

CONTRIBUTED PAPER

Representation of the world's biophysical conditions by the global protected area network

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Article Impact Statement

Protected areas unevenly cover the world's abiotic conditions; many conditions of climate, topography, and bathymetry lack protection.

Abstract

Protected areas (PAs) are often implemented without consideration of already existing PAs, which is likely to cause an overrepresentation of certain biophysical conditions. We assessed the representativeness of the current PA network with regard to the world's biophysical conditions to highlight which conditions are underprotected and where these conditions are located. We overlaid terrestrial and marine PAs with information on biophysical conditions (e.g., temperature, precipitation, and elevation) and then quantified the percentage of area covered by the PA network. For 1 variable at a time in the terrestrial realm, high temperature, low precipitation, and medium and very high elevation were underrepresented. For the marine realm, low and medium sea surface temperature (SST), medium and high sea surface salinity (SSS), and the deep sea were underrepresented. Overall, protection was evenly distributed for elevation across the terrestrial realm and SST across the marine realm. For 2 variables at a time, cold and very dry terrestrial environments had mostly low protection, which was also the case for low SST and low and medium SSS across most depths for marine environments. Low protection occurred mostly in the Sahara and the Arabian Peninsula for the terrestrial realm and along the Tropic of Capricorn and toward the poles for the marine realm. Although biodiversity measures are of prime importance for the design of PA networks, highlighting biophysical gaps in current PAs adds a frequently overlooked perspective. These gaps may weaken the potential of PAs to conserve biodiversity. Thus, our results may provide useful insights for researchers, practitioners, and policy makers to establish a more comprehensive global PA network.

KEYWORDS

abiotic conditions, bathymetry, elevation, marine, precipitation, salinity, temperature, terrestrial

Resumen

Las áreas protegidas (AP) son frecuentemente implementadas sin considerar las ya existentes, lo que probablemente ocasiona una sobrerrepresentación de ciertas condiciones biofísicas. Analizamos la representatividad de la red actual de AP con respecto a las condiciones biofísicas del mundo para resaltar que condiciones están subprotegidas y en dónde se encuentran localizadas. Superpusimos las AP terrestres y marinas con la información sobre las condiciones biofísicas (p. ej.: temperatura, precipitación y elevación) y luego cuantificamos el porcentaje de área cubierta por la red de AP. Para el análisis de una variable a la vez, en el ámbito terrestre, la alta temperatura, baja precipitación y las elevaciones media y muy alta estuvieron subrepresentadas. Para el ámbito marino, la baja y media temperatura de la superficie marina (TSM), la media y alta salinidad de la superficie marina (SSM) y el mar profundo estuvieron subrepresentados. En general, la protección para la elevación en

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el ámbito terrestre y para la TSM en el ámbito marino se distribuyó uniformemente. Para el análisis de dos variables a la vez, los ambientes terrestres fríos y muy secos tuvieron en su mayoría una baja protección, lo que también ocurrió para la baía TSM y la baja y media SSM en casi todas las profundidades de los entornos marinos. La baja protección para el ámbito terrestre estuvo presente en su mayoría en el Sahara y en la Península Arábiga, y en el ámbito marino, a lo largo del Trópico de Cáncer y hacia los polos. Aunque las medidas de biodiversidad son de suma importancia para el diseño de las redes de AP, resaltar los vacíos de información biofísica en las actuales AP añade una perspectiva que con frecuencia se ignora. Estos vacíos pueden debilitar el potencial que tienen las AP para conservar la biodiversidad. Por lo tanto, nuestros resultados pueden proporcionar información útil para que investigadores, profesionales y tomadores de decisiones establezcan una red mundial de AP más completa.

PALABRAS CLAVE:

batimetría, condiciones abióticas, elevación, marino, precipitación, salinidad, temperatura, terrestre

摘要

保护区 (Pas) 的建立通常没有考虑已有的保护区, 这可能导致某些生物物理条件出现的比例过高。本研究评估了当前的保护区网络对全球生物物理条件的代表性, 以突出哪些条件受到的保护不足, 并描述了它们的分布情况。我们将陆地和海洋保护区与生物物理条件(如温度、降水、海拔)的信息叠加, 量化了这些条件被保护区网络覆盖的面积比例。结果显示, 在陆地范围的单个变量中, 保护区网络对高温、低降水量、中等和极高海拔的代表性不足。在海洋范围内, 保护区网络对中低海表温度 (SST)、中高海表盐度 (SSS) 和深海的代表性不足。总体来看, 不同海拔的陆地和不同海表温度的海洋都得到了保护区的均匀覆盖。当同时考虑两个变量时, 我们发现寒冷和极度干燥的陆地环境的保护程度大多较低, 而海洋大部分深度的低海表温度和中低海表盐度的环境也是如此。保护程度低的区域主要分布在撒哈拉沙漠和阿拉伯半岛的陆地领域, 以及沿南回归线和靠近两极的海洋领域。尽管生物多样性指标在保护区网络设计中至关重要, 但强调当前保护区中的生物物理空缺引入了一个经常被忽视的视角。这些空缺可能会削弱保护区保护生物多样性的潜力。因此, 我们的研究结果可以为研究者、实践者和决策者建立更全面的全球保护区网络提供有用的见解。【翻译: 胡怡思; 审校: 聂永刚】

关键词: 温度, 降水, 盐度, 海拔, 海洋测深, 海洋, 陆地, 非生物条件

INTRODUCTION

Anthropogenic impacts on biodiversity often vary between land and ocean as well as geographically, thus requiring different conservation priorities for mitigation (Bowler et al., 2020). Protected areas (PAs) are the most effective tool for in situ conservation (Chape et al., 2005) and are crucial for reducing habitat loss (Geldmann et al., 2013), protecting endangered species (Pacifi et al., 2020), safeguarding biodiversity, and conserving ecosystem services (Stolton & Dudley, 2010).

The global PA network has been growing steadily in number and extent, which confirms government commitments to the conservation of natural ecosystems. To improve the status of biodiversity, the Aichi Biodiversity Target 11 was set to protect at least 17% of terrestrial and inland water and 10% of coastal and marine areas by 2020 (CBD, 2011). As of February 2021, around 15.4% of terrestrial areas and inland waters, 17.8% of coastal and marine areas within national jurisdiction,

and 1.2% of the global ocean (areas beyond national jurisdiction) were covered by PAs (UNEP-WCMC et al. 2021). The target calls for the PA network to be ecologically representative (CBD, 2011), and a focus on representativeness of ecoregions is recommended. Although this will likely enhance coverage of geographically distinct species assemblages, it is not necessarily equal to the representativeness of species or other biological properties (Visconti et al., 2019). Various strategies, aiming to enhance the ecological representativeness of PAs, have been developed, ranging from coverage of genetic traits (Pollock et al., 2017), groups of individual species (i.e., species of conservation concern; Venter et al., 2018), or mountain biodiversity (Rodríguez-Rodríguez et al., 2011) to wider aspects, including the maintenance of phylogenetic (Rosauer et al., 2017), functional (Guilhaumon et al. 2015), and geodiversity (Tukiainen et al., 2017) as well as ecosystem functions (Harvey et al., 2017) and services (Eastwood et al., 2016).

Accounting for future direct and indirect impacts of climate change is also becoming increasingly important in conservation planning, and various spatial prioritization approaches incorporating potential impacts have been developed (Jones et al., 2016; Maxwell et al., 2020). With regard to climate change, establishing a PA network that will be ecologically representative in the future is difficult, whereas protecting a representative set of current abiotic conditions is likely to provide the required diversity of environments to support the maintenance and establishment of biodiversity under future climatic conditions (Ackerly et al., 2010; Anderson & Ferree, 2010; Lawler et al., 2015). It further allows forecasting of representativeness in the face of future climate change (Elsen et al., 2020).

Given that nature is often considered as a continuous gradient of biophysical conditions, rather than a set of discrete units (from vegetation types to realms), evaluating the representativeness of nature in PA networks based on biophysical gradients may be a promising approach. The representation of climatic and topographic conditions across terrestrial protected areas (TPAs) has been assessed at various spatial scales, from local to global (e.g., Batllori et al., 2014; Elsen et al., 2018; Rouget et al., 2003). Baldi et al. (2017, 2019) included the representation of human and biological factors, whereas Sayre et al. (2020) assessed the representation of terrestrial ecosystems. The representation of biophysical conditions across marine protected areas (MPAs) has been less studied (but see Devillers et al. [2015] and Roberts et al. [2019]). To our knowledge, no one has examined the biophysical representativeness of MPAs at a global level.

We aimed to assess the protection coverage of the different biophysical conditions globally and compare the current level of protection between the marine and terrestrial realm. Thus, we assessed the global protection of terrestrial and marine areas with respect to biophysical factors: temperature, precipitation, topography, sea surface temperature (SST), sea surface salinity (SSS), and bathymetry. We analyzed the protection coverage of each individual biophysical factor across their respective conditions and compared how the coverage of biophysical conditions differed among protection categories, because PAs with a low protection (e.g., IUCN categories IV–VI) have only limited restrictions on resource exploitation (Shafer, 2015). We specifically tested how evenly the biophysical factors were covered by PAs and highlighted under which conditions protection coverage was lower or higher than expected. Given that biophysical variables often interact strongly, we also analyzed the protection coverage of the pairwise interaction of biophysical conditions and, to provide recommendations for the establishment of future PAs, considered how protection coverage of individual biophysical factors and their pairwise combinations were distributed geographically.

METHODS

To evaluate the global protection coverage of biophysical conditions among the terrestrial and marine realm, we combined the

global PA and the biophysical data in a common grid which we used to perform our analysis.

Protected areas

Global PA data were derived from the World Database on Protected Areas (UNEP-WCMC & IUCN, 2020) and contained polygon data for 225,098 PAs (208,796 terrestrial, 10,724 coastal, 5578 marine). We excluded PAs for which only point information was available (21,250 PAs) because these only provide information on their overall spatial position and areal coverage, not on their exact spatial extent. The PA data were split into marine (coastal and marine) and terrestrial (coastal and terrestrial) PAs and then further divided into 4 IUCN protection categories: Ia, Ib, and II (I–II); III and IV (III–IV); V and VI (V–VI); and not reported, not applicable, and not assigned (Non-designated).

These categories group PAs according to their management objectives. Categories Ia, Ib, and II include strict nature reserves, wilderness areas, and national parks and focus on the protection of intact ecosystems (Dudley, 2008). Categories III and IV include natural monuments or features and habitat or species management areas, and categories V–VI include protected land- and seascapes and PAs with sustainable use of natural resources.

For each protection category, we calculated the percentage of protection cover for each grid cell of a raster with 30 arc seconds resolution and a spatial extent corresponding to the extent of the respective biophysical data (Figure 1a). This resulted in a gridded layer of percentage protection cover for each protection category for marine and terrestrial areas. These layers were transformed into Mollweide equal-area projection (ESRI:54009) and covered 162,067,794 and 421,197,812 cells for terrestrial and marine areas, respectively (Appendix S1).

We also calculated the percentage of protection cover for all categories combined (total percentage protection) to determine where PAs of different designation types overlapped (Deguignet et al., 2017). Total percentage protection was then used to adjust cells of overlapping extents (cells where the sum of the area protected of the individual protection category layers was larger than the total area protected): we added the area protected by each protection category, starting with the strictest protection category, until the sum of the individual areas reached the total area protected. This resulted in a nonoverlapping data set, always keeping the strictest protection category in areas with overlapping polygons. This was necessary because if overlapping PAs were not resolved, the underlying biophysical space would be counted multiple times when calculating the total percentage protection.

Terrestrial data

Annual mean temperature and annual precipitation were obtained from Worldclim 2 (Fick & Hijmans, 2017), which

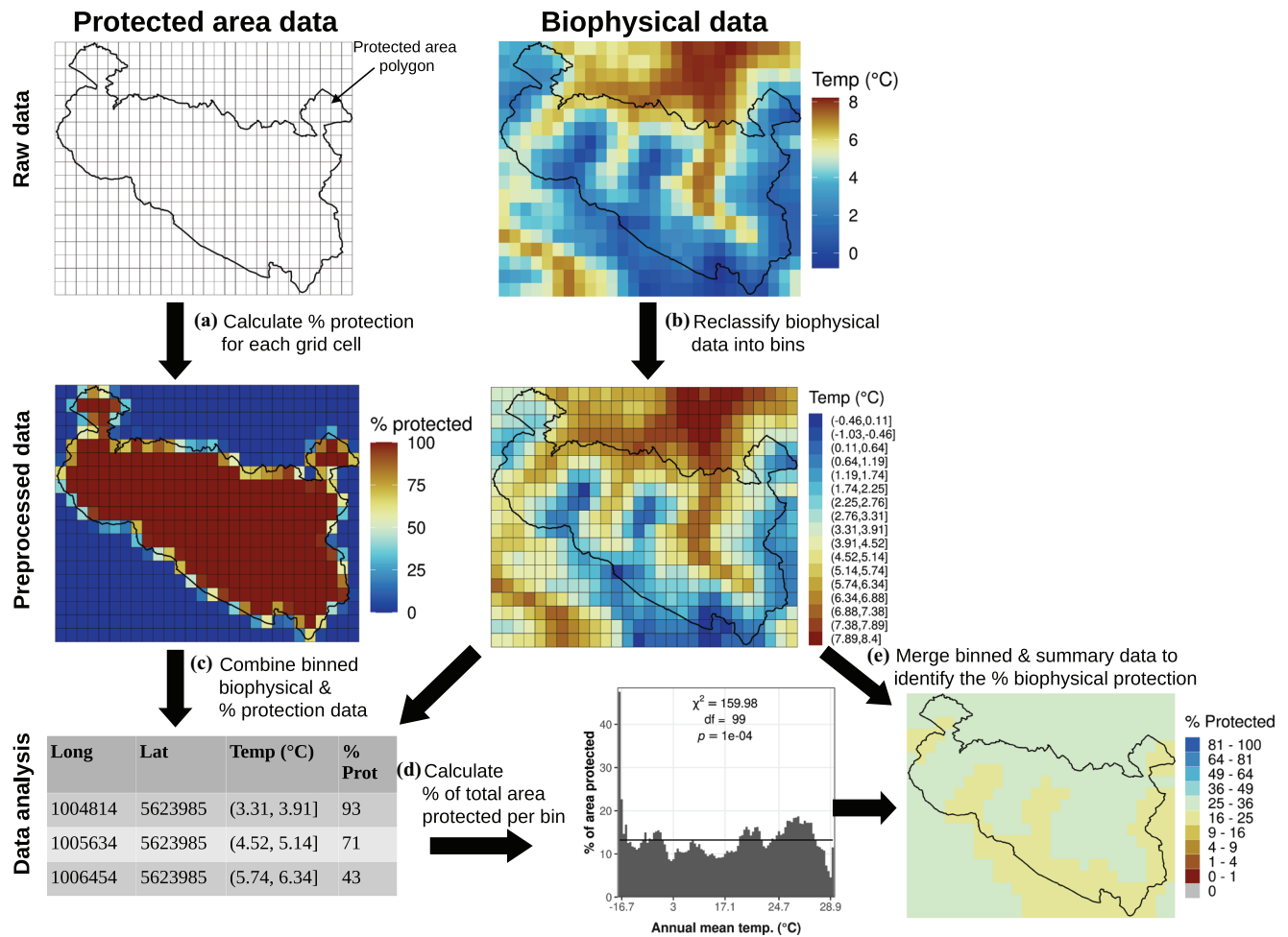


FIGURE 1 Methodological approach used to identify the protection coverage of the different conditions for each biophysical variable: (a) calculation of percentage of protection for each grid cell, (b) reclassification of data for each biophysical variable into bins observed with equal frequency, (c) merging of binned environmental and gridded percentage of protection data, (d) summarization of merged data by calculating percentage of total area protected per bin, and (e) merging of summary data with the geographic locations of each bin to identify the protection coverage of each grid cell for a particular biophysical variable

compiled climatic information from 1970 to 2000 at a resolution of 30 arc seconds. We chose these 2 variables because they are the main determinants of the world's terrestrial biomes (Holdridge, 1947; Whittaker, 1975). We also examined temperature and precipitation seasonality and temperature annual range, which we also obtained from Worldclim 2 (Appendix S3). Worldclim 2 interpolates observations from weather stations based on elevation and distance to coast and maximum and minimum land surface temperature and cloud cover derived from MODIS satellite data (Fick & Hijmans, 2017).

Elevation data were obtained from EarthEnv (Amatulli et al., 2018). These data are based on the global 250-m GMTED2010 digital elevation model output and averaged into a 30 arc seconds grid (Amatulli et al., 2018). We used elevation because it is a strong explanatory variable for species richness (Kaufman & Willig, 1998). The EarthEnv data set does not include latitudes above 84°N and below -56°S, so we excluded these areas from terrestrial analyses. Worldclim and EarthEnv layers were

transformed into Mollweide equal area projection (ESRI:54009; Appendix S2).

Marine data

Mean annual SST, mean annual SSS, and bathymetry were obtained from MARSPEC (Sbrocco & Barber, 2013). This high-resolution global marine data set is a 10-fold improvement in spatial resolution over Bio-ORACLE (Tyberghein et al., 2012). It combines different satellite and in situ observations of SST, SSS, and bathymetry of the global ocean into a harmonized data set at a spatial resolution of 30 arc seconds. Bathymetry data were derived from SRTM30_PLUS 6.0, and the climatic layers were derived from the World Ocean Atlas (SSS) and Ocean Color Web (SST). The climatic variables range over varying time periods (SSS = 1955–2006, SST = 2002–2010), but information about interannual means and their variance is provided (Sbrocco

& Barber, 2013). We also analyzed annual range and annual variance in SSS and SST, which were also obtained from MARSPEC (Appendix S3). All marine layers were transformed into Mollweide equal area projection (ESRI:54009; Appendix S2).

Protection coverage

We divided the amplitude of each biophysical variable into bins observed with equal frequency. The respective optimal number of bins ($n \leq 100$) was identified using the bins function of the binr package (Izrailev, 2015) in R (R Core Team, 2020). For most variables, the maximum number of bins ($n = 100$) was reached. Some strongly skewed variables resulted in a much smaller number of bins. For each variable, we combined the binned biophysical layer with the different percentage-of-protection layers and summarized them into the overall percentage of each bin protected (hereafter protection coverage) (Figure 1c,d).

An expected value of protection for each bin was calculated by dividing the total global terrestrial and marine area protected equally among the area covered by each bin. This represents a world where all conditions of a biophysical variable were evenly protected. For each individual variable, we compared the protection coverage with the expected value of protection for each bin and assessed the evenness in the distribution (by comparing it with the expected value) with a chi-square goodness-of-fit test. The chi-square value denoted the sum of error values. A high value indicated a large deviance between observed and expected values and thus implied a low evenness in distribution.

Given that using bins observed with equal frequency puts a stronger emphasis on a small range of conditions (i.e., SSS 34–35.4 PSU), we also assessed the protection coverage across each variable with equally spaced bins (1°, 100 mm, 100 m, and 1 PSU for temperature and SST, precipitation, elevation and bathymetry, and SSS, respectively [Appendix S4]). Although this puts the focus on discrete biophysical conditions, it specifically highlights conditions that might be rare on a global level; thus, it is not meaningful for assessing the biophysical representativeness of the global PA network.

To examine the protection interaction across multiple variables, we used the same procedure for each pairwise combination of all terrestrial and all marine variables separately.

To derive a map of protection coverage for each variable and their respective pairwise combinations, which indicates how well the underlying environmental condition of a given location is protected globally, we combined the binned data with the protection coverage of each individual bin and each pairwise combination (Figure 1e). We summarized the derived maps into the area covered by each zoogeographic and marine realm (Appendix S3).

All analyses were performed in R 4.0 (R Core Team, 2020). Among others, we used R packages specifically designed for handling large spatial data: sf (Pebesma, 2018), fasterize (Ross, 2020), exactextractr (Baston, 2020), and terra (Hijmans, 2020) and high-performance computers. The full code is publicly available from <https://github.com/RS-eco/globePA/>.

RESULTS

Overall coverage

For the terrestrial realm, mostly very high (≥ 27 °C) and low to intermediate (0.6–20 °C) temperature conditions were underprotected (Figure 2a). Low (≤ 151 mm), intermediate (270–571 mm), and some high (1074–1610 mm) annual precipitation conditions were underprotected (Figure 2b), as were elevational conditions from 92 to 407 m, 452 to 729 m, and above 3944 m (Figure 2c). The observed distribution of temperature and precipitation significantly differed from the expected distribution ($p \leq 0.05$) (Figure 2a–c). Toward their upper range, all additional terrestrial variables were underrepresented. Only temperature annual range differed significantly from the expected distribution ($p \leq 0.05$) (Appendix S3). When we considered only PAs with category I–II (strict protection), only annual mean temperature and precipitation differed significantly from the expected distribution ($p \leq 0.05$). For category III–IV, all variables were evenly distributed (Appendix S3). Considering the protection coverage across equally spaced bins, rare conditions, in particular low temperature and high elevation, usually had a higher protection coverage than common ones (Appendix S4).

For the marine realm, particularly low and medium SST were underprotected (Figure 2d). Intermediate (32.7–34.9 PSU) and high (≥ 36 PSU) SSS conditions were underprotected (Figure 2e), as was most of the deep sea (–3634 to 5999 m), in stark contrast to intermediate and very shallow depths and depths below 6000 m (Figure 2f). For the marine realm, SSS and bathymetry showed a significant difference ($p \leq 0.05$) in goodness of fit between the expected and observed distribution, but the contribution of the protection category varied strongly across conditions, at least for SST and SSS (Figure 2d–f). Variance and annual range in SST were underprotected for distinct lower and upper conditions, whereas almost all conditions in annual range and annual variance in SSS were underprotected. Only annual variance in SST differed significantly from the expected distribution ($p \leq 0.05$) (Appendix S3). For bathymetry, annual range in SST, and all SSS variables, the protection coverage was evenly distributed across all protection categories, whereas mean annual and annual variance in SST differed significantly from the expected distribution ($p \leq 0.05$) for categories III–IV and Non-designated (Appendix S3). For equally spaced bins, rare conditions, specifically low SSS and very deep conditions, usually had higher protection coverage than more common ones (Appendix S4).

Interaction coverage

For temperature and precipitation pairwise interactions, primarily conditions at the lower temperature and upper precipitation limit had a high protection coverage, whereas conditions that were either at the upper temperature limit or at the lower precipitation limit tended to be only marginally protected.

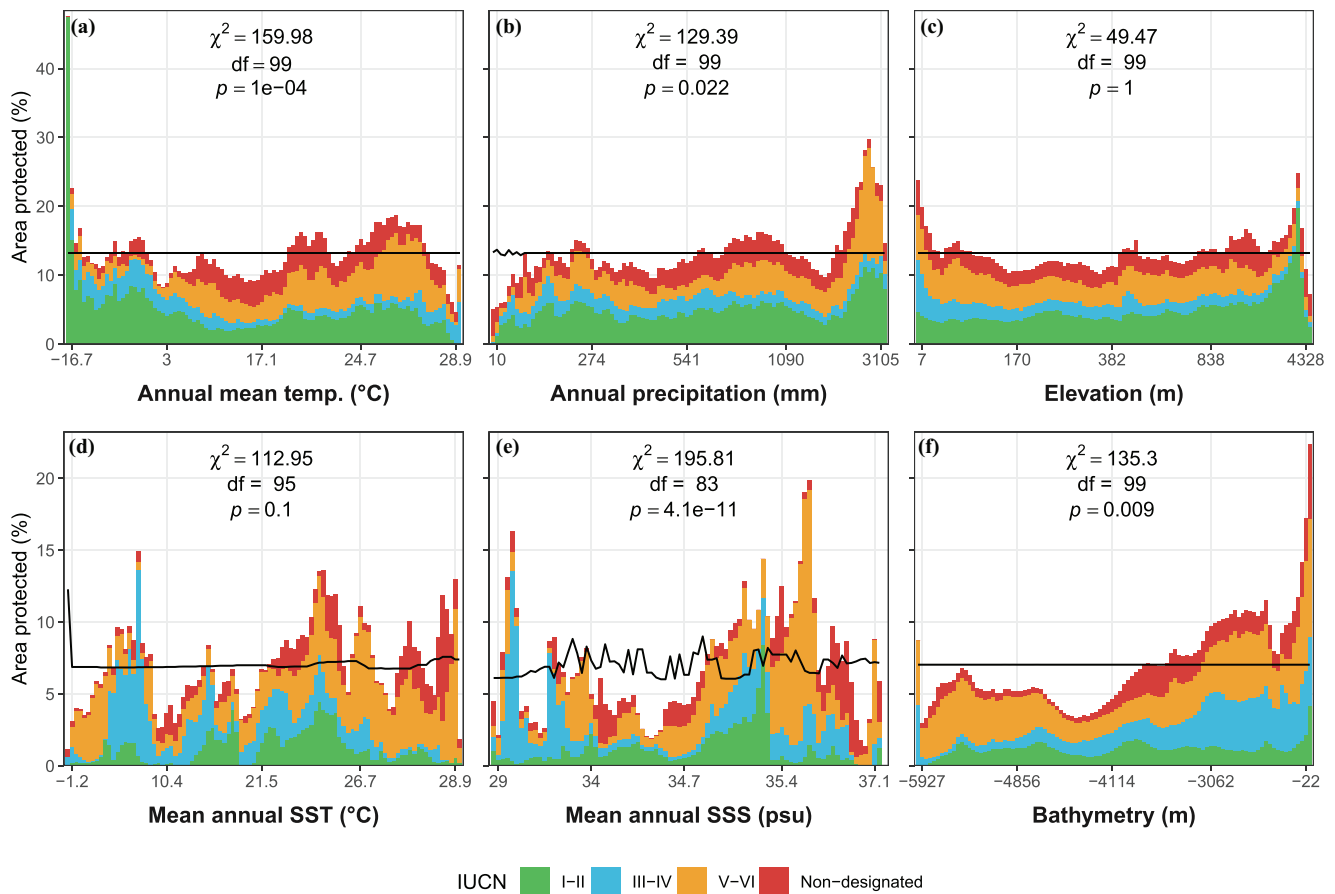


FIGURE 2 Percentage area protected (Figure 1d) divided by the different International Union for Conservation of Nature categories across biophysical conditions for different variables in the terrestrial ([a] temperature, [b] precipitation, and [c] elevation) and marine ([d] sea surface temperature [SST], [e] sea surface salinity [SSS], and [f] bathymetry) realms. To calculate the percentage area protected, the different biophysical conditions were divided into bins observed with equal frequency. The optimal number of bins ($n \leq 100$) was derived iteratively for each variable: (a) $n = 100$, (b) $n = 100$, (c) $n = 100$, (d) $n = 96$, (e) $n = 84$, and (f) $n = 100$. Black lines indicate the expected percentage area protected given equal protection of all conditions. For some variables, this line is not flat because the underlying data are strongly skewed, so no bins observed with absolute equal frequency could be calculated. Individual bins of each variable represent percentile ranges and so cover a different extent, which is also reflected in the irregular intervals of the x-axis. See Appendix S4 for a similar figure based on equally spaced bins

There were discrete conditions with very low temperatures and low and high precipitation that were completely unprotected (Figure 3a). For the temperature and elevation interaction, areas with low temperature and low elevation were very strongly protected, whereas mostly very high temperature and high elevation conditions were only marginally protected (Figure 3b). For precipitation and elevation, the majority of the upper precipitation limits had high protection coverage across all elevational bands, whereas conditions with low precipitation and very high elevation were either marginally protected or completely unprotected (Figure 3c). Overall, the combination of temperature and elevation was best protected (largest area with high protection), whereas the combination of temperature and precipitation had the largest area with low protection (Figure 3d).

For the marine realm, patterns were less clear. Most SSS and SST conditions were only marginally or completely unprotected. A few well-protected conditions occurred most frequently at high SSS across various SST conditions (Figure 3e).

For bathymetry and SST (Figure 3f) and bathymetry and SSS (Figure 3g), very well-protected conditions occurred mostly at very shallow depths (0–46 m) across all SSS and SST conditions (Figure 3f,g), in depths deeper than 5755 m with very low (around 0 °C) SST (Figure 3f) and at SSS conditions of 32–32.5 and 35.4–35.7 PSU across most depths (Figure 3g). Low and no protection occurred mostly with low SST (around 10 °C) across various depths (Figure 3f) and very low (around 20 PSU) and medium (around 34.5 PSU) SSS across various depths (Figure 3g). For the marine realm, the combination of SST and SSS showed the largest area with low protection, and all pairwise combinations had a considerable area with unprotected conditions (Figure 3h).

Spatial patterns

Sixty-eight percent of the terrestrial realm had temperature conditions that were protected by 10–16%. Greenland

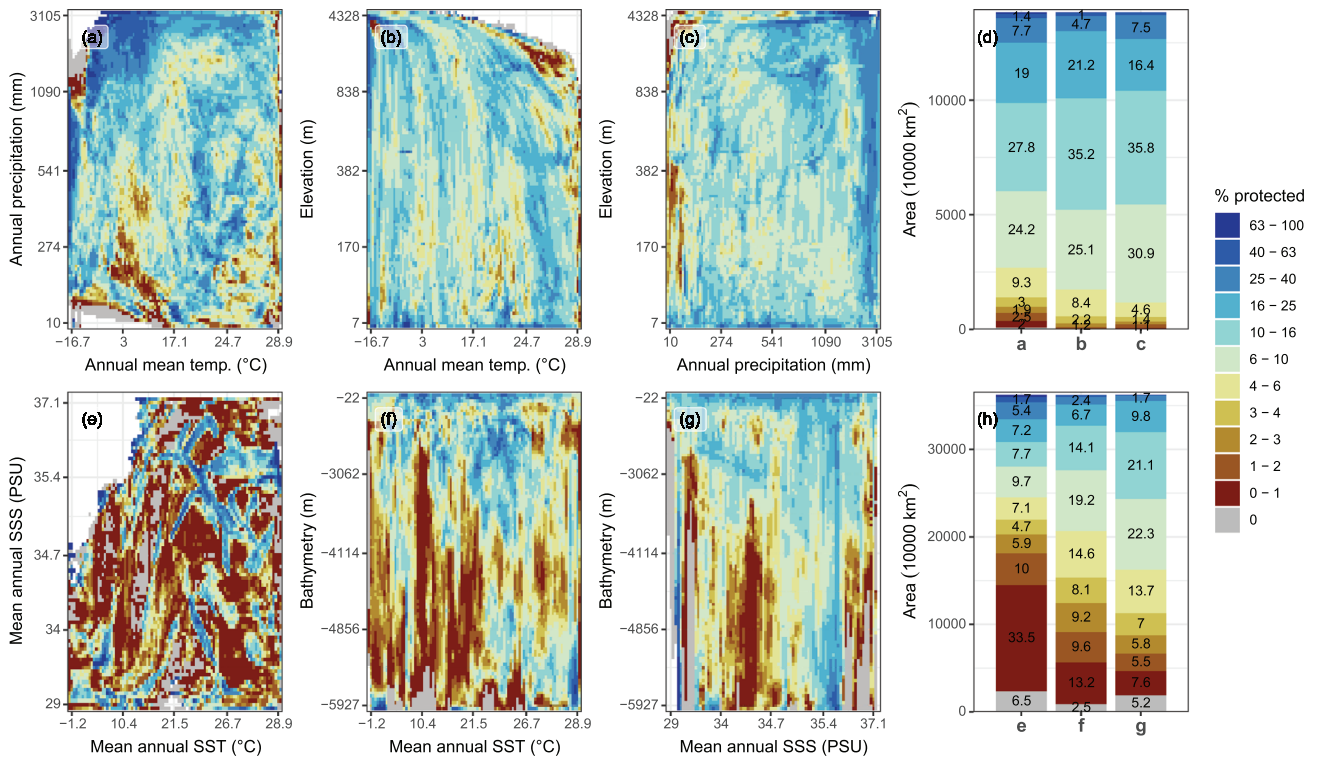


FIGURE 3 Percentage of land area (a, b, c) and marine area (d, e, f) protected by each pairwise combination of the biophysical variables considered (temperature vs. precipitation, temperature vs. elevation, and precipitation vs. elevation; sea surface temperature [SST] vs. sea surface salinity [SSS], SST vs. bathymetry, and SSS vs. bathymetry). Pixels are based on the bins observed with equal frequency shown in Figure 2 (see Appendix S4 for a similar figure based on equally spaced bins). Total area covered by certain levels of protection (d, h). The percent area protected was calculated considering all International Union for Conservation of Nature protection categories (I–II, III–IV, V–VI, and Non-designated) together. Because percentage of area protected is not normally distributed, the color key is divided into 10 intervals reflecting a log₁₀-transformed continuous scale

exhibited unique temperature conditions that had high protection, whereas large parts of the Sahara and the Arabian Peninsula exhibited temperatures that were only marginally protected (Figure 4a). Around 77% of the terrestrial realm had precipitation levels that were protected by 10–16% and 9% that were protected by 16–25%. The northern part of South America (mostly Colombia, Peru, Bolivia, and Brazil), some tropical regions in West Africa, and parts of Indonesia and China (mostly Himalayans) had precipitation levels with high protection (Figure 4b). Eighty-nine percent of the terrestrial realm had elevational bands that were protected by 10–16% and 9.9% that were protected by 16–25%. Elevational conditions with high protection were located mostly in Greenland and China (Figure 4c). For the spatial overlap of different terrestrial variables, we found that unique combinations of temperature and precipitation that were protected by ≤16% occurred all over the world, covering about 71% of the terrestrial realm (Figure 3d). Areas with low protection were mostly located in the western United States, large parts of the Sahara, the Arabian Peninsula, and parts of Central Asia (Figure 4d). Unique combinations of temperature and elevation that were protected by ≤16% covered around 73% of the terrestrial realm (Figure 3d). Areas where the combination of temperature and elevation conditions was highly protected occurred mostly in Greenland and parts of South America and Russia and China, whereas areas that were little pro-

ected occurred mostly in the western Sahara and the Arabian Peninsula, but also across Argentina, Australia, Russia, and the United States (Figure 4e). Areas that were protected by ≤16% of unique combinations of precipitation and elevation conditions covered 75% of the terrestrial realm (Figure 3d). Locations with low protection of this combination were in Chile, parts of the Sahara, the Arabian Peninsula, and China, whereas locations with highly protected conditions covered large parts of northern South America, eastern Africa, Indonesia, New Guinea, the Himalayan Mountains, and Greenland (Figure 4f). Overall, protection coverage strongly differed among zoogeographic realms and the variable or variable combination considered (Appendix S3).

Forty-three percent of marine areas had SST conditions that were protected by 1–6% and 57% that were protected by 6–16% (Figure 5a). Forty-six percent of marine areas had SSS conditions that were protected by 1–6% and 54% that were protected by 6–25% (Figure 5b). Forty-nine percent of marine areas had a depth level that was protected by 2–6% and 33% that was protected by 6–10% (Figure 5c). The SST conditions had relatively high levels of protection in the Tropic of Cancer, Tropic of Capricorn, the Arctic, and Antarctic Circle (Figure 5a), whereas areas with low protection were mostly at the poles and east of New Guinea. SSS was well-protected along the west coast of the United States and Canada and the east coast of

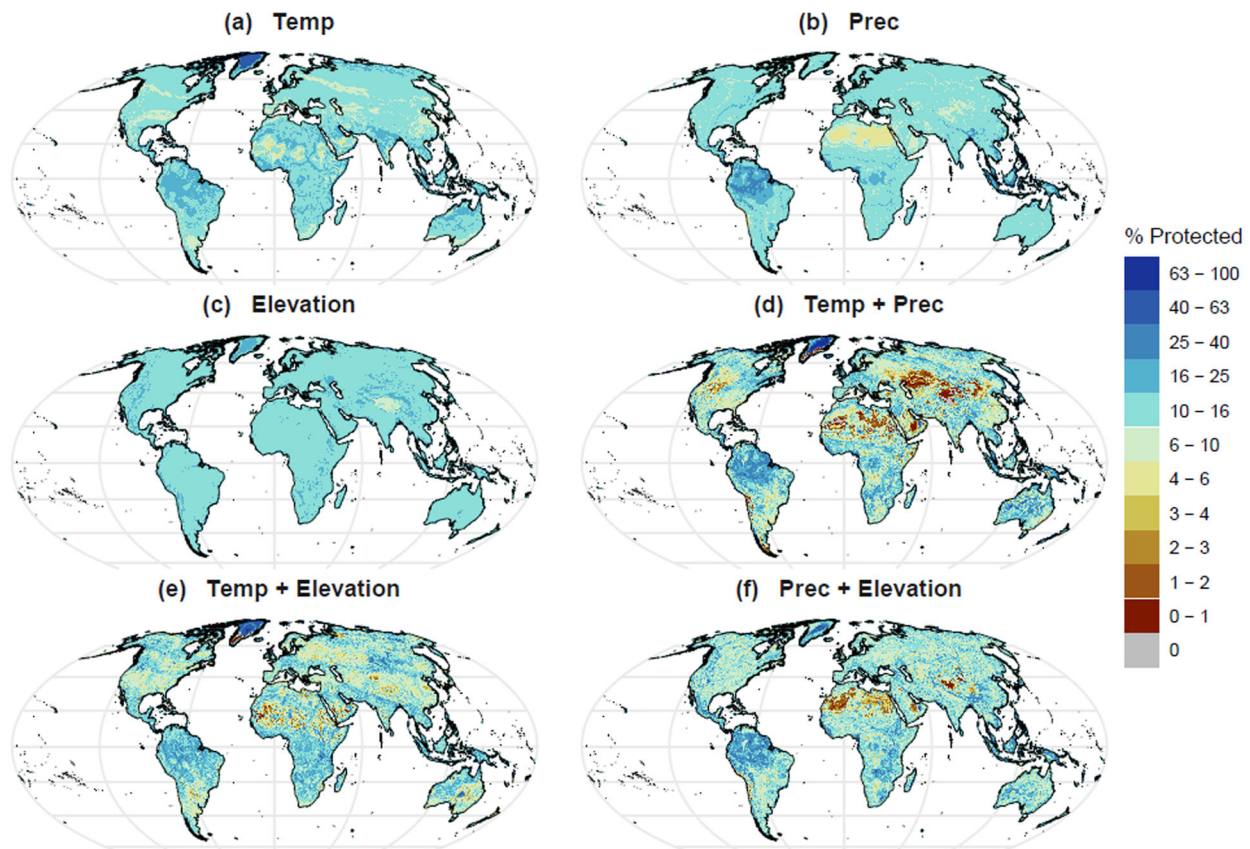


FIGURE 4 Percentage of the terrestrial realm protected by each biophysical condition—(a) temperature (Temp), (b) precipitation (Prec), and (c) elevation—and their pairwise combinations—(d) temperature and precipitation, (e) temperature and elevation, and (f) precipitation and elevation. The percent area protected is based on the bins observed with equal frequency shown in Figures 2 and 3 and was calculated considering all International Union for Conservation of Nature protection categories (I–II, III–IV, V–VI, and Non-designated) together. Because percent protected is not normally distributed, the color key is divided into 10 intervals reflecting a \log_{10} -transformed continuous scale. See Appendix S4 for maps based on equally spaced bins. Maps are in Mollweide projection (ESRI:54009)

Australia, whereas areas with low SSS protection occurred mostly in the Atlantic, Indian and South Pacific Oceans, and the Gulf of Oman (Figure 5b). Well-protected bathymetry conditions were mostly located along the coasts and the ocean trenches, and very well-protected bathymetry conditions occurred along the coast of Australia, most of the South China Sea, and most of the Arctic Ocean.

Areas that exhibited conditions that were not well protected covered the remaining marine realm and occurred in all major oceans (Figure 5c). All 3 variables had only a marginal area ($\leq 3.5\%$) with protection coverage $\geq 16\%$ (Figure 5a–c). The spatial patterns of the pairwise comparison of SST, SSS, and bathymetry showed that mostly the South Pacific Ocean exhibited unique conditions of pairwise combinations of biophysical variables that were highly protected, whereas, particularly, the Tropic of Capricorn and parts of the Atlantic and North Pacific Oceans had conditions that were only marginally protected (Figure 5d–f). Overall, protection coverage differed among marine realms and each variable and the pairwise combinations (Appendix S3).

DISCUSSION

Overall coverage

The protected area network provided a wide coverage of current biophysical conditions across the terrestrial realm. However, for the terrestrial realm low to intermediate and very high temperature and low and medium precipitation conditions lacked protection (Figure 2a,b). These conditions represent the majority of temperate regions and thus are quite common. Rare biophysical conditions were usually much better protected (Appendix S4). This bias might reflect historical human settlement preferences; terrestrial protected areas (TPAs) are typically biased toward isolated locations with low population density and low suitability for agriculture and are mostly driven by opportunistic forces rather than preferential and representative motivations (Joppa & Pfaff, 2009; Baldi et al., 2017).

Low and very high elevational levels were less protected than expected, although overall elevation was evenly represented by the TPA network (Figure 2c). This is consistent with results of

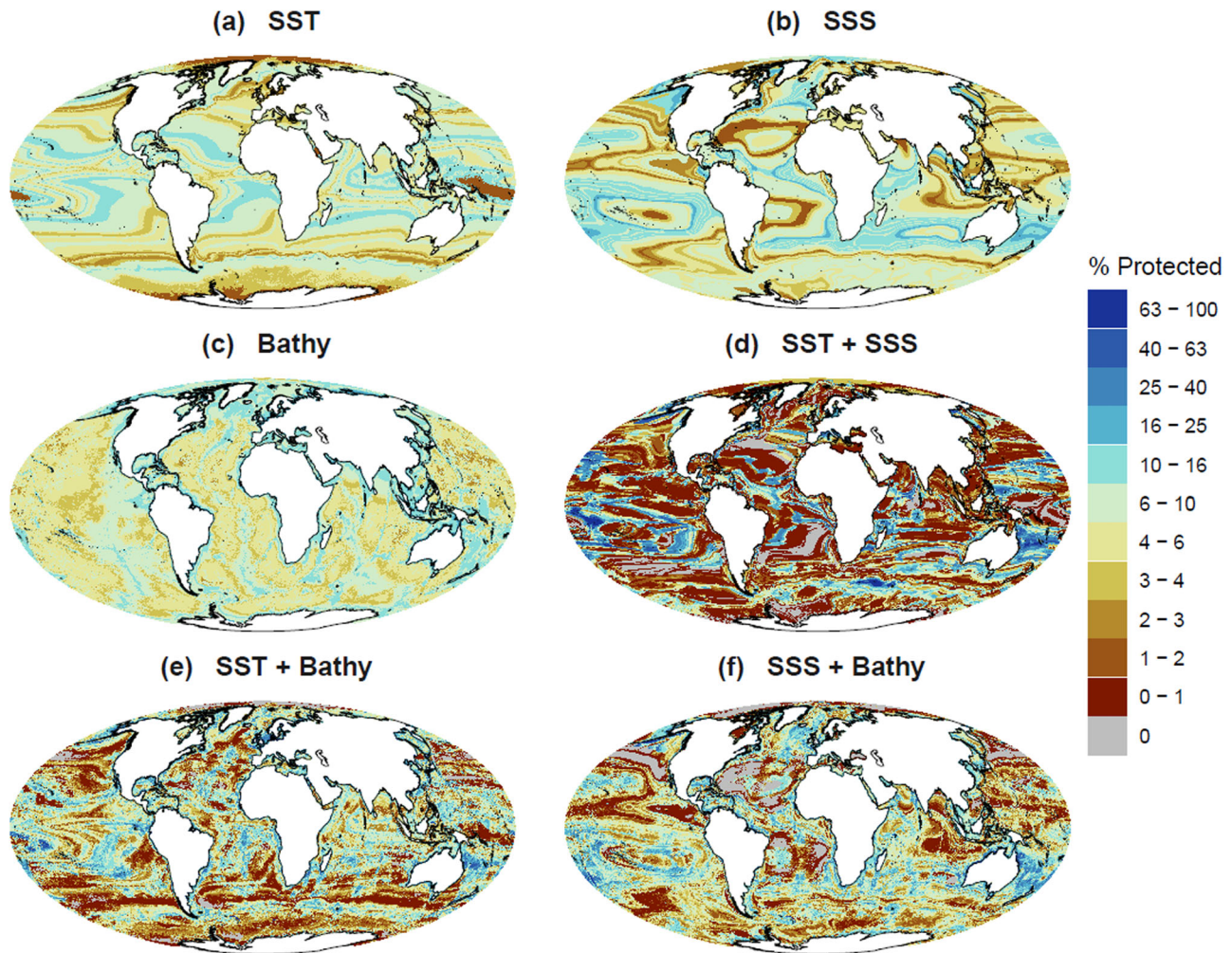


FIGURE 5 Percentage of the marine realm protected by each biophysical condition—(a) sea surface temperature (SST), (b) sea surface salinity (SSS), and (c) bathymetry—and their pairwise combinations—(d) SST and SSS, (e) SST and bathymetry, and (f) SSS and bathymetry. The percent area protected is based on the bins observed with equal frequency shown in Figures 2 and 3 and was calculated considering all International Union for Conservation of Nature protection categories (I–II, III–IV, V–VI, and Non-designated) together. Because percent protected is not normally distributed, the color key is divided into 10 intervals reflecting a \log_{10} -transformed continuous scale. See Appendix S4 for maps based on equally spaced bins. Maps are in Mollweide projection (ESRI:54009)

Joppa and Pfaff (2009) who found that in the United States areas from 1000 to 4000 m elevation are disproportionately protected. In contrast to Elsen et al. (2018), we did not find a bias in TPAs toward high mountain systems. This is because we considered elevational levels of equal frequency rather than discrete levels (comparison in Appendix S4). Although our approach (equal frequency bins) led to a larger number of bins with low or medium elevations, because these are more common, it may also be more meaningful when assessing the representation of global biophysical conditions by PAs. Another confounding factor, especially with regard to elevation (You et al., 2018), is that some countries have stopped reporting their PAs to UNEP-WCMC, so some PAs are not included in the World Database on Protected Areas (Bingham et al., 2019).

The patterns across the marine realm were less clear, as low and medium SST and medium and high SSS were underrepresented. For bathymetry, only the deep sea was underrepresented (Figure 2d–f). The lack of deep-sea protection is cause for con-

cern because the abyssal plain (2000–4000 m) is by surface area the largest habitat on Earth (Angel, 1993) and its biodiversity is largely unexplored (Webb et al., 2010). Even more concerning was the uneven distribution in SSS and bathymetry protection. This could be because marine protected areas (MPAs) are typically much larger in size, but fewer in number than TPAs, which results in the protection of large areas with similar biophysical conditions and thus an overrepresentation of these conditions on a global level. This again highlights the importance to consider biophysical conditions when designing and implementing new MPAs in order to establish a representative global MPA network that helps safeguard current and future biodiversity and ecosystem services. At the same time, the establishment of new MPAs in places of low economic interest without considering their value for conservation (Devillers et al., 2015) needs to be avoided. Given that most marine areas are beyond national jurisdiction, a globally coordinated establishment of representative MPAs presents an enormous challenge, yet such an effort

could considerably help to protect biodiversity and simultaneously boost food provisioning and carbon storage (Sala et al., 2021).

Protection categories in the terrestrial realm seemed to be evenly represented, whereas for the marine realm certain SST, SSS, and bathymetry conditions were mostly protected by category V–VI or non-designated MPAs (Figure 2). This is cause for concern given that PAs in stricter protection categories are more likely to provide effective conservation (Jones et al., 2018; Leberger et al., 2020) than PAs in low protection categories (e.g., V–VI).

Interaction coverage

In the terrestrial realm, the combination of low temperature and high precipitation (Figure 3a) had a high protection coverage, as did the combination of both low temperature and high precipitation with all elevational levels (Figure 3b,c). Dry and hot as well as hot conditions had a low protection coverage across all elevations (Figure 3a–c). This is consistent with Sayre et al.'s (2020) finding that cold and moist ecosystems are well represented, whereas warm and dry environments are not, and also with Elsen et al.'s (2020) finding that there is a protection bias toward rare portions of climate space, particularly cold and wet environments (although they used equally spaced conditions; comparison in Appendix S4).

For the marine realm, well-protected conditions were mostly present at the upper limits of SSS across almost all SST conditions (Figure 3e) and at very shallow depths (0–46 m) across all SSS and SST conditions (Figure 3f,g), whereas very deep locations across various SST and low SSS conditions across most depths were completely unprotected (Figure 3f,g). This again highlights a lack of protection in the marine realm. In order to create a fully representative MPA network, these areas need to be specifically targeted, irrespective of national jurisdictions (Liu et al., 2020), when establishing new MPAs.

Spatial patterns

Our assessment of how the representation of certain biophysical conditions by the PA network is distributed across space at the global level is important because, even though biophysical conditions are well represented, these conditions might only occur in a single location (e.g., mountain top) or be protected at a geographically distinct region (e.g., Europe). This in turn may weaken the overall representativeness of these biophysical conditions because the protected location or region could be particularly vulnerable to anthropogenic impacts and climate change, even if they are strictly protected.

Large parts of the terrestrial realm had temperature (68%), precipitation (77%), and elevation (89%) conditions that were protected by 10–16 % (Figure 4a–c). Greenland, most of which is protected by a single PA, the Northeast Greenland National Park, exhibited unique temperatures that had high protection

coverage. The northern part of South America had high protection coverage with regard to precipitation conditions. However, this was mostly due to a large number of PAs in low protection categories (V–VI) (Baldi et al., 2019). Low protection in the terrestrial realm mostly occurred in parts of China (Figure 4d), the Sahara, and the Arabian Peninsula (Figure 4d). Protection of these regions is unlikely to conflict with human population pressure or agricultural use (both should be relatively low). Thus, although biodiversity is low in these areas, increasing the protection level may help conserve parts of the last areas on the planet that remain largely uninfluenced by humans (Watson et al., 2018).

For the marine realm, 50% of SST, 46% of SSS, and 42% of bathymetry conditions were protected between 7–16% (Figure 5a–c). Well-protected biophysical conditions occurred mostly along the coasts and in the Tropics, whereas areas with low protection were mainly located along the Cancer of Capricorn and toward the poles. But this is counteracted by anthropogenic threats to marine ecosystems that concentrate on continental shelves (Halpern et al., 2015) and so co-occur with areas that exhibit well-protected conditions. Most marine areas had low protection of pairwise combinations of biophysical variables, whereas a few areas, mostly east of Australia, had multiple variables protected by $\geq 16\%$ (Figure 5d–f). However, this result depended on the overall spatial extent considered. For local representativeness of Australian MPAs, Roberts et al. (2019) found that Australian MPAs overrepresent warm, offshore waters and underrepresent temperate environments.

Challenges and potential caveats

Although the variables considered are important in explaining the distribution of biomes and species richness, they do not fully represent the biophysical conditions of the world and there are other factors, such as geology, soil, current velocity, and availability of resources, that influence species distribution, composition, and diversity (Anderson & Ferree, 2010; Lawler et al., 2015; Rees et al., 1999). We did not consider variability in climate or topography within a grid cell, although microclimate and terrain ruggedness are also important surrogates for biodiversity and potentially also ecosystem services (Bramer et al., 2018; Amatulli et al., 2018).

Even if the current global PA network fully represented the diversity of current biophysical conditions, which would likely favor the maintenance and establishment of biodiversity under climate change (Ackerly et al., 2010; Lawler et al., 2015), the representativeness of nature exceeds biophysical conditions and there are many other factors that affect conservation effectiveness (Watson et al., 2014). Given that the Aichi Biodiversity Target 11 calls for “ecologically representative PAs of particular importance for biodiversity and ecosystem services”, biotic measures (e.g., number of threatened species [Venter et al., 2018]; biotic interactions [Lawler et al., 2015]; phylogenetic [Rosauer et al., 2017], functional [Guilhaumon et al. 2015], and geodiversity [Tukiainen et al., 2017]; the coverage of climatic niches [Hanson et al., 2020]; and ecosystem functions

[Harvey et al., 2017] and services [Eastwood et al., 2016]) are additional factors to be considered. Nevertheless, currently neither the world's most diverse nor the most productive ecosystems are the most protected (Lindgren et al., 2018; Maxwell et al., 2020), although on the level of ecoregions the global PA network is strongly related to biodiversity measures (Loucks et al., 2008).

While topographic conditions (elevation, bathymetry) remain relatively constant through time, climatic conditions are subject to drastic change in the near and far future (IPCC, 2013). This will have strong effects on the PA network because some of the protected abiotic conditions will disappear and new nonanalog climates may appear (Elsen et al., 2020).

We did not consider whether cells that covered a biophysical condition were protected by 1 large or multiple small PAs or assess the extent of the cells covered or their connectivity. Given that connectivity among PAs will become even more important when species that are currently under protection shift their ranges to track changing climatic conditions (Littlefield et al., 2017), one also needs to consider the size and connectivity of PAs and the protection retention of future climatic conditions (Elsen et al., 2020) when assessing the representativeness of the global PA network.

Our results highlight potential gaps in the global coverage of biophysical conditions by the current PA network. To conserve global biodiversity and ecosystem services, PAs need to represent all of the world's ecosystems and the areas that contain exceptional or endemic species and habitats (Olson & Dinerstein, 2002; Davidson & Dulvey, 2017). Thus, future conservation actions need to be driven by preferential and representative motivations rather than opportunistic forces (Baldi et al., 2017).

Given the rising challenges of climate change, a conservation planning approach that increases the coverage of species, ecosystems, and ecological processes is crucial because climate change may lead to new species communities and even new ecosystem types (Mawdsley et al. 2009). Although biodiversity measures are of prime importance for PA planning strategies, precise knowledge of species distributions is still lacking for many species, particularly non-iconic ones. Our assessment of the representativeness of biophysical conditions thus adds a frequently overlooked perspective. We believe our results provide useful insights for researchers, conservation practitioners, and policy makers that will improve prioritization efforts for a more comprehensive future global PA network.

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