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Towards climate-smart, three-dimensional protected areas for biodiversity conservation in the high seas

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Marine species are moving rapidly in response to warming, often in different directions and with variations dependent on location and depth. Given the current impetus to increase the area of protected ocean to 30%, conservation planning must include the 64% of the ocean beyond national jurisdictions, which in turn requires associated design challenges for conventional conservation to be addressed. Here we present a planning approach for the high seas that conserves biodiversity, minimizes exposure to climate change, retains species within reserve boundaries and reduces conflict with fishing. This is developed using data from across four depth domains, considering 12,932 vertebrate, invertebrate and algal species and three climate scenarios. The resultant climate-smart conservation areas cover 6% of the high seas and represent a low-regret option that provides a nucleus for developing a full network of high-seas marine reserves.

Human threats—including fishing and climate change—are impacting marine biodiversity, from the ocean surface to the deepest and most remote places on Earth[1,2]. Marine protected areas (MPAs) are the most effective and widely used tools in conservation to mitigate threats[3]. Well-enforced MPAs can protect biodiversity[4], enhance ecological resilience[5], enrich local fish stocks[6] and provide scientific reference sites in modified seascapes[7,8]. Climate change is considered in the design of some MPA networks, most commonly by using marine species distribution models under different climate scenarios[9] and by making management recommendations on how to incorporate climate change into conservation plans[10,11]. Although most MPA conservation plans include some aspects of both benthic (that is, seafloor) and pelagic (that is, water-column) biodiversity[12], and some include climate change, almost all are in relatively shallow environments with strong mixing where benthic and pelagic environments are considered together. However, in the high seas, we question whether it is appropriate to aggregate biodiversity in the top 200 m of the ocean with the distinct and largely separate biodiversity at 8 km depth, especially given that oceanography, biology and climate change impacts vary greatly with depth[1,13].

Ensuring that MPAs are climate-smart (that is, considering climate change in their design) is challenging[14]. As the climate warms, species are rapidly shifting towards cooler regions[15–19], potentially moving beyond MPA boundaries. The retention of species in MPAs is further complicated by the three-dimensional nature of the open ocean. Because rates of ocean warming and spatial temperature gradients change with depth, the speed and the direction of species' movement are also likely to vary across the water column, a phenomenon that will be more pronounced in the future[13]. As MPAs have mostly been designed and declared in coastal and shelf regions without explicit consideration of different depth domains, a new paradigm for the design of MPAs in the open ocean[20,21] is needed[22]—one that considers both its three-dimensional nature and the potential consequences of climate change.

Compared with the high seas, national jurisdictions experience intense competition between conservation and human uses, but have higher MPA coverage. For example, while 17% of national waters in exclusive economic zones (EEZs) are in partially protected MPAs, only 1.2% of the high seas is similarly protected, and 0.7% is fully protected[23]. This shortfall in the protection of the high seas means that currently only ~7.5% of the ocean is within MPAs[24], well short of the goal of protecting 10% of the ocean by 2020 (Aichi Target 11 by the Convention on Biological Diversity). Furthermore, momentum is growing under the Post-2020 Global Biodiversity Framework to increase protection targets to 30% of the ocean by 2030[25]. Since the inception of protection goals, policymakers have recognized that they would need to use the high seas to meet marine targets, but they have been hindered by fragmented governance regimes and the absence of global mechanisms to implement MPAs in the high seas[26]. The imminent agreement of a new treaty for the conservation and sustainable use of biodiversity beyond national

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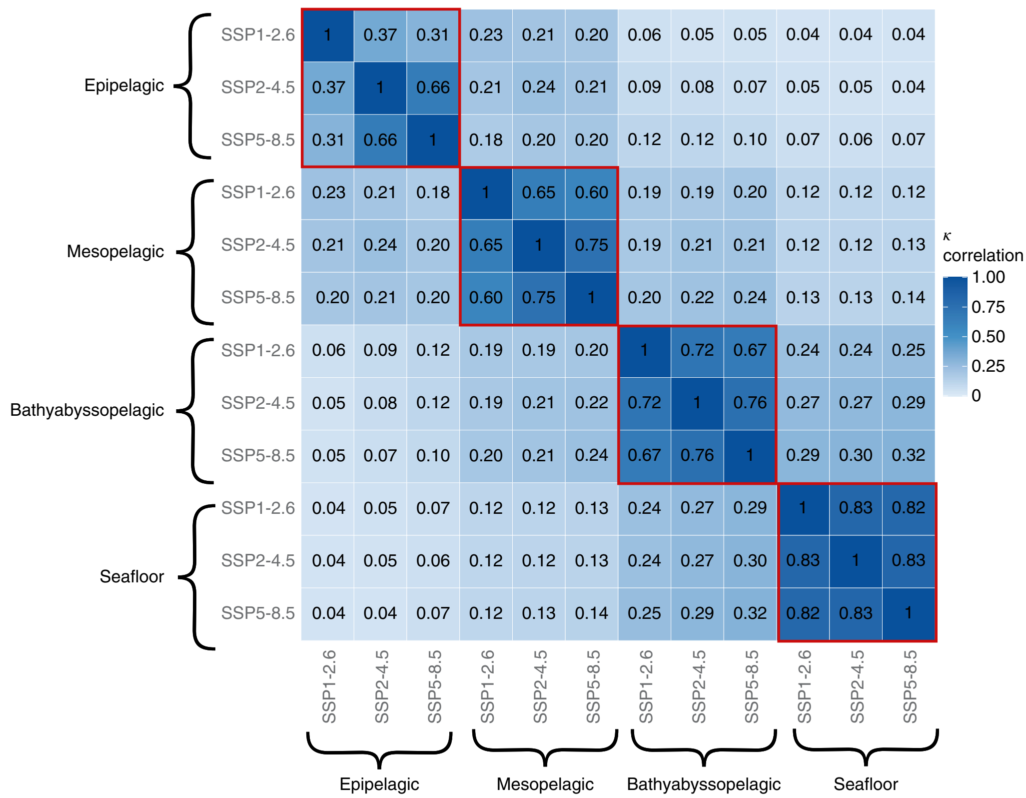

Fig. 1 | The degree of agreement between the climate-smart MPA networks for different planning domains and climate scenarios. The κ index for the relationship between each prioritized climate-smart network design for the four ocean planning domains: epipelagic, mesopelagic, bathyabyssopelagic and the seafloor.

jurisdiction will establish just such a mechanism[24], finally providing an opportunity for policymakers to address arguably the biggest gap in biodiversity protection on the planet[22]. High seas or areas beyond national jurisdiction are thus likely to be a primary focus of marine conservation in the future as global commitments to develop ecologically representative MPA networks increase.

To inform the development of MPAs in the high seas, we present a climate-smart planning approach across different depth domains that prioritizes the conservation of marine biodiversity and excludes fishing[27], while minimizing impacts on the fishing industry. Some studies argue that current MPA networks cannot effectively protect biodiversity against climate change[5,28] because individual MPAs are too small to retain species undergoing range shifts in response to changing environmental conditions. We address this criticism by identifying ecological climate refugia[29]—areas where biodiversity is likely to be least affected by climate change—and targeting these for protection.

To identify climate refugia, which will have lower exposure to future climate change and in which biodiversity will be more likely to be retained within MPAs, we used two climate-smart metrics. For biodiversity retention, we used climate velocity[15], a generic predictor of the expected speed of species' distribution shifts under climate change[18,30,31]. Areas with the slowest velocities are likely to see the smallest range shifts and are therefore considered more stable across time. As a metric of relative climate exposure (RCE), we used the temporal rate of temperature change divided by the mean annual temperature range (Methods). This assumes that species exposed to larger annual temperature ranges within any given bioregion (Methods) will exhibit greater thermal plasticity and, along with those exposed to slower warming (that is, where the numerator of the RCE is small), will be more resilient to climate change.

We have focused on temperature because of its fundamental importance as a driver of species' distributions[32] and because it is correlated with nutrient availability, dissolved oxygen concentration and pH, thereby also controlling system structure and function[33]. These latter correlations, together with our focus on refugia related to temperature, also mean that these areas will probably experience less overall change in terms of interlinked environmental variables than would be experienced in non-refuge areas. Species in climate refugia are thus likely to be more resilient to climate change, irrespective of whether their spatial distribution is towards the centre of the species' range or near their edge. Temperature also has a symmetrical functional relationship with species' biological performance, which is relevant in applications of climate velocity[34].

We created spatial plans for three alternative futures based on ocean temperatures from the IPCC Shared Socioeconomic Pathways (SSPs): SSP1-2.6 (an optimistic scenario with peak emissions in 2020), SSP2-4.5 (an intermediate scenario with peak emissions in 2040) and SSP5-8.5 (an unrestrained emission scenario). Both climate-smart metrics were estimated globally across a 0.5°×0.5° grid in four depth domains: three pelagic (epipelagic, mesopelagic and bathyabyssopelagic) and one benthic (seafloor). Each spatial plan included a set proportion of the distribution of 12,932 species of vertebrates (fish, birds, mammals and reptiles), invertebrates (molluscs, arthropods and corals) and macroalgae (green, red and brown) present within each depth zone and bioregion (Extended Data Fig. 1d–g and Supplementary Table 1). It also included 12 geomorphic features recognized for being hotspots of seafloor biodiversity (Methods and Extended Data Fig. 2). Taxa reported as threatened in the IUCN Red List were assigned high protection targets[35], whereas those not reported as threatened were assigned targets on the basis of the size of their global distribution (Methods).

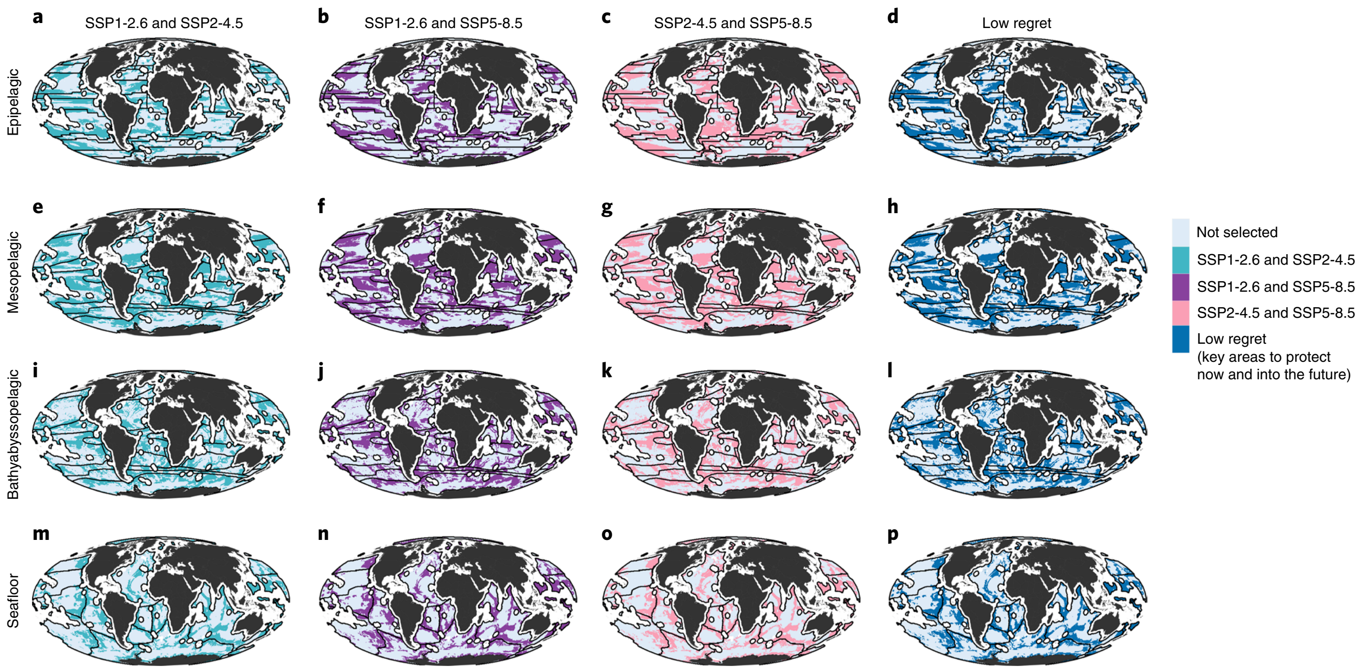

Fig. 2 | Climate-smart networks in the high seas. a–p, Coherence of prioritized networks in the high seas across different combinations of IPCC SSPs (SSP1-2.6, SSP2-4.5 and SSP5-8.5) and low-regret conservation areas, across four depth domains: epipelagic (**a–d**), mesopelagic (**e–h**), bathyabyssopelagic (**i–l**) and the seafloor (**m–p**). The polygons represent Longhurst provinces for the epipelagic domain, Glasgow provinces for the mesopelagic and bathyabyssopelagic domains, and Global Open Oceans and Deep Seabed provinces for the seafloor domain.

Because high-seas fisheries are a key economic resource[36], we minimized the cost to fishing, defined as the product of fish catch and fish value at any point in space (Methods) using the fish catch dataset of Watson[37], which includes estimates of illegal, unregulated and unreported catch and discards at sea. We then used integer linear programming to identify priority conservation areas for each depth domain and climate scenario using the R package prioritizr[38]. Our intent is to answer one pressing conservation question: can we identify climate-smart areas common to all future climate scenarios and across depth domains? These are areas that could form a nucleus around which a network of high-seas MPAs could be built.

When we apply a climate-smart planning approach independently within each depth domain, there is moderate to substantial agreement among configurations of climate-smart MPA networks across emission scenarios in the epipelagic (Cohen's κ coefficient, $\kappa=0.31$ to 0.66), the mesopelagic ($\kappa=0.60$ to 0.75), the bathyabyssopelagic ($\kappa=0.67$ to 0.76) and the seafloor ($\kappa=0.82$ to 0.83) (Figs. 1 and 2 and Extended Data Fig. 3). This high degree of spatial correspondence implies that climate-smart conservation networks for particular depth domains could be robust to different climate futures. Given that we do not know the future climate, having substantial agreement among climate scenarios at each depth domain will be key to successful climate-smart conservation and could maximize the protection of biodiversity[34].

Running the prioritization analyses without a cost layer had relatively little influence on the spatial pattern of selected planning units ($\kappa=0.91$ to 0.95 between the MPA networks with and without a cost layer; Extended Data Figs. 4 and 5). But when estimating the total cost of the scenarios, it was higher for every depth domain and climate scenario (Extended Data Figs. 4 and 5). This suggests that most key conservation areas from a biodiversity perspective are retained when minimizing the cost to fisheries.

Priority areas common across emission scenarios could be considered 'low-regret conservation areas' because they can be conserved independent of the future climate. Low-regret areas for

Table 1 | Proportion of the high seas (%) covered by all slow conservation feature priorities under different climate scenarios

Depth domain	SSP1-2.6	SSP2-4.5	SSP5-8.5	Climate-smart network (all three SSPs)
Epipelagic (0–200 m)	47.8	55.2	56	35.7
Mesopelagic (200–1,000 m)	57.1	57	57.7	47.7
Bathyabyssopelagic (>1,000 m)	48.4	47.4	46.3	39.3
Seafloor	37.6	38	38.2	33.7
Pelagic climate-smart network	–	–	–	12
Pelagic + seafloor climate-smart network	–	–	–	6

conservation include substantial proportions of the mesopelagic (47.7%), bathyabyssopelagic (39.3%), epipelagic (35.7%) and seafloor (33.7%) in the high seas (Fig. 2 and Table 1). These prioritized areas represent biodiversity by depth domain and bioregion that is likely to be both retained and less exposed to warming (Extended Data Fig. 6a). To date, conservation planning in the high seas has largely focused on individual depth domains, usually either the epipelagic[39] or the seafloor[40]. In a warming ocean, networks of MPAs that are vertically coherent across depth domains would be the easiest to enforce and implement[13,34], but knowing where those areas are located might be the first challenge to address in future marine conservation initiatives.

Identifying vertically coherent low-regret areas for protection is difficult not only because costs differ among depth domains (Extended Data Fig. 1a–d) but also because the threat posed by

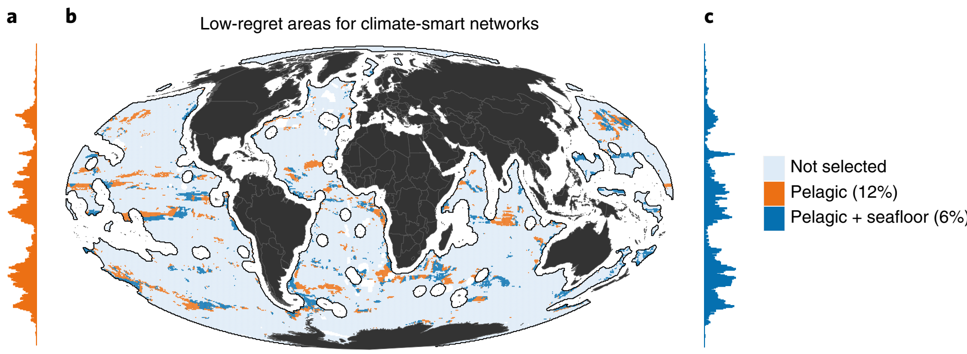

Fig. 3 | Low-regret climate-smart networks in the high seas. a–c, Climate-smart prioritization networks as low-regret conservation areas throughout the water column of the ocean for the pelagic domains (epipelagic, mesopelagic and bathyabyssopelagic) and for the pelagic plus the seafloor domains (**b**). The lateral panels show the latitudinal distribution of the prioritized climate-smart network as a proportion of ocean area for the pelagic domains (**a**) and the pelagic plus the seafloor domains (**c**).

disparate warming futures varies across depths (Extended Data Figs. 7 and 8). For example, due to the flatter spatial temperature gradient exhibited in the mesopelagic layer (Extended Data Fig. 7), its future climate velocity is projected to be faster than in the epipelagic layer, even with strong mitigation of future emissions[13]. This could cause dissociation of bioregions across depths and compromise the functioning, effectiveness and ecosystem services of climate-uninformed MPAs.

This variability in biodiversity, climate metrics and cost among pelagic depth domains (that is, epipelagic, mesopelagic and bathyabyssopelagic) across emission scenarios means that climate-smart MPA network configurations exhibit more spatial agreement between epipelagic and mesopelagic domains ($\kappa=0.18$ to 0.24 across emission scenarios) and between mesopelagic and bathyabyssopelagic domains ($\kappa=0.19$ to 0.24) than between epipelagic and bathyabyssopelagic domains ($\kappa=0.05$ to 0.12) (Fig. 1). The benthic (seafloor) domain exhibits some agreement with the bathyabyssopelagic domain across emission scenarios ($\kappa=0.24$ to 0.32) but little agreement with the mesopelagic ($\kappa=0.12$ to 0.14) and the epipelagic domains ($\kappa=0.04$ to 0.07) (Fig. 1). The spatial agreement (or disagreement) in prioritized networks across depth domains (Fig. 2) highlights not only differences in the cost of fishing with depth (Extended Data Fig. 1a–d) but also the vertical coherence across depths. This vertical coherence, in turn, is the result of vertically structured oceanographic phenomena, the vertical migration of biodiversity and the passive sinking of surface production, particularly through the epipelagic and mesopelagic[41]. The declining coherence with greater separation between domains is unsurprising, given that many species are unique to each depth domain[42] and few vertically migrate far enough to span multiple depth domains. The spatial coherence in the placement of MPAs in the epipelagic and mesopelagic domains is encouraging in terms of establishing vertically coherent climate-smart MPAs in the upper ocean, but the lack of coherence with the bathyabyssopelagic domain and the seafloor suggests that in some cases, separate conservation plans might be needed for upper and lower ocean layers. Vertical zoning of MPAs in the ocean is currently rare[43], but examples include the Mexican Caribbean Biosphere Reserve and the Deep Mexican Pacific Biosphere Reserve[44].

A benefit of targeting ocean protection in areas where responses to climate change are coherent across vertical depth domains and scenarios (Fig. 3 and Extended Data Fig. 3) is that it decreases the risk of decoupling trophic relationships and may allow for the movement of MPA boundaries in response to novel climates[13,34]. Our results show that 6% of the high seas are such 'low-regret conservation areas' (Fig. 3 and Supplementary Table 2). They represent key areas to conserve pelagic and benthic biodiversity in the high seas now and into the future across depth domains (Extended Data Fig. 6b). Considering only pelagic depth domains (that is, excluding the seafloor), the amount of ocean within low-regret conservation areas expands to 12% (Fig. 3 and Supplementary Table 2). Such low-regret sectoral management measures that operate in parts of the water column (for example, pelagic and benthic) represent 'other effective area-based conservation measures' and could serve as part of a global conservation network[43] (Extended Data Fig. 6b).

Biodiversity targets are key in motivating conservation actions, but to date politics and expediency have dominated ecology in the international policy arena[45], which has dictated how conservation targets are applied in global prioritization exercises[35,46]. To perform a sensitivity analysis of how representation targets alter the global climate-smart MPA network identified here, we created several alternative climate-smart MPA networks with varying conservation targets for the 12,932 species distributions and the 12 seafloor geomorphic features (Methods). We ran seven additional prioritization analyses with new sets of targets (10% minimum with 10% increments to a maximum of 90%) for every restricted conservation feature (that is, species and geomorphic features in climate refugia in each bioregion) (Extended Data Figs. 9 and 10). As expected, the total area required to achieve these targets in vertically coherent low-regret MPA networks scales positively with target size (Supplementary Table 2), with less area prioritized for targets of 10–30% (targets for wide- and narrow-ranged features; 0.10% of the total high seas) and more area prioritized for targets of 10–90% (3.2% of the total high seas) (Supplementary Table 2). Importantly, despite varying targets for protection, considerable spatial agreement remains among prioritized climate-smart networks across climate scenarios, and with greater spatial agreement in configurations between epipelagic and mesopelagic depth domains than between the epipelagic and either the bathyabyssopelagic or seafloor domains (Extended Data Fig. 9). Higher biodiversity-protection targets in a climate-smart prioritization would increase the size of low-regret conservation areas, not only across different climatic scenarios but also in a coherent way across depth domains. This would provide substantial benefits to the Conservation of Biological Diversity agenda in a warming world.

There are several caveats in our analyses that should be considered. First, while our study focuses on the high seas because they are underprotected, we strongly believe that representative conservation of all coastal and marine habitats is necessary. Protection of the high seas should not replace or undermine efforts to protect critical coastal environments. Second, we focus on placing MPAs in climate refugia, but there are other possible design approaches, including placing MPAs in areas of high chronic but low acute thermal stress to increase resistance, and potentially providing greater protection for species in areas of rapid change to mitigate non-climate threats[14]. Third, by focusing on temperature, we do not consider other climate change impacts that may affect the spatial prioritization. For example, primary productivity influences the community structure of pelagic food webs[47], and its magnitude and spatial pattern are likely to change in the future[48], although uncertainty in this regard is high. Fourth, our climate metrics do not directly link climate warming with a species' thermal preference. For example, a species in a rapidly changing environment may be at relatively low risk if it has a broad thermal safety margin[49]. Nevertheless, by targeting climate refugia[29] rather than a broad spectrum of climate change characteristics[14], we focus on areas where the least change is expected, rendering the thermal preferences of resident species less important. Fifth, our approach did not consider the three main aspects of a well-connected marine MPA network in its design[50]: structural connectivity, functional connectivity and climate connectivity. We consider the areas identified to be a nucleus around which to build a larger, broader, more connected MPA network that considers additional criteria. For example, climate-connected MPAs could be designed to enable biodiversity to shift along climate pathways[51], either by moving MPAs with climate change[52,53] or by designing stepping-stone MPAs[34]. Sixth, our study assumes that all parts of a species' range are equally important, and meeting a conservation target for a species range will thus not necessarily confer the protection necessary to conserve metapopulation structure or species viability. Seventh, we assume that fishing is the primary driver of cost. In the future, data on the increasing number of mining licences to explore the deep-ocean seafloor could also be included[54], although they are currently proprietary and unavailable to public scrutiny[55]. International cooperation will be vital in generating open-access information that can be used to minimize political and socio-economic conflicts in the design of open-ocean MPAs. Last, the fisheries cost layer quantifies only current fish catch and prices, both of which could change with future climate, economic and social changes.

Designed and enforced appropriately, a global network of climate-smart MPAs in the high seas will help conserve marine biodiversity in a warming world. An initial priority could be the protection of the low-regret areas across depth domains that we identified (6% of the high seas) because they are vertically coherent, are robust to different climate futures and protect key threatened species. Such protection would increase the coverage of the global MPA network from ~7.5% to ~11.3%. However, because our low-regret climate-smart areas do not consider other ecological criteria, such as spatial connectivity or adequacy[21], they should be considered a nucleus around which a comprehensive MPA network can be built. In constructing an expanded network, society might need to consider separate reserve networks for different depth domains, if they are to be robust to different climate futures. Since climate-smart low-regret areas are geographically similar between the epipelagic and mesopelagic layers, a second priority could be to focus on the development of sectoral spatial management measures in the upper 1,000 m of the ocean; this could add another 10% of the high seas to the area conserved, mainly representing 'other effective area-based conservation measures'. A greater focus on a separate planning process for the bathyabyssopelagic and the seafloor could consider potential costs beyond deep-sea fishing, including mining and underwater cabling[55].

As momentum builds towards protection of 30% of the ocean by 2030[25], the expansion of the current MPA network is a primary goal of the 2021–2030 Decade of Ocean Science for Sustainable Development. To be effective, conservation and management will need to include the high seas. The climate-smart MPAs proposed here are not meant to be prescriptive but rather to advance the idea that MPA design in the high seas should consider multiple depth domains and multiple climate futures. We hope that the three-dimensional, climate-smart approach developed here will help inform MPA negotiations among member states and allow managers to better incorporate the deep and dynamic nature of the ocean into future spatial planning studies.

Online content

Any methods, additional references, Nature Research reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at https://doi.org/10.1038/s41558-022-01323-7.

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Methods

Study domain. We used the most recent global dataset of marine regions to define the spatial extent of the high seas (v.11, https://www.marineregions.org/). We defined the high seas as marine areas outside of the EEZs, which represent 95% of habitat on Earth by volume, 64% of the surface of the ocean and 46% of the surface of the Earth[24]. By excluding EEZs from this study, we omit parts of the ocean that contain most known marine biodiversity and are relatively well protected, and focus instead on areas beyond national jurisdiction, which are likely to be central to efforts to protect 30% of the ocean by 2030. MPAs in the deep ocean also address growing threats. Bottom trawling occurs to depths of 2,200 m (refs. [56,57]), and indirect impacts of epipelagic and midwater trawls have been described down to 2,500 m (ref. [58]). Beyond fisheries, deep-sea mining is set to begin in 2023 off Nauru, and deepwater cables can also damage habitat on the seafloor at virtually any depth. Here we classified the high seas into three pelagic layers (epipelagic, 0–200 m; mesopelagic, 200–1,000 m; and bathyabyssopelagic, >1,000 m) and one benthic layer (seafloor) using the ETOPO1 bathymetry dataset[59]. We treated each layer as a separate planning domain containing equal-area hexagonal planning units of 2,620 km^2 (~0.5° at the equator). This yielded a total of 90,065 planning units for the epipelagic domain, 88,528 planning units for the mesopelagic domain and 87,170 planning units for the bathyabyssopelagic domain; there are fewer planning units by depth because of seamounts and underwater mountain ranges. For the seafloor domain, there were 90,065 planning units. Information about climate metrics, species and fishing data were assigned to each depth domain (as described below), each of which could then be prioritized for inclusion in a climate-smart MPA network.

Climate change metrics: sources and processing. Climate change metrics (that is, climate velocity and RCE) were estimated using future ocean temperatures from the Coupled Model Intercomparison Project Phase 6 (Earth System Grid Federation, https://esgf.llnl.gov). For the three pelagic domains, we used sea temperature from a multi-model ensemble mean derived from 11 general circulation models (GCMs), and for the seafloor, we used bottom temperatures from a multi-model ensemble mean derived from 12 GCMs (Supplementary Tables 3 and 4). We used models under three IPCC SSPs[60]: SSP1-2.6, SSP2-4.5 and SSP5-8.5. Pathway SSP1-2.6 represents an optimistic scenario, characterized by a shift to a more sustainable economy and a reduction in inequality, resulting in a peak in radiative forcing of ~3 W m^{-2} before 2100. SSP2-4.5 represents an intermediate scenario, with a stabilization of radiative forcing levels at ~4.5 W m^{-2} by 2100. SSP5-8.5 is characterized by a continued increase of greenhouse gas emissions resulting from a fossil-fuel-based economy and increased energy demand, with a radiative forcing >8.5 W m^{-2} by 2100, rising thereafter.

To construct the multi-model ensemble, we followed published methods[13]. Briefly, for each climate model, we regridded from the original grid to a uniform 0.5° spatial grid using an area-weighted bilinear interpolation[61]. We then extracted sea temperature data from the GCMs by depth according to three different ocean layers: epipelagic (0–200 m), mesopelagic (200–1,000 m) and bathyabyssopelagic (>1,000 m)[62]. For each depth layer, we averaged temperatures using a volume-weighting approach, with volumes of 0.5° grid squares in each depth layer. Finally, to avoid artefacts caused by inconsistent numbers of grid cells available by depth for different models, we included only grid cells common to all models within each depth layer[13]. We have assumed that integrating temperatures across broad ocean depths is a reasonable approximation of habitat conditions in the ocean[34,43,62,63]. Although temperature varies continuously by depth, these ocean layers have been defined on the basis of consistency in their physical, chemical and biological environments[63], and these conditions are further integrated by the extensive vertical migration of many marine species[41]. Using temperature alone, instead of other climate variables, means that our results reflect only the potential impact of warming on biodiversity. All analysis was undertaken using the software tools Climate Data Operators (version 1.9)[64] and R (version 3.5)[65] (Supplementary Tables 3 and 4).

Calculation of climate velocity and RCE metrics. Climate change has been considered in previous conservation planning exercises, particularly in coastal regions[66–68]. Global conservation planning exercises have used sea surface temperature as the metric of climate change[39,69], with none using data throughout the water column. Here, to prioritize a climate-smart MPA network, we focused on areas across depth domains (including the seafloor) that accomplish two objectives: (1) high retention of biodiversity and (2) low levels of exposure to future climate warming. We used two metrics of climate change to represent these objectives: climate velocity and RCE. Climate velocity is a metric that gives expectations for species' range shifts under projected future ocean warming[15,18,30]. It is expected that in areas of slow climate velocity, species' distributions are likely to shift less, promoting their retention within a given area. We estimate local climate velocity at 0.5° resolution for the second half of the century (2050–2100) at each depth domain of the multi-model CMIP6 ensemble. The temporal trend (that is, the numerator of climate velocity) was calculated as the slope of a linear regression of mean annual temperatures (°C yr^{-1}) for the corresponding climate scenario time period. The spatial gradient (that is, the denominator of climate velocity) was calculated from the vector sum of the latitudinal and longitudinal pairwise differences of the mean temperature across the corresponding climate scenario and time period at each focal cell using a 3 × 3 neighbourhood window (°C km^{-1})[15]. All calculations were performed using the R package VoCC[70].

RCE is a metric that we developed to obtain information about the amount of exposure to climate warming that local populations of a species would face relative to its experience of variation in seasonal temperatures. We define exposure to climate change as the presence of a species, ecosystem or habitat at a location where it might be adversely affected by climate change. We calculated RCE as the ratio of the slope of a linear regression of projected mean annual temperatures (°C yr^{-1} in 2050–2100) to the current mean seasonal temperature range (°C in 2015–2020):

$$\mathrm{RCE} = \frac{\text{Slope of temperature change}(^\circ\mathrm{C\,yr}^{-1})}{\text{Current seasonal range }(^\circ\mathrm{C})}$$

It is expected that by prioritizing areas with a low climate-exposure index, we will select MPAs that will be more likely to minimize the potential exposure of species to future warming. Although some metrics of exposure have already been incorporated in marine spatial planning[28,71], our metric considers not only information on warming but also the local change relative to seasonal variation, and therefore, presumably, the relative vulnerability of resident biodiversity to projected future temperatures. It is important to mention that the RCE metric developed here is only weakly correlated with latitude ($r < 0.1$ for almost all depth domains and climate scenarios) and shows a similar pattern to climate velocity in terms of greater exposure to warming for species living below the epipelagic layer and under higher emissions (that is, the SSP5-8.5 climate scenario) (Extended Data Fig. 8). For each depth domain, we calculated climate velocity and RCE separately for all three SSPs.

We have chosen to analyse three pelagic depth domains and the seafloor rather than vertical climate velocity for several reasons. First, because species fill their thermal niches[72,73], species are likely to move both horizontally and vertically into available habitat. The large horizontal movements (kilometres) are greater than the vertical movements (metres) of species with warming, so our approach of using horizontal climate velocity is best suited to exploring the retention of species within MPA boundaries[34]. Second, recent empirical evidence[74] suggests that depth provides refuge from ocean warming only in areas of steep vertical temperature gradients. However, vertical temperature gradients are gentle over most of the open ocean (>500 m depth). Thus, in most of the high seas, vertical shifts would need to be much greater than in coastal areas to avoid climate warming and are less likely[74]. Such large vertical shifts are rendered less likely because they could dissociate distributions of animals from their food, especially for herbivores, and risk increasing exposure to other climate hazards, such as shoaling oxygen-minimum zones. In the high seas, horizontal climate velocity is likely to be a more useful proxy for community-level responses to climate change than vertical velocity. This is especially pertinent in our analysis because we integrate across large depth domains within which vertical temperature responses might operate. Last, it is not straightforward to assign the relative importance of the horizontal and vertical dimensions of climate velocity in a three-dimensional conservation plan.

Conservation features. To solve the minimum-set conservation prioritization problem, it is necessary to specify a protection target a priori for each conservation feature, which indicates the minimum amount of each feature (that is, species or habitat) to be included within the final prioritized network[75]. Although there are multiple criteria for identifying areas for biodiversity conservation[76], our conservation features here were marine species distribution maps from AquaMaps[77] (v.2019) and seafloor geomorphic features[78] from the Blue Habitats dataset (www.bluehabitats.org).

The AquaMaps dataset predicts marine species distributions using a probability of occurrence (0–1) derived from an environmental niche model based on depth, temperature, salinity and oxygen at 0.5° spatial resolution. It includes 33,518 marine species, 23,700 of which we considered, as their environmental envelopes were generated using at least ten observations[13]. Since published studies have concluded that varying the probability of occurrence to select thresholds in prioritization analysis has little impact in prioritized networks[35], we applied the commonly used minimum threshold of 0.5 probability of occurrence[13,69] to set range maps for our high-seas depth domains. Since most biodiversity in the ocean is located in coastal regions, our selection criteria yielded 12,932 species distribution maps across the depth domains within the high seas (Supplementary Table 1).

We classified the AquaMaps species into those that were pelagic and benthic using information from FishBase[79] and SeaLifeBase[80]. Pelagic species were those classified as pelagic–neritic, pelagic, bathypelagic, pelagic–oceanic or epipelagic. Benthic species were those that are classified as sessile, demersal, benthic, reef-associated, benthopelagic or bathydemersal. We assigned the pelagic species to each of the three pelagic depth domains on the basis of their depth range from the AquaMaps depth envelopes. This yielded 1,081 conservation features in the epipelagic domain (0–200 m), 1,300 in the mesopelagic domain (200–1,000 m) and 519 in the bathyabyssopelagic domain (>1,000 m; Extended Data Fig. 1e–h and Supplementary Table 1). We also assigned each of the benthic species to the seafloor domain, which yielded 10,860 conservation features.

In addition to the seafloor conservation features derived from AquaMaps, we included geomorphic features[78] in the seafloor domain. Geomorphic features are often associated with highly productive zones and are hotspots for biodiversity[81,82]. We used the 12 categories that best represent biological species-associated information as conservation features for the seafloor domain (Extended Data Fig. 2). These features (basins, bridges, canyons, escarpments, fans, guyots, plateaus, ridges, seamounts, sills, trenches and troughs) bring the total number of conservation features in the seafloor domain to 10,872.

To obtain a better representation of conservation features in the global climate-smart MPA network across latitudes and ocean planning domains, we ensured that each feature is represented in every marine biogeographical province that it overlaps with a threshold of 0.5. We used different biogeographical provinces for different depth domains. For the epipelagic domain, we used Longhurst provinces, which are widely recognized by policymakers[83,84] and which reflect major oceanographic regions and boundaries that are compatible with the current climate-smart approach, although there are other available bioregionalizations[85]. For the mesopelagic and bathyabyssopelagic depth domains, we used the Glasgow provinces[86], and for the seafloor domain, we used the Global Open Oceans and Deep Seabed provinces[87]. Since most conservation features appear in multiple provinces, this categorization process yielded a total of 66,093 conservation features: 12,791 for the epipelagic domain, 15,141 for the mesopelagic domain, 7,083 for the bathyabyssopelagic domain and 31,078 for the seafloor domain.

Opportunity cost of fishing. When solving the minimum-set problem in spatial prioritization, the objective is to identify areas where MPAs can meet conservation targets at a minimum cost[75]. In our global prioritization analysis, we used the value of fisheries as a cost layer because it is the most common cost layer used in marine planning, as resulting priority areas avoid valuable fishing grounds where possible[88]. Our use of a fisheries cost layer is predicated on the reality that biodiversity conservation in the high seas relies on sectoral implementation of protection measures and their need to balance competing objectives of conservation and fisheries[24]. However, we have also run a climate-smart prioritization analysis without a cost layer (that is, the base scenario) to focus solely on conservation objectives.

To estimate the fisheries value (US$) of each planning unit in each depth domain, we used a global database of catch (kg)[37] and price (US$ kg^{-1})[89] for each species caught. The catch data contained fishing records for 1,242 species of fish and invertebrates from different publicly available databases from 1950 to 2014[37]. This dataset includes landings at 0.5° spatial resolution, is interpolated to account for missing values and includes an estimate of illegal, unreported and unregulated fishing recorded as discards[37]. For the cost layer, we used a subset of the total catch for the period 2005–2014 in each 0.5° cell (Extended Data Fig. 1a–d) and obtained the mean price of each species (US$)[89] from the Sea Around Us project dataset. Note that these prices are not absolute and are likely to change in the future due to economic factors and fish availability. To obtain a species' price for each depth domain, we categorized species by pelagic and benthic habitats using the same approach as described in 'Conservation features'. For pelagic species, we also used the FishBase database (https://www.fishbase.se/) to classify species by depth range preferences. This process yielded a total of 1,076 prices for species (US$), 221 prices for the epipelagic layer, 232 prices for the mesopelagic layer, 55 prices for the bathyabyssopelagic layer and 834 prices for benthic species associated with the seafloor. To obtain a final cost layer for each depth layer, we created a cost per square metre for each species and then multiplied it by the number of square metres that each species covers in each pelagic domain. We calculated a total price by adding prices for all species within each 0.5° cell. Finally, we overlapped each cost layer generated with the corresponding depth domain to obtain an area-weighted mean total cost (US$) for each planning unit (Extended Data Fig. 1a–d). Because fishing is limited in deep ocean layers, we assigned a zero cost in areas or depths where fishing was absent.

Spatial conservation prioritization. We used integer linear programming to find climate-smart MPA networks across depth domains that minimize the overall cost (that is, fishing value in US$) of the MPA network and achieve the representation targets for each conservation feature. We solved the minimum-set objective[75] using the R package prioritizr[38] and Gurobi optimization software (version 9.0)[90]. We set Gurobi to achieve a solution within 10% of the optimal solution (that is, the solution that achieves the coverage target with the lowest possible cost). This is a relatively arbitrary number that establishes the difference between the upper and lower bounds of the objective function[91]. For example, a value of 0.10 results in the optimizer stopping and returning solutions when the difference between the bounds reaches 10% of the upper bound.

Targets for conservation features were generated as follows (Extended Data Fig. 10). First, each conservation feature was intersected with both climate velocity and RCE maps to obtain its corresponding climate change condition in each planning unit. Then, for each conservation feature, we selected only the planning units in which the conservation feature experienced slow climate change. We defined slow climate change as values in the lowest quartile for each of climate velocity and RCE (that is, slow climate velocity and low RCE) within the range of the species under consideration (Extended Data Fig. 10). This process reduced the distribution size of each conservation feature (that is, the number of cells represented in the high seas) to one quarter of its initial distribution (Extended Data Fig. 10), yielding 'restricted' conservation features. Next, for each of these restricted conservation features, we assigned targets on the basis of the conservation status reported by the IUCN Red List[92]. For this, we used the R package rredlist[93] to obtain the IUCN classification for each conservation feature. For taxa reported as threatened (that is, vulnerable, endangered or critically endangered), every associated restricted conservation feature was assigned a fixed target of 100%[35] (that is, 100% of its distribution within the first quartile of our climate-smart metrics for its overall distributional range) (Extended Data Fig. 10). For conservation features not reported as threatened in the IUCN Red List, we assigned relative targets on the basis of the size of their global distribution (that is, the restricted conservation feature) represented in each depth domain, with a minimum of 10% for features with broad ranges and 100% for features with limited ranges (10–100% of its restricted distribution for each conservation feature) (Extended Data Fig. 10 and 'Sensitivity analyses'). We calculated these relative targets using the equation:

$$\mathrm{Target}(\%) = \mathrm{Target}_{\mathrm{max}}\,(\%) - \frac{\mathrm{PU}_i}{\mathrm{PU}_{\mathrm{total}}} \times \left[\mathrm{Target}_{\mathrm{max}}\,(\%) - \mathrm{Target}_{\mathrm{min}}\,(\%)\right]$$

where $\mathrm{Target}_{\mathrm{max}}$ and $\mathrm{Target}_{\mathrm{min}}$ refer to the maximum and minimum protection targets (%) for restricted conservation feature i, PU_i is the number of planning units represented for slow conservation feature i, and $\mathrm{PU}_{\mathrm{total}}$ refers to the total number of planning units for each high-seas depth planning region. By using relative targets instead of fixed targets, we ensured the representation of multiple areas where widely distributed restricted conservation features were conserved, as well as the protection of restricted conservation features within limited distribution ranges[35].

We created different prioritization planning scenarios to determine how the incorporation of climate change metrics (that is, slow climate velocity and low RCE) drives the selection of a climate-smart MPA network under alternative climatic futures. We ran three scenarios: one where we included restricted conservation features under SSP1-2.6, one with restricted conservation features under SSP2-4.5 and one with restricted conservation features under SSP5-8.5. The resultant mean and median targets (%) across scenarios and depth domains were 79 ± 12 ($n = 12$, ±s.d.) and 74 (70, 82; range as the first and third quartiles), respectively. Each prioritization scenario locked in protection in existing MPAs (data extracted from www.protectedplanet.net) and Vulnerable Marine Ecosystems (data extracted from www.fao.org).

To determine the spatial similarity of selected planning units among prioritization scenarios and depth domains, we calculated the Cohen's κ coefficient[94]. Cohen's κ is a pairwise statistic that indicates the degree of agreement among scenarios, ranging from −1 to 1, where −1 represents complete disagreement, 0 represents agreement due to chance and 1 represents complete agreement[94].

Sensitivity analyses. The total area protected in a prioritization analysis is highly correlated with the initial target assigned to each conservation feature. To test the sensitivity of our analysis, we tested different targets of protection for the climate-smart prioritization planning approach, with a minimum of 10% and sequentially adding 10% up to a maximum of 90% (10–90% of the restricted distribution for each conservation feature). This gave a total of seven new and different planning scenarios (Supplementary Table 2). For each set of targets (that is, planning scenarios) and for the base scenario, we performed a prioritization analysis using the R package prioritizr and the Gurobi software. As in the main design, we set Gurobi to achieve a solution within 10% of the optimum solution. Given that thousands of marine species were used in this study, a species-by-species and habitat assessment of vulnerabilities and sensitivities to all specific threats was not possible.

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

The data used in this study (except the AquaMaps biodiversity and geomorphic features data) are available at Zenodo[95] under the identifier https://doi.org/10.5281/zenodo.5912047. The AquaMaps[77] data are freely available via www.aquamaps.org. The geomorphic features[78] data are freely available via www.bluehabitats.org.

Code availability

All the scripts are available at Zenodo[95] under the identifier https://doi.org/10.5281/zenodo.5912047.

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Author contributions

I.B.-M., D.S.S. and A.J.R. conceived the research. J.D.E. generated the fishing cost layer. I.B.-M. analysed the data. I.B.-M. wrote the first draft with input from D.S.S., A.J.R., C.J.K. and D.C.D. I.B.-M., D.S.S., A.J.R., C.J.K., D.C.D., J.D.E., J.G.M., M.T.B., K.C.V.B., R.M.D. and H.P.P. contributed equally to the discussion of ideas and analyses, and all authors commented on the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

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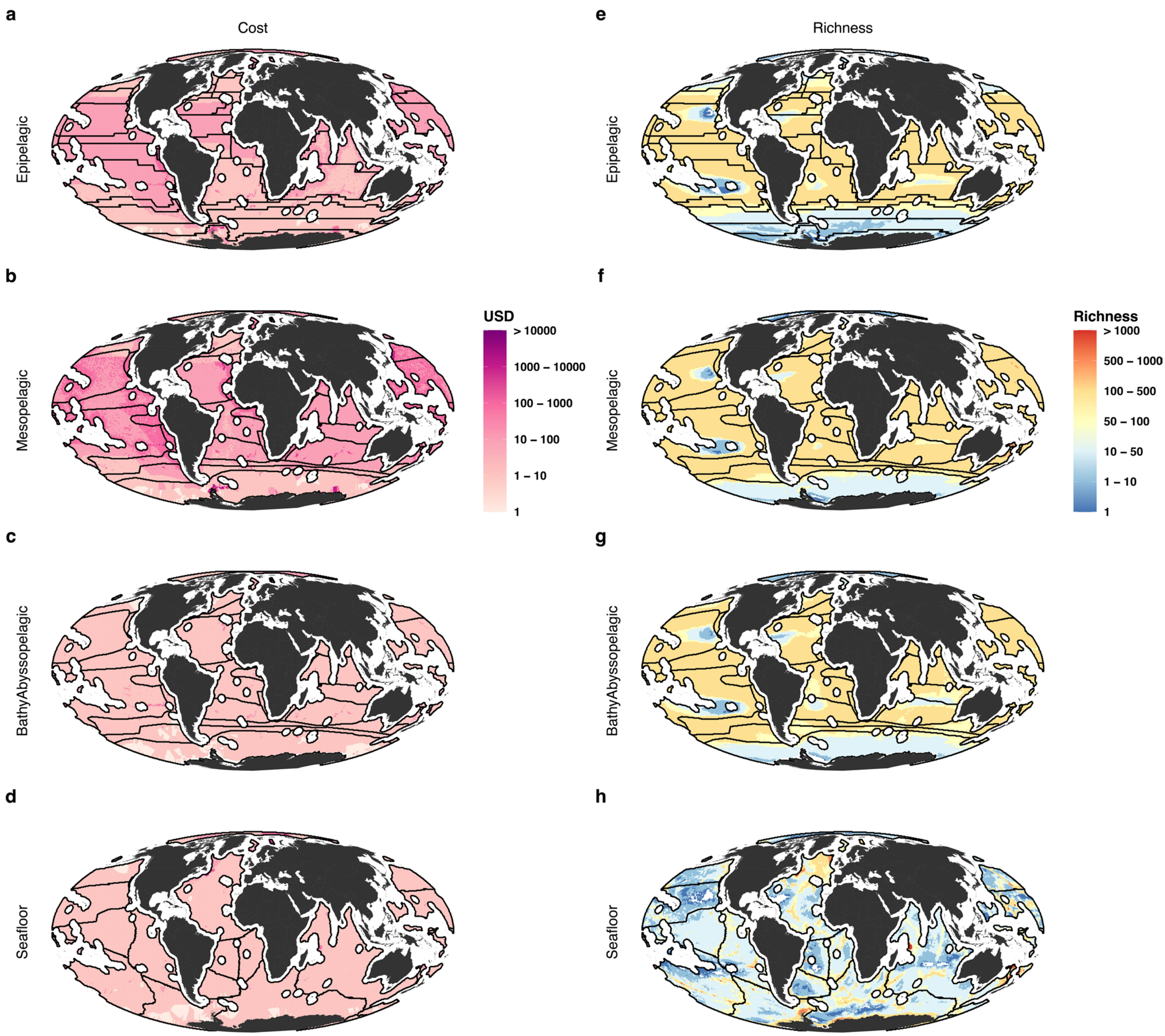
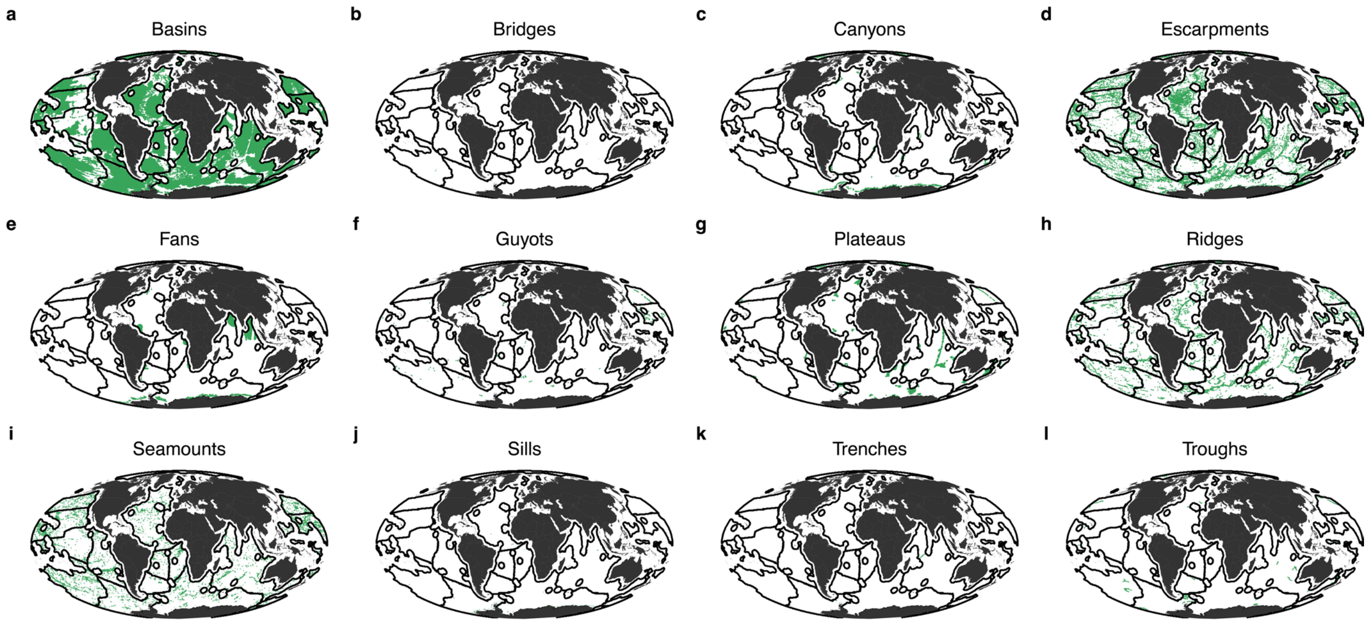
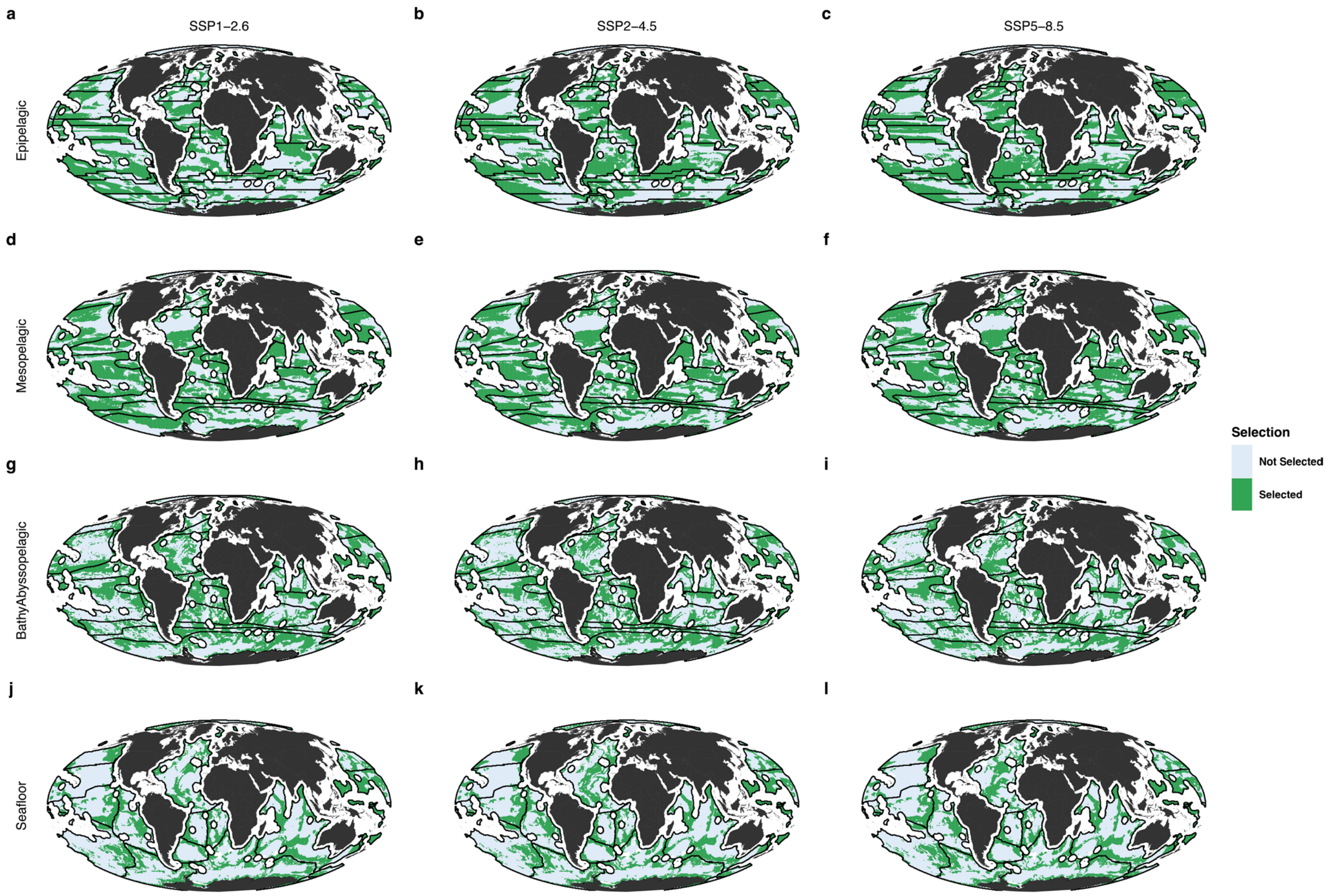


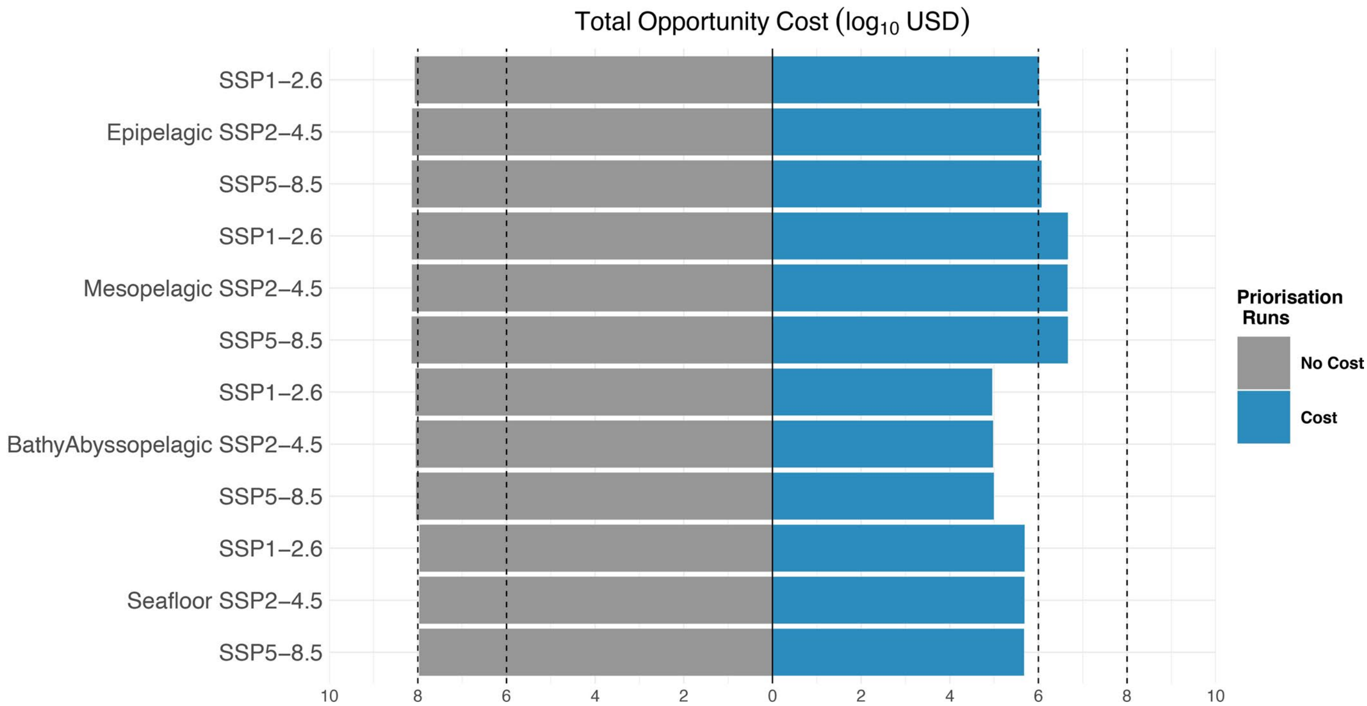
Extended Data Fig. 1 | Map of monetary value of fishing and biodiversity in the high seas. Opportunity cost of fishing (a, b, c, d) and species richness (number of species) with a probability of occurrence > 0.5 (d, e, f, g) in the high seas at four depth domains. Polygons represent Longhurst provinces for the epipelagic domain (a, e), Glasgow provinces for the mesopelagic (b, f) and bathyabyssopelagic domains (c, g), and the GOOD provinces for seafloor domain (d, h).



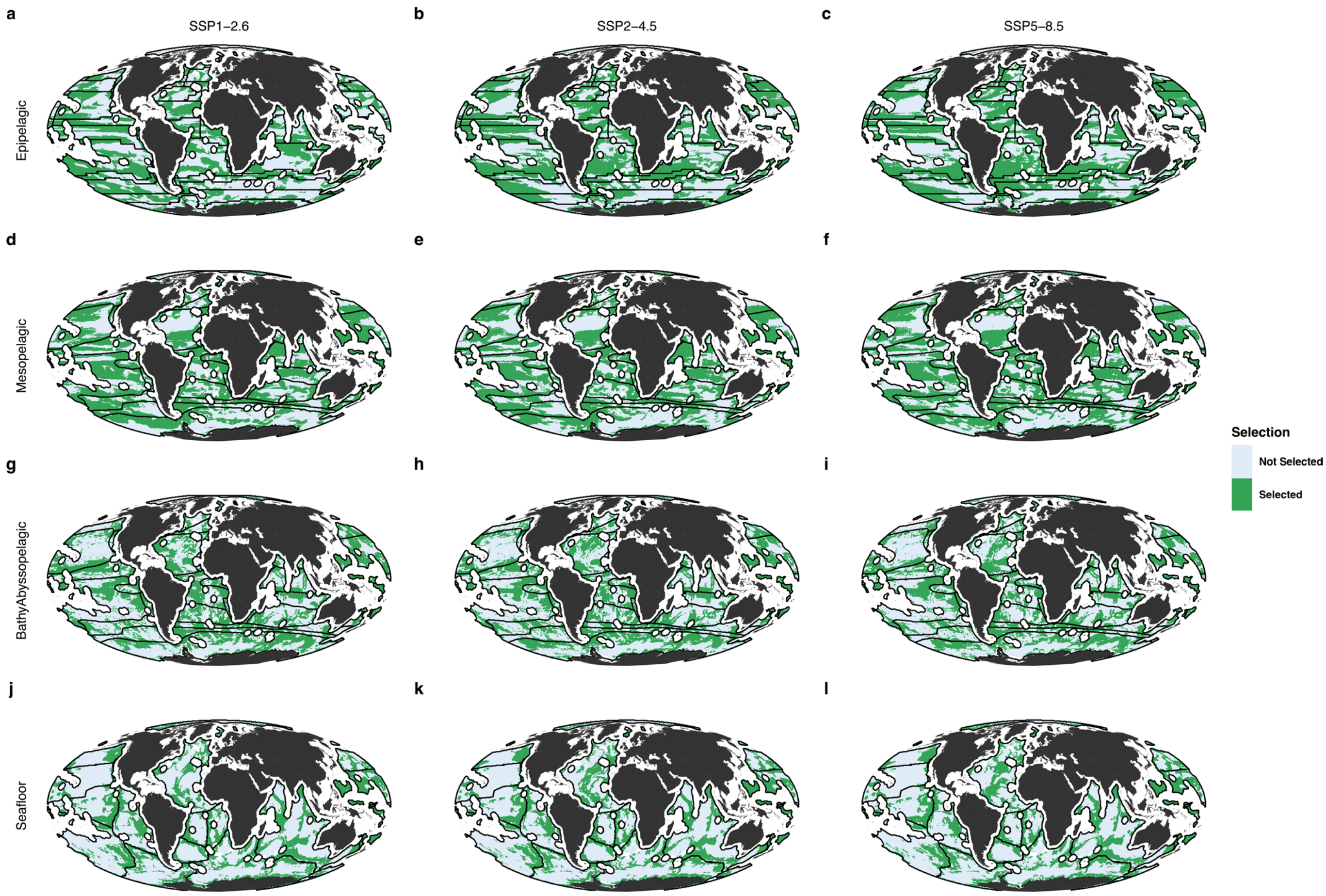
Extended Data Fig. 2 | Geomorphic conservation features in the seafloor domain[78]. For each map, green hexagons indicate the presence of each geomorphic feature in each planning unit. Polygons represent the GOODS provinces[87].



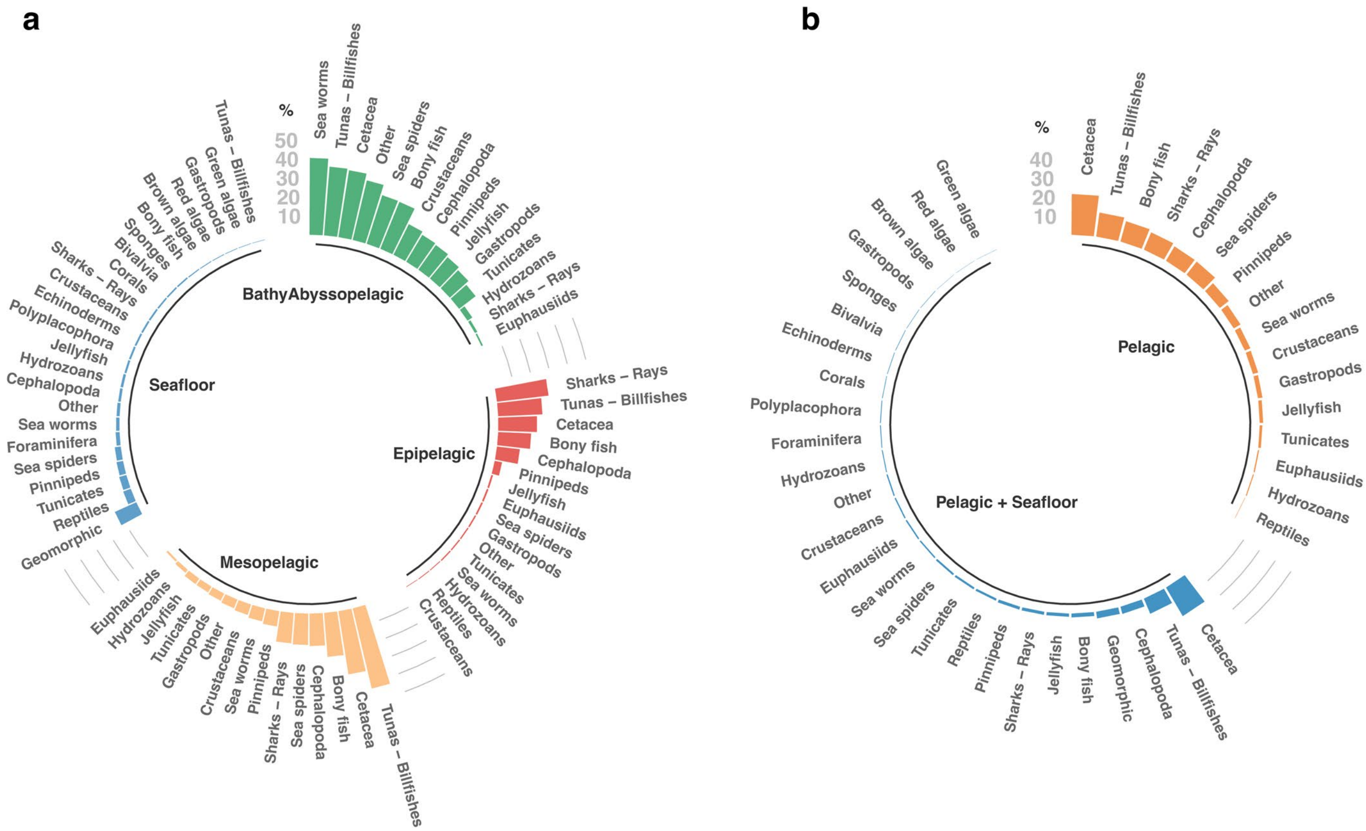
Extended Data Fig. 3 | Prioritised climate-smart networks in the high seas. Prioritised networks for the high seas at three pelagic depth domains and the seafloor, under three IPCC Shared Socioeconomic Pathways (SSP1-2.6, SSP2-4.5 and SSP5-8.5). For each map, green hexagons represent selected planning units while light blue hexagons represent non-selected planning units. Polygons in each map represent Longhurst provinces for the epipelagic domain (a, b, c), Glasgow provinces for the mesopelagic (d, e, f) and bathyabyssopelagic (g, h, i) domains, and the GOODS provinces for seafloor domain (j, k, l).



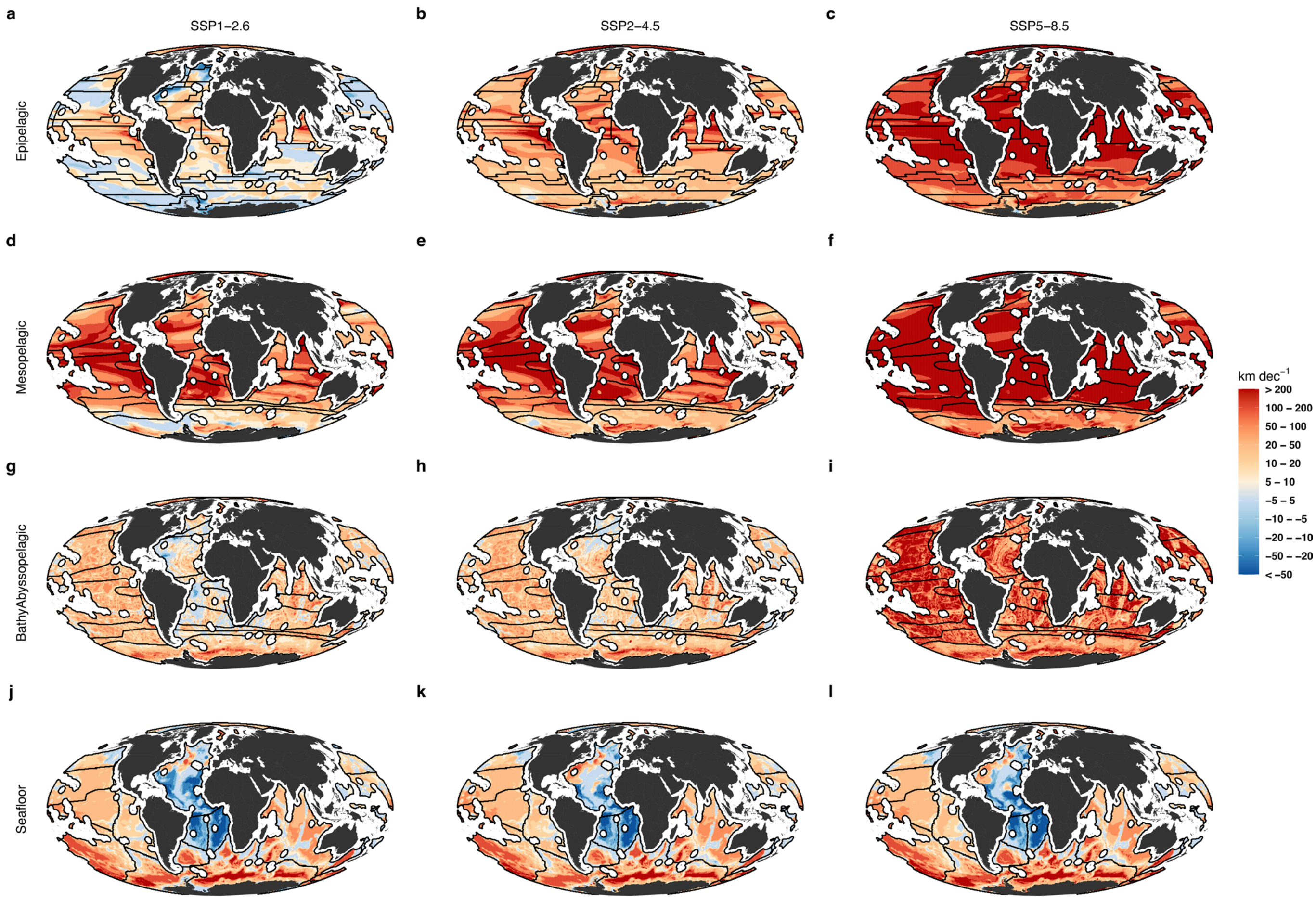
Extended Data Fig. 4 | The relationship between climate-smart networks with and without the cost layer. Total Opportunity cost among the prioritised base scenario (that is, no cost) and the climate-smart prioritisation scenarios under three IPCC emission pathways (SSP1-2.6, SSP2-4.5 and SSP5-8.5).



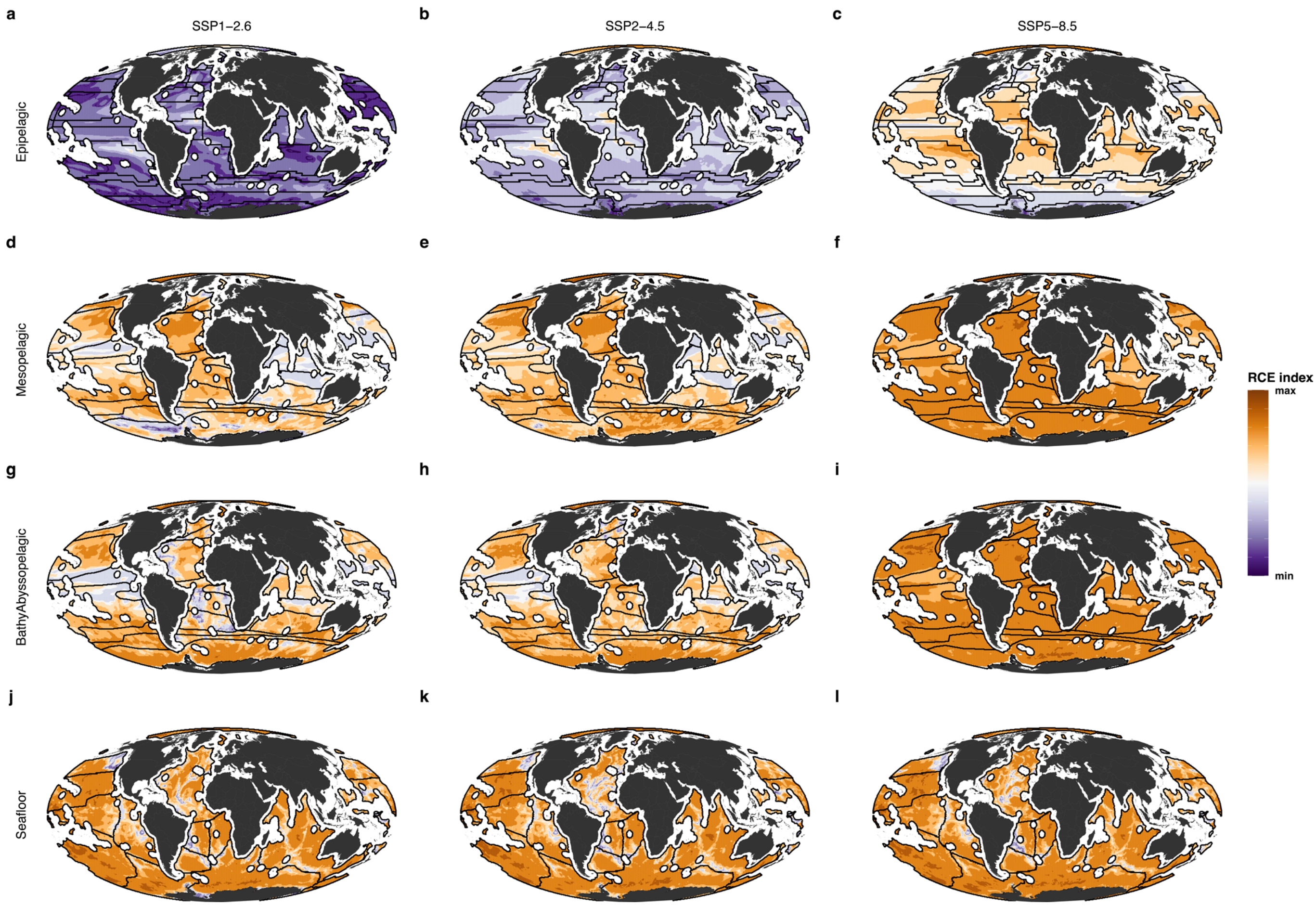
Extended Data Fig. 5 | Prioritised climate-smart networks in the high seas for the base scenario. Prioritised networks for a base scenario (that is, no cost) for the high seas at three pelagic depth domains and the seafloor, under three IPCC Shared Socioeconomic Pathways (SSP1-2.6, SSP2-4.5 and SSP5-8.5). For each map, green hexagons represent selected planning units while light blue hexagons represent non-selected planning units. Polygons in each map represent Longhurst provinces for the epipelagic domain (a, b, c), Glasgow provinces for the mesopelagic (d, e, f) and bathyabyssopelagic (g, h, i) domains, and the GOODS provinces for seafloor domain (j, k, l).



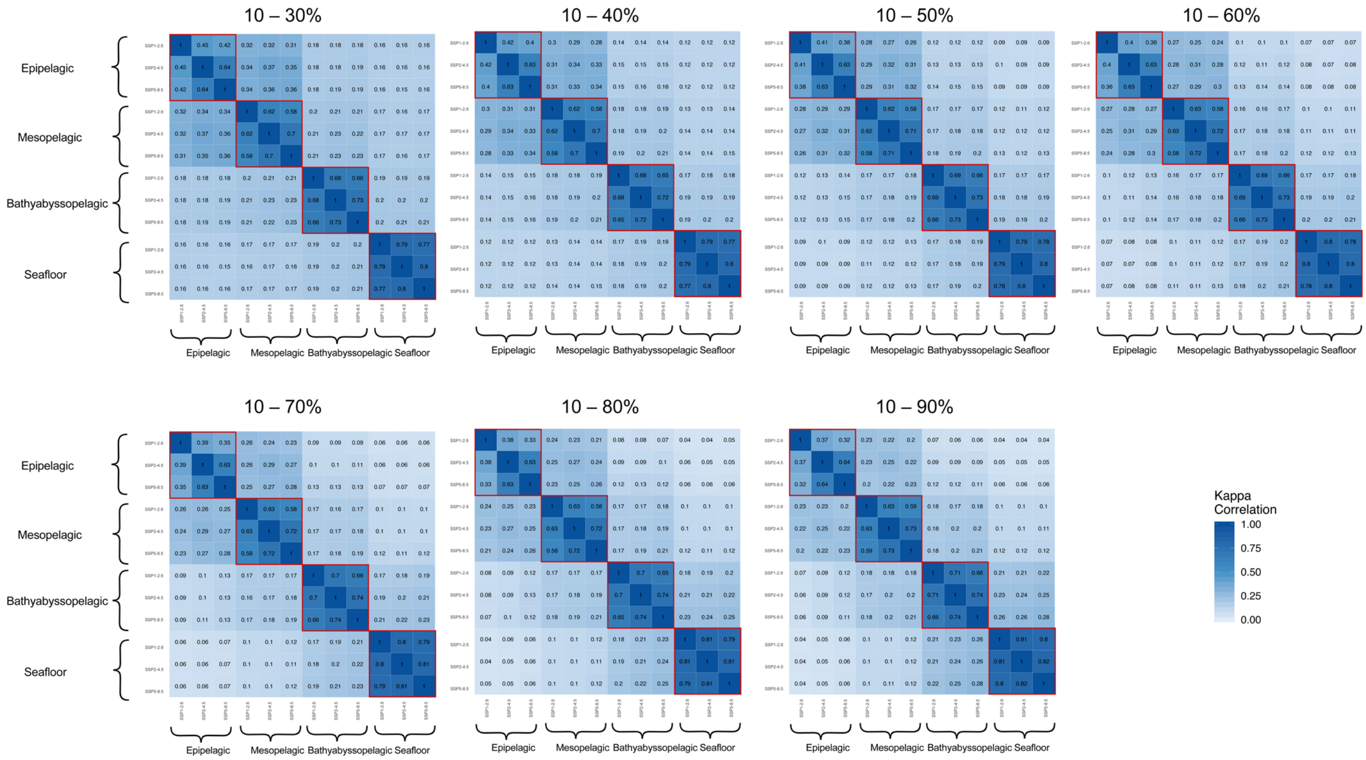
Extended Data Fig. 6 | Biodiversity representation for climate-smart networks in the high seas. Average taxonomic group representation (%) in low-regret conservation areas for three pelagic depth domains and the seafloor (a), and throughout the water column for the pelagic domains and pelagic plus the seafloor domain under three IPCC Shared Socioeconomic Pathways: SSP1-2.6, SSP2-4.5, and SSP5-8.5.



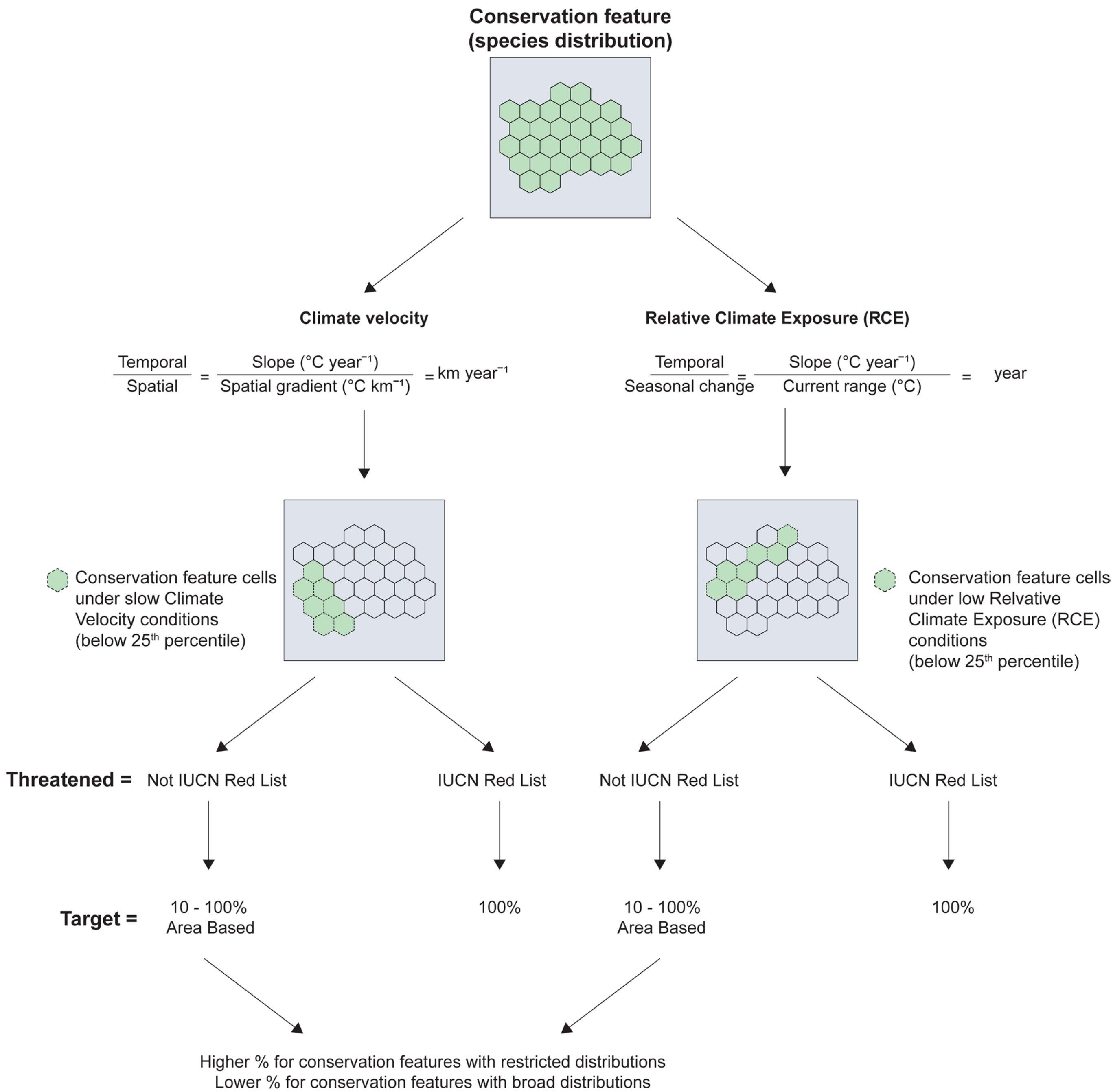
Extended Data Fig. 7 | Climate velocity in the high seas. Climate velocity (km decade^{-1}) in the high seas for projected sea temperatures (2050–2100) at three pelagic depth domains and the seafloor, under three IPCC Shared Socioeconomic Pathways (SSP1-2.6, SSP2-4.5 and SSP5-8.5). Polygons in each map represent Longhurst provinces for the epipelagic domain (a, b, c), Glasgow provinces for the mesopelagic (d, e, f) and bathyabyssopelagic (g, h, i) domains, and the GOODS provinces for the seafloor domain (j, k, l).



Extended Data Fig. 8 | Relative Climate Exposure (RCE) index in the high seas. RCE index (years) in the high seas for projected sea temperatures (2050–2100) at three pelagic depth domains and the seafloor, under three IPCC Shared Socioeconomic Pathways (SSP1-2.6, SSP2-4.5 and SSP5-8.5). Polygons in each map represent Longhurst provinces for the epipelagic domain (a, b, c), Glasgow provinces for the mesopelagic (d, e, f) and bathyabyssopelagic (g, h, i) domains, and the GOODS provinces for the seafloor domain (j, k, l).



Extended Data Fig. 9 | The degree of agreement between the climate-smart MPA networks for different sets of conservation targets. The Kappa index for the relationship between each prioritised climate-smart network MPA for different area-based protection targets under four depth domains: Epipelagic, Mesopelagic, Bathyabyssopelagic and the Seafloor. The percentages represent the minimum and maximum targets of protection in each prioritisation analysis.



Extended Data Fig. 10 | Process for setting climate-smart conservation targets. Schematic representation for setting targets for conservation features in the climate-smart prioritisation planning approach.

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Reporting Summary

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n/a	Confirmed	
☐	☒	The exact sample size (n) for each experimental group/condition, given as a discrete number and unit of measurement
☐	☒	A statement on whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
☒	☐	The statistical test(s) used AND whether they are one- or two-sided *Only common tests should be described solely by name; describe more complex techniques in the Methods section.*
☒	☐	A description of all covariates tested
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☐	☒	A full description of the statistical parameters including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)
☒	☐	For null hypothesis testing, the test statistic (e.g. F, t, r) with confidence intervals, effect sizes, degrees of freedom and P value noted *Give P values as exact values whenever suitable.*
☒	☐	For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
☒	☐	For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
☒	☐	Estimates of effect sizes (e.g. Cohen's d, Pearson's r), indicating how they were calculated

Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection	No software was used to collect data in this study. All data came from different existing sources listed in the Methods section.
Data analysis	We used CDO (climate data operators) and R 3.5.0 to analyse the data in this study. Codes and Scripts are available at Zenodo under the identifier https://doi.org/10.5281/zenodo.5510748

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors and reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Research guidelines for submitting code & software for further information.

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- Accession codes, unique identifiers, or web links for publicly available datasets
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Data used in this study can be found at Zenodo under the identifier https://doi.org/10.5281/zenodo.5510748

Field-specific reporting

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Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	We collected and used global ocean data on climate models, biodiversity, and fisheries and conducted climate-smart 3D prioritisation analyses to identify a global climate-smart network of marine protected areas across different ocean depths
Research sample	We used data on: Climate models: Coupled Model Intercomparison Project Phase 6 (Earth System Grid Federation, https://esgf-node.llnl.gov). The ensemble model for each climate scenario and depth domain as been provided in the Zenodo repository. Bathymetry: ETOPO1 Global Relief Model. Included in the Zenodo repository Biodiversity: AquaMaps (standardized distribution maps) and IUCN Red List. These dataset are not provided in the Zenodo repository but can be downloaded from https://www.aquamaps.org/ and https://www.iucn.org/ Marine provinces: Longhurst Provinces from Marine Regions (www.marineregions.org), Glasgow Provinces from Sutton et al. (2017), and the GOODS provinces (Global open oceans and deep seabed: biogeographic classification). These datasets have been provided in the Zenodo repository Fishing data: Sea Around Us and FishBase datasets. Data layers with the costs per fishing are included in the Zenodo repository. Marine Protected Areas from protected planet. Not included in the repository but free available at www.protectedplanet.net Vulnerable Marine Ecosystems from FAO. Not included in the repository but free available at www.fao.org
Sampling strategy	We used all free available databases that contained global information which allowed us to conduct our 3D climate-smart prioritisation analyses
Data collection	Data were obtained from online repositories. The previous section describes the sources and availability.
Timing and spatial scale	We used the most recent databases. Sea temperature from climate models (IPCC Shared Socioeconomic Pathways) range from 2020 to 2100. The previous section describes the sources and availability.
Data exclusions	No data were excluded from our study
Reproducibility	N/A - No experiments were performed
Randomization	N/A - No experiments were performed
Blinding	N/A - No experiments were performed

Did the study involve field work? ☐ Yes ☒ No

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study
☒	☐ Antibodies
☒	☐ Eukaryotic cell lines
☒	☐ Palaeontology and archaeology
☒	☐ Animals and other organisms
☒	☐ Human research participants
☒	☐ Clinical data
☒	☐ Dual use research of concern

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
☒	☐ MRI-based neuroimaging