CellPress
OPEN ACCESS

Trends in
Ecology & Evolution

Opinion

Ecologically representative Marine Protected Area planning can think globally and act locally

Qianshuo Zhao (赵千硕)[1,*] and Mark John Costello [1,2,*]

To date, Marine Protected Area (MPA) planning has been regional. Over half of the current MPA are outside the areas identified as a priority for the protection of global biodiversity in all global and High Seas studies. Using systematic planning, an MPA network could be representative of all marine biodiversity in half of the ocean area and could be representative of between 70% and 90% of biodiversity in 30% of the ocean area. We found that 1% of the ocean was overlapped by the global studies. This 1% should be prioritised internationally and nationally as fully protected MPA which prohibit people from killing wildlife and damaging habitats. Species range maps suggest this 1% may include up to half of some groups of marine species.

Highlights

Best practice in nature conservation is to use systematic conservation planning to maximise representation of biodiversity within ecologically coherent networks of protected areas.

Current Marine Protected Areas (MPA) have not been located considering the global distribution of biodiversity.

MPA planning would be more effective if it combined the perspective of areas of consensus across systematic global studies with local conservation action.

We found that 1% of the ocean overlaps current global MPA prioritisations and is likely to contain disproportionally more species, perhaps half of all of some groups of marine species.

Systematic planning for representativity

In response to the global scale decline of **biodiversity** (see Glossary), over 100 countries have pledged to conserve at least 30% of the planet in 'ecologically representative … systems of protected areas' by 2030 as part of commitments within the Convention of Biological Diversity (CBD; https://www.cbd.int/gbf/targets). 'Representative' means that, collectively, the protected areas should include (i.e., represent) as much biodiversity as possible, that is, as many species, **habitats**, **ecosystems**, and other measures of biodiversity as possible. Because biodiversity varies geographically, the most area-efficient way to achieve this is to use systematic conservation planning [1]. As a first step, this takes a top-down approach to identify which combination of areas would include the most biodiversity using geographically standardised data on biodiversity. Several measures of biodiversity are desirable so that the available data act as a surrogate for missing data. This top-down approach is analogous to the situation in which, when prioritising individual species for conservation action at a national scale, those species threatened with global extinction are generally given higher priority than declines in populations at local scales (i.e., threatened with extirpation) but which may not be threatened elsewhere. Thus, in both area-based and individual species conservation, a global perspective provides context that informs local scale conservation priorities.

To date, conservation has taken a regional and national approach in identifying areas important for biodiversity in the ocean, including the CBD Ecological or Biologically Significant Areas (EBSA), Food and Agriculture Organization of the United Nations, Regional Fisheries Management Organizations Vulnerable Marine Ecosystems, Barcelona Convention Specially Protected Areas of Mediterranean Importance, and the environmental nongovernmental organisation–identified Key Biodiversity Areas (KBAs), Important Bird Areas, and Important Marine Mammal Areas. In addition, there are places managed for protection of aspects of nature (not necessarily biodiversity), including the World Heritage Convention Sites, Ramsar Convention Wetlands of International Importance, UNESCO Biosphere Reserves, and MPA listed by the OSPAR Commission for the North-East Atlantic. Gownaris *et al.* [2] compared these and other *ad hoc*

[1]Ocean University of China, Qingdao, China
[2]Faculty of Biosciences and Aquaculture, Nord University, Bodo, Norway

*Correspondence:
zqs@ouc.edu.cn (Q. Zhao) and
mark.j.costello@nord.no (M.J. Costello).

mapping of areas of conservation importance and found they occupied 55% of the ocean and had 14% overlap but were mostly (88%) unprotected. They called for a more science-driven approach to selecting areas as MPA that can reconcile alternative proposals.

A classification of MPA based on fishing impacts found that partially protected MPA covered 9% of the ocean and had a surprisingly high proportion of marine species recorded in them [3]. It found that half of all species and 70% of threatened species in the Ocean Biodiversity Information System (www.obis.org) have been reported at least once in these MPA, and half of threatened species have been reported in fully (or strictly) protected MPA. Yet, only about 3% of the ocean is designated for full or high (minimal fishing) protection (mpatlas.org, navigatormap.org). It is not known how well-enforced this is, but there are indications enforcement is less than half (e.g., [4–7]). Thus, it may be more effective to focus conservation on a most representative network of fully protected MPA rather than on area targets that do not aim to protect or enforce protection of biodiversity. These areas should be as fully protected as practicable from human impacts, with no hunting, fishing, or other killing of marine life or damage to habitats allowed (Box 1).

Fortunately, for the oceans, countries have a choice of studies that systematically used the best available data to identify priorities for where to locate MPA. However, none of these studies have been referenced by the CBD or used in guiding the selection of where to place MPA. If there is considerable overlap across these studies, despite their varying data and methodologies, this would indicate that we know enough to prioritise the most area-efficient places to protect biodiversity globally. Countries should consider all these studies in their conservation planning. Where multiple studies map the same priority areas, it indicates that despite their varying data sources and methods, these places emerge as high priority for protection. Here, we overlaid the areas prioritised by these studies to identify areas of consensus. Details of the overlaying process are provided in the supplemental information online.

Box 1. What does 'protection' mean?

The word 'protection' is meaningless without qualification. All of the ocean has been protected since 1963 from testing of nuclear bombs, but less than 3% has been protected from fishing. Because over 90% of so-called MPA permit fishing, and because fishing changes food webs and ecosystems (i.e., biodiversity), they may be better considered as attempts for ecologically sustainable use than what most people would expect of MPA (i.e., for biodiversity to be natural) [36] (see Figure 3 in the main text). These areas may help contribute to UN Sustainable Development Goals and CBD Global Biodiversity Framework targets for sustainable use but are not true MPA. However, countries have also committed to sustainable use in all of the ocean in the CBD GBF and in the High Seas according to UNCLOS commitments. The fact that most 'MPA' aim for sustainable use rather than protecting biodiversity in a natural condition suggests that the rest of the ocean is being used unsustainably, as indicated by an assessment of 280 fish stocks [37].

Areas may be protected for their human heritage, architecture, history, culture, and traditionally managed landscapes. Most of the IUCN categories for Protected Areas aim to protect 'nature' but do not aim to protect biodiversity as defined by the CBD (see Glossary and Outstanding questions). Rather, most aim to protect geological features, landscapes, seascapes, or manage single species or habitats (IUCN categories IV to VI) (Figure 3). Only category I aims for biodiversity to be in a natural or wild state, and category II partially (e.g., a national park with tourism services). The intention of the 30% by 2030 target is to protect biodiversity so only IUCN categories I and II apply, the first for full (strict) protection and the second for partial protection. These conservation areas may be legally protected as protected areas, or 'other effective area-based conservation measures' (OECMs). If these areas do not allow the killing of wildlife (hunting or fishing) or destruction of natural habitats, they can be considered fully protected.

It seems necessary to emphasise that protected areas cannot protect wildlife by allowing the killing of wild animals or plants or destroying their habitat. Yet, in the European Union, 86% of so-called MPA are so lightly protected that they would not qualify as protected, including many allowing fishery trawling of the seabed [7]. That only 0.2% of the area of European Union seas qualify as fully protected MPA reflects the hypocrisy of wealthy countries proclaiming their support for marine conservation [38].

Glossary

Biodiversity: the Convention of Biological Diversity definition encompasses the variation within species (genetic, phenotypic), between species, and of ecosystems (habitats, productivity, processes).
Biomes: a large geographic area dominated by a plant life form that provides physical habitat for other species. Used on land for deciduous forests, tundra, and grasslands. Comparable marine biomes are seagrass beds, kelp and mangrove forests, and coral reefs with symbiotic algae.
Ecoregions: a large geographic area defined by environmental features considered ecologically important. Typically nested within a biogeographic realm. Most have been defined as areas of conservation interest.
Ecosystem: an enduring, spatially bounded environment (not only one area) where biological and energy interactions are greater within than with other ecosystems. Note that although species are part of ecosystems, the concept is agnostic as to regarding what species are present.
Endemic species: species only known to occur at one location or area of defined extent, such as a country or sea area.
Habitat: the environment (not an area) where an individual, species, or group of species live that can be repeatedly found in nature.
High Seas: means 'all parts of the sea that are not included in the territorial sea or in the internal waters of a State' (1958 Convention on the High Seas) and 'all parts of the sea that are not included in the Exclusive Economic Zone (EEZ), in the territorial sea or in the internal waters of a State' (1982 UN Convention on the Law of the Sea). It includes the water, seabed, and living organisms. This longer-established term is favoured here over the acronym and synonym ABNJ (areas beyond national jurisdiction).
Realm: a biogeographic region defined by an assemblage of species distinct from other regions, with characteristic endemic (geographically rare or localised) species. Distinct from habitat, which is characterised by its dominant species (often common species), ecosystem, and biome (see above).
Topographic heterogeneity: the variation in seabed topography, generally measured as variation in slope of the seabed from bathymetry.

Prioritisations

There have been six independent data-driven studies prioritising where best to protect marine biodiversity, four covering all the oceans [8–11] and two only the **High Seas** [12,13] (Table 1). We synthesise these studies in this opinion paper. In addition, experts have prioritised marine **ecoregions** for conservation based on their knowledge of species richness and **endemicity**, and 18 other studies identified areas of high marine biodiversity, although biased toward particular areas, habitats, or groups of species and without using globally standardised data [14]. Differences between the studies reflected the availability of biodiversity data at the time of their analysis, spatial resolution, and how wide a range of measures of biodiversity they incorporated (Table 1).

Table 1. Recent prioritisations for global marine biodiversity conservation based on data-driven priority analysis compared with criteria for designated protected areas in international agreements as reviewed by Asaad *et al.* [39]

Prioritisation criteria	Selig *et al.* [8]	Visalli *et al.* [12]	Jones *et al.* [9]	Zhao *et al.* [10]	Sala *et al.* [11]	Brito-Morales *et al.* [13]
Scale	Global	High Seas	Global	Global	Global	High Seas
Species diversity (richness)	Species ranges	Species ranges	X	Species ranges	Species ranges	Pelagic species ranges
Number of species	12 497	12 013	22 885	24 904	4242	12 932
Restricted range (endemic)	Range rarity, an indicator of endemism	X	X	Biogeographic realms based on 65 000 species endemicity	X	X
Of conservation concern	Some species included but not given extra weighting	Species extinction risk	The percent of species within MPA, KBAs, and/or marine wilderness	Some species included but not given extra weighting	(i) Species directly or indirectly affected by threats abatable by MPA or (ii) species reported in global catch databases	Threatened species given higher protection target
Life history sites (e.g., nesting)	X	X	X	X	X	X
Habitat						
Rare, unique	X	X	X	X	X	X
Fragile, sensitive	X	X	X	Biomes included seagrass, laminarian kelp, mangroves, shallow coral reefs	X	X
Representativeness	X	X	X	Biogeographic realms based on species' endemicity data	Biogeographic provinces by experts' opinion	Expert mapped pelagic areas and depth zones
Geomorphology	X	Seamounts, hydrothermal vents	X	Physical habitat as topographic rugosity	Seamounts	12 categorical seabed features
Integrity	Human impact	Fishing effort	Human stressors	X	Human impacts on the world's ocean including area of seabed trawled	Fishery catch estimates
Total area of ocean prioritised	<5%[a]	13% of all the ocean, 24% of the High Seas)	2%	30%	21% to protect 90% of maximum potential biodiversity benefits	6%
Spatial resolution	0.5°	0.5°	50 km	100 km	50 km	0.5°

X = not included.
[a]3.2% for priority areas of species richness, 2.7% for priority areas of range rarity, 4.3% for priority areas of proportional range rarity within EEZs and High Seas.

Following the CBD definition of biodiversity, a global network of protected areas should represent as many species, habitats, ecosystems, and related measures of diversity as possible. Because it will never be possible to have comprehensive data on all measures of biodiversity, alternative measures are used as surrogates. For example, the habitats for well-sampled species will also contain less well-known species. Thus, the marine prioritisation analyses have used a range of measures (Table 1), including data on: thousands of species; biogeographic **realms** based on data on species' endemicity; marine **biomes** (kelp forests, mangroves, seagrass meadows, coral reefs); **topographic heterogeneity** (highly correlated with species richness because it indicates variability in physical habitat); phytoplankton productivity; and they sometimes considered fishing effort and species' extinction risk status (Table 1).

If we knew the geographic ranges of all species, then systematic prioritisation could map where to protect all species. However, ranges are only available for 10% of all 243 000 named marine species, and currently available species range maps include artefacts of the modelling process that may bias the areas prioritised (see the supplemental information online Figure S7). This gap in knowledge emphasises the need to prioritise protection of habitats, biomes, and biogeographic realms of high endemicity to help account for the other 90% of the species, as applied in studies to date (Table 1).

Consensus areas

Despite the variability in data used across studies, we see that there are areas of consensus across all the systematic, data-driven prioritisation studies (Figure 1A). These align well with prior data-driven studies and expert-identified marine biodiversity rich spots (supplemental information online, Figures S1–S6). Collectively, the priority areas identified by the four global studies covered 37% of the ocean, and all six studies (including the two only on the High Seas) covered 52% of the ocean (Figure 1B,C). The areas overlapped by at least three of the four global prioritisations occupied 1% of the ocean (Figure 1B).

The 1% area of consensus across at least three of the four global studies would include a disproportionally high number of species for its area. For example, the AquaMaps global dataset of 24 901 marine species ranges, at a 0.5° spatial resolution, predicts 55% of the species ranges (13 578 species) and overlaps the 1% consensus area. The International Union for the Conservation of Nature (IUCN) Red List also provides alternative species range maps, and this predicts that 29% of 1190 fish species and 52% of 912 invertebrate and seaweed species may occur in the 1% consensus area. However, how well species ranges predict the local presence of species and how much area threatened marine species need to survive are outstanding questions.

Available global maps of the major biomes are spatially coarse and may over- and underestimate their characterising species distribution. When they are compared with the 1% consensus area, they have less than 1% overlap, namely ~0% for kelp [15], <0.1% for seagrass [16], 0.1% for mangrove [17], and 0.5% for shallow coral reef [18] biomes. This is to be expected because, for example, even if all of the 1% consensus area was in the coral biome, it would only occupy 2% of the biome. Thus, protecting all marine biodiversity needs to cover closer to 50% of the ocean as indicated in Figure 2.

None of the 1% consensus area is currently in fully protected areas (IUCN categories I and II), based on the World Database of Protected Areas [19]. Partially protected areas are also underrepresented, with 0.4% in the 1% consensus area.

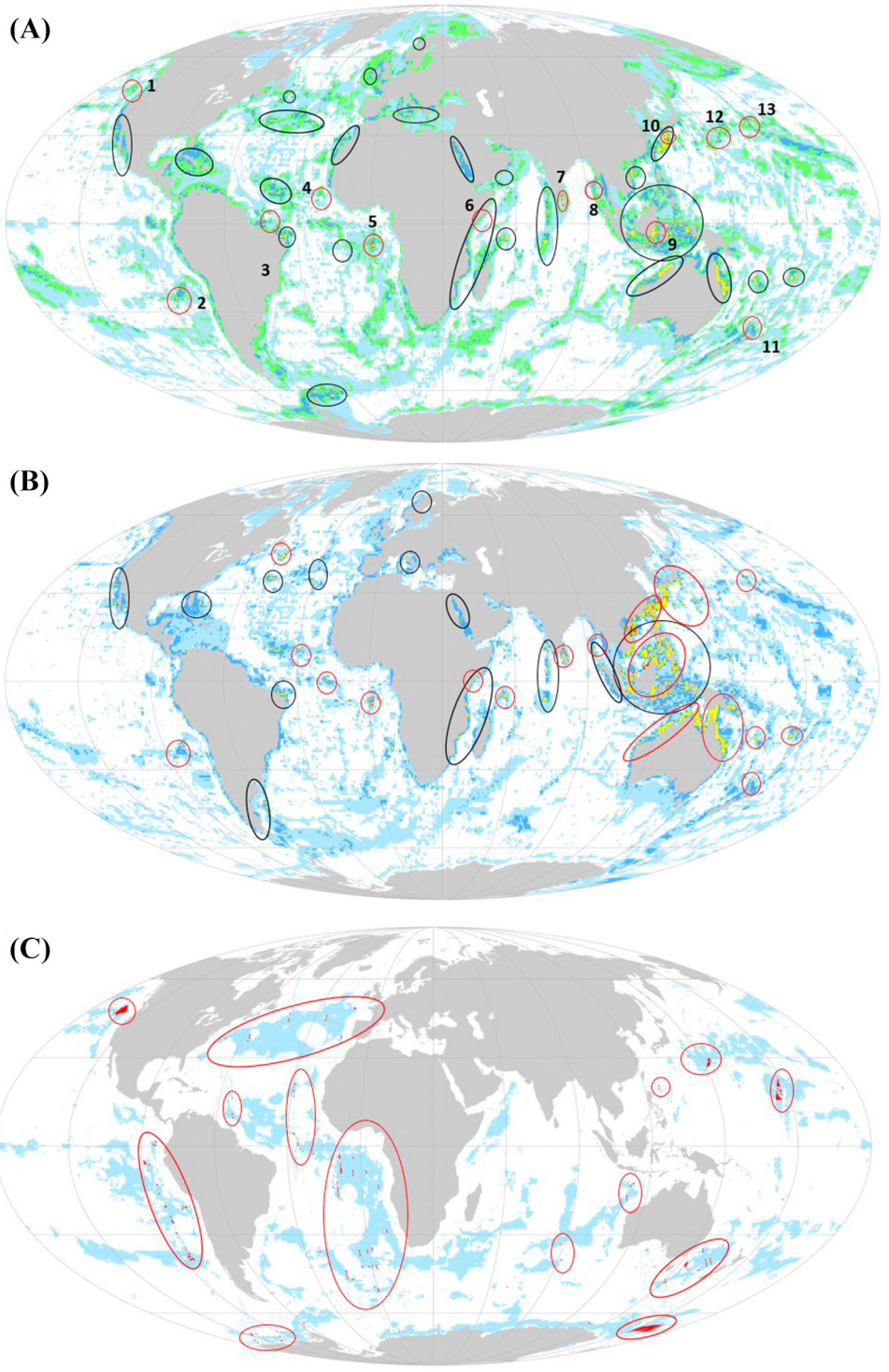

Figure 1. The areas prioritised for conservation. (A) The areas covered by six prioritisations for marine biodiversity at a global scale, namely by data-driven priority analysis (Table 1) and expert opinion [40]. Areas covered by five or more of the six

(Figure legend continued at the bottom of the next page.)

Biodiversity included in percentage area targets

Instead of focusing on a simple area target, systematic conservation planning can estimate how many species and other measures of biodiversity can theoretically be included with increasing area. Although the available studies (Table 1) did not provide such relationships, we have the data to show the relationships for one (Figure 2). This example indicates that all major marine biomes and species could be included in half the ocean area and between 70% and 90% respectively, in 30%, ~60% in 20%, and ~40% in 10% (Figure 2). Thus, the biggest gain is possible in the smallest area, assuming that that area is selected to be optimal.

The limitations of species range maps and prioritisations include that the occurrence of a species at local scales depends on the presence of suitable habitat conditions, and we do not know how large an area most species need to survive (see Outstanding questions). Thus, local field studies are essential for conservation management, and species in danger of extinction need species-tailored conservation measures.

The current selection of places recommended by present efforts to protect biodiversity is not optimal from a global perspective. For example, about 53% of present MPA and 82% of CBD-documented EBSA do not fall within the optimal 30% area mapped by Zhao *et al.* [10] (Figure S6 in the supplemental information online). This reflects the regional *ad hoc* selection of EBSA that do not use systematic conservation planning, although they identify local data that support their potential importance for biodiversity. However, this coverage is changing as new MPA are designated.

High Seas

Alternative prioritisations can be selected using different combinations of areas. For example, closing the High Seas to fisheries would protect 61% of the ocean and has been calculated to increase yields and profits of fisheries through spillover into adjacent countries' Exclusive Economic Zones (EEZ) and to reduce fishing costs [20,21]. The High Seas contribute just 4% or less of total marine fisheries [16,22], and half of these may be profitable only because of government subsidies [23]. Thus, the closure of the High Seas to fisheries would save governments having to subsidise them and have negligible effects on the global fishery catch. The evidence from fully protected (no fishing) MPA shows that the spillover effects can more than compensate for any fishery displacement [24–27].

Although most marine biodiversity, including the marine biomes, are concentrated in coastal zones, a significant proportion occurs in the High Seas, partly because of their large area (Figure 1A,C and Figures S1–S6 in the supplemental information online). The Zhao *et al.* [10] top 30% area for ocean biodiversity, called Representative Biodiversity Areas (RBAs) because they included species richness, endemicity, biomes, habitats and ecosystems, contained 90% of species across biogeographic realms, and of this, 42% was in High Seas and 58% in EEZs. Should all the High Seas be protected, then the area of EEZs that would need to be protected would fall from 58% to 7% of the RBAs.

prioritisation studies are circled in red, and by four (yellow areas) are circled in black. The most prioritised areas were (1) seamounts in Northeast Pacific, (2) San Juan Bautista Island, (3) São Luís offshore, (4) the middle of the Mid-Atlantic Ridge, (5) seamounts between Saint Helena and São Tomé e Príncipe, (6) offshore Kenya and Tanzania, (7) West Sri Lanka, (8) Andaman Islands, (9) East Borneo (and Coral Triangle), (10) the Ryukyu Islands, (11) Cape Reinga (northernmost New Zealand), and (12) and (13) seamounts in the north mid-Pacific. (B) The 'consensus' areas covered by three or four data-driven prioritisations for marine biodiversity on global oceans (Table 1). The areas covered by four prioritisations in (B) and by two in (A) are circled in red, and the ones covered by three in (B) are circled in black. The 1% consensus area is the sum of the black and red circled areas. (C) The areas covered by two data-driven prioritisations for marine biodiversity on High Seas only (Table 1). The areas overlapped by both prioritisations are in red and their region circled.

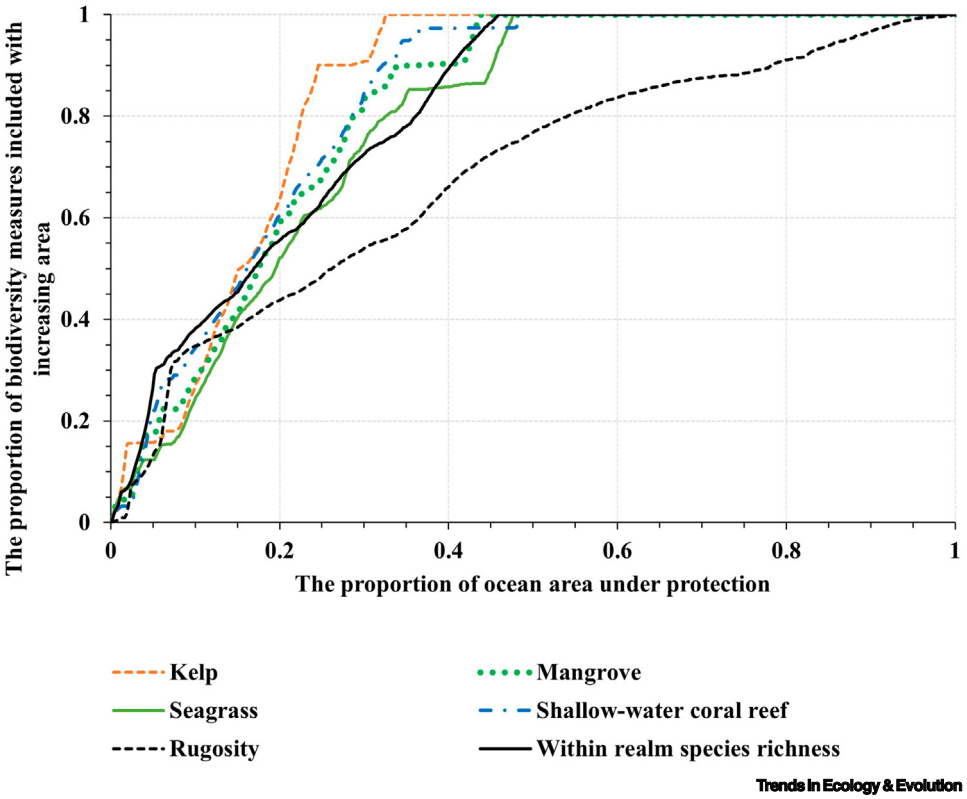

Figure 2. An example of how choosing the optimal areas using systematic conservation planning can include an increasing number of species; area of kelp, seagrass, mangrove and shallow coral reef biomes; and topographic habitat diversity (rugosity) with ocean area. This suggests that 100% of biological variables could be included in half and 70–90% in one-third of the ocean area (data from [10]).

This full protection of the High Seas combined with 7% of EEZs may be a more politically manageable way to achieve conservation of marine biodiversity, because its inclusion of biodiversity would be the same as 30% of the area globally but with less conflict with the many coastal resource users [16]. The High Seas Agreement under the United Nations Convention on the Law of the Sea (UNCLOS) also commits countries to protect 30% of the High Seas in MPA. It provides a new international definition of MPA that avoids ambiguity about whether protection is of biodiversity or uses of biodiversity as 'a geographically defined marine area that is designated and managed to achieve specific long-term biodiversity conservation objectives and may allow, where appropriate, sustainable use provided it is consistent with the conservation objectives … using the best available science ... with ecologically representative and well-connected networks.' Achieving this UNCLOS goal for High Seas protection will be most effective in ecological representation if it uses systematic conservation planning placed in the context of a global network based on variables representative of biodiversity from species to ecosystems.

Threatened species

Prioritisations may give extra weight to threatened species as several studies have done (Table 1). Jefferson *et al.* [28] showed that if we wanted to protect 30% of the geographic range of all 969 species listed as threatened and with range maps on the IUCN Red List, 40% of the ocean would be needed to protect biodiversity and these threatened species. This is because a threatened species does not necessarily occur where biodiversity is richest or in places of high endemicity,

and some threatened marine species, such as wide-ranging megafauna, are not a good indicator of the geographic distribution of biodiversity. Asaad *et al.* [29] found positive correlations between the geographic distribution of the richness and endemicity of species, habitats, biomes, and topographic variation in the Coral Triangle, but these variables were not correlated with the distribution of sea turtles that traveled widely but congregated at beach nesting sites. Thus, in addition to selecting the best places to protect biodiversity, highly threatened species need species-specific management measures to safeguard their populations.

Regional implementation

The expectation of the CBD and European Union is that each country would protect 30% of its EEZs, although what protection means is not clear (Box 1). However, biodiversity is not equally distributed by country and species cross national borders, some species doing so as annual migrations, others during their life cycle, and thousands are now shifting their distribution due to climate change [30–32]. A recent marine biodiversity prioritisation found from 0% to 100% of individual countries' EEZs were included in the top 30% of the global ocean prioritised [10]. Thus, protecting 30% of each EEZ, although it would be a major advance in marine conservation, cannot include as many species as protecting 30% of the ocean. Nevertheless, some protection somewhere is better than none, and systematic planning analyses can be repeated to see where else needs to be protected to provide a representative network of protected areas.

A limitation of all these global prioritisation schemes is their spatially coarse resolution (50–100-km grids; Table 1). However, given suitable data, the same process of prioritisation can be conducted at regional scales under finer spatial resolution. Regional Marine Spatial Planning is better positioned to ensure sustainable use of natural resources and conservation of biodiversity than global prioritisations. Thus, local habitat and species distribution knowledge can be used to determine MPA boundaries and management plans within the wider context of global conservation.

If spatial planning places MPA where there may be fewer conflicts with other users into so-called residual areas, it cannot optimise protection of biodiversity within protected areas. Furthermore, as with migratory birds and other mobile species on land, protected areas can help the conservation of wide-ranging species if suitably located but cannot protect all species all of the time. This means that sustainable use outside MPA needs to pay special attention to maintenance of populations of threatened species while accepting that human use will modify food webs and ecosystems (as it has on land).

At regional scales, MPA boundaries may be drawn to minimise perceived conflicts with fisheries and thus may not be the best locations to protect either biodiversity or fisheries. In part this is due to misunderstandings about the benefits of fully protected MPA to fisheries and to vested interests benefiting from business as usual. There are 46 examples of fishery benefits from MPA, 91% of which were fully protected MPA, due to spillover effects, and no evidence of a fishery loss due to an MPA anywhere [18]. These spillover effects lead to fishing effort declines around fully protected MPA due to increased catch per unit effort and more trophy fish caught by recreational fishermen [19–21]. Claims of fishery displacement and that MPA cannot work for pelagic fish are unfounded [18,33,34]. Thus, Marine Spatial Planning (MSP) that recognises areas of global conservation importance (Figure 1) can benefit both biodiversity and associated renewable natural resources [35]. Generally, coastal communities already recognise the benefits of biodiversity and will want it protected within the context of wider sustainable use. Thus, bottom-up MSP involving local communities is essential for effective MPA management and can be guided by top-down systematic conservation planning. Best practice is thus both bottom-up and top-down MSP.

Concluding remarks

The effectiveness of protecting global biodiversity will depend on how representative the areas protected are. The systematic conservation studies reviewed here (Table 1) provide the most cost-efficient places to protect all biodiversity. We recommend that the 1% of the ocean prioritised by most of the systematic conservation planning analyses should be prioritised to be fully protected from human impacts. As is already the practice for species conservation, these areas of global importance should be the highest priority for national conservation and international cooperative conservation, including in the High Seas. New data and analyses are unlikely to alter these areas of overlap between these studies. Thus, we propose these consensus areas as a top priority for fully protected MPA.

Cooperation between countries by protecting the High Seas may reduce the amount of area required for MPA within their EEZ. However, countries also need to recognise that some countries have more marine biodiversity than others, and species are already moving geographically as they adapt to climate change. Considering these globally important priority areas will enable more biodiversity to be included in MPA, thereby benefiting all countries and their natural resources into the future.

Outstanding questions

How well do species range maps predict the local occurrence of marine species?

How much area do threatened marine species need to survive?

Considering CBD targets and OECM and the need to protect biodiversity as a whole, are the IUCN categories of protected areas out of date?

Should protected areas be redefined by their impacts on wildlife rather than their management aims (i.e., have nature- rather than human-centered definitions)?

Acknowledgments

This study is a contribution to the *MPA Europe* project cofunded by Horizon Europe, grant agreement 101059988, under 'HORIZON-CL6-2021-BIODIV-01-12,' and was supported by the Fundamental Research Funds for the Central Universities (3005000/842161022) from the Ocean University of China. We thank the referees for suggestions that improved the paper.

Declaration of interests

The authors have no interests to declare.

Supplemental information

Supplemental information associated with this article can be found online https://doi.org/10.1016/j.tree.2025.05.007.

References

1. Margules, C. and Pressey, R.L. (2000) Systematic conservation planning. *Nature* 405, 243–253
2. Gownaris, N.J. *et al.* (2019) Gaps in protection of important ocean areas: a spatial meta-analysis of ten global mapping initiatives. *Front. Mar. Sci.* 6, 650
3. Appeltans, W. *et al.* (2024) Biodiversity knowledge and threats on marine life: assessing no-take zones as a refuge for marine species. In *IOC-UNESCO State of the Ocean Report (IOC Technical Series, 190)*, IOC-UNESCO
4. Normander, B. *et al.* (2021) Denmark's marine protected areas assessed according to IUCN's international definition. *Parks* 27, 69–74
5. Relano, V. and Pauly, D. (2023) The 'paper park index': evaluating Marine Protected Area effectiveness through a global study of stakeholder perceptions. *Mar. Policy* 151, 105571
6. Pike, E.P. *et al.* (2024) Ocean protection quality is lagging behind quantity: applying a scientific framework to assess real marine protected area progress against the 30 by 30 target. *Conserv. Lett.* 17, e13020
7. Aminian-Biquet, J. *et al.* (2024) Over 80% of the European Union's marine protected area only marginally regulates human activities. *One Earth* 7, 1–16
8. Selig, E.R. *et al.* (2014) Global priorities for marine biodiversity conservation. *PLoS One* 9, e82898
9. Jones, K.R. *et al.* (2020) Area requirements to safeguard Earth's marine species. *One Earth* 2, 188–196
10. Zhao, Q. *et al.* (2020) Where Marine Protected Areas would best represent 30% of ocean biodiversity. *Biol. Conserv.* 244, 108536
11. Sala, E. *et al.* (2021) Protecting the global ocean for biodiversity, food and climate. *Nature* 592, 397–402
12. Visalli, M.E. *et al.* (2020) Data-driven approach for highlighting priority areas for protection in marine areas beyond national jurisdiction. *Mar. Policy*, 103927
13. Brito-Morales, I. *et al.* (2022) Towards climate-smart, three-dimensional protected areas for biodiversity conservation in the High Seas. *Nat. Clim. Chang.* 12, 402–407
14. Jefferson, T. and Costello, M.J. (2020) Hotspots of marine biodiversity. In *Encyclopedia of the World's Biomes* (4) (Goldstein, M.I. and DellaSala, D.A., eds), pp. 586–596, Elsevier
15. Jayathilake, D.R.M. and Costello, M.J. (2020) A modelled global distribution of the kelp biome. *Biol. Conserv.* 252, 108815
16. Jayathilake, D.R.M. and Costello, M.J. (2018) A modelled global distribution of the seagrass biome. *Biol. Conserv.* 226, 120–126
17. Worthington, T.A. *et al.* (2020) A global biophysical typology of mangroves and its relevance for ecosystem structure and deforestation. *Sci. Rep.* 10, 14652
18. UNEP-WCMC *et al.* (2021) *Global Distribution of Coral Reefs, Compiled from Multiple Sources Including the Millennium Coral Reef Mapping Project*, UNEP-MCMC
19. UNEP-WCMCIUCN (2022) *Protected Planet: The World Database on Protected Areas (WDPA)*, UNEP
20. White, C. and Costello, C. (2014) Close the High Seas to fishing? *PLoS Biol.* 12, e1001826
21. Sumaila, U.R. *et al.* (2015) Winners and losers in a world where the High Seas is closed to fishing. *Sci. Rep.* 5, 8481
22. Schiller, L. *et al.* (2018) High Seas fisheries play a negligible role in addressing global food security. *Sci. Adv.* 4, eaat8351
23. Sala, E. *et al.* (2018) The economics of fishing the High Seas. *Sci. Adv.* 4, eaat2504
24. Costello, M.J. (2024) Economic benefits of MPA to fisheries and tourism. *Sci. Mar.* 88, e080

25. Franceschini, S. *et al.* (2024) A global test of MPA spillover benefits to recreational fisheries. *Sci. Adv.* 10, eado9783
26. McDonald, G. *et al.* (2024) Global expansion of marine protected areas and the redistribution of fishing effort. *Proc. Natl. Acad. Sci. U. S. A.* 121, e2400592121
27. Bode, M. *et al.* (2025) Marine reserves contribute half of the larval supply to a coral reef fishery. *Sci. Adv.* 11, eadt0216
28. Jefferson, T. *et al.* (2021) Conserving threatened marine species and biodiversity requires 40% ocean protection. *Biol. Conserv.* 264, 109368
29. Asaad, I. *et al.* (2018) Delineating priority areas for marine biodiversity conservation in the Coral Triangle. *Biol. Conserv.* 222, 198–211
30. Chaudhary, C. *et al.* (2021) Global warming is causing a pronounced dip in marine species richness at the equator. *Proc. Natl. Acad. Sci. U. S. A.* 118, e2015094118
31. Gordó-Vilaseca, C. *et al.* (2023) Three decades of increasing fish biodiversity across the north-east Atlantic and Arctic Oceans. *Proc. Natl. Acad. Sci. U. S. A.* 120, e2120869120
32. Gordó-Vilaseca, C. *et al.* (2023) Over 20% of marine fishes shifting in the North and Barents Seas, but not in the Norwegian Sea. *PeerJ* 11, e15801
33. Lynham, J. *et al.* (2020) Impact of two of the world's largest protected areas on longline fishery catch rates. *Nat. Commun.* 11, 1–9
34. Medoff, S. *et al.* (2022) Spillover benefits from the world's largest fully protected MPA. *Science* 378, 313–316
35. Costello, M.J. *et al.* (2016) Sustainable fisheries need reserves. *Nature* 540, 341
36. Costello, M.J. and Ballantine, B. (2015) Biodiversity conservation should focus on no-take Marine Reserves: 94% of Marine Protected Areas allow fishing. *Trends Ecol. Evol.* 30, 507–509
37. Edgar, G.J. *et al.* (2024) Stock assessment models overstate sustainability of the world's fisheries. *Science* 385, 860–865
38. Anon. (2023) The hypocrisy threatening the world's oceans. *Nature* 621, 7
39. Asaad, I. *et al.* (2017) Ecological criteria to identify areas for biodiversity conservation. *Biol. Conserv.* 213, 309–316
40. Olson, D.M. and Dinerstein, E. (2002) The Global 200: priority ecoregions for global conservation. *Ann. Missouri Bot. Garden* 199–224