Climate change will displace habitats prioritised for marine protected areas in the high seas

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Abstract

A redistribution of marine biodiversity with climate change may compromise the effectiveness of static marine area-based management tools (ABMTs). Under the High Seas Treaty, EBSAs (Ecologically or Biologically Significant Areas) are first candidates for new ABMTs. Here, we explore the projected shifts in habitat conditions from low to high carbon emissions scenarios for high seas EBSAs. We find that the distance of geographical shifts by EBSA habitat conditions can nearly triple by 2100, depending on emissions scenario, but none sustain Arctic EBSAs. Under low emissions, 94% of analysed EBSAs are likely to retain at least half of their original habitat. Habitat persistence declines to 78% and 57% of EBSAs under medium and high emissions, as habitat velocities increase 2.5-4-fold. Only about a third of high seas EBSAs appeared suited for static protection. In most other cases, the inclusion of nearby, equivalent habitats would allow protection of original EBSA conditions. Next to emissions scenario, geographical location and size predicted EBSA habitat suitability. Our analyses demonstrate the importance of carbon emission reduction and of dynamic protection measures for effective protection of marine biodiversity.

Introduction

Marine biodiversity provides society with resources and services but is under severe pressure from human impacts (UN, 2026). One effective way to protect it from fishing, pollution, and mining is by area-based management tools (ABMTs; including marine protected areas, MPAs) (Bates et al., 2019; Maxwell et al., 2020). However, few ABMTs consider the biodiversity redistributions anticipated from anthropogenic climate change (Brito-Morales et al., 2022; Garciá Molinos et al., 2015; IPCC, 2019). Marine waters beyond national jurisdiction present a particular challenge for ABMTs, being unbound to fixed seabed features, difficult to police, and complex to govern in multilateral regimes (De Santo, 2018; Fourchault et al., 2024; Visalli et al., 2020). Nevertheless, the protection of their ecosystem services, including food and genetic resources, is of global importance. Entering into force January 2026, the High Seas Treaty (also known as the 'BBNJ Agreement') (UN, 2023) anticipates a major role for ABMTs. These will help meet the protection target of 30% of land, waters and seas by 2030 ("30 x 30", Global Biodiversity Framework Target 3) set by the Kunming-Montreal Global Biodiversity Framework (CBD, 2022).

Since 2011, the Secretariat of the Convention on Biological Diversity has coordinated regional workshops to agree high ecological value areas, called Ecologically or Biologically Significant Marine Areas (EBSAs) (CBD, 2021; Dunn et al., 2025). EBSAs must meet at least one of seven criteria (Bax et al., 2016; Dunstan et al., 2016; Harris et al., 2022), rarity of taxa, communities, or habitat, importance for life history stages, threat, vulnerability, productivity, diversity, and naturalness, which all emphasise a uniqueness of biological and environmental features. EBSAs owe their political success to this easily applicable approach without considering management goals (Dunn et al., 2025; Harris et al., 2022; Johnson et al., 2018). Although management goals were excluded from the EBSA process, EBSAs are now discussed as viable candidates for new ABMTs under the High Seas Treaty (e.g. Prip, 2022). However, their vulnerability to climate change is unclear (Visalli et al., 2020), despite the availability of state-of-the-art climate projections (Assis et al., 2024). With the recently ratified High Seas Treaty, more knowledge is needed on spatial prioritisation of potential ABMTs in areas beyond national jurisdiction in the face of climate change (Jones et al., 2016). While success in previous MPAs was linked to their age and size (Edgar et al., 2014), these characteristics may change as climate change progresses. Here, we analyse the future of habitats covered by EBSAs under climate change forecasted for different greenhouse gas emissions scenarios (Shared Socioeconomic Pathways, SSPs), until 2100.

Climate-driven changes of biodiversity, including those within MPAs, can be anticipated by modelling how the environmental variables supporting species' habitats shift (Beaugrand et al., 2015; Garciá Molinos et al., 2015; Hodapp et al., 2023). Forecasting habitat shifts for individual species often requires species-specific modelling to fully parameterise their niches (Elith & Leathwick, 2009; Hodapp et al., 2023). However, species-specific models often underestimate documented range shifts (Oliveira et al., 2026). Meanwhile, occurrence databases often focus on larger or higher trophic level species, miss difficult-to-sample environments including the open ocean, and may underestimate wider, ecosystem-level changes (Jones et al., 2016). Instead, expectations of how species in general are challenged as their ranges shift can be revealed by purely physical, spatio-temporal metrics like marine climate velocity (Burrows et al., 2011; Garciá Molinos et al., 2015). Indeed, temperature is a fundamental driver of individual species and assemblage changes (Antão et al., 2020; Benedetti et al., 2021; Pinsky et al., 2025). While often predicting changes in species richness and composition, changing habitat variables may also indicate more difficult-to-quantify changes in dominance and abundance (Beaugrand & Kirby, 2018; Hillebrand et al., 2018).

Of all 338 EBSAs, 45 are in transboundary areas (both within and beyond national jurisdiction) and 22 are solely in the high seas, excluding those with a purely benthic focus. We consider these 67 EBSAs, covering nearly 70 of the 200 million km^2 of ocean beyond national jurisdiction. As climate change progresses, we expect that many static protected areas will cumulatively lose their similarity to their original defining habitat. Thus, these areas will be losing the environmental conditions they presented when originally proposed as an EBSA, likely challenging originally resident species. Although various environmental conditions can drive species range shifts, we concentrate on annual means of sea surface temperature, salinity, and chlorophyll, which are dominant drivers of organism distributions over broad spatial scales (e.g. Hodapp et al., 2023). We trained machine learning, habitat suitability models to best distinguish the environment within each EBSA boundary from background environment during a temporal baseline (the 2010–2020 decade). We validate the fitting of each EBSA habitat

model via historical hindcasting, testing its predictions against EBSA configurations, before projecting habitat changes for each decade until the end of the century. We assess what characteristics of EBSAs maintain a high habitat suitability by 2100 for each SSP, i.e. what makes an EBSA 'climate-proof'. We expected the rate of losing habitat similarity, and velocity travelled by habitat conditions matching the original EBSA, to increase with higher SSPs. We also expect static ABMTs to be insufficient for protection in some regions under projected climate change, especially in equatorial and polar areas. However, we anticipate that the area covered by original habitat could be maintained, on average, if EBSA boundaries dynamically track equivalent environmental conditions shifting outside existing boundaries, except at high latitudes where suitable analogues disappear. Our results indicate which EBSAs might provide most effective biodiversity protection with static boundaries and which might require more flexible management solutions.

Results

EBSA habitat fidelity

We quantify habitat similarity to EBSA baseline conditions in two ways. Firstly, we used the mean probability of habitat suitability within the EBSA's spatial boundaries. At baseline conditions, this probability averages 0.7 (Fig. S2A) rather than 1, reflecting model specificity (influence of environmental heterogeneity and environmental overlap of EBSA with its surroundings). Mean habitat suitability by 2100 was low for Arctic EBSAs but varied for tropical EBSAs (Fig. 1, Fig. S1). Over time, EBSA mean habitat suitability tended to decline in any scenario, but the shape of the trend curve depends on SSP (Figs. 2A, S3, Table S1A). If global emissions are kept low, average EBSA habitat suitability plateaus during the 2060s before beginning recovery, trending back towards baseline conditions. The trajectory after 2030 under high emissions is closer to linear, with no clear deceleration. Change in habitat suitability under medium and high emission scenarios was mostly driven by temperature change from the EBSA's baseline (Table S3A).

EBSA habitat area change

By binarizing the probability of habitat suitability about an EBSA-specific threshold, we calculate the area of most-likely suitable habitat within the EBSA's spatial boundaries, given relative to its baseline area as the *relative suitable area* (see Methods). If emissions are kept low, 63 of the 67 EBSAs, or 94%, maintain at least half their original suitable area by 2100, and only EBSAs from the Arctic, North-West Indian Ocean, and Eastern Pacific regions show significant declines. Even at this low emission scenario, three northern high latitude EBSAs suffer severe decreases to < 10% suitable area already by the 2050s to 2070s (the two Arctic and the North-East Atlantic Rockall EBSAs: ARC_1, ARC_2, and NEA_17; Fig. S5, Fig. 1, Table S1B). Under medium and high emissions, the proportion of EBSAs with at least half their area suitable by 2100 declines to 77.6%, and 56.7%, respectively (Table S2).

Drivers of EBSA habitat suitability to climate change

Random forest models predicting EBSA habitat suitability by 2100 identified geographical region and latitude as the most important predictors across all SSPs, although unexplained variance increased rapidly with higher SSPs (Fig. 3A). Regional rankings based on average annual change in habitat suitability were broadly consistent among SSPs. The main exception was the Mediterranean, which increased from intermediate EBSA susceptibility under low emissions to the second-most susceptible region under high emissions (Fig. 3B). By contrast, losses in habitat suitability were not significant for EBSAs of the Western South Pacific, North-East Indian Ocean, and Western Mid-Atlantic under any emissions scenario (Fig. 3B). Random forests agreed that EBSAs north of 52°N lose habitat suitability, with this latitudinal threshold shifting southwards to 37°N with medium or high emissions by 2100 (Table S6). The importance of other EBSA characteristics varied among SSPs (Fig. 3A). Under low and medium emissions, the contribution of temperature to EBSA uniqueness was the third-most important predictor of habitat-suitability change. Under high emissions, this was replaced by EBSA area as the third-most important predictor, with larger areas associated with greater maintenance of habitat suitability (Fig. 3A). Specifically, most EBSAs smaller than 49,500 km^2 lost habitat suitability under medium or high emissions, while this threshold increased to 288,000 km^2 under high emissions (Table S6).

Distance and direction of change

The distance shifted by EBSA habitat centroids provides an estimate of how far protected areas would need to move per year to protect the status quo of present-day habitat conditions. This distance increases with time and higher SSPs as climate change progresses (Figs. 2B, S7; Table S1D). Centroid movements tended not to align with a simple north-south direction, instead following the often-oblique trajectories of climate velocities (Fig. S8, Table S4). Under low and medium emissions, movement rates are most rapid early this century but gradually slow by the end of the century, even beginning to retreat under low emissions (Fig. 2B). They nevertheless average 147.5 ± 113.8 km and 349.2 ± 231.3 km (median ± MAD), respectively, from their original positions by the end of the century. However, under high emissions, distances increase unabated, reaching 483.8 ± 319.2 km from their original positions by 2100. Distances shifted by habitat centroids from each EBSA's baseline were particularly driven by SSP-dependent temperature changes, while chlorophyll change had a strong but highly variable influence (Table S3B).

Change beyond EBSA boundaries

In the high emissions scenarios, habitat matching the EBSA baseline conditions is often projected to lie outside their original boundaries, but within the potential species dispersal range (see Methods) (Fig. S6, Table S1C). Thus, protecting these equivalent nearby habitats could be an effective dynamic strategy to protect components of the EBSA's original biodiversity. Of those EBSAs unlikely to meet 50% of their original suitable area within their boundary, an increasing proportion of 20% under medium emissions, and 34% under high emissions could meet 50% suitable area if given dynamic boundaries. The average dynamism required increases with higher SSPs, with median (± MAD) rates of habitat shift of 13.2 ± 14.7, 39.1 ± 29.0, and 65.6 ± 43.1 km per decade respectively under low, medium, and high emissions (Fig. 4). Original habitat conditions for one Arctic and one North-Atlantic EBSA disappears entirely in all scenarios (Fig. S6).

Discussion

Our results quantify the climate change impacts for high seas EBSAs and show, how higher emissions increase their rate of habitat change, widen the distance between present and future habitat conditions, and increase the chance that original EBSA habitat conditions will regionally disappear. These projected environmental changes are consistent with studies on climate-induced species range shifts (Benedetti et al., 2021; Garciá Molinos et al., 2015; Hodapp et al., 2023). This is expected as the predicted changes in species distributions and habitat conditions are based on similar climate change projections.

The habitat conditions characterising EBSAs in the open ocean will change for the rest of the century and beyond, to the extent that the static protection of baseline conditions is on course to miss its purpose for more than half of EBSAs by 2100, assuming a medium emissions scenario. This result has two major implications: First, emissions reduction remains a very effective way to minimise the changes projected for high seas ABMTs (Bates et al., 2019; Hodapp et al., 2023). Emissions reduction increases chances that ABMTs (such as MPAs) based on EBSAs protect the habitat they were proposed for. Furthermore, emissions reduction may be critical to maintain polar-type habitat. Second, climate change transforms the design requirements for biodiversity protection, so that adaptive and dynamic ABMTs are required, for example by dynamic MPAs following the species and ecosystems they are intended to protect. Dynamic protection measures would still be necessary even if anthropogenic greenhouse gas emissions were reduced to zero, because of the time lag in the reaction of the climate system (Lee et al., 2026) leads habitats to still shift geographically. Hence, a combination of emission reduction and dynamic protection measures is the most effective way to protect marine biodiversity from climate change impacts

By tying emissions scenario to habitat change in ABMTs, our results imply that each year of continued high emissions increases the probability that conservation measures will be applied to a location for which the ecological target that motivated protection in the first place has already moved away. Continued high emissions also increase the likelihood of permanent ecological change (Beaugrand et al., 2015; Yasuhara et al., 2020), including species extinctions (IPCC, 2019). Higher global emissions increase uncertainty in predicting climate change impacts (requiring more precautionary and thereby more difficult decision-making) and increase the need for ABMTs to be larger, and/or more dynamic, to maintain their effectiveness (Fig. 4) (Tittensor et al., 2019). Meanwhile, lower emissions limit climate change pressure on species, even initiating recovery before the end of the century in some EBSAs. Climate mitigation and marine protection should therefore not be treated as separate agendas.

Consistent with the accelerating divergence in biodiversity responses among emissions scenarios seen in other marine climate studies (Beaugrand et al., 2015; Garciá Molinos et al., 2015), our results indicate that differences among emissions scenario futures are not proportional over time, rather, they widen as climate change accumulates. This means that, particularly under medium-to-high emissions trajectories, the length of delay between assessment of an area as worthy of protection and the legal implementation of this protection may determine whether the protection area remains ecologically relevant. Our results allow for sorting EBSAs according to their expected persistence (Table S7), rather than assuming that all EBSAs will retain similar conservation value over a common planning horizon.

Only about a third of the analysed high seas EBSAs, often the larger ones, appeared climate-proof regardless of emissions scenario (relative suitable area > 87.5% by 2090 under SSP 3-7.0), clearly qualifying them for static MPAs sensu climate-refugia (Brito-Morales et al., 2022). These included the Atlantic Equatorial Fracture Zone (WC_20), the Upwelling System of Papagayo and adjacent areas (ETTP_7, 64% within national jurisdiction, Eastern Pacific), and The Sargasso Sea (WC_21). Large EBSAs beyond national jurisdiction often encompass the full dynamic or ephemeral nature of oceanographic features, partly because they reflect the scale at which important open-ocean processes operate (Dunn et al., 2025). Hence, large MPAs may offer advantages for ecological representation, connectivity and resilience, and our findings add climate-proofing to that list (Edgar et al., 2014; Weaver & Johnson, 2012). These aspects interact, with climate change able to decrease larval connectivity in MPAs by 50% (Arafeh-Dalmau et al., 2023), so that larger MPAs may offer disproportionately higher value under climate change.

Around ten high seas EBSAs may be unsavable in the sense of retaining their initially surveyed conditions (relative suitable area < 10% by 2090 under SSP 2-4.5), including the Northern Lord Howe Ridge Petrel Foraging Area (SP_20, South Pacific), and South of Java Island (SIO_38,

Southern Indian Ocean). Here, consequences are likely for ecosystem functioning and services (Tittensor et al., 2019), such as the unique spawning habitat for the southern bluefin tuna in SIO_38. The number of unsustainable EBSAs increased to 15 with high global emissions. The protection of unique Arctic ecosystems is a special case (Wenzel et al., 2016). Arctic conservation planning should recognise that the present-day environmental conditions are highly likely to disappear within decades, regardless of the emissions scenario, leading to ecosystem changes effectively permanent on human timescales (IPCC, 2019). Although no EBSAs were designated south of 60°S (Wenzel et al., 2016), evidence from past rapid warming suggests that extinctions of polar taxa are a general feature of global warming (Reddin et al., 2022). Under low emissions, however, a late-century climatic stabilisation or recovery could allow Arctic habitat conditions eventually to return towards their 2010-2020 baselines. Protecting Arctic ecosystems and species in the meantime would maximise their resilience and recovery potential, potentially averting extinctions, in a climate reversal scenario (Wenzel et al., 2016).

For the remaining high seas EBSAs, projections were perhaps less bleak, but still indicated substantial change, likely requiring dynamic management schemes, for instance the important tuna habitat Zone de Production Equatoriale de Thons (SEA_30, Central Atlantic). Where environmental conditions are projected to shift rapidly (Hodapp et al., 2023), protected areas should be designed to track the relevant ecological features rather than remain fixed to areas that lose their original conservation value. Although static protection may be appropriate for EBSAs with relatively stable habitat conditions (Dunn et al., 2016; Wright et al., 2019), our analysis suggests that a universal spatially-fixed approach will increasingly mismatch the biodiversity it is intended to protect. EBSAs based around seasonal fronts, migratory corridors, or other features that already move in space or time may need particular flexibility as climate change advances (Brito-Morales et al., 2022; Dunn et al., 2025; Johnson et al., 2018). This is especially so in tropical marine regions, where climate-driven species turnover is expected to be high (Blowes et al., 2019; Hodapp et al., 2023; Reddin et al., 2022; Yasuhara et al., 2020) yet where data availability is relatively low (Menegotto & Rangel, 2018).

Flexible and dynamic protection of marine biodiversity could include periodic boundary review, scenario-based boundary setting, seasonal rules, inter-connected ABMTs, nested designs that combines a static core with adaptive surrounding measures, or shifting whole ABMTs/MPAs to respond to shifts in the occurrence of protected species or ecosystems (Bates et al., 2019; Brito-Morales et al., 2022; Hannah et al., 2024; Jones et al., 2016; Tittensor et al., 2019). These solutions require a substantial amount of data and monitoring (Roe et al., 2022), and our directional analysis shows how the direction of habitat shift needs reviewing for each EBSA individually (Table S7). Compared with coastal or terrestrial protected areas, high-seas ABMTs may opportunely face fewer stakeholders competing for their resources, potentially increasing the chances of their implementation. However, conflicts may emerge if spatially-adaptive ABMTs intersect with existing or future stakeholder interests, making early coordination important (Hannah et al., 2024). Legal implementation of protective measures in areas beyond national jurisdiction remains challenging (Dunn et al., 2025; Wright et al., 2019) and will likely depend on regional governance capacity.

Several limitations of this study should be considered. First, our models are based on broad environmental envelopes, which have an established role in climate change ecology, especially at broad spatial scales (Beaugrand et al., 2015; Brito-Morales et al., 2018; Burrows et al., 2019; Pinsky et al., 2013). Temperature is a fundamental driver of broad-scale biodiversity change (Antão et al., 2020; Benedetti et al., 2021; Hodapp et al., 2023; Lenoir et al., 2020; Pinsky et al., 2025); however, environmental envelopes do not explicitly capture species interactions, population differences, dispersal ability and limits, climate variability and phenology (Hodapp et al., 2023; Jones et al., 2016; Oliveira et al., 2026). Some high seas EBSAs are also tied to static seabed features, like sea mounts and ridges. Our projections may therefore represent an optimistic estimate of ecological trackability, especially at higher global emissions (Arafeh-Dalmau et al., 2023), by assuming that species can track their general abiotic preferences.

Second, climate change is inherently broad-scale in space and time, so we used relatively coarsely-gridded environmental data. This resolution may reduce precision for smaller EBSAs, although even the smallest EBSAs analysed here (~6600km^2) covered more than 300 environmental grid cells, allowing substantial environmental heterogeneity. Thirdly, although established habitat suitability models like Maxent remain highly competitive with newer approaches (Kellenberger et al., 2026), deep learning may allow utilisation of a broader informational array than numerical environmental data. Finally, our projections do not consider ecological impacts of extreme, short-term events (Jones et al., 2016). These caveats mean that our projections should be interpreted as a precautionary screening tool for ABMTs, supporting a “precautionary approach” required in the BBNJ Agreement (UN, 2023, Art. 7), rather than as final design specifications for individual EBSAs.

By presenting a moving target, the large-scale redistribution of life under anthropogenic climate change poses a profound challenge for effective biodiversity conservation (Garciá Molinos et al., 2015). We demonstrate that linking area-based protection with climate adaptation (Global Biodiversity Framework Targets 3 and 8, respectively), to anticipate high seas biodiversity changes over the coming century and beyond, is essential for effective conservation of the high seas (Brito-Morales et al., 2022; Tittensor et al., 2019).

Methods

Environmental and EBSA data

Annual means of sea surface temperature, salinity, and chlorophyll were downloaded between 19th and 24th November 2025 from Bio-ORACLE v3 as NetCDF files for the globe at 0.05° spatial resolution, using the BiooracleR package (Assis et al., 2024). These variables are projections from the Coupled Model Intercomparison Project Phase 6 (CMIP6), integrating over an ensemble of approximately 50 models. The temporal coverage was the recent two decades 2000-2010 and 2010-2020, and the future decades from 2020-2030 until 2090-2100 for three SSPs 1-2.6, 2-4.5, and 3-7.0. These files were converted to raster files to facilitate handling in R, using packages *sf, sp* and *terra*. The decade 2010-2020 was used as the environmental baseline, for training the habitat suitability model, since most EBSAs were proposed as candidates to the Convention on Biological Diversity during this timeframe (e.g. Roe et al., 2022). To use later as a covariate, we calculated the change in environmental variable means relative to their baseline means. The decade 2000-2010 was kept as a testing dataset. The boundaries of EBSAs were downloaded as shapefiles (.shx), or in the case of the North-East Atlantic region, geoJSON files (.json) from the EBSA repository of the Convention on Biological Diversity (https://www.cbd.int/ebsa/repository/) between 11th and 15th April 2025. Additional EBSA details were sourced from Appendix A of Dunn et al. (2025). We excluded EBSAs with zero area beyond national jurisdiction, which included all Baltic Sea, Black and Caspian Sea EBSAs, and excluded EBSAs intended solely to protect benthic habitat, which removed the remaining East Asian Seas EBSA. This narrowed the original total of 336 EBSAs to a subset of 67 EBSAs that had a median 74% of their area beyond national jurisdiction.

EBSA habitat suitability modelling

We considered our EBSA-habitat modelling as presence-only since the habitat (combination of temperature, salinity, and chlorophyll) inside the EBSA boundary was known (Fig. S9). While environmental conditions were available throughout the study region, it was unknown whether the combination of conditions characterising each EBSA occurred exclusively within the EBSA boundary (i.e. habitat absence outside EBSA is true) or also in surrounding areas (i.e. habitat present outside EBSA but not identified as part of the EBSA). We chose the machine-learning algorithm Maxent as the habitat suitability model for its well-documented discrimination ability (Elith et al., 2011; Phillips et al., 2006), maximising the ratio between the probability densities of presences (e.g. of a species, of an EBSA) against those of background points across the environmental gradients. We used the implementation of Maxent available in R package *predicts (Hijmans, 2024)*. 500 raster cells or, for smaller EBSAs, as close to this total as possible (>300 cells) were randomly sampled without replacement from within the EBSA boundaries, and used as 'presence' points. For background sampling, we adopted a widely used approach that is the default setting for Maxent in the package *predicts* (Hijmans, 2024; Waldock et al., 2022). This was to extract 10,000 background points randomly sampled from the marine environment within and surrounding each EBSA, so long as they were within a buffer distance considered reachable by species range shifts by the end of the century. This buffer distance was calculated using the mean velocity of the leading edges of species ranges reported in Poloczanksa et al. (2013). Although the most rapid range shifts therein were reported for phytoplankton, phytoplankton are rarely if ever targets for marine protected areas, so the slightly lower leading-edge range shift estimates for bony fishes were used instead (277.5 ± 76.9km dec^{-1}, or ~2497.5km by 2100, rounded to 2500km) (Poloczanska et al., 2013). These distances are similar to but slightly higher than a more recent compilation (Lenoir et al., 2020).

Maxent uses nonlinear and interactive functions of environmental variables, known as 'features', to capture their complexity, while using regularisation to manage overfitting. To give a smoother predictive function of the environment that better resembles how water masses mix over EBSA boundaries, hinge and threshold features of Maxent were not used. Moreover, it was considered unlikely that species populations (i.e. abundance, biomass) were so sharply restricted by the environmental conditions within the EBSA boundaries, but more likely that most species had ranges continuing outside the EBSA boundaries via their wider climate envelopes.

Model evaluation used 2000-2010 environmental data as out-of-bag testing data where the location of the EBSA habitat was known. Predictions of EBSA habitat conditions were compared with 10,000 random absences from within and outside the EBSA (again, within a 2500km buffer) and 500 presences from within the EBSA. From these were used to calculated true positive rate (sensitivity) and true negative (specificity) rate, used to calculate the overall diagnostic power (ODP), and Area Under the receiver operator Curve (AUC) for each Maxent model. All models had very few classification errors (ODP > 0.95), and all except one (AUC = 0.73) had "good" discriminatory power (AUC >0.8).

The model was then used to forecast habitat suitability at baseline conditions and into future decades at the three SSPs. Raw maps of relative suitability were converted to binary presence/absence maps, which are generally required for conservation applications, for instance here to calculate the area covered by suitable habitat, both within and outside the EBSA boundaries. Binarisation used maximum TSS complementary log-log ('cloglog') as the optimal discrimination threshold, which was chosen for the same reasons as which Maxent features were included. A threshold that retains a broader representation of suitable conditions, like maximum TSS, also fits better with the expectation that EBSA boundaries will rarely match the ranges of their objects of conservation, the original species. To facilitate comparison of areal change

between EBSAs of vastly different sizes (Q1 = 1717 km^2, Q3 = 109,000 km^2, max = 11.1 million km^2), we calculated the log-ratio of the area relative to the EBSA's baseline area, both for area within and area unrestricted to the EBSA boundaries.

We also trialled using the annual ranges of surface temperature and salinity alongside the three mean variables for Maxent (downloaded and handled as described above for annual means). For 19 EBSAs, this resulted in the sudden collapse of forecasted binary habitat suitability area, from the typical baseline ~70% of the EBSA area (Fig. S2) to <10% within 2020-2030, even in SSP1-2.6. The two range variables had particularly high contributions to these collapsing EBSAs, and had the highest collinearity among all five variables (Table S5). We suspected inclusion of temperature and salinity ranges to lead to model overfitting, which would unlikely represent the behaviour of species as the climate changed.

Quantifying habitat change

We used two ways to assess habitat change within EBSA boundaries: (A) the mean probability of habitat suitability projected within the EBSA's spatial boundaries. This value, the mean of the geographically-projected Maxent output, typically falls around median = 0.70 (IQR = 0.68—0.74, Fig. S2) at baseline. Another intuitive value is the degree to which EBSA habitat is or is not present, akin to a projected species range of presence and absence, relative to its baseline state, which facilitates comparison among EBSAs of differing sizes. This second approach, (B) the relative suitable area, was the natural log ratio of the area occupied by EBSA habitat under different carbon emission scenarios to the initial area occupied by EBSA habitat (during the 2010-2020 baseline),

$$\text{Log}(\text{habitat\_area} / \text{habitat\_area}_{\text{baseline}})$$

Whether a spatial cell is occupied by EBSA habitat or not is defined by whether the habitat suitability for that cell is above or below a threshold, a value estimated by Maxent to best differentiate the probability of true presences against true absences (see methods, Fig. S2B). The habitat area can be calculated only within the EBSA boundary, as above, or additionally including area outside it. Plotted or values in the text are in % by calculating the exponent of the log-ratio and multiplying by 100. Thus, 100% suitable area would have been a log-ratio of zero, meaning the EBSA habitat covers exactly the same area as it did at baseline.

To estimate the distance and direction of habitat shifts, we calculated the Haversine distance and bearing between the centre of gravity (habitat suitability-weighted centroid of coordinates) of baseline habitat suitability and the centre of gravity for each projected decade thereafter. Larger EBSAs tended to exhibit larger distances but this was likely because larger areas simply represent a different spatial scale of environmental uniqueness.

Statistical analysis

We used mixed-effect linear models to test the temporal trend (slope) and its interaction with SSP on the EBSA response variables. When the temporal trend (decade) was not a direct predictor variable, temporal dependence was accounted for using a lag 1 autoregressive term. In all cases, a random intercept was included for each EBSA (R package *nlme*). Distance was log-transformed for statistical analysis. When using direction as a dependent variable, latitude was included as an independent variable to account for polewards being in the opposite direction in the southern hemisphere.

For judging the variables most important for predicting which EBSAs are more or less susceptible to progressing climate change, we used random forests from R package *randomForest* (Liaw & Wiener, 2002). One random forest was grown per SSP to predict EBSA habitat suitability by 2100. These use a set number of decision trees (here, n = 500). Since any individual tree will likely be wrong, random forests essentially give each tree a vote on the predictive outcome, utilising the "wisdom of the crowd". Rather than focussing on decisions of any single regression tree, we document stable decision rules based on a random forest for each SSP using SIRUS in R, with the default maximum of 10 rules (Bénard et al., 2019).

Sensitivity tests

In addition to the previously-mentioned annual means, we explored adding annual ranges of temperature and salinity to the habitat conditions of EBSAs. Among the environmental variables in the training data (2010-2020), the two range variables had the highest collinearity, by both their individual coefficients with other variables and the sum of their pairwise correlations. Adding the ranges to the environmental envelope resulted in some EBSAs' relative suitable area collapsing to below 10% within the first decade forecast, 2020-2030, at SSP 1-2.6. Although such projections of environmental envelope change are likely correct, salinity and temperature seasonal changes are not expected to themselves result in complete loss of habitat within our current decade for many protected species. This is especially likely given natural

decadal cyclicity inherent in most high seas habitats (e.g. ENSO, Atlantic Decadal Oscillation). Given the higher collinearity and likelihood of overfitting, we decided to base our analyses on projections of the annual means

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Figures

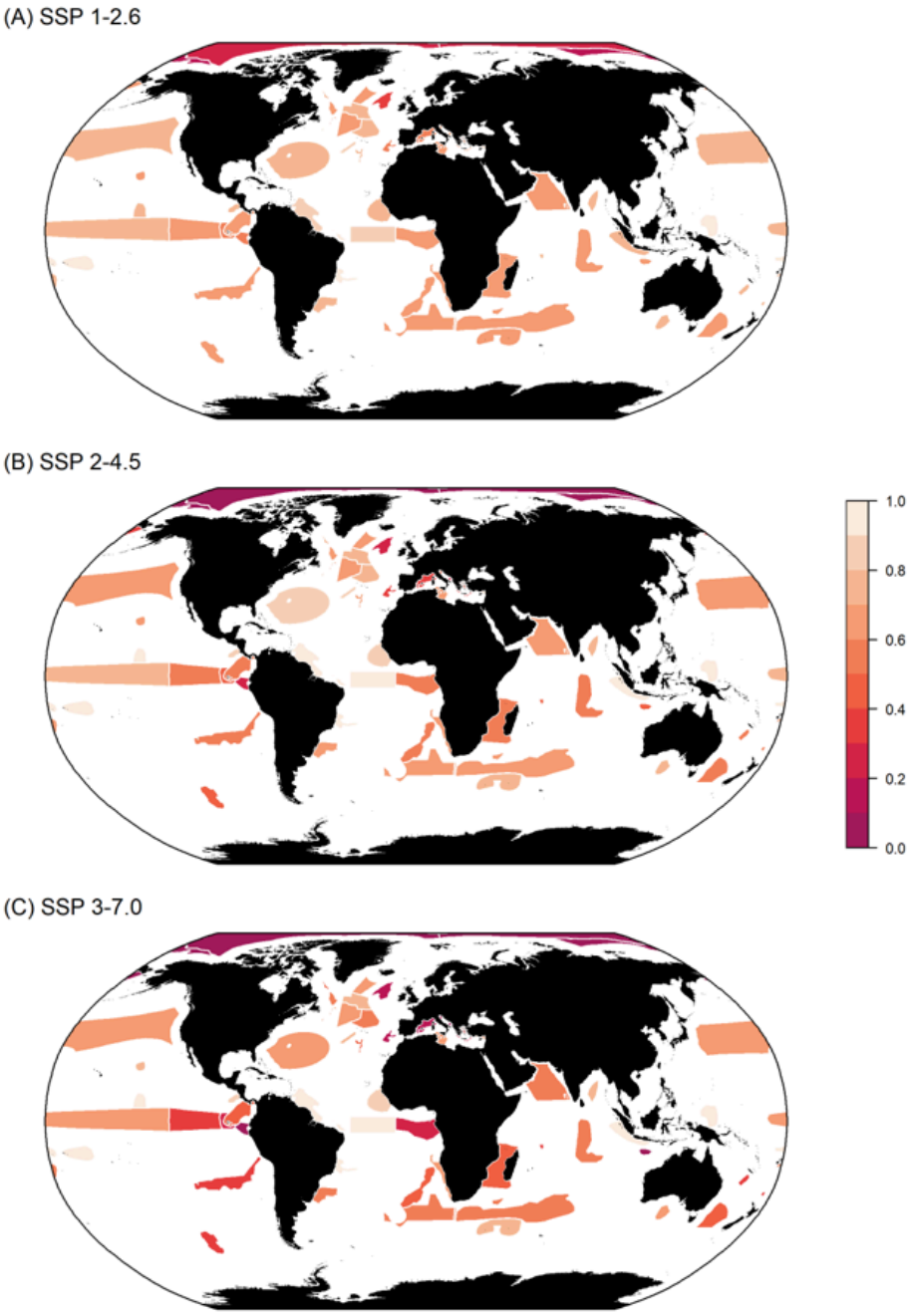

Figure 1

Mean habitat suitability of high seas EBSAs within their spatial boundaries for the decade 2090-2100 under three emissions scenarios. (A) low emissions, SSP1-2.6; (B) medium emissions, SSP2-4.5; (C) high emissions, SSP3-7.0. Warmer, darker colours indicate a greater change in environmental conditions relative to those characterising each EBSA (n = 67) during the 2010–2020 baseline period (model training data)

anticipating greater biodiversity change. Baseline mean suitability values typically ranged around 0.7 (Fig. S2). Note that values represent Maxent modelled suitability and not a normalised change metric relative to the baseline.

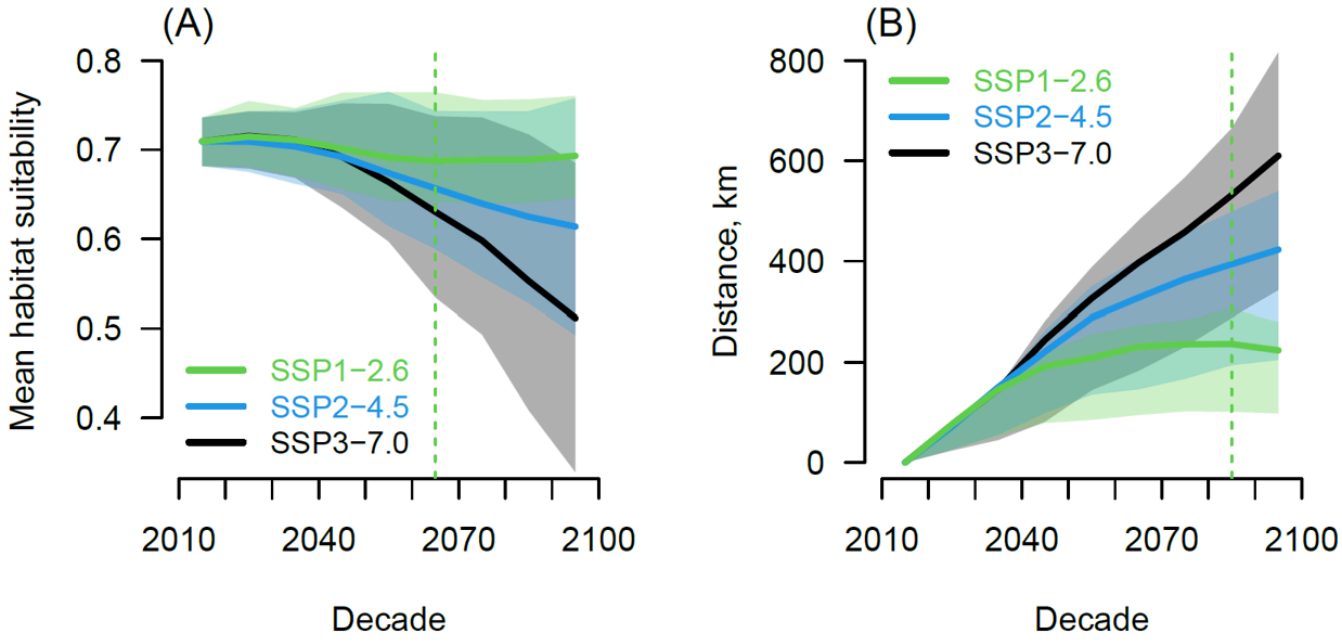

Figure 2

Temporal change in high seas EBSA (A) mean habitat suitability within their boundaries, and (B) mean distance travelled by their original habitat centroid, under three different carbon emissions scenarios. Each coloured line is the median among EBSA forecasts for each SSP. Coloured polygons are the interquartile ranges among EBSAs. Y-axis variables are plotted at the x-axis mid-point of each time bin (e.g. 2065 for the decade 2060-2070). Vertical dashed lines show the SSP1-2.6 habitat suitability low point (2060-2070) and distance high point (2080-2090). In (B), distance is calculated from the baseline (2010-2020) habitat centre of gravity to its centre of gravity for each decade thereafter.

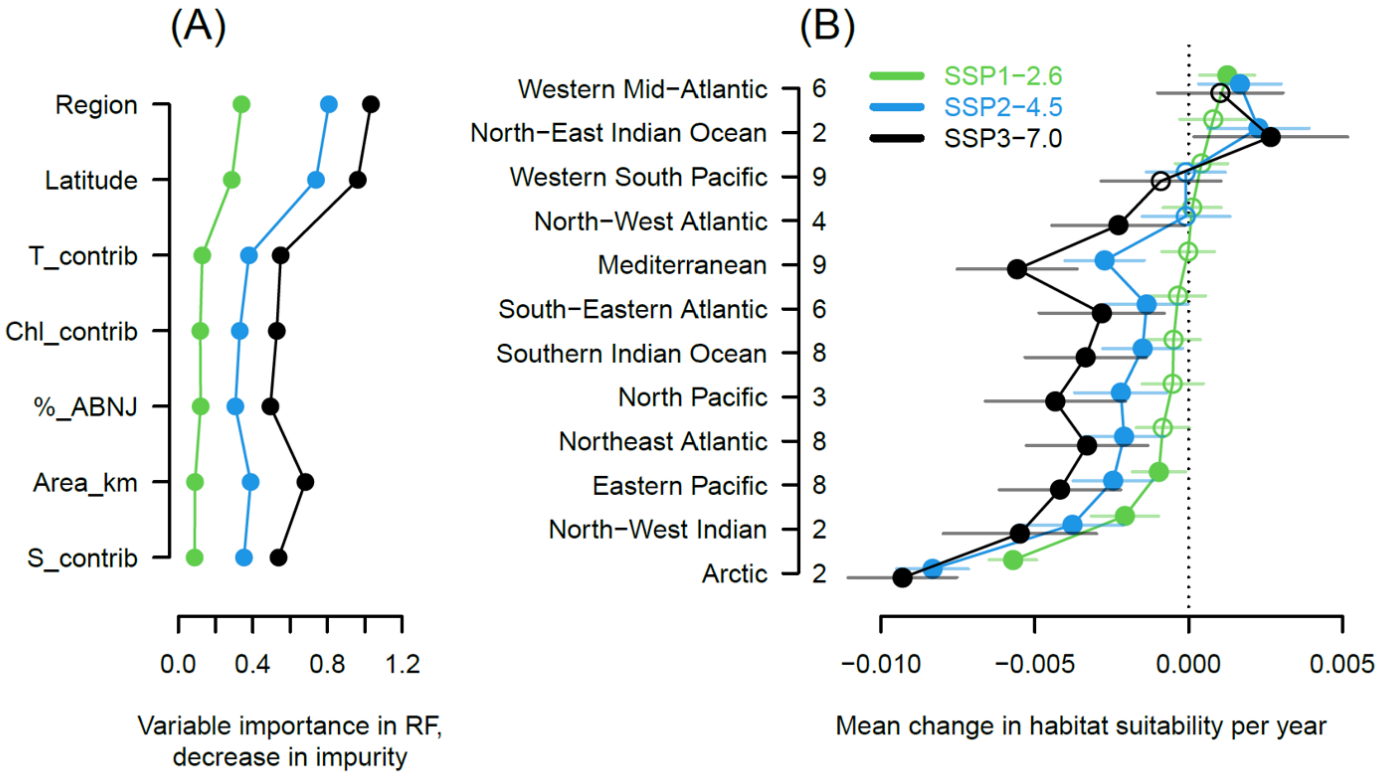

Figure 3

EBSA design features that predict loss of their projected habitat suitability, and their rank changes, under three different carbon emissions scenarios. (A) shows the importance of multiple predictor variables in a random forest (RF) of 500 regression trees for 2100 mean habitat suitability, separately for each SSP, ranked according to SSP 1-2.6 importance. Area_km = area in km^2; %_ABNJ = % of EBSA area lying beyond national jurisdiction; Chl_contrib, S_contrib, T_contrib = the respective contributions of chlorophyll, salinity, and temperature to EBSA habitat uniqueness at baseline (SSP 1-2.6). (A) x-axis shows mean decrease in impurity (MDI), which quantifies the total reduction in node impurity attributable to a feature across the trees in the forest. Variance explained (R^2) decreased with SSP, with 38.8%, 25.6%, and 22.2%, for SSPs 1-2.6, 2-4.5, and 3-7.0, respectively. (B) geographical regions ranked based on their mean annual change in habitat suitability under SSP1-2.6. Points and 95% confidence intervals were calculated by one mixed effects regression per SSP, as the interaction between decade and region, with a random intercept per EBSA. Number of EBSAs per region given by numbers. Open points indicate confidence intervals overlapping with zero.

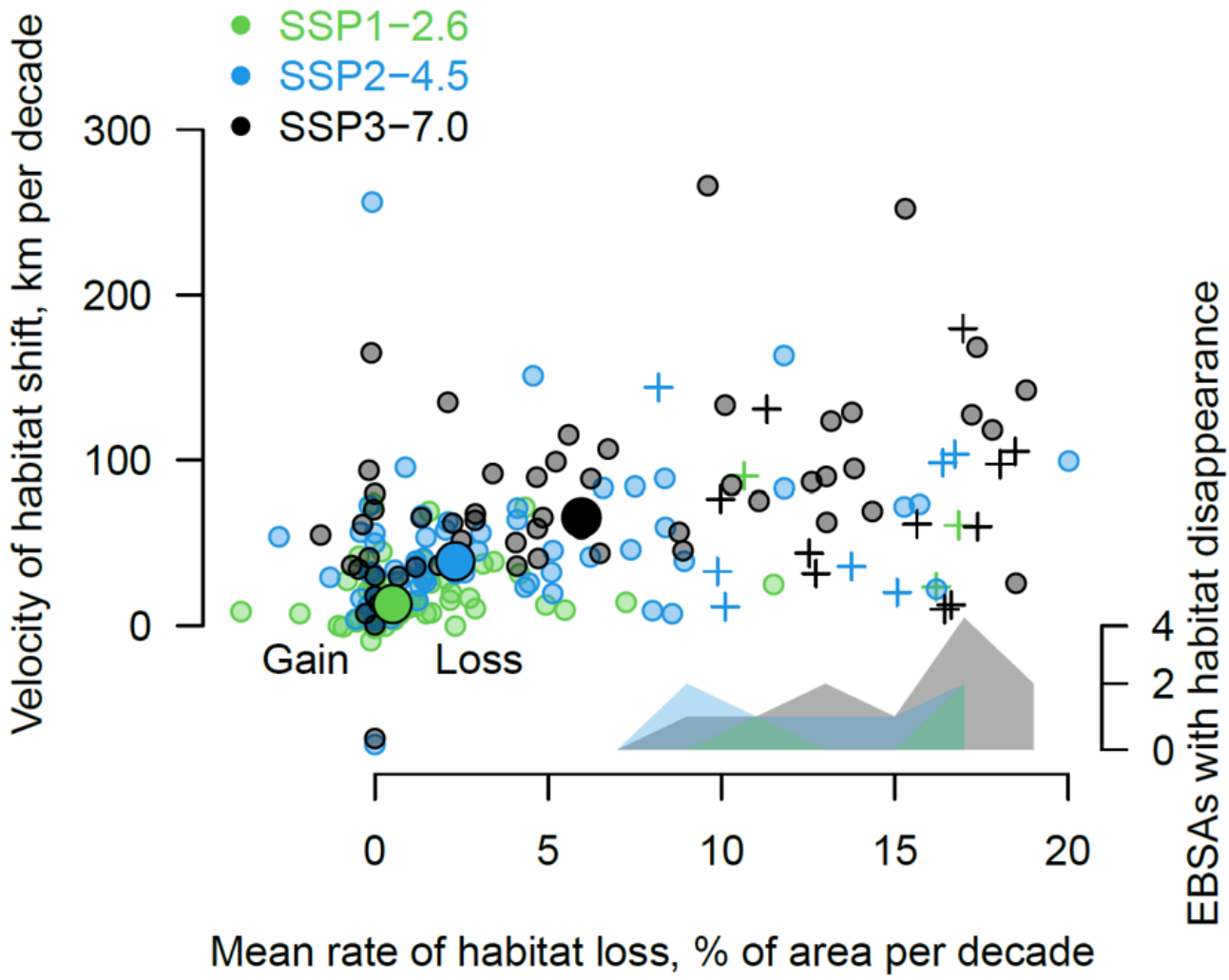

Figure 4

Higher emissions lead to higher temporal rates of habitat loss within EBSAs, greater velocities of the original habitat conditions, and greater rates of entire habitat disappearance. Small points on scatterplot are EBSAs plotted once per SSP: X-axis is calculated by the regression slope between areal change of binarized maps of habitat suitability against time; left Y-axis is calculated by the regression slope between the distance shift of the centre of gravity of baseline habitat conditions against time. Velocity of habitat shift was weak-to-moderately correlated with loss rate of baseline habitat area (Rho = 0.41, 0.34, 0.41, respectively for low, medium, and high SSPs). The large points are the scatterplot geometric medians for each SSP. The crosses (+) are those EBSAs where suitable habitat conditions entirely disappear, even outside the EBSA boundaries. Right x-axis histogram polygons mark the increasing incidence (number of EBSAs) of habitat disappearance per 2%-bin of the x-axis. "gain"/"loss" in the figure refer to EBSAs being above/below zero on the x-axis.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- TableS6.SIRUSrulessheet.xlsx
- SupplementaryInformation.docx
- TableS7.FullEBSAResponses.xlsx