from 0.00 to 1.00) at a resolution of 0.5-degree cells. It is assumed that the preferred range is where probability is 1, outside the range limits is where probability is 0, and between these two thresholds the relative environmental suitability decreases linearly. As there is no recommended threshold to use, we follow previous studies and report on results using probability threshold of 0.5 or greater.¹⁷ We did explore other probability thresholds and found that the results varied very little (Table S4).

To assess coverage of marine species distributions in MPAs, KBAs, and wilderness areas, we determined the proportion of PA (MPA, KBA, and wilderness) in each 0.5-degree cell. As we do not know the exact distribution of

species within each cell, we assumed that the area of a species' range represented in PAs was equal to the PA coverage for grid cells in which the species was present.

Spatial Prioritization Analysis

We used integer linear programming to identify spatial priorities that meet a percentage coverage target for each of the 22,885 AquaMaps species, while accounting for the level of protection in existing MPAs, KBAs, and wilderness, and minimizing the total cost of selected cells, with area as the cost, after previous studies.^{4,23} This is frequently referred to as the minimum-set problem in spatial conservation planning. We used the software package Gurobi (version 5.6.2) to find solutions to this minimum-set problem. Gurobi is proprietary software that uses several algorithms, including simplex and branch and bound algorithms, to solve linear programming problems and is guaranteed of finding optimal solutions given enough time. We set Gurobi to achieve a solution within 0.5% of the optimum (i.e., when the current solution was within 0.005 times the guaranteed lower boundary of the optimal solution). The optimal solution is that which achieves the coverage target with the lowest possible cost. We explored three different coverage targets: 10% of species range (reported in main text), 20% of species range, and a set of targets that varied depending on the total range size of each species (reported in [Sensitivity Analysis](#) below).

We used 0.5-degree cells as our planning units (areas which can be selected or not selected for conservation), as this is the same scale as our species distribution data. We extracted all planning units containing species distribution records from AquaMaps ($n = 178,234$) and assigned each planning unit a cost value equal to the area of the cell that is not covered by an MPA, KBA, or marine wilderness area. All MPAs, KBAs, and marine wilderness areas were locked into the analysis (i.e., they were always selected), and if these areas only partially covered a planning unit then we split that planning unit into two parts and only locked in the area covered by MPAs, KBAs, or wilderness. For example, if a planning unit was half covered by an MPA, we always selected the portion covered by the MPA and left the other half open for selection in our analysis. The cost of selecting the planning unit was always proportional to the area not covered by existing MPAs, KBAs, or wilderness areas. Thus, the cost value reflects the additional area per cell that requires management if selected for conservation. Similarly, because our AquaMaps species distributions use the same 0.5-degree cells as our planning units, the amount of a species range covered if a planning unit is selected is equal to the area of that planning unit which is not already covered by MPAs, KBAs, and marine wilderness areas.

Assessing Threats Facing Priority Areas

We assessed the anthropogenic threats facing priority areas using normalized data on cumulative human impact to marine ecosystems.²⁴ This threat database includes 19 individual human stressors, but we excluded four climate-change stressors. We then categorized threats as ocean-based or land-based, depending on their origin (see [Table S1](#) for full list). Ocean-based threats have clear marine origins, such as fishing and shipping, and can therefore potentially be managed through effective MPAs of other ocean-use regulations, whereas land-based threats (e.g., nutrient runoff, coastal armoring) originate on land and will require land management to address. All measures of fishing pressure, shipping (shipping lanes and ship-based pollution), and ocean structures (e.g., oil rigs) were considered as "ocean based" in our analysis, whereas all other threats were considered land based. We summed the values for each individual stressor layer within the ocean-based and land-based stressor groups to give final ocean-based and land-based human impact values. Using this information, we used the zonal statistics tool in ArcMap 10.5 to calculate the mean level of ocean-based and land-based threat within each planning unit selected as a priority area in our spatial prioritization analysis.

Sensitivity Analyses

The AquaMaps species distribution maps we used for our gap analysis and spatial prioritization predict relative probabilities of species occurrence (ranging from 0.00 to 1.00) at a resolution of 0.5-degree cells. It is assumed

that the preferred range is where probability is 1, outside the range limits is where probability is 0, and between these two thresholds the relative environmental suitability decreases linearly. To test the sensitivity of our results to the probability threshold used to determine species distributions within each 0.5-degree cell, we repeated our gap analysis using four probability thresholds: 0.25, 0.5, 0.75, and 1 (results presented in the main text use 0.5).

When using various probability thresholds to determine species distributions, the number of species within each coverage group (e.g., no coverage, 0%–2% coverage, and so forth) varied by less than 1% across all probability thresholds tested ([Table S4](#)), and thus our results are not sensitive to species distribution modeling uncertainties. Furthermore, previous studies using AquaMaps data found that varying probability thresholds makes very little difference to global scale analyses.^{7,16}

To test the sensitivity of our results to the species representation target used, we explored three targets in our spatial prioritization analyses, all of which aimed to minimize the total area of selected planning units: 10% of species range, 20% of species range, and range-size-based targets that vary depending on the total range size of each species. For the latter case, we set a 100% coverage target for species with ranges <10,000 km², whereas for wide-ranging species (>390,000 km²) the target was reduced to 10% coverage, and where geographic-range size was intermediate between these extremes the target was log-linearly interpolated. The 390,000-km² threshold is arbitrary, but it follows previous studies²⁹ and corresponds to roughly one-third of all species analyzed. For each set of targets, we set Gurobi to achieve a solution within 0.5% of the optimum (i.e., when the current solution was within 0.005 times the guaranteed lower boundary of the optimal solution). The optimal solution is that which achieves the coverage target with the lowest possible cost. As such, the prioritizations conducted in this sensitivity analysis identify sets of planning units that meet each species representation target (10% of all species ranges, 20% of all species ranges, and species range size-based targets) in the least possible area.

When using various species-range targets in our spatial prioritization analysis there was a high level of overlap between selected planning units, although the total area of priorities changed substantially. More than half of all the planning units selected when using a 10% coverage target were also selected when using a 20% target ([Table S5](#)). As expected, considerably more area was required to meet the range-size-based targets, although 56% of planning units selected under the range-size-based targets were also selected when using a 10% target. This suggests that our priority areas are robust to different target-setting approaches, as over 50% of planning units are always selected, regardless of the specific species representation target used. As such, future conservation agreements and priority setting exercises, which might use representation targets different from the 10% coverage target we report on in the main text, can efficiently build on the priority areas we identify.

Bird-Range Overlap

To explore how our conservation priority areas overlap with seabird ranges, we obtained data on the distribution of birds from BirdLife International (<http://datazone.birdlife.org/species/requestdis>). We extracted all birds classified as seabirds and calculated the area of overlap between each seabird species range and our conservation priority areas. We found that our priority areas overlap with 67.4% ($n = 247$) of all seabird ranges and cover 12.2% of individual species-range area on average. In 42.8% ($n = 157$) of species, our priority areas cover >10% of their range.

DATA AND CODE AVAILABILITY

Input data are available for download from <https://doi.org/10.5063/F1GF0RVK>.

SUPPLEMENTAL INFORMATION

Supplemental Information can be found online at <https://doi.org/10.1016/j.oneear.2020.01.010>.

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AUTHOR CONTRIBUTIONS

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DECLARATION OF INTERESTS

The authors declare no competing interests.

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