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Kelp forest diversity under projected end-of-century climate change

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Abstract

Aim: Future climate change threatens marine forests across the world, potentially disrupting ecosystem function and services. Nonetheless, the direction and intensity of climate-induced changes in kelp forest biodiversity remain unknown, precluding well-informed conservation and management practices.

Location: Global.

Methods: We use machine-learning models to forecast global changes in species richness and community composition of 105 kelp forest species under contrasting Shared Socioeconomic Pathway (SSP) scenarios of climate change (decade 2090–2100): one aligned with the Paris Agreement and another of substantially higher emissions.

Results: A poleward and depth shift in species distributions is forecasted, translating into ~15% less area in the extent of the global biome, coupled with marked regional biodiversity changes. Community composition changes are mostly projected in the Arctic, the Northern Pacific and Atlantic, and Australasia, owing to poleward range expansions and wide low latitude losses.

Main Conclusions: By surpassing the Paris Agreement expectations, species reshuffling may simplify and impair ecosystem services in numerous temperate regions of Australasia, Southern Africa, Southern America and the Northern Atlantic, and in the tropical Pacific, where complete species losses were projected without replacement. These estimates, flagging threatened regions and species, as well as refugial areas of population persistence, can now inform conservation, management and restoration practices considering future climate change.

KEYWORDS
biodiversity, climate change, kelp forests, macrophytes, Paris Agreement, range shifts

1 | INTRODUCTION

Climate change is anticipated to trigger significant shifts in marine species distributions (Assis, Araújo, & Serrão, 2017; Gouvêa et al., 2022; Hodapp et al., 2023), reshuffling global patterns of species richness and community composition (Boavida-Portugal et al., 2022; Brown et al., 2022; Garciá Molinos et al., 2016), particularly if the targets of the Paris Agreement are not met (Martins et al., 2021; Warren et al., 2018). Impacts can be intensified when elicited on ecosystem structuring species, which support a wide range of ecological and economic services. Their loss or altered state may have far-reaching effects, compromising ecosystem functioning, even if regional diversity is maintained through replacements of species that share the same or closely related traits (Teagle & Smale, 2018).

Kelp forests, here defined as large brown algae belonging to the orders Desmarestiales, Laminariales and Tilopteridales (Eger, Aguirre, et al., 2023; Fragkopoulou et al., 2022; Wernberg & Filbee-Dexter, 2019), are a critical case of ecosystem structuring species facing the effects of climate change. They play a pivotal role in many ecosystem services, particularly in provisioning essential habitat for associated communities, many of which with notable commercial, ecological and conservation significance (Eger, Marzinelli, et al., 2023; Pessarrodona et al., 2022). However, population declines have been recorded on a global scale, impacting their structure and capacity to provide essential ecosystem services (Araújo et al., 2016; Assis, Berecibar, et al., 2017; Coleman et al., 2022; Krumhansl et al., 2016). Accordingly, kelp forest conservation was considered in international conventions (e.g., the Convention for the Protection of the Marine Environment of the North-East Atlantic) (de Bettignies et al., 2021), and restoration initiatives have been promoted globally (Eger et al., 2022). Despite the recognized role and potential threats posed to kelp forests, global projections of climate-induced changes in their patterns of species richness and community composition are still missing. Current research is limited to present-day biodiversity patterns (Fragkopoulou et al., 2022) and to future impacts on particular species and regions (Assis et al., 2022; Assis, Araújo, & Serrão, 2017; Martínez et al., 2018; Raybaud et al., 2013). Global estimation of the future of kelp forests across species would allow pinpointing hotspots of species turnover and refugial areas that sustain long-term persistence of ancient marine forest populations (Fragkopoulou et al., 2021).

We examine the direction and intensity of future net changes in the global patterns of kelp forests' biodiversity under contrasting Shared Socioeconomic Pathway (SSP) scenarios of climate change, from low carbon emissions aligned with the Paris Agreement goals to higher emissions under limited mitigation strategies. To that end, we used machine learning species distribution modelling (SDM) linking a comprehensive dataset of kelp forest records with biologically meaningful predictor variables to quantify changes in species richness and community composition, as well as identify climatic refugia supporting the long-term persistence of kelp forests. The assessment highlights the benefits of stringent compliance with the Paris Agreement, limiting carbon emissions and consequently kelp forest changes, and serves to inform conservation, management, and restoration practices in the face of global change.

2 | METHODS

The direction and intensity of future net changes in the patterns of kelp forests' diversity were explored with SDM (Peterson et al., 2011) following well-established standards for biodiversity assessments (Araújo et al., 2019) and taking advantage of three high-performance machine learning algorithms, namely Boosted Regression Trees (BRT) (Elith & Leathwick, 2011), Adaptive Boosting (AdaBoost) (Hofner et al., 2011) and Extreme Gradient Boosting (XGBoost) (Chen & Guestrin, 2016). These algorithms are known for (1) capturing complex relationships and interactions between predictor and response variables (Elith et al., 2006), (2) dealing well with low prevalence biodiversity datasets (Barbet-Massin et al., 2012) and (3) reducing overfitting through hyperparameter tuning and forcing of monotonic responses (Elith & Leathwick, 2011; Hofner et al., 2011), a key step to improve model transferability (Elith & Leathwick, 2009; Yates et al., 2018).

Climate data for modelling were obtained from Bio-ORACLE v3.0 (Assis et al., 2024). Data included present-day "baseline" climate (decade 2010–2020) and two contrasting Shared Socioeconomic Pathway (SSP) scenarios of end-of-century climate (decade 2090–2100): the "sustainability" SSP1-1.9 scenario, following the Paris Agreement of reduced greenhouse gas emissions, and the "regional rivalry" SSP3-7.0 scenario of rising emissions over time. For each time period and scenario, multiple biologically meaningful predictor variables were considered for the benthic realm, along the typical depth range of kelp forests (0 to 30 m depth) (Assis et al., 2022), in particular, ocean temperature (long-term average of monthly maximum and minimum), salinity (long-term minimum), nutrient conditions (long-term minimum of nitrate), sea ice cover (long-term minimum) and wave energy (Assis et al., 2022; Assis, Araújo, & Serrão, 2017).

Occurrence records of 105 taxonomically accepted kelp forest species belonging to the orders Desmarestiales, Laminariales and Tilopteridales (Table S1) were gathered from the fine-tuned global distribution dataset of marine forests (Assis et al., 2020). The data included 584,504 records, unbiased regarding the known distribution of species as it integrates expert and published information. Because the algorithms need to consider zeros for fitting and absence data were unavailable for all species globally, we randomly generated pseudo-absences per species (i.e., presence-only modelling) in regions where no occurrences were recorded. To mitigate the impact of sampling bias and spatial autocorrelation in the models, a thinning process was implemented on both occurrences and pseudo-absences, by random selection of one record from the pool found within a species-specific distance, where predictor variables showed no significant autocorrelation (Segurado et al., 2006). To estimate this distance, a correlogram was built to evaluate Pearson's correlation coefficient of predictors as a function of increasing geographic distance. Pseudo-absences were subsequently pruned using a balanced 1:1 ratio with occurrence records for species with more than 1000 occurrences. For species with fewer occurrences, 10 model runs were conducted with a minimum of 100 pseudo-absences, following (Barbet-Massin et al., 2012). To reduce the chance of producing redundant information for modelling, pseudo-absences were segregated based on climate conditions, by assigning to each one a membership based on the K-means clustering algorithm using the predictor variables and setting the k parameter to the desired number of pseudo-absences (Senay et al., 2013). This additional step was instrumental in addressing the issue of class imbalance, which is key in machine learning (Johnson et al., 2012) and improved the isolation of the relative contribution of predictor variables to the output of the models (Senay et al., 2013).

Model parameter tuning and predictive error were assessed with a cross-validation framework with 10 random folds (Roberts & Hamann, 2012; Valavi et al., 2019). Both for parameter tuning and predictor error assessment, independent spatial blocks were defined as equal-area hexagons with the size matching the previously inferred climatic uncorrelated distances (Valavi et al., 2019). All hyperparameter combinations were tested per algorithm (i.e., "grid search" method). For BRT, learning rate from 0.1 to 0.01 (step 0.001), tree complexity from 1 to 4, and number of trees from 50 to 1000 (step 50); for AdaBoost, the number of interactions ranged from 50 to 250 (step 50), with degrees of freedom varying from 1 to 12 and shrinkage from 0.25 to 1 (step 0.25); for XGBoost, gamma varied from 0 to 5, interaction depth ranged from 1 to 4, shrinkage from 0.1 to 0.5 (step 0.1) and number of rounds from 10 to 100 (step 10). Competitive models were trained with data distributed in nine random folds, with one-fold reserved at a time for testing predictive error. To mitigate overfitting and enhance model generalization, monotonicity constraints were used by forcing a positive or negative fit for each predictor variable according to their expected biological effect on the response of models (Assis, Araújo, & Serrão, 2017; Hofner et al., 2011). Specifically, we hypothesize that maximum temperature, sea ice cover and wave energy have a negative effect on the response of models, while minimum temperatures, salinity and nutrient conditions have a positive one. Pearson's correlation coefficient (r) and Variance Inflation Factor (VIF) were determined between predictors.

The assessment of predictor error was conducted using the Boyce index, a measure particularly appropriate for presence-only models, sensitivity (true positive rate), and the area under the curve (AUC). The Boyce index ranges between −1 to +1, while sensitivity and AUC between 0 and 1. Boyce values greater than 0, or sensitivity and AUC above 0.5, indicate predictions better than random, while higher values towards 1 indicate predictions corresponding to observed patterns (Hirzel et al., 2006).

Models considering all predictor variables and the combination of hyperparameters retrieving the lowest prediction error in cross-validation were built to explore the relative contribution of predictors and to develop partial dependency plots reflecting the effect of each predictor on the response of models (Elith et al., 2008). Distribution maps per species were developed for present-day conditions and the different SSP future climate change scenarios by averaging the predictive responses of the three algorithms and the multiple cross-validation rounds (i.e., ensemble modelling) (Araújo & New, 2007). These maps were reclassified to represent presence and absence (i.e., binomial maps) with the minimum training area threshold, which is based on setting a minimum predicted area, while maintaining sensitivity higher or equal to 0.95 (Vignali et al., 2020). Lastly, to reduce overprediction, the maps were clipped to include only the potential areas reachable by dispersal, an important step in SDM for low-dispersal species, such as kelp forests (Fragkopoulou et al., 2022). This assumed that dispersing propagules (e.g., spores and rafts) cannot traverse regions of unsuitable habitats unless demonstrated by records of occurrence (Mendes et al., 2020) within a range of up to 200 km, a typical maximum distance of dispersal between marine forest populations (Fourqurean et al., 2012).

Species richness patterns were inferred for present-day conditions and the SSP scenarios by summing the species' distribution maps (i.e., stacked-SDM) (Fragkopoulou et al., 2022). Regions of high (i.e., hotspots), moderate and poor species richness were identified in cells with ≥30 species, <30 species and ≥15 species, and ≤2 species, respectively (Fragkopoulou et al., 2022). The uncertainty of estimates was accessed by mapping the average standard deviation of the predictive responses of the algorithms and cross-validation rounds. Additionally, the number of species gained (G) and lost (L) per pixel under the SSP scenarios was inferred. Community turnover was determined by (L + G)/(SR + G), where SR refers to species richness per pixel for present-day conditions (Thuiller et al., 2005). Summary tables were produced to report habitat coverage and diversity per marine ecoregion (Spalding et al., 2007). For coverage, a post-filtering process was applied to restrict estimates to areas where kelp forests can vertically occur. Specifically, the high-resolution General Bathymetric Chart of the Oceans (15 arc-second, approximately 450 m) (GEBCO, 2023) considered depths down to 30 m^2.

All analyses were performed in R (R Development Core Team, 2023). The data and code used in SDM, as well as the predicted distribution layers (per species at a 0.05° resolution) are openly available in a permanent repository (please refer to the data availability statement).

3 | RESULTS

The performance of SDMs in cross-validation (CV) and final predictions is high across the 3 algorithms (average CV AUC 0.93 ± 0.01; AUC 0.93 ± 0.02; CV Boyce 0.69 ± 0.02; Boyce 0.87 ± 0.01; CV sensitivity 0.94 ± 0.01; sensitivity 0.96 ± 0.02; Table S2). Performance further improved when ensembling the models into a unique consensus and when considering dispersal constraints (average AUC 0.99 ± 0.01; Boyce 0.88 ± 0.07; sensitivity 0.97 ± 0.02; Figure 1; Table S2). The uncertainty of SDMs, given by the standard deviation of probability of occurrence, is low across the algorithms and cross-validation runs (maximum standard deviation ≤0.04; Figure S1).

At the biome level (i.e., combining all kelp forest species), minimum and maximum ocean temperature play a crucial role in explaining the variability of species distribution (average combined contribution of 79.78%; Figure 1; refer to Table S3 for information on the species and algorithm levels), followed by nutrient conditions (nitrate) and wave energy (average contributions of 9.33% and 4.92%, respectively). The models show a residual impact of salinity and ice coverage (average contributions of 2.64% and 3.21%).

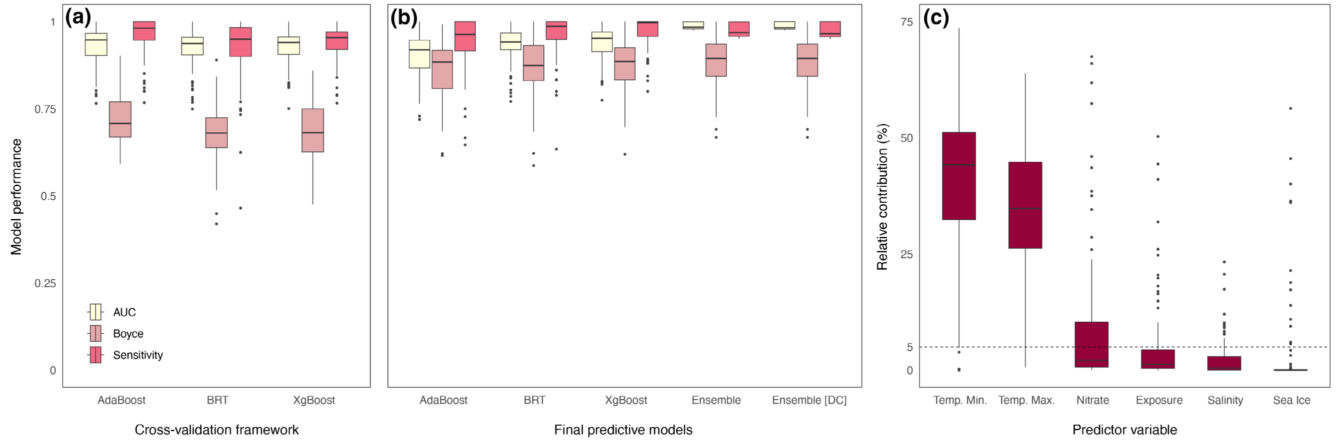

FIGURE 1 Performance of Adaptive Boosting (AdaBoost), Boosted Regression Trees (BRT), Extreme gradient boosting (XGBoost), and the ensemble of algorithms (dispersal constrain; DC) estimated with AUC, Boyce (reclassified to 0–1 for representation) and sensitivity in (a) the cross-validation framework and (b) the final predictions. (c) The relative contribution of predictor variables estimated with the ensemble of algorithms (Please refer to Figure S2 for estimates per order).

Nevertheless, salinity is relevant for species with distributions proximal to major hyposaline regions like the Hudson Bay, the Baltic Sea and the Siberian shelf (e.g., *Alaria angusta*, *Desmarestia kurilensis* and *Saccorhiza dermatodea*; contribution of salinity >20%). In the same way, ice coverage is relevant for species with polar distributions (e.g., *Alaria pylaiei*, *Haplospora globose*, *Laminaria* solidungula, *Saccorhiza dermatodea*, Saccharina *longicruris* and *Saccharina nigripes*; contribution of sea ice >=20%). These results were further verified when combining species per order, however with some exceptions. In particular, the effect of nutrient conditions was more important in explaining the distribution of species of the order Desmarestiales (average contribution of 19.72%) and ice coverage in species of the order Tilopteridales (average contribution of 9.02%; refer to Figure S2 for information at the order level). The relative contribution of predictor variables to the models is sustained by the generally low levels of collinearity found between them. Only maximum and minimum temperatures show high collinearity (Pearson's correlation 0.84 ± 0.07, on average); however, implementing monotonicity constraints mitigates any potential confounding effects concerning their individual contributions to the outcome of the models.

Stacked individual SDM predict a present-day global extent of kelp forests of 641,224 km^2 (739,185 km^2 without considering dispersal constraints), at an average depth of 4.61 ± 1.95 m (Table S4). Areas of great concentrations of kelp species (henceforth hotspots of species richness) are predicted to occur in several regions of the Northeast Pacific, from Southern California Bight to the Gulf of Alaska (species richness ≥30; Figure 2; Table S5). The Arctic, additional regions of the Northwest Pacific (the Northeaster Honshu, the Oyashio Current and the Seas of Japan and Okhotsk) and the Temperate Northern Atlantic are characterized by moderate species richness, with regional hotspots in the Aleutian Islands, the Bering and the North Seas, the Gulf of Maine, the South European Atlantic Shelf (Lusitanian region) and the Scotian Shelf (species richness >=15; Figure 2; Table S5). Conversely, poor spots of 1–2 species are predicted in the tropical Pacific and the tropical Atlantic, and in the highest latitudes of both the Arctic and Antarctic (inc. the Southern Ocean). Some temperate regions are also predicted to have low species richness, specifically, in South America (e.g., Southeastern Brazil), Australasia (e.g., Shark Bay and Tweed-Moreton) and the Northern Atlantic (e.g., the warm and oligotrophic Aegean Sea in the Mediterranean Sea; Figure 2; Table S5). Please refer to Figures S3–S5 for present-day biogeographic patterns predicted per order.

End-of-century projections capture an expected poleward redistribution of species following the increasing trend of warming temperatures. Consequently, a negative net change in the extent of kelp forests worldwide is expected, at 8.27 to 15.69% (SSP1-1.9 vs. SSP3-7.0). Concurrently, the models projected a redistribution of suitable habitats towards greater depths, specifically lowering the mean depth from 0.78 to 2.37 m below current levels (SSP1-1.9 vs. SSP3-7.0; Table S4). Species range gains are asymmetrical between hemispheres, mainly expected in the higher latitudes of the Arctic (e.g., High Arctic Archipelago, the Barents, Bering and White Seas, in North Greenland and Northern Labrador) and the cold-temperate Northern Pacific (e.g., Oyashio Current and the Gulf of Alaska) and North Atlantic Oceans (e.g., Scotian Shelf), with species richness increasing by 3 or more species under SSP3-7.0 (Figure 3; Table S5). Range losses are mostly projected in the lower latitudes of the temperate Northern Pacific and Australasia, with species richness reduced by 5 or more species in the Northeastern Honshu, Southern California Bight (remarkedly, a present-day hotspot), Southeast Australian Shelf and in Northeastern New Zealand (Figure 3; Table S5; please refer to Figures S3–S5 for future biogeographic patterns projected per order). Additionally, in specific temperate regions of Australasia, Southern Africa, South America and Northern Atlantic, and in the tropical Indo-Pacific, where kelp forests are currently cryptically distributed, complete losses without species replacements are projected under SSP3-7.0 (Table S5). This is the case of the species *Arthrocladia villosa* in Carolinian (Northwest Atlantic), *Desmarestia ligulata* in the Australian Shelf and Hawaii, *Ecklonia radiata* in the Australian Shelf, Shark Bay and Tweed-Moreton (Australasia), in Northern New Zealand and Lord Howe and Norfolk Islands (Central

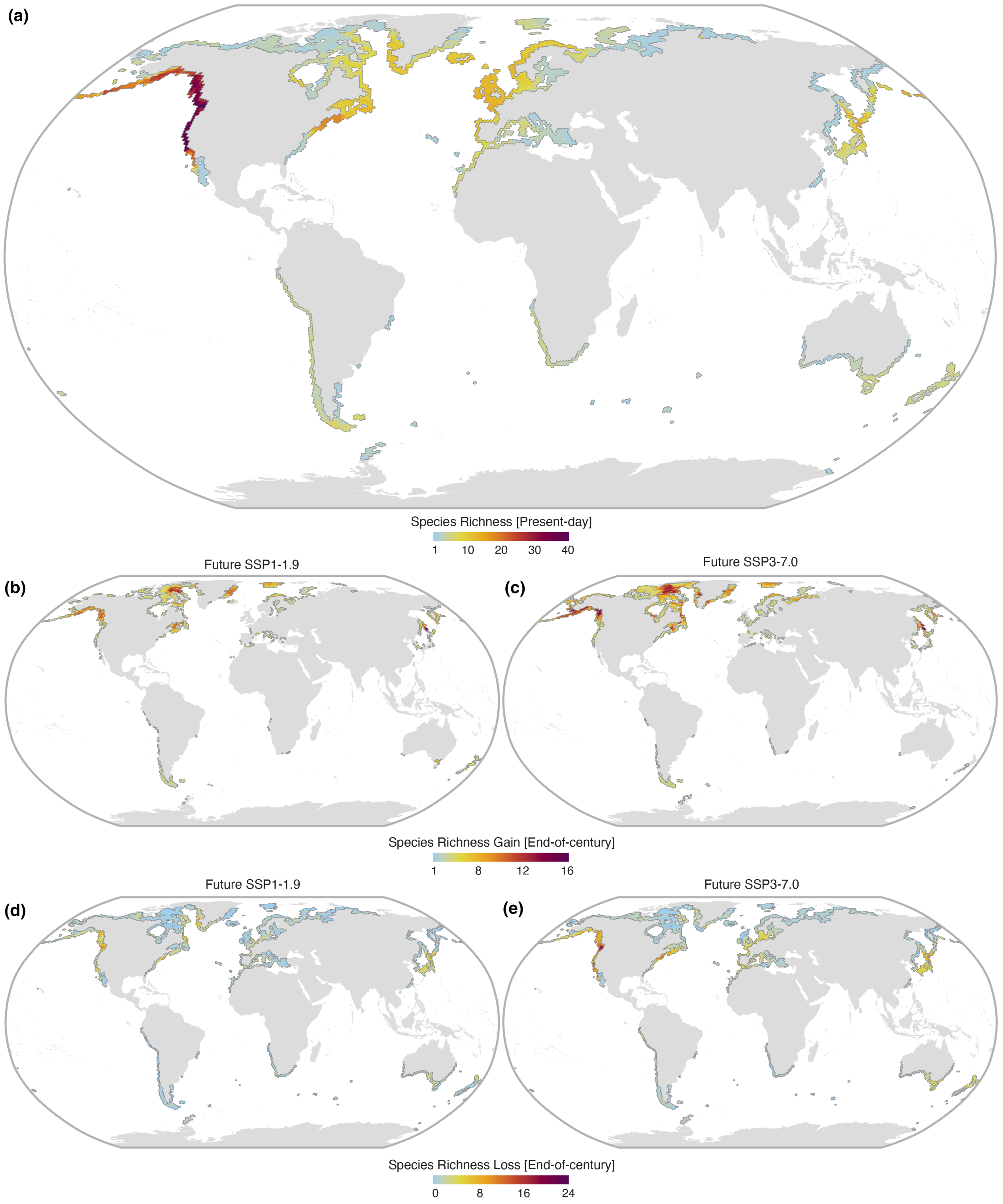

FIGURE 2 (a) Present-day species richness patterns of kelp forests predicted with Species Distribution Modelling (SDM). Future projected (b, c) gains and (d, e) losses of species richness under contrasting Shared Socioeconomic Pathway (SSP) scenarios of end-of-century climate change conditions. To improve visualization, raster cells were aggregated into hexagons of 100 km (Please refer to Figures S3–S5 for estimates per order).

Indo-Pacific), *Ecklonia richardiana* in the Australian Shelf and Delagoa (Western Indian Ocean), *Laminaria pallida* in Amsterdam-Saint-Paul Islands, *Laminaria platymeris* in Carolinian (Northwest Atlantic), *Lessonia corrugata* and *Lessonia variegata* in the Australian Shelf and *Macrocystis pyrifera* in Amsterdam-Saint-Paul Islands, the Australian Shelf and the Uruguay-Buenos Aires Shelf (Table S6).

The projected shifts in ranges of kelp forest species lead to substantial changes in their community composition (Figure 3) stemming

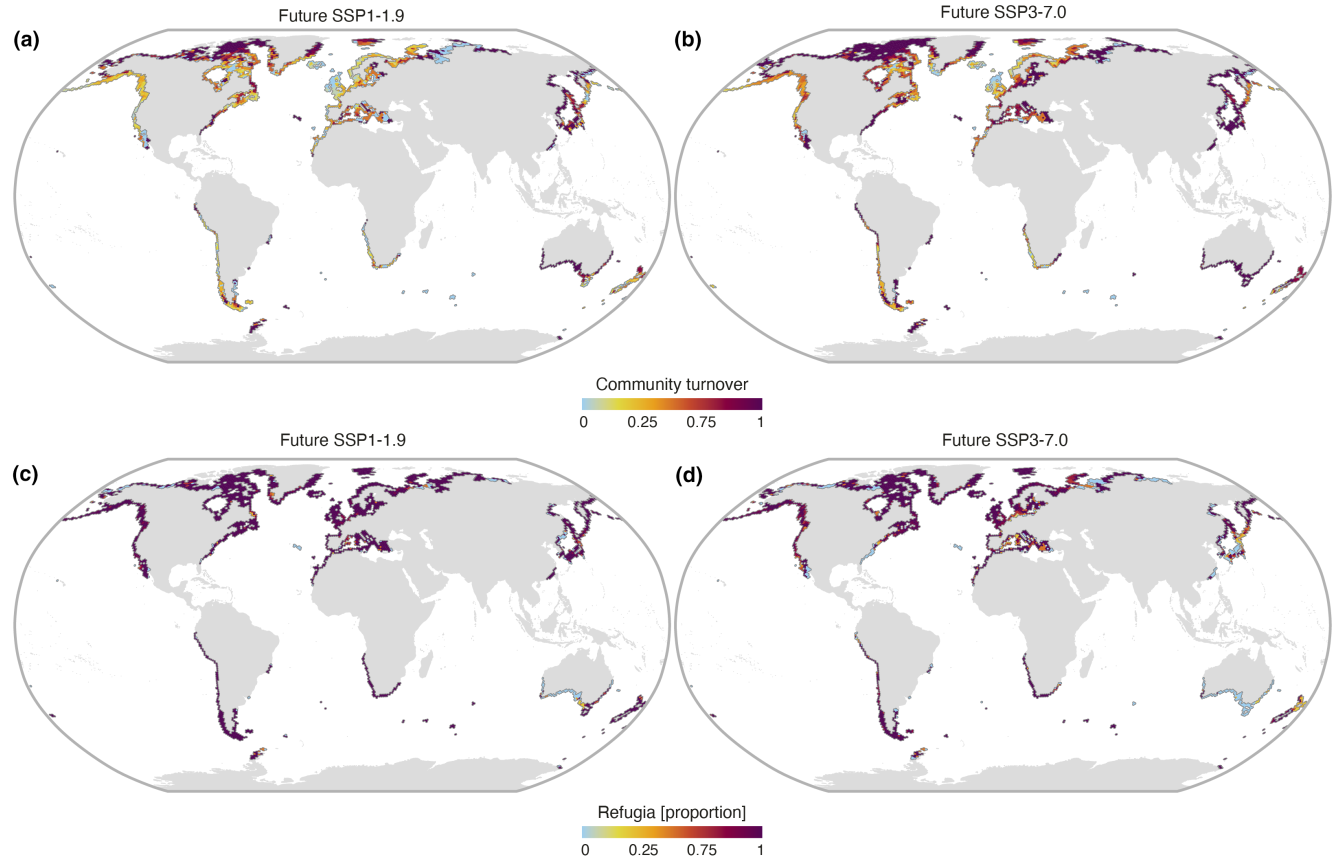

FIGURE 3 (a, b) Community turnover and (c, d) refugia (proportion of species persisting regionally) projected under contrasting Shared Socioeconomic Pathway scenarios (SSP1-1.9 and SSP3-7.0) of end-of-century climate change conditions. To improve visualization, raster cells were aggregated into hexagons of 100 km (Please refer to Figures S6–S8 for estimates per order).

from a combination of species gains, losses, or both gains and losses (Figure 2). Within the present-day distribution of kelp forests, a total area of 74,491 km^2 is projected to experience near complete turnover ratio (0.95 or higher) under SSP1-1.9. In stark contrast, this turnover area substantially expands to 193,004 km^2 under SSP3-7.0 scenario, reflecting the profound impact of differing carbon emission pathways. Against this background of change, climatic refugia are projected under all scenarios and across the majority of the global kelp forest distribution, however, species persistence is also dependent on the specific scenario considered. As carbon emissions escalate, there is a notable decline in global climatic refugia from 356,172 to 188,013 km^2 when comparing scenario SSP1-1.9 against SSP3-7.0. This decline is particularly striking in regions such as the Temperate Australasia, the lower latitudes of the temperate Northern Pacific and the temperate Northern Atlantic, where regional species persistence becomes increasingly eroded (Figure 3).

4 | DISCUSSION

Our study reports the expected direction and intensity of future (end-of-century) net changes in kelp forest biodiversity under contrasting scenarios of climate change. We show negative net changes in the global area of these ecosystems, coupled with widespread northern poleward range shifts, which may strongly rearrange the regional patterns of species richness and community composition of kelp forests, particularly under increased carbon emissions. Biodiversity changes associated with poleward range expansions were asymmetrical among hemispheres, as expected due to the absence of coastlines for range expansions along the Southern Ocean, for as long as the Antarctic remains an endemism hotspot, mostly unsuitable and isolated (Fragkopoulou et al., 2022). Expansions of kelp forests were mostly projected in the Arctic and the cold-temperate Northern Pacific and Atlantic Oceans, while changes associated with range losses were mostly projected for the temperate regions of the Northern Pacific and along Australian and New Zealand coastlines. Without stringent compliance with the Paris Agreement, the degree of changes may simplify ecosystem functioning and impair the numerous ecological and economic services provided (Eger, Marzinelli, et al., 2023). Importantly, some temperate regions of Australasia, Southern Africa, South America, and Northern Atlantic, and the tropical Pacific Ocean might undergo complete losses without species replacements. The findings also anticipate the location of key refugial areas for kelp forests' persistence, which are baselines to inform conservation and management priorities in the face of future climate change. This information is especially relevant for initiatives involving blue carbon (Wedding et al., 2021), designation of marine protected areas (Wilson et al., 2020), and potential donor populations for restoration (Eger et al., 2022).

4.1 | Performance and significance of SDM

The ensemble of machine learning algorithms fitting expert-verified data and a set of biologically meaningful predictor variables retrieved high performance and low uncertainty, aligning with cutting-edge advancements in predictive modelling techniques for species distributions. Notably, integrating dispersal constraints, a valuable but often-overlooked approach in SDM, effectively reduced overprediction without requiring prior knowledge of species dispersal ecology (Cooper & Soberón, 2018; Mendes et al., 2020), which is often particularly challenging to obtain and highly uncertain for marine species as a whole (Assis et al., 2021; Gouvêa et al., 2023). Overall, the models revealed that the distribution of kelp forests at biogeographical scales is predominantly influenced by physiological (ocean temperature and nutrient conditions) and disturbance (wave energy) constraints. These results, also verified for the three taxonomic orders analysed, are consistent with previous empirical and theoretical studies (Assis, Araújo, & Serrão, 2017; Fragkopoulou et al., 2022). Further, the relevance of salinity for species with distributions proximal to regions like Hudson Bay, the Baltic Sea, and the Siberian shelf, where very large rivers drain, and sea ice coverage for species with polar distributions, also aligns with previous research (Assis et al., 2022).

Stacking the models into a single layer provided a comprehensive view of the present-day biome, which spanned an extent of 641,224 km^2. This estimate is lower than previous reports (ranging between 1.7 and 2.0 million km^2) although distributed across the same exact regions (Fragkopoulou et al., 2022; Jayathilake & Costello, 2020). This difference in area resulted from the post-filtering process, which used a high-resolution bathymetric layer to restrict predictions to realistic areas where kelp forests can occur (Gouvêa et al., 2022). The species richness patterns revealed, characterized by significant hotspots in the temperate Northeast Pacific and Northern Atlantic, along with poor spots in the high Arctic, Antarctic, and tropical regions, are consistent with the established biogeographic patterns of kelp forests, which reflect evolutionary opportunities for species' radiation and diversification (Fragkopoulou et al., 2022).

4.2 | Kelp forest diversity under future climate change

Transferring the models to contrasting SSP scenarios of climate change revealed negative net changes in the global extent of kelp forests (by up to ~15% globally), coupled with generalized poleward shifts at the species level, which can significantly alter the regional future patterns of diversity, particularly under the SSP3-7.0 scenario. As species track climate change, the higher latitudes of the Arctic and the cold-temperate Northern Pacific and Atlantic Oceans may experience an increase in regional diversity of 3 or more species, as observed with the recent expansion rates of pan-Arctic subtidal macroalgae (Krause-jensen et al., 2020). In contrast, the lower temperate latitudes of the Northern Pacific and Australasia may experience a reduction of diversity of 5 or more species. Importantly, the present-day diversity hotspots of Southern California Bight may be subject to substantial diversity reduction and specific temperate regions of Australasia, Southern Africa, South America, Northern Atlantic and the tropical Pacific Ocean, where kelp forests are cryptically distributed, may undergo extinctions, adding up to ongoing reports of kelp forest local extinctions (Assis, Berecibar, et al., 2017; Coleman et al., 2022). Such changes in species richness are anticipated to impact the patterns of community composition. In particular, turnover, integrating both gains and losses at the regional level, is expected to peak in the Arctic, and the temperate regions of the Northwestern Pacific, Northern Atlantic and Australasia. Notably, with increasing carbon emissions, 30.09% of the present-day distribution of kelp forests may experience near-complete turnover.

These projected changes in the regional patterns of diversity and community structure may have contrasting effects, influencing associated biodiversity from the microbial to macrofauna levels, demanding careful consideration. On the expansion zones, the new forests in previously unfavourable regions, like the Arctic, may boost regional biodiversity levels and ecosystem services (Dijkstra et al., 2017), including carbon sequestration (Krause-Jensen & Duarte, 2016), or disrupt biotic interactions, by outcompeting native species and changing community composition (Fossheim et al., 2015). Additionally, the expansion of kelp forests can decrease the abundance and diversity of species not associated with them, like sessile invertebrates or suspension feeders (Lebrun et al., 2022). In the threatened regions, in contrast, losses may have profound and far-reaching consequences. Where models projected severe or complete diversity losses, a reduction in habitat provisioning and other ecosystem services is anticipated. Additionally, the disruption of food webs and ecological interactions that rely on the presence of large brown algae may occur, ultimately leading to the loss of essential habitats for numerous associated species, some of which are of high commercial value (Eger, Marzinelli, et al., 2023). Even where diversity levels are maintained through replacements by structurally similar or taxonomically closely related species, negative consequences are hypothesized. Studies focused on marine forest replacements have reported impacts on key ecological functions like organic matter cycling (Pessarrodona et al., 2019), ability to withstand wave disturbance (Smale et al., 2015), susceptibility to disease, habitat complexity and overall diversity levels of associated species (Smale et al., 2022; Teagle & Smale, 2018). All in all, broad compliance with the Paris Agreement holds the potential to halt the projected distribution changes and, in turn, safeguard their key ecosystem services.

Despite generalized range shifting, climatic refugia with hotspots of persistence were projected across most of the global distribution of kelp forests, in regions with higher species richness. This suggests that regions that currently harbour higher species richness may also display greater diversity in the future. However, the extent of projected refugia was highly dependent on the SSP scenario considered, with increasing carbon emissions reducing these areas from 356,172 to 188,013 km^2, challenging kelp forests in temperate regions of Australasia, Northern Pacific and Northern Atlantic. Interestingly, depth refugia, where colder waters may safeguard end-of-century populations, were projected by the deepening of suitable habitats up to 2.37 m on average. Deep refugia for kelp forests have been reported across the globe, e.g., in the low latitude populations of *Ecklonia radiata*, *Laminaria ochroleuca*, *Saccorhiza polyschides* and *Macrocystis pyrifera* (Assis et al., 2016, 2018; Davis et al., 2021), encompassing higher genetic diversity owing to long-term population stability (Assis et al., 2016, 2018). Refugia for kelp forests constitute priority areas for conservation. If properly managed, such regions can act as future sources of population replenishment and genetic variability (Bongaerts et al., 2010). Additionally, they may contribute significantly to the export of higher levels of carbon to marine sediments (Pessarrodona et al., 2023). There is therefore value in establishing new marine protected areas with the specific goal of conserving kelp forest refugia, also adding opportunity to advance the successful implementation of the post-2020 Global Biodiversity framework that calls for the protection of 30% of the oceans. It should however be highlighted that marine protected areas may be beneficial but may not protect kelp forests from either climate change or anthropogenic threats to kelp forests, which are typically caused by land (terrestrial) management leading to increasing nutrient and particle loads on the coast.

4.3 | SDM limitations

Despite the high performance and low uncertainty of the models, there are inherent uncertainties associated with SDM and climate change projections that should be acknowledged. First, potential data gaps driven by uneven sampling, particularly in regions like Northeastern Russia and Western and Northern Africa, may have influenced niche estimates and therefore the predicted biodiversity patterns (Assis et al., 2020). Second, the models were built on climate conditions alone, neglecting biotic interactions that may influence species' abilities to successfully colonize newly suitable areas (Pinsky et al., 2020). Also, despite the inclusion of dispersal constraints, dispersal trajectories driven by oceanographic transport were not considered, potentially creating inconsistencies between projected and realized future expansions where major oceanographic barriers play a role (Legrand et al., 2023). Third, the models did not consider the potential for local adaptation to new climate conditions, although the short time frame of our predictions (up to end-of-century) compared to evolutionary times renders this process unlikely (Henson et al., 2017). Finally, the models missed additional important variables, such as light at the bottom and substrate type, which are not available at the global scale (light is only available for present-day conditions) (Assis et al., 2024; Assis, Tyberghein, et al., 2017). Therefore, models might have overestimated the extent of kelp forests and, accordingly, the projections provided represent a best-case scenario, potentially underestimating future climate change impacts in some regions where benthic light and hard substrate limitation might create additional challenges. Acknowledging these uncertainties is crucial for proper interpretation of results to be used to inform conservation strategies in the face of future climate change.

5 | CONCLUSIONS

Our study underscores the hidden vulnerability of kelp forests to future climate change. The projected changes in species richness and community composition, highly dependent on the SSP scenario considered, call for urgency in the implementation of climate change mitigation strategies consistent with the objectives of the Paris Agreement. Particularly, the extensive expansions into highly sensitive regions like the Arctic, coupled with the potential drastic losses at low latitude regions, some of which without any species replacements, emphasize the need to meet the ambitious targets set by the agreement. Continuous research and monitoring are therefore critical to better understand and manage the potential impacts of projected changes and to ensure the conservation and sustainability of these critical coastal ecosystems. Ultimately, the results provided (also at the species level and also under the reduced mitigation scenario SSP5-8.5; please refer to the data availability statement) are baselines to, among other uses, inform climate-smart conservation frameworks in line with the post-2020 Global Biodiversity Framework (Wilson et al., 2020) and identify donor populations for restoration actions of previously impacted regions (Eger et al., 2022).

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

The data and code used in Species Distribution Modelling, the coefficient of correlation of climatic predictors, the cross-validation data splits, the spatial autocorrelation estimates per species, as well as the distribution layers (at a 0.05° resolution) per species and climate scenario are available at: https://www.doi.org/10.6084/m9.figshare.24182559.

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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