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RESEARCH ARTICLE

Seagrass Biodiversity Under the Latest-Generation Scenarios of Projected Climate Change

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ABSTRACT

Aim: The potentially cascading consequences of climate changes on redistribution of habitat-forming species, like seagrasses, remain a major research gap. Empirical demonstrations of local population changes are increasingly reported without a globally integrated predictive framework as a leading testable hypothesis. Therefore, here, we aimed to estimate changes in species richness, community composition, and areas of climatic refugia under future climate scenarios.

Location: Global scale.

Time Period: Present-day conditions (from 2010 to 2020) and for three Shared Socioeconomic Pathway (SSP) scenarios of future climate change (from 2090 to 2100).

Major Taxa Studies: Seagrasses (plantae).

Methods: We coupled seagrass occurrences with environmental predictors (temperature, salinity, nitrate, wave energy, and ice) in stacked species distribution modelling.

Results: Models estimated a present global extent of 917,169 km^2 with high species richness in Temperate Australasia, Indo-Pacific, and Temperate North Pacific. Future projections predicted widespread spatial redistribution, with Arctic expansions, losses in lower latitudes, and deeper vertical ranges, while globally maintaining the area extent occupied worldwide by seagrass species (only 5% of change). Species richness increased poleward under more drastic scenarios (SSP3-7.0 and SSP5-8.5), with losses in tropical zones (30°N to 30°S). Local climatic refugia are retained in all scenarios but decrease under higher emissions. Additionally, even where seagrass species remain, widespread community composition changes were predicted.

Main Conclusions: Our findings serve as baselines to inform, anticipate, and mitigate cascading consequences of shifts in seagrass ecosystems that provide essential services for humanity.

Lidiane Gouvêa and Eliza Fragkopoulou contributed equally to this work.

1 | Introduction

A major global problem for the future of humanity is the change in the extent and distribution of structural species that create ecosystems upon which many other species and ecosystem services depend. In the oceans, marine structural habitats that play a disproportionately large role in supporting marine biodiversity tend to be very environmentally restricted and susceptible to change. Concomitantly, under increased carbon emissions, not aligned with the Paris Agreement goals (United Nations Framework Convention on Climate Change), future climate change is expected to redistribute global marine biodiversity through a generalised pattern of poleward range expansions and losses at lower, warmer latitudes (Assis et al. 2017; Assis et al. 2022; Gorman et al. 2016; Hodapp et al. 2023). Distribution range shifts can alter patterns of species richness and community composition (Boavida-Portugal et al. 2018, 2022; Brown et al. 2022; Garciá Molinos et al. 2016) potentially disrupting the structure of marine food webs (Hillebrand et al. 2018). Such impacts can be amplified when changes are elicited on ecosystem structuring species (Hoegh-Guldberg and Bruno 2010; Monserrat et al. 2022) that support essential habitats for numerous associated species. Their loss or altered state can lead to the simplification and impairment of ecosystem functioning (Agostini et al. 2018; Harvey et al. 2021), even when species are replaced by others with similar ecological roles (James et al. 2020; Muthukrishnan et al. 2020; Teagle and Smale 2018).

In the global ocean, essential marine ecosystem services are provided by seagrasses, as they create a habitat for mating, nursery (Nordlund et al. 2018), food and shelter for numerous associated species, including those with high commercial value. They are efficient in carbon sequestration, nutrient cycling, and coastal protection (Erzini et al. 2022; Mtwana Nordlund et al. 2016) and serve as biological and ecological indicators of the well-being of their connected communities and ecosystems (Purvaja et al. 2018). Ongoing climate change, coupled with other human disturbances, e.g., eutrophication, has caused seagrass declines globally (Espel et al. 2019; Lafratta et al. 2019) impacting their ecological services (Macreadie et al. 2019; Pansini et al. 2021). Due to their high importance and vulnerability, seagrasses are included in several directives and legislation (e.g., European Water Framework Directive; European Biodiversity Strategy), international conventions (e.g., the Convention on Biological Diversity), and restoration initiatives (Da Ros et al. 2021; de los Santos et al. 2019; van Katwijk et al. 2016). Yet, the persistence of seagrass ecosystem services in the future is contingent on their future distributions, as the leading hypothesis is that projected climate change might continue or even accelerate seagrass declines (Chefaoui, Duarte, and Serrão 2018). A comprehensive predictive assessment of future global seagrass distribution and diversity, including turnover by species replacements, is an important current research gap for the reasons highlighted above. Available projections are currently limited to a few species (e.g., *Zostera marina*, *Posidonia oceanica and Cymodocea nodosa*) and regions (e.g., the Arctic, the Mediterranean Sea, and western Africa; Assis et al. 2022; Chefaoui, Duarte, and Serrão 2018; Chefaoui et al. 2021). One study projected future seagrass changes at the global scale (Daru and Rock 2023), yet it did not consider identifying climatic refugia to guide prioritisation of conservation (e.g., Marine Protected Areas). Additionally, it overlooked key predictors for seagrass modelling, like nutrient conditions, wave energy, and sea ice cover. The study also neglected the latest-generation data of the Coupled Model Intercomparison Project (CMIP phase 6) that contributes to the latest IPCC Assessment Report on Climate Change. Importantly, these data include new predictor variables for modelling, better capture the variability (spatial and temporal) of the physical and biogeochemical properties of the ocean (Kwiatkowski et al. 2020), and output the new Shared Socioeconomic Pathway (SSP) scenario. These allow to estimate future biodiversity patterns under the Paris Agreement expectations, aligned with international climate policies (Sanderson, O'Neill, and Tebaldi 2016), contrasting with the previous RCPs scenarios.

In this study, our goal is to conduct the first systematic assessment of how climate change will impact the richness and community composition of seagrass species under the latest-generation Shared Socioeconomic Pathway (SSP) scenarios of the CMIP 6. These spanned from low carbon emissions, aligned with the goals of the Paris Agreement, to high emissions under no mitigation strategies. We hypothesised that future climate change will lead to significant shifts in the distribution, species richness, community composition, and areas of climatic refugia for seagrasses globally. To make projections, we used ensembles of species distribution modelling (Araújo and New 2007) and stacked modelled individual distributions to investigate patterns of diversity (Fragkopoulou et al. 2022) and community turnover. We used a suite of sophisticated machine learning algorithms linking the most comprehensive and quality-controlled datasets of seagrass occurrence records available with high-resolution, biologically meaningful climatic predictors. Our results provide quantitative estimates of future global seagrass species richness and community turnover and identify areas of climatic refugia estimated to support seagrass persistence over the long term. These estimates highlight the benefits of broad compliance with the Paris Agreement in reducing carbon emissions. They also serve as baselines to inform conservation, management, and restoration planning by flagging threatened and stable seagrass regions under different climate change scenarios.

2 | Methods

The direction and magnitude of seagrass biodiversity shifts were explored using Species Distribution Modelling (SDM; Peterson and Araujo 2012) under alternative climate change scenarios to guide well-informed conservation and management decisions (Villero et al. 2017) (e.g., in the scope of the Intergovernmental Panel on Climate Change framework). These models were constructed based on widely agreed standards for biodiversity assessments (Araújo et al. 2019) and were published following the ODMAP protocol (Supporting Information S1; Overview, Data, Model, Assessment and Prediction; Zurell et al. 2020) with open-source code to ensure proper reproducibility (please refer to data availability statement). Three high-performance machine learning algorithms were chosen, namely Adaptive Boosting (AdaBoost; Krause-Jensen et al. 2020), Boosted Regression Trees (BRT; Elith, Leathwick, and Hastie 2008; Krause-Jensen et al. 2020), and Extreme Gradient Boosting (XGBoost; Chen and Guestrin 2016). In addition to capturing complex interactions between predictor and response variables, these tools also cope well when there are few data available (Barbet-Massin et al. 2012) and allow tuning specific hyperparameters for reducing overfitting and improving model transferability (Elith, Leathwick, and Hastie 2008).

Environmental layers for modelling were generated at a 0.05° resolution (approx. 5 km at the equator) based on Bio-ORACLE computational pipelines (Assis et al. 2018) for present-day conditions (from 2010 to 2020) and for three Shared Socioeconomic Pathway (SSP) scenarios of future climate change (from 2090 to 2100): (1) a "sustainability" scenario SSP1-1.9 following the target of Paris Agreement of reduced greenhouse gas emissions, (2) the "regional rivalry" SSP3-7.0 scenario, which represents the medium-to-high end of the range of future forcing pathways, and (3) the "fossil-fuelled development" SSP5-8.5 scenario of high emissions and low challenges to adaptation (Figures S1–S3). Predictor variables reflecting seawater conditions were based on the biological relevance for seagrass meadows. Specifically, sea temperatures (long-term average of monthly maximum and minimum), salinity (long-term minimum), nutrient conditions (long-term minimum of nitrate), sea ice cover (long-term mean), and wave energy (Donatelli et al. 2019; Grech and Coles 2010; Jayathilake and Costello 2018; Short, Coles, and Short 2001). The long-term values, encompassing minimum, mean, and maximum, represent the average conditions recorded annually within the climatology. Such a subset of relevant predictors was designed to achieve parsimony while increasing the temporal transferability of the models (Araújo and Guisan 2006; Wenger and Olden 2012). Environmental predictor data for present-day conditions were acquired from the Copernicus Marine Service. Future projections of these predictor data layers were used through SSP scenarios derived from the ensemble (average of multiple atmosphere–ocean general circulation models "*AOGCMs*," see Table S1) (Assis et al. 2018). These models are provided as part of the 6th version of the Coupled Model Intercomparison Project (CMIP). Because information on the light at the sea bottom is unavailable for the future, the predictor variables were restricted to the typical maximum depth range of seagrasses (down to 20 m depth; Larkum, Kendrick, and Ralph 2018).

Records of seagrass occurrences used for modelling were compiled from (1) the global distribution of seagrasses from the United Nations Environment World Conservation Monitoring Centre (UNEP-WCMC 2021) and (2) the fine-tuned global distribution dataset of marine forests (Assis et al. 2020). These data comprised 1,547,562 records of 58 species belonging to 13 genera and 5 families (Cymodoceaceae, Hydrocharitaceae, Posidoniaceae, Zosteraceae and Ruppiaceae; Table S2). Due to lack of absence data, pseudo-absences were randomly generated for every species. To minimise the influence of spatial autocorrelation and sampling bias in distribution models (Araújo et al. 2005), a filtering process was applied to the occurrences and pseudo-absences by randomly selecting one record from the pool found within the minimum distance exhibiting significant spatial autocorrelation (Di Cola et al. 2016; Segurado, Araújo, and Kunin 2006). This distance was estimated by evaluating Pearson's correlation coefficient of predictor variables as a function of geographical distance (Boavida et al. 2016). Following the recommendations of Barbet-Massin et al. (2012), the number of pseudo-absences was set to a 1:1 ratio with occurrence records. However, to reduce the likelihood of generating redundant information for modelling, the pseudo-absences were climatically structured by applying to each one a unique membership attributed by *K*-means clustering performed on the predictors and setting the *k* clustering parameter to the number of occurrence records (Senay, Worner, and Ikeda 2013). This step further allowed removing the potential negative effect of class imbalance, which is particularly important for machine learning algorithms and provided a straightforward approach to isolate the potential contribution of predictor variables (Senay, Worner, and Ikeda 2013).

Model performance and predictive error were assessed with a 10-fold cross-validation framework (Roberts et al. 2017; Valavi et al. 2019) using spatially independent hexagons with sizes matching the previously determined uncorrelated distance (Mendoza and Araujo 2022; Valavi et al. 2019). Cross-validation also allowed identifying the optimal combination of hyperparameters for each algorithm (Elith, Leathwick, and Hastie 2008) by training competitive models in nine random folds of data, while one-fold was held at each run to test performance. The process was performed using the grid search method, which involved testing a span of learning rate (0.1, 0.01 and 0.001), tree complexity (1–4) and number of trees (50–1000, step 50) for BRT, number of interactions (50–250, step 50), degrees of freedom (1–12) and shrinkage (0.25–1, step 0.25) for AdaBoost (Krause-Jensen et al. 2020), and gamma (0 to 5, step 1), interaction depth (1 to 4), shrinkage (0.1 to 0.5, step 0.1) and number of rounds (10 to 100, step 10) for XGBoost (Valavi et al. 2022). To reduce overfitting, monotonic responses (Hofner, Muller, and Hothorn 2011) were forced either positively or negatively according to expected outcomes on species' habitat suitability. Maximum temperature, sea ice cover and wave energy were hypothesised to have a negative effect on seagrass distribution, while minimum temperatures, salinity and nutrient conditions were hypothesised to have a positive one. Pearson's correlation coefficient (r) and Variance Inflation Factor (VIF) were calculated among predictor pairs.

The performance of SDMs was determined with the Boyce index, which is an appropriate metric for presence-only models (Boyce et al. 2002), as well as with the area under the receiver operating characteristic curve (AUC) and sensitivity (Allouche, Tsoar, and Kadmon 2006). Boyce index varies between −1 and +1, while AUC and TSS are between 0 and 1. Positive Boyce index values above 0, or AUC and TSS above 0.5, indicate model predictions better than random, while values close to 1 suggest that predictions agree with the observed patterns (Hirzel et al. 2006). For each species and algorithm, full models, including all predictor variables, were built using the combination of hyperparameters retrieving higher performance in cross-validation. The significance of these models was inferred by determining the relative contribution of predictors to the performance of models and by developing partial dependence plots, from which hypothetical physiological tolerance limits were extracted (minimum or maximum, depending on the predictor; Assis et al. 2017; Elith, Leathwick, and Hastie 2008).

Habitat suitability maps per species were produced for present-day conditions and for the different SSP scenarios by ensembling the responses of the three algorithms (i.e., weighted averaged ensemble modelling; Araújo, Thuiller, and Pearson 2006). These were then reclassified into binomial maps to represent presence and absence records, using the minimum training area threshold, which sets the minimum predicted area while keeping sensitivity higher or equal to 0.95 (Vignali et al. 2020). To reduce overprediction, maps were clipped by considering potential reachable areas through dispersal (Ballesteros-Mejia et al. 2017; Cooper and Soberón 2018; Fragkopoulou et al. 2022; Mendes et al. 2020), an important step when analysing species with low dispersal ability, such as seagrasses (Kendrick et al. 2017). This considered the typical maximum dispersal distance among seagrass populations of up to 200 km (Kendrick et al. 2012) and avoided regions of unsuitable habitats.

Species richness maps for present-day and SSP scenarios were inferred by summing species' binomial maps (i.e., stacked SDM). The number of species gained (G) per pixel (assuming species are able to reach suitable areas) was determined under the three future SSP scenarios considered. Species lost (L) per pixel were also determined and divided by estimated species richness per pixel for present-day conditions (SR). Community turnover was calculated using the familiar metric (L + G)/(SR + G) (Thuiller et al. 2005). For visualisation purposes, maps were aggregated at a 60 km resolution using Uber's hexagonal hierarchical spatial index (Fragkopoulou et al. 2022). Summary tables were also produced to report estimates per marine realm, province, and ecoregion (Spalding et al. 2007a) and for the Exclusive Economic Zones (EEZs).

3 | Results

The performance of the individual models was high across the 3 algorithms, both in cross-validation and the final predictions, with further improvement when combined into a unique ensemble and when considering dispersal constraints based on a distance threshold of 200 km (Figure 1; Table S3). The ensemble models had low uncertainty (based on the standard deviation of the algorithms; Figure S1). Multiple predictors were considered in the models, but minimum and maximum ocean temperatures played a key role in explaining the distribution of seagrass species (relative combined contribution of ~71%, on average; Figure 1c; Table S4), followed by wave energy and nitrate (average contributions of 17.90% and 8.31%). Salinity had a residual contribution to the models (3.37%), and ice coverage was important for *Zostera marina* only (6.40%; per species estimates available in Table S4), the unique seagrass species with an Arctic distribution, and no species occurring in Antarctica. These results are supported by the generally low collinearity found between predictors. Only minimum and maximum temperatures showed stronger collinearity (Pearson's correlation 0.84 ± 0.08, on average; VIF 10.70 ± 11.24, on average), yet implementing monotonicity in the algorithms removed potentially unreliable estimates of model coefficients and improved the interpretability of the relative contribution of the two variables for the models' outcome. Overall, suitable environments for seagrasses were predicted in areas with temperatures ranging between 11.79°C and 29.14°C, wave energy equal to or below 5 (index ranging between 1 and 6, reflecting increasing energy), salinity above 25.14, nutrients above oligotrophic conditions ($9.97 \cdot 10^{-4}$ mol.m^{-3}) and with no ice (per species estimates available in Table S5).

3.1 | Seagrass Distribution and Biodiversity Patterns

Individual SDM were produced at 0.05° resolution and stacked into unique layers depicting the global distribution and diversity patterns of seagrasses (Figure 2a; Figure S2). The global extent of suitable habitats for seagrasses at present-day conditions was estimated to be 917,169 km^2 (Figure 2), at an average predicted depth of 2.26 m (Table S6). To describe geographic patterns of species richness, estimates were aggregated at the marine ecoregion level (Table S7; Spalding et al. 2007b). Accordingly, areas of high species richness were predicted in Temperate Australasia,

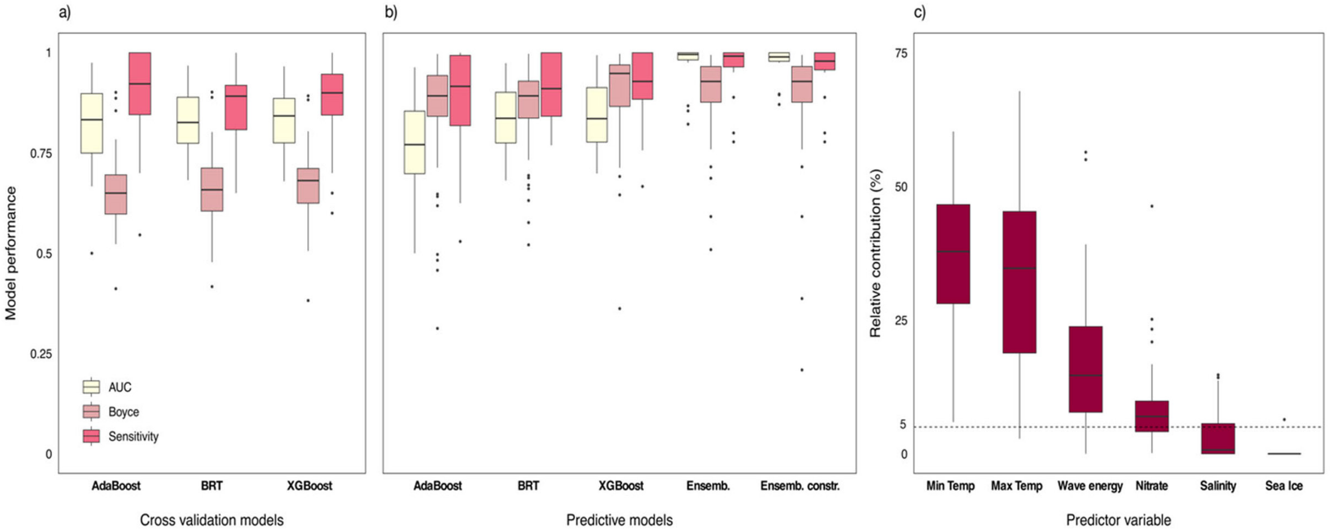

FIGURE 1 | Performance of species distribution modelling inferred with (a) cross-validation and (b) the final predictive models based on Adaptive Boosting (AdaBoost), Boosted Regression Trees (BRT), Extreme gradient boosting (XGBoost), and the ensemble of algorithms (without and with dispersal constraints; Ensemb. and Ensemb. constr., respectively), estimated with AUC, Boyce, and Sensitivity (yellow, light pink, and pink, respectively). (c) The relative contribution of each predictor variable to the ensemble of the algorithms. For more information, refer to Tables S3, S4.

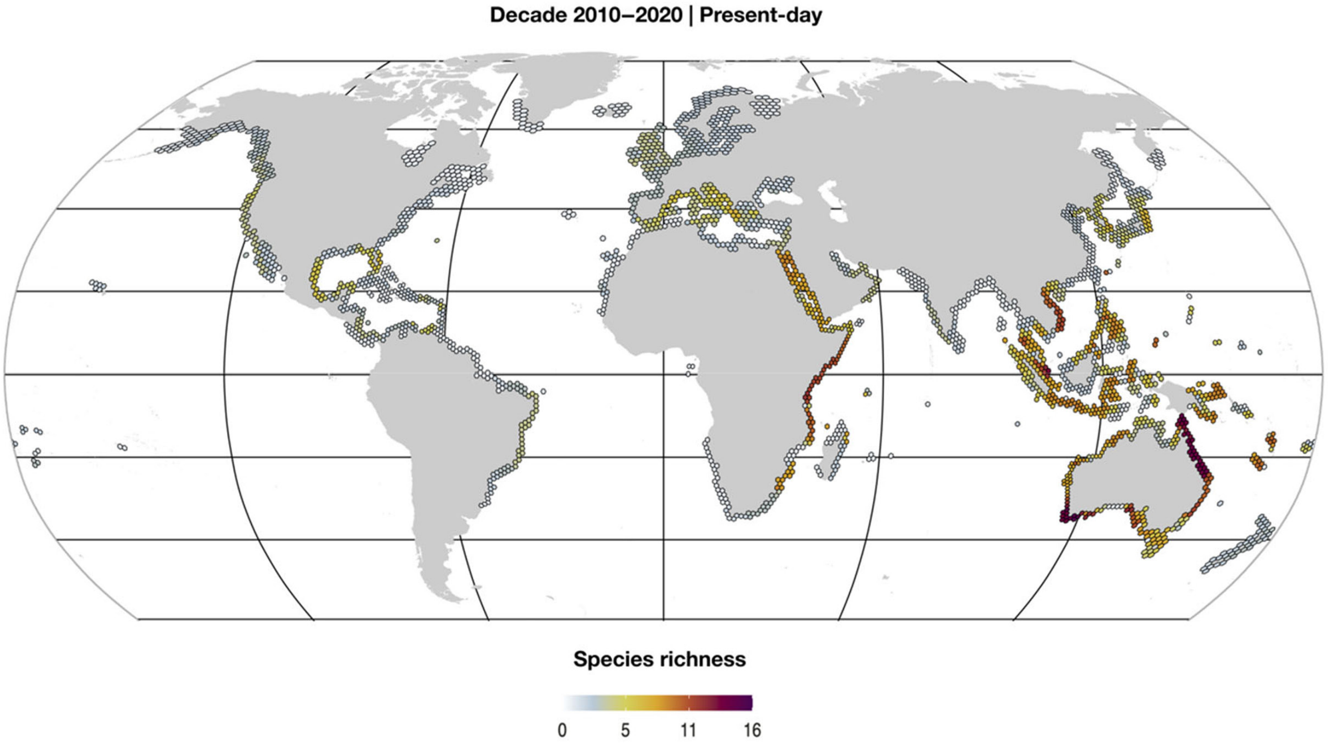

FIGURE 2 | Seagrass species richness patterns predicted at the global scale for present-day conditions. To improve visualisation, spatial information was aggregated to hexagon of 60 km edge length.

the Indo-Pacific, and the Temperate North Pacific (Figure 2; Table S7). The highest species richness was identified in the Leeuwin and the Houtman (16 species) ecoregions of Western Australia (Figure 2; Table S7). The Pacific and Atlantic Oceans were characterised by moderate richness (maximum 7 species), with regional higher diversity in the China and Mediterranean Seas (Figure 2; Table S7). Conversely, species-poor areas with up to 4 species were mainly predicted in the higher latitudes of both hemispheres (e.g., Arctic and South America), and along the western African coastline (Figure 2; Table S7).

Future projections considering dispersal constraints estimated limited net changes in the global extent of seagrasses, characterised by poleward expansions in the Arctic and regional losses at lower latitudes. The extent of suitable areas decreased by 5% under the low-emission SSP1-1.9 scenario and increased by 5% under the higher emission SSP3-7.0 (Figure 3; Figure S2a). The deepening of the average vertical distribution of seagrasses was estimated from 0.30 to 0.53 m (maximum: 9.20 m; SSP3-7.0; Table S6). Future projections anticipate extensive spatial redistribution, encompassing both latitude and longitude, as well as across depth levels. According to our models, as depth increases, it is likely that environmental conditions will become more suitable for seagrasses, as estimated in the SSP5-8.5 scenario and observed and projected elsewhere (Chefaoui et al. 2021).

Broad changes in species richness and community composition were projected globally, particularly under the higher emission scenarios SSP3-7.0 (Figure 3) and SSP5-8.5 (Figure S2a). Overall, a poleward shift of species richness was projected, coupled with losses between 30ºN to 30ºS that coincided with areas that currently hold great numbers of species (Figures 2, 3). The largest changes in regional species richness were estimated in numerous ecoregions of the Central Indo-Pacific and Temperate Australasia, with losses reaching up to 13 species (e.g., Torres Strait Northern Great Barrier Reef), and gains up to 12 species (e.g., Leeuwin) under SSP3-7.0 (Table S7). Regions losing up to 100% of their present-day seagrass species were also predicted at ecoregions of the Tropical Atlantic (e.g., Gulf of Guinea Islands), Tropical Eastern Pacific (e.g., Chiapas-Nicaragua), Indo-Pacific (e.g., Southeast Papua New Guinea), and Temperate Australasia (e.g., Three Kings-North Cape), without replacement by new species (Table S7).

Against this background of change, regions providing climatic refugia, i.e., suitable conditions for seagrass species under present and future conditions, were estimated in all future scenarios, although decreasing in extent with increasing gas emissions (global extent of refugia ranging between 917,169 and 817,865 km^2; Figure 4; Figure S2b). Under the SSP1-1.9 scenario, climatic refugia were estimated across the global distribution of seagrasses, in contrast to the increased emission SSP3-7.0 scenario, where refugia were mostly confined to mid (e.g., Adriatic Sea) and high latitude ecoregions (e.g., Aleutian Islands), as well as in upwelling regions (e.g., Saharan upwelling; Figure 4; Figure S3; Table S7).

Changes in community composition caused by localised range losses and gains (i.e., turnover) were projected across the global distribution of seagrasses (Figure 5). Regardless of the climate scenario considered, turnover peaked across the Arctic, the Central Indo-Pacific, Temperate Australasia, and Northern Pacific, either in areas experiencing pronounced gains (e.g., Hudson complex, Papua and Cape Howe) or regions with severe losses of species richness (e.g., Yellow and Japan Seas; Figure 5). Even some refugia regions showed some degree of

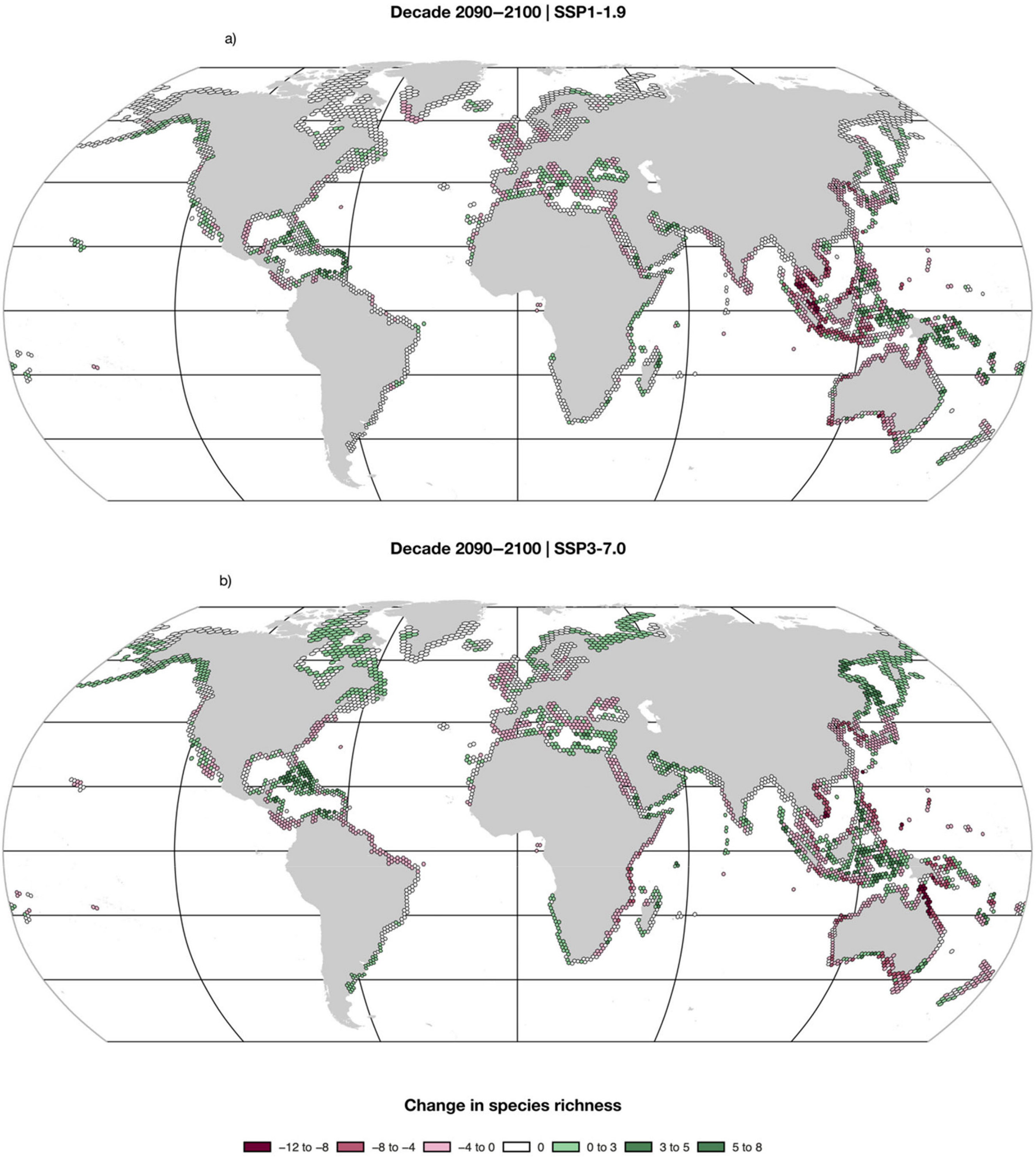

FIGURE 3 | Changes in species richness (green and purple gradients indicating gains and losses richness, respectively) under the scenarios of climate (a) SSP1-1.9 and (b) SSP3-7.0 (for the additional scenario SSP5-8.5 refer to Figure S2a).

community composition changes due to species gains and losses (Figure 5), despite the overall regional persistence of most species (Table S7).

4 | Discussion

We show that, despite limited net changes in the global extent of the seagrass biome, species are likely to experience poleward range shifts in the scenario of increased carbon emissions, as predicted by high-performance machine learning species distribution models for the latest-generation scenarios of climate change. These shifts may have profound consequences for regional patterns of species richness and community composition. The changes are particularly drastic across the Central Indo-Pacific, the Temperate Australasia and the Tropical Atlantic, some of which (e.g., Southeast Papua New Guinea and Chiapas-Nicaragua) are projected to

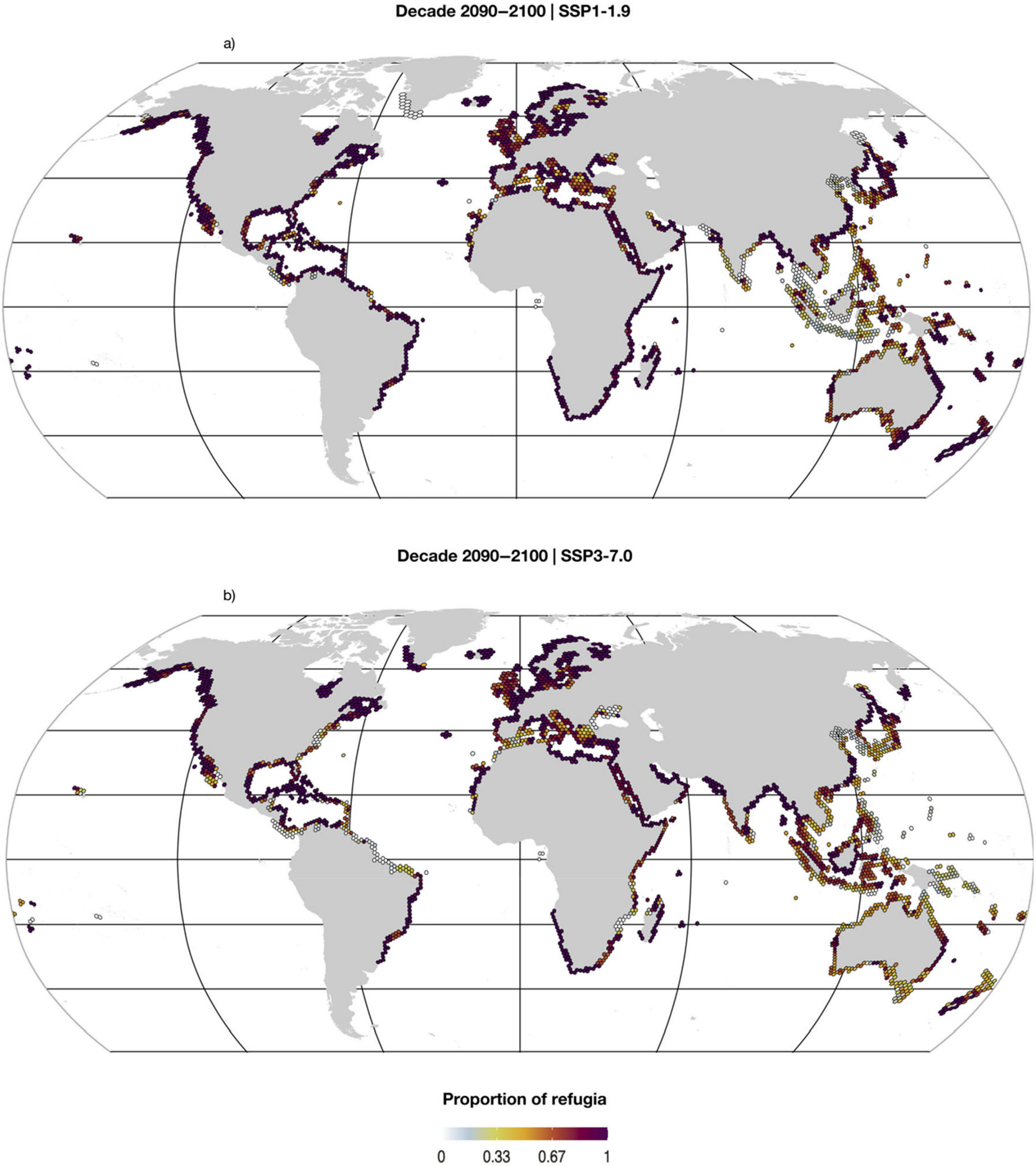

FIGURE 4 | The proportion of species finding refugia under the scenarios of climate change (a) SSP1-1.9 and (b) SSP3-7.0 (for the additional scenario SSP5-8.5 refer to Figure S2b).

lose up to 100% of their present seagrass species. By considering the new SSP scenarios of the current version of the CMIP (phase 6), our results are policy-relevant in the context of the latest IPCC Assessment Report on Climate Change and current international climate policies (e.g., the Paris Agreement). Importantly, our estimates indicate that strong climate action in line with the Paris Agreement is extremely worthwhile, as it has been predicted in broader climatic refugia, enhancing the prospects of seagrass persistence, as well as the multiple ecosystem services provided. Furthermore, by identifying areas that serve as important refugia for seagrasses, as well as those particularly vulnerable to the impacts of climate change, we provide crucial information in the context of Blue Economy (Alongi 2018; Chanda and Ghosh 2022). These will guide where efforts in conservation, management, and restoration for seagrass ecosystems can yield a more enduring positive

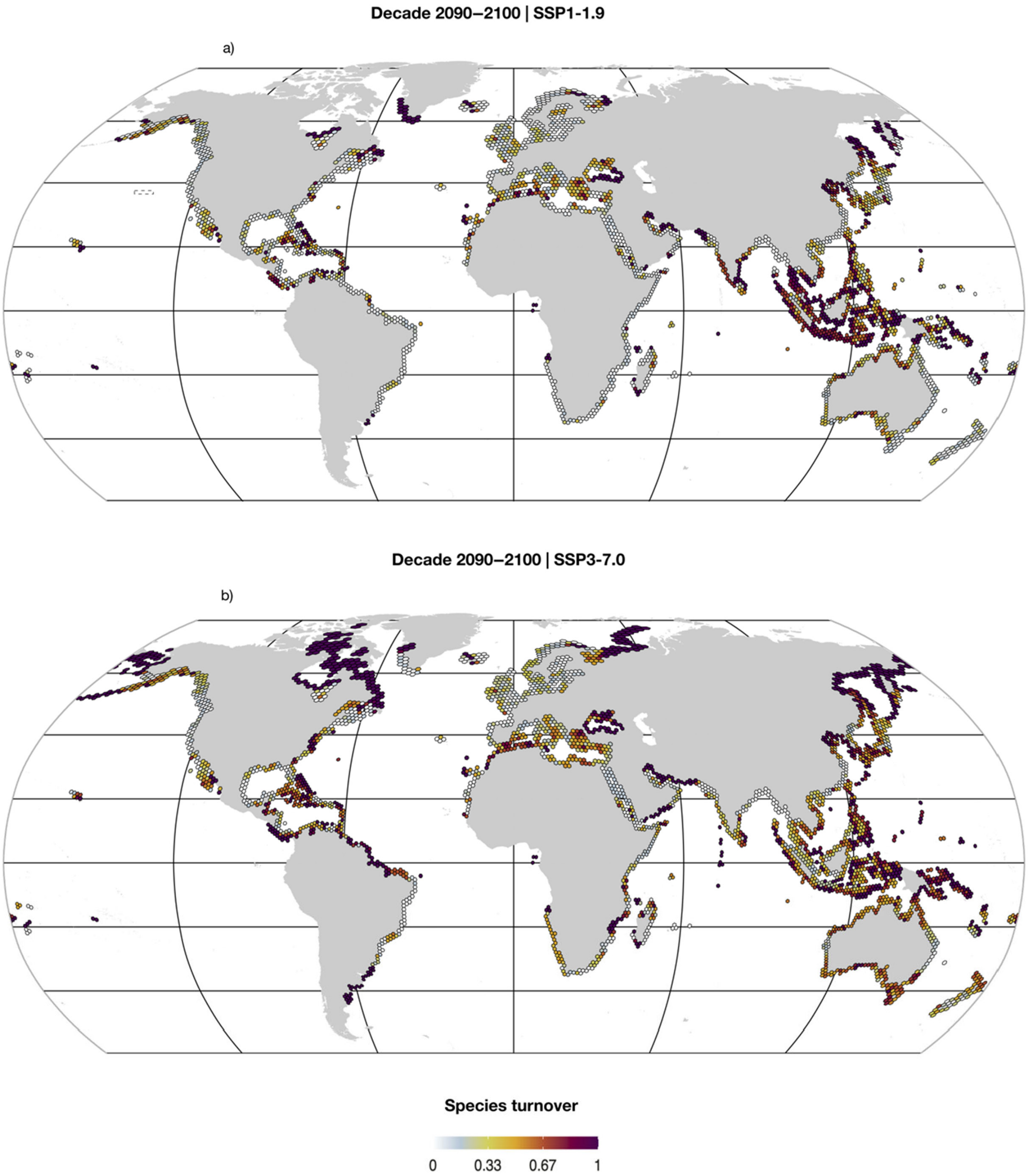

FIGURE 5 | Seagrass species' turnover projected under the scenarios of climate change (a) SSP1-1.9 and (b) SSP3-7.0 (for the additional scenario SSP5-8.5 refer to Figure S3).

impact, enhanced by the benefits to the associated biodiversity reliant on seagrass habitat.

The machine learning algorithms fitting expert-verified occurrence data per species against biologically meaningful predictors retrieved high performance. Their predictions averaged in a unique ensemble resulted in a robust approach, as expected in this line of modelling (a.k.a., ensemble modelling; Araújo and New 2007). Additionally, the integration of dispersal constraints further improved performance. This often-neglected SDM approach allows for reducing overprediction (Mendes et al. 2020) without prior information on species' dispersal ecology (Cooper and Soberón 2018), which is largely unavailable and uncertain for most marine species

(Assis et al. 2021; Gouvêa et al. 2023). Overall, the models indicate that the distribution of seagrasses is largely explained by physiological constraints (ocean temperature and nitrate) and disturbance (wave energy), in line with previous empirical and modelling studies (Assis et al. 2022; Jayathilake and Costello 2018; Pereda-Briones et al. 2018). The effect of nutrient conditions and sea ice is also supported by additional studies. While non-limiting nutrient concentrations have been linked to seagrass growth (Mazarrasa et al. 2018), the effect of ice, detected for *Zostera marina*, can regulate its occurrence by direct disturbance or by changing the light environment conditions (Assis et al. 2022; Krause-Jensen et al. 2020).

Stacking the individual models into a unique layer for the present-day conditions allowed an overview of the global seagrass biome, which largely matched its known distribution (Jayathilake and Costello 2018; Short et al. 2007), with a total predicted extent of 917,169 km^2, an estimate within the range of previous studies (300,000 to 1,646,788 km^2; Duarte, Middelburg, and Caraco 2005; Duarte et al. 2010; Jayathilake and Costello 2018; McKenzie et al. 2020). Similarly, the inferred patterns of seagrass species richness matched previous studies, with higher diversity estimated in Temperate Australasia and the Central Indo-Pacific (Larkum, Kendrick, and Ralph 2018; Short et al. 2007) and moderate species richness in the Pacific and Atlantic Oceans. These estimated biodiversity patterns reflect biogeographic and evolutionary expectations, supporting previous studies that have proposed the radiation and diversification of seagrasses in the Indo-Pacific and Australian regions (Larkum, Kendrick, and Ralph 2018; Short et al. 2007). Moreover, such a link between stacked SDM outcomes and biogeographic and evolutionary hypothesis has also been demonstrated for additional ecosystem structuring species at global scale, specifically marine forests of large brown algae (Fragkopoulou et al. 2022).

Stacking the individual models under future conditions revealed a limited degree of change in the global extent of seagrasses (by up to 5% globally). However, the generalised poleward range shifts of seagrass species may lead to changes in regional patterns of richness and community composition, aggravated under higher emission scenarios. Species like *Phyllospadix scouleri*, *Phyllospadix serrulatus*, *Zostera caespitosa* and *Zostera marina* may expand to the high latitudes of the Arctic (as projected elsewhere; Assis et al. 2022; Krause-Jensen et al. 2020). On the other hand, range contractions at lower and warmer latitudes are expected, as populations are already living near their upper thermal tolerance limits (Poloczanska et al. 2016). Losses are projected to impact species diversity in numerous countries (e.g., Australia, Vietnam, Japan, and Indonesia), some of which may entirely lose seagrass in specific areas. Such regional projections may add up to the losses already reported across the globe, whether by disease outbreaks, community structure shifts, or diebacks (Strydom et al. 2020; Tang and Hadibarata 2022). Despite generalised range shifts, broad regions were projected as climate refugia where seagrasses may find favourable conditions for the long-term. These areas were mainly identified in higher latitudes and also, interestingly, at deeper and upwelled regions of lower latitudes, where cold-richer waters may safeguard populations from detrimental stressful surface conditions (Graham et al. 2023), as observed for additional taxa (e.g., macroalgae; Lourenço et al. 2016) and gorgonian coral (Pilczynska et al. 2019). However, increased carbon emission scenarios projected a reduction in climate refugia from 917,169 to 817,865 km^2, specifically in regions like the Yellow and Japan Seas and Northern Brazil, challenging the long-term persistence of the seagrass and ecosystem services.

The generalised projected pattern of range shifts may bring contrasting positive and negative effects. The projected poleward expansions, by increasing seagrass area in previously unfavourable regions, can boost local ecosystem services (Viana et al. 2019) but also affect biotic interactions, outcompeting native species (Chiquillo et al. 2023; James et al. 2020) and altering the functioning of local ecosystems (Muthukrishnan et al. 2020). Concomitantly, at the lower latitudes, potential seagrass losses should have multiple consequences resulting from the loss of their ecosystem services. Where complete or severe losses are projected, consequences in ecological services are expected. These include reductions in carbon sequestration or even extremely severe loss of long-term carbon reserves, increased coastal erosion, changes in nutrient cycling, besides loss of essential habitat provisioning for numerous associated species (Dahl, Björk, and Gullström 2021; James et al. 2023; Nguyen et al. 2021; Pansini et al. 2021). Where species replacements preserve regional richness, consequences can be unpredictable. For instance, the replacement of the large seagrass *Thalassia testudinum* by the non-native smaller-sized *Halophila stipulacea* in the Caribbean resulted in decreased food availability, altered associated assemblages, and reduced coastal protection (James et al. 2020; Muthukrishnan et al. 2020). In contrast, the replacement of *Ruppia maritima* by *Halodule wrightii* had no significant impacts on the observed ecosystem services provided in two shallow lagoons of the Florida Gulf coast (Christiaen et al. 2016). The complexity of range shift outcomes highlights the need for additional research to understand the potential impacts of community turnover and well-informed management strategies for seagrass conservation in a rapidly changing world.

Despite the high performance of the models, limitations should be acknowledged. Potential data gaps and uneven sampling could have affected biodiversity estimates (Taheri et al. 2021; Tessarolo et al. 2014; Waycott et al. 2009), especially in under-sampled regions like Africa and Northeastern Russia. Uncertainties could also arise when projecting climate change impacts on seagrass distributions in regions where future conditions may be non-analog to those experienced by species anywhere in the present-day, such as in the Gulf of Oman and the Persian Gulf (Gouvêa et al. 2022). Additionally, projections did not consider additional drivers, such as anthropogenic disturbances in current and future distributions (e.g., degradation, eutrophication) (Faurby and Araújo 2018) or biotic interactions between species (e.g., competition, commensalism) that can further affect habitat suitability predictions (Araújo and Guisan 2006; Lemes et al. 2022). Integrating such additional drivers would be important to increase the realism of projections, however, such data are not available at the global extent of the study. Additionally, the lack of information on the available substrata, typically muddy to coarse sand, and future light conditions could have resulted in overpredicting suitable habitats (Krause-Jensen et al. 2020). To overcome this shortcoming, seagrass distribution was restricted to a maximum depth of 20 m, a typical maximum depth of seagrasses (Larkum et al. 2018). However, such conditions may change in the future, especially in higher latitudes, due to melting glaciers and increases in river outflow. Potential consequences of future sea level rise altering available coastlines were also not considered but may affect individual estimates of suitable habitat (Chefaoui et al. 2021). Concerning the nutrient forms assimilated by seagrasses, only one of them was considered in the models due to the strong correlation among these predictors (e.g., nitrate and phosphate). Some studies have suggested the nutrient source used for seagrass is dependent on species, but DIN (dissolved inorganic nitrogen) or ammonium could be better predictors than only nitrate (Han et al. 2023; Short and McRoy 1984). However, at global scales and community level, thermal conditions were the main drivers for the seagrass's distribution, and the influence of nutrients was residual in the models ($< 10\%$ of relative contribution; Figure 1). Additionally, although this is not directly reflected in the model predictions, since nutrient layers might not capture localised gradients of eutrophication, it is important to highlight that these events combined with warming conditions are a major stressor on seagrass and have led to declines of meadows (Helber et al. 2021). Future studies should consider additional drivers under present-day conditions and future climate scenarios to better capture localised stressors of seagrasses.

Considering all the above, our climate change impact assessment is likely to be overestimating seagrass habitat suitability. Nevertheless, it provides important new baseline information on present-day and future seagrass biodiversity patterns at global scales. As global change research advances, more and better data are being developed and made available that could be used to refine our results.

Our results highlight the benefits of complying with the Paris Agreement to reduce the magnitude of changes in seagrass biodiversity. Through high-resolution forecasts produced (0.05° resolution per species and stacked to unique layers; Supporting Information S2), we have provided baseline data to inform conservation and restoration actions. This enables the identification of regions with threatened species richness and stable seagrass ecosystems under different climate change scenarios. For example, countries like Somalia, Kenya, Australia, Brazil and Japan may see seagrass ecosystems and associated services dramatically reduced if broad compliance with the Paris Agreement is not achieved. This information supports a climate-smart conservation framework (Brito-Morales et al. 2022) and aligns with the new post-2020 Global Biodiversity Framework aiming to protect 30% of our seas by 2030 (CBD 2021; Leadley et al. 2022a). Identifying and protecting seagrass areas from additional cumulative disturbances, such as pollution or degradation caused by fishing gear, is crucial because these factors, combined with the impacts of climate change, could further compromise ecosystem health and resilience of meadows (Costello 2022a, 2022b; Leadley et al. 2022b). It could also be used to pinpoint candidate donor populations for restoration actions in impacted regions, in particular, stable seagrass in refugial areas (e.g., countries like Australia, New Zealand, and some islands of the South Pacific, Table S8). Finally, considering that seagrass ecosystems are major blue carbon sinks, the information provided can allow countries to manage and incorporate blue carbon strategies with the main target of enhancing CO_2 sequestration (Mazarrasa et al. 2018).

Author Contributions

L.G., E.F. and J.A. contributed to the study conception, design and defined the methodology; L.G., E.F. and J.A. led the writing of the manuscript; and all authors contributed to the draft and gave final approval for publication.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The ODMAP protocol (Supporting Information S1), high-resolution species richness maps (Supporting Information S2), and codes of species distribution modelling are available in Figshare at https://doi.org/10.6084/m9.figshare.23284019.

References

Agostini, S., B. P. Harvey, S. Wada, et al. 2018. "Ocean Acidification Drives Community Shifts Towards Simplified Non-Calcified Habitats in a Subtropical–Temperate Transition Zone." *Scientific Reports* 8, no. 1: 11354. https://doi.org/10.1038/s41598-018-29251-7.

Allouche, O., A. Tsoar, and R. Kadmon. 2006. "Assessing the Accuracy of Species Distribution Models: Prevalence, Kappa and the True Skill Statistic (TSS)." *Journal of Applied Ecology* 43, no. 6: 1223–1232. https://doi.org/10.1111/j.1365-2664.2006.01214.x.

Alongi, D. M. 2018. "The Blue Economy: Mitigation and Adaptation." https://doi.org/10.1007/978-3-319-91698-9_6.

Araújo, M. B., W. Thuiller, and R. G. Pearson. 2006. "Climate Warming and the Decline of Amphibians and Reptiles in Europe." *Journal of Biogeography* 33, no. 10: 1712–1728. https://doi.org/10.1111/j.1365-2699.2006.01482.x.

Araújo, M. B., R. P. Anderson, A. M. Barbosa, et al. 2019. "Standards for Distribution Models in Biodiversity Assessments." *Science Advances* 5, no. 1: aat4858. https://doi.org/10.1126/sciadv.aat4858.

Araújo, M. B., and A. Guisan. 2006. "Five (Or So) Challenges for Species Distribution Modelling." *Journal of Biogeography* 33, no. 10: 1677–1688. https://doi.org/10.1111/j.1365-2699.2006.01584.x.

Araújo, M. B., and M. New. 2007. "Ensemble Forecasting of Species Distributions." *Trends in Ecology & Evolution* 22, no. 1: P42–P47. https://doi.org/10.1016/j.tree.2006.09.010.

Araújo, M. B., R. G. Pearson, W. Thuiller, and M. Erhard. 2005. "Validation of Species-Climate Impact Models Under Climate Change." *Global Change Biology* 11, no. 9: 1504–1513. https://doi.org/10.1111/j.1365-2486.2005.01000.x.

Assis, J., E. Berecibar, B. Claro, et al. 2017. "Major Shifts at the Range Edge of Marine Forests: The Combined Effects of Climate Changes and Limited Dispersal." *Scientific Reports* 7, no. February: 1–10. https://doi.org/10.1038/srep44348.

Assis, J., P. Failler, E. Fragkopoulou, et al. 2021. "Potential Biodiversity Connectivity in the Network of Marine Protected Areas in Western Africa." *Frontiers in Marine Science* 8, no. November: 1–12. https://doi.org/10.3389/fmars.2021.765053.

Assis, J., E. Fragkopoulou, D. Frade, et al. 2020. "A Fine-Tuned Global Distribution Dataset of Marine Forests." *Scientific Data* 7, no. 1: 119. https://doi.org/10.1038/s41597-020-0459-x.

Assis, J., E. A. Serrão, C. M. Duarte, E. Fragkopoulou, and D. Krause-Jensen. 2022. "Major Expansion of Marine Forests in a Warmer Arctic." *Frontiers in Marine Science* 9, no. March: 1–10. https://doi.org/10.3389/fmars.2022.850368.

Assis, J., L. Tyberghein, S. Bosch, H. Verbruggen, E. A. Serrão, and O. De Clerck. 2018. "Bio-ORACLE v2.0: Extending Marine Data Layers for Bioclimatic Modelling." *Global Ecology and Biogeography* 27, no. 3: 277–284. https://doi.org/10.1111/geb.12693.

Ballesteros-Mejia, L., I. J. Kitching, W. Jetz, and J. Beck. 2017. "Putting Insects on the Map: Near-Global Variation in Sphingid Moth Richness Along Spatial and Environmental Gradients." *Ecography* 40, no. 6: 698–708. https://doi.org/10.1111/ecog.02438.

Barbet-Massin, M., F. Jiguet, C. H. Albert, and W. Thuiller. 2012. "Selecting Pseudo-Absences for Species Distribution Models: How, Where and How Many?" *Methods in Ecology and Evolution* 3, no. 2: 327–338. https://doi.org/10.1111/j.2041-210X.2011.00172.x.

Boavida, J., J. Assis, J. Reed, E. A. Serrão, and J. M. S. Gonçalves. 2016. "Comparison of Small Remotely Operated Vehicles and Diver-Operated Video of Circalittoral Benthos." *Hydrobiologia* 766, no. 1: 247–260. https://doi.org/10.1007/s10750-015-2459-y.

Boavida-Portugal, J., F. Guilhaumon, R. Rosa, and M. B. Araújo. 2022. "Global Patterns of Coastal Cephalopod Diversity Under Climate Change." *Frontiers in Marine Science* 8: 740781. https://doi.org/10.3389/fmars.2021.740781.

Boavida-Portugal, J., R. Rosa, R. Calado, et al. 2018. "Climate Change Impacts on the Distribution of Coastal Lobsters." *Marine Biology* 165, no. 12: 186. https://doi.org/10.1007/s00227-018-3441-9.

Boyce, M. S., P. R. Vernier, S. E. Nielsen, and F. K. A. Schmiegelow. 2002. "Evaluating Resource Selection Functions." *Ecological Modelling* 157, no. 2–3: 281–300. https://doi.org/10.1016/S0304-3800(02)00200-4.

Brito-Morales, I., D. S. Schoeman, J. D. Everett, et al. 2022. "Towards Climate-Smart, Three-Dimensional Protected Areas for Biodiversity Conservation in the High Seas." *Nature Climate Change* 12, no. 4: 402–407. https://doi.org/10.1038/s41558-022-01323-7.

Brown, S. C., C. Mellin, J. García Molinos, E. D. Lorenzen, and D. A. Fordham. 2022. "Faster Ocean Warming Threatens Richest Areas of Marine Biodiversity." *Global Change Biology* 28, no. 19: 5849–5858. https://doi.org/10.1111/gcb.16328.

CBD. 2021. "First Draft of the Post-2020 Global Biodiversity Framework." Cbd/Wg2020/3/3, July, 1–12.

Chanda, A., and T. Ghosh. 2022. "Blue Carbon Potential of India: The Present State of the Art." *Blue Economy: An Asian Perspective*: 159–180. https://doi.org/10.1007/978-3-030-96519-8_10.

Chefaoui, R. M., C. M. Duarte, and E. A. Serrão. 2018. "Dramatic Loss of Seagrass Habitat Under Projected Climate Change in the Mediterranean Sea." *Global Change Biology* 24, no. 10: 4919–4928. https://doi.org/10.1111/gcb.14401.

Chefaoui, R. M., C. M. Duarte, A. I. Tavares, et al. 2021. "Predicted Regime Shift in the Seagrass Ecosystem of the Gulf of Arguin Driven by Climate Change." *Global Ecology and Conservation* 32: e01890. https://doi.org/10.1016/j.gecco.2021.e01890.

Chen, T., and C. Guestrin. 2016. "XGBoost: A scalable tree boosting system." *Proceedings of the ACM SIGKDD International Conference on Knowledge Discovery and Data Mining, 13–17-August-2016*. https://doi.org/10.1145/2939672.2939785.

Chiquillo, K. L., P. H. Barber, M. I. Vasquez, et al. 2023. "An Invasive Seagrass Drives Its Own Success in Two Invaded Seas by Both Negatively Affecting Native Seagrasses and Benefiting From Those Costs." *Oikos* 2023, no. 3: e09403. https://doi.org/10.1111/oik.09403.

Christiaen, B., J. C. Lehrter, J. Goff, and J. Cebrian. 2016. "Functional Implications of Changes in Seagrass Species Composition in Two Shallow Coastal Lagoons." *Marine Ecology Progress Series* 557: 111–121. https://doi.org/10.3354/meps11847.

Cooper, J. C., and J. Soberón. 2018. "Creating Individual Accessible Area Hypotheses Improves Stacked Species Distribution Model Performance." *Global Ecology and Biogeography* 27, no. 1: 156–165. https://doi.org/10.1111/geb.12678.

Costello, M. J. 2022a. "Biodiversity Conservation Through Protected Areas Supports Healthy Ecosystems and Resilience to Climate Change and Other Disturbances." *Imperiled: The Encyclopedia of Conservation* 1-3. https://doi.org/10.1016/B978-0-12-821139-7.00164-1.

Costello, M. J. 2022b. "Restoring Biodiversity and Living With Nature (Based Solutions)." *Imperiled: The Encyclopedia of Conservation* 1-3. https://doi.org/10.1016/B978-0-12-821139-7.00233-6.

Da Ros, Z., C. Corinaldesi, A. Dell'Anno, C. Gambi, F. Torsani, and R. Danovaro. 2021. "Restoration of Cymodocea Nodosa Seagrass Meadows: Efficiency and Ecological Implications." *Restoration Ecology* 29, no. S2. https://doi.org/10.1111/rec.13313.

Dahl, M., M. Björk, and M. Gullström. 2021. "Effects of Seagrass Overgrazing on Sediment Erosion and Carbon Sink Capacity: Current Understanding and Future Priorities." *Limnology and Oceanography Letters* 6, no. 6: 309–319. https://doi.org/10.1002/lol2.10211.

Daru, B. H., and B. M. Rock. 2023. "Reorganization of Seagrass Communities in a Changing Climate." *Nature Plants* 9: 1034–1043. https://doi.org/10.1038/s41477-023-01445-6.

de los Santos, C. B., D. Krause-Jensen, T. Alcoverro, et al. 2019. "Recent Trend Reversal for Declining European Seagrass Meadows." *Nature Communications* 10, no. 1: 3356. https://doi.org/10.1038/s41467-019-11340-4.

Di Cola, V., O. Broennimann, B. Petitpierre, et al. 2016. "Ecospat: An R Package to Support Spatial Analyses and Modeling of Species Niches and Distributions." *Ecography* 40, no. 6: 774–787. https://doi.org/10.1111/ecog.02671.

Donatelli, C., N. K. Ganju, T. S. Kalra, S. Fagherazzi, and N. Leonardi. 2019. "Changes in Hydrodynamics and Wave Energy as a Result of Seagrass Decline Along the Shoreline of a Microtidal Back-Barrier Estuary." *Advances in Water Resources* 128: 183–192. https://doi.org/10.1016/j.advwatres.2019.04.017.

Duarte, C. M., J. J. Middelburg, and N. Caraco. 2005. "Major Role of Marine Vegetation on the Oceanic Carbon Cycle." *Biogeosciences* 2, no. 1: 1–8. https://doi.org/10.5194/bg-2-1-2005.

Duarte, C. M., N. Marbà, E. Gacia, et al. 2010. "Seagrass Community Metabolism: Assessing the Carbon Sink Capacity of Seagrass Meadows." *Global Biogeochemical Cycles* 24, no. 4. https://doi.org/10.1029/2010GB003793.

Elith, J., J. R. Leathwick, and T. Hastie. 2008. “A Working Guide to Boosted Regression Trees.” *Journal of Animal Ecology* 77, no. 4: 802–813. https://doi.org/10.1111/j.1365-2656.2008.01390.x.

Erzini, K., F. Parreira, Z. Sadat, et al. 2022. “Influence of Seagrass Meadows on Nursery and Fish Provisioning Ecosystem Services Delivered by ria Formosa, a Coastal Lagoon in Portugal.” *Ecosystem Services* 58: 101490. https://doi.org/10.1016/j.ecoser.2022.101490.

Espel, D., N. J. Diepens, O. Boutron, et al. 2019. “Dynamics of the Seagrass Zostera Noltei in a Shallow Mediterranean Lagoon Exposed to Chemical Contamination and Other Stressors.” *Estuarine, Coastal and Shelf Science* 222: 1–12. https://doi.org/10.1016/j.ecss.2019.03.019.

Faurby, S., and M. B. Araújo. 2018. “Anthropogenic Range Contractions Bias Species Climate Change Forecasts.” *Nature Climate Change* 8, no. 3: 252–256. https://doi.org/10.1038/s41558-018-0089-x.

Fragkopoulou, E., E. A. Serrão, O. De Clerck, et al. 2022. “Global Biodiversity Patterns of Marine Forests of Brown Macroalgae.” *Global Ecology and Biogeography* 31, no. 4: 636–648. https://doi.org/10.1111/geb.13450.

Garciá Molinos, J., B. S. Halpern, D. S. Schoeman, et al. 2016. “Climate Velocity and the Future Global Redistribution of Marine Biodiversity.” *Nature Climate Change* 6, no. 1: 83–88. https://doi.org/10.1038/nclimate2769.

Gorman, D., A. Turra, E. R. Bergstrom, and P. A. Horta. 2016. “Population Expansion of a Tropical Seagrass (Halophila Decipiens) in the Southwest Atlantic (Brazil).” *Aquatic Botany* 132: 30–36. https://doi.org/10.1016/j.aquabot.2016.04.002.

Gouvêa, L. P., E. Fragkopoulou, K. Cavanaugh, et al. 2023. “Oceanographic Connectivity Explains the Intra-Specific Diversity of Mangrove Forests at Global Scales.” *Proceedings of the National Academy of Sciences* 120, no. 14: 2209637120. https://doi.org/10.1073/pnas.2209637120.

Gouvêa, L. P., E. A. Serrão, K. Cavanaugh, C. F. D. Gurgel, P. A. Horta, and J. Assis. 2022. “Global Impacts of Projected Climate Changes on the Extent and Aboveground Biomass of Mangrove Forests.” *Diversity and Distributions* 28, no. 11: 2349–2360. https://doi.org/10.1111/ddi.13631.

Graham, O. J., T. Stephens, B. Rappazzo, et al. 2023. “Deeper Habitats and Cooler Temperatures Moderate a Climate-Driven Seagrass Disease.” *Philosophical Transactions of the Royal Society, B: Biological Sciences* 378, no. 1873: 20220016. https://doi.org/10.1098/rstb.2022.0016.

Grech, A., and R. G. Coles. 2010. “An Ecosystem-Scale Predictive Model of Coastal Seagrass Distribution.” *Aquatic Conservation: Marine and Freshwater Ecosystems* 20, no. 4: 437–444. https://doi.org/10.1002/aqc.1107.

Han, Q., C. Qiu, W. Zeng, et al. 2023. “Effect of DIN and DON Sources on the Nitrogen Uptake of the Seagrass Zostera Japonica and the Macroalgae Ulva Pertusa Previously Grown in Different Light Levels.” *Frontiers in Marine Science* 10. https://doi.org/10.3389/fmars.2023.1015323.

Harvey, B. P., K. Kon, S. Agostini, S. Wada, and J. M. Hall-Spencer. 2021. “Ocean Acidification Locks Algal Communities in a Species-Poor Early Successional Stage.” *Global Change Biology* 27, no. 10: 2174–2187. https://doi.org/10.1111/gcb.15455.

Helber, S. B., G. Procaccini, E. F. Belshe, et al. 2021. “Unusually Warm Summer Temperatures Exacerbate Population and Plant Level Response of Posidonia Oceanica to Anthropogenic Nutrient Stress.” *Frontiers in Plant Science* 12. https://doi.org/10.3389/fpls.2021.662682.

Hillebrand, H., T. Brey, J. Gutt, et al. 2018. “Climate Change: Warming Impacts on Marine Biodiversity.” *Handbook on Marine Environment Protection*. https://doi.org/10.1007/978-3-319-60156-4_18.

Hirzel, A. H., G. Le Lay, V. Helfer, C. Randin, and A. Guisan. 2006. “Evaluating the Ability of Habitat Suitability Models to Predict Species Presences.” *Ecological Modelling* 199, no. 2: 142–152. https://doi.org/10.1016/j.ecolmodel.2006.05.017.

Hodapp, D., I. T. Roca, D. Fiorentino, et al. 2023. “Climate Change Disrupts Core Habitats of Marine Species.” *Global Change Biology* 29: 3304–3317. https://doi.org/10.1111/gcb.16612.

Hoegh-Guldberg, O., and J. F. Bruno. 2010. “The Impact of Climate Change on the world's Marine Ecosystems.” *Science* 328, no. 5985. https://doi.org/10.1126/science.1189930.

Hofner, B., J. Muller, and T. Hothorn. 2011. “Monotonicity-Constrained Species Distribution Models.” *Ecology* 92, no. 10: 1895–1901.

James, R. K., L. M. Keyzer, S. J. van de Velde, P. M. J. Herman, M. M. van Katwijk, and T. J. Bouma. 2023. “Climate Change Mitigation by Coral Reefs and Seagrass Beds at Risk: How Global Change Compromises Coastal Ecosystem Services.” *Science of the Total Environment* 857: 159576. https://doi.org/10.1016/j.scitotenv.2022.159576.

James, R. K., M. J. A. Christianen, M. M. van Katwijk, et al. 2020. “Seagrass Coastal Protection Services Reduced by Invasive Species Expansion and Megaherbivore Grazing.” *Journal of Ecology* 108, no. 5: 2025–2037. https://doi.org/10.1111/1365-2745.13411.

Jayathilake, D. R. M., and M. J. Costello. 2018. “A Modelled Global Distribution of the Seagrass Biome.” *Biological Conservation* 226: 120–126. https://doi.org/10.1016/j.biocon.2018.07.009.

Kendrick, G. A., R. J. Orth, J. Statton, et al. 2017. “Demographic and Genetic Connectivity: The Role and Consequences of Reproduction, Dispersal and Recruitment in Seagrasses.” *Biological Reviews* 92, no. 2: 921–938. https://doi.org/10.1111/brv.12261.

Kendrick, G. A., M. Waycott, T. J. B. Carruthers, et al. 2012. “The Central Role of Dispersal in the Maintenance and Persistence of Seagrass Populations.” *Bioscience* 62, no. 1. https://doi.org/10.1525/bio.2012.62.1.10.

Krause-Jensen, D., P. Archambault, J. Assis, et al. 2020. “Imprint of Climate Change on Pan-Arctic Marine Vegetation.” *Frontiers in Marine Science* 7, no. December: 1–28. https://doi.org/10.3389/fmars.2020.617324.

Kwiatkowski, L., O. Torres, L. Bopp, et al. 2020. “Twenty-First Century Ocean Warming, Acidification, Deoxygenation, and Upper-Ocean Nutrient and Primary Production Decline From CMIP6 Model Projections.” *Biogeosciences* 17, no. 13: 3439–3470. https://doi.org/10.5194/bg-17-3439-2020.

Lafratta, A., O. Serrano, P. Masqué, et al. 2019. “Seagrass Soil Archives Reveal Centennial-Scale Metal Smelter Contamination While Acting as Natural Filters.” *Science of the Total Environment* 649: 1381–1392. https://doi.org/10.1016/j.scitotenv.2018.08.400.

Larkum, A. W. D., G. A. Kendrick, and P. J. Ralph. 2018. “Seagrasses of Australia: Structure, Ecology and Conservation.” In *Seagrasses of Australia: Structure, Ecology and Conservation*. Switzerland: Springer Nature, Switzerland AG. https://doi.org/10.1007/978-3-319-71354-0.

Larkum, A. W. D., M. Pernice, M. Schliep, et al. 2018. “Photosynthesis and Metabolism of Seagrasses.” *Seagrasses of Australia: Structure, Ecology and Conservation*. https://doi.org/10.1007/978-3-319-71354-0_11.

Leadley, P., A. Gonzalez, D. Obura, et al. 2022a. “Achieving Global Biodiversity Goals by 2050 Requires Urgent and Integrated Actions.” *One Earth* 5, no. 6. https://doi.org/10.1016/j.oneear.2022.05.009.

Leadley, P., D. Obura, E. Archer, et al. 2022b. “Actions Needed to Achieve Ambitious Objectives of Net Gains in Natural Ecosystem Area by 2030 and Beyond.” *PLOS Sustainability and Transformation* 1, no. 12. https://doi.org/10.1371/journal.pstr.0000040.

Lemes, P., F. G. Barbosa, B. Naimi, and M. B. Araújo. 2022. “Dispersal Abilities Favor Commensalism in Animal-Plant Interactions Under Climate Change.” *Science of the Total Environment* 835: 155157. https://doi.org/10.1016/j.scitotenv.2022.155157.

Lourenço, C. R., G. I. Zardi, C. D. McQuaid, et al. 2016. "Upwelling Areas as Climate Change Refugia for the Distribution and Genetic Diversity of a Marine Macroalga." *Journal of Biogeography* 43, no. 8: 1595–1607. https://doi.org/10.1111/jbi.12744.

Macreadie, P. I., T. B. Atwood, J. R. Seymour, et al. 2019. "Vulnerability of Seagrass Blue Carbon to Microbial Attack Following Exposure to Warming and Oxygen." *Science of the Total Environment* 686: 264–275. https://doi.org/10.1016/j.scitotenv.2019.05.462.

Mazarrasa, I., J. Samper-Villarreal, O. Serrano, et al. 2018. "Habitat Characteristics Provide Insights of Carbon Storage in Seagrass Meadows." *Marine Pollution Bulletin* 134, no. January: 106–117. https://doi.org/10.1016/j.marpolbul.2018.01.059.

McKenzie, L. J., L. M. Nordlund, B. L. Jones, L. C. Cullen-Unsworth, C. Roelfsema, and R. K. F. Unsworth. 2020. "The Global Distribution of Seagrass Meadows." *Environmental Research Letters* 15, no. 7. https://doi.org/10.1088/1748-9326/ab7d06.

Mendes, P., S. J. E. Velazco, A. F. A. de Andrade, and P. De Marco. 2020. "Dealing With Overprediction in Species Distribution Models: How Adding Distance Constraints Can Improve Model Accuracy." *Ecological Modelling* 431: 109180. https://doi.org/10.1016/j.ecolmodel.2020.109180.

Mendoza, M., and M. B. Araujo. 2022. "Biogeography of Bird and Mammal Trophic Structures." *Ecography* 2022, no. 7: 6289. https://doi.org/10.1111/ecog.06289.

Monserrat, M., S. Comeau, J. Verdura, et al. 2022. "Climate Change and Species Facilitation Affect the Recruitment of Macroalgal Marine Forests." *Scientific Reports* 12, no. 1: 18103. https://doi.org/10.1038/s41598-022-22845-2.

Mtwana Nordlund, L., E. W. Koch, E. B. Barbier, and J. C. Creed. 2016. "Seagrass Ecosystem Services and Their Variability Across Genera and Geographical Regions." *PLoS One* 11, no. 10: e0163091. https://doi.org/10.1371/journal.pone.0163091.

Muthukrishnan, R., K. L. Chiquillo, C. Cross, et al. 2020. "Little Giants: A Rapidly Invading Seagrass Alters Ecosystem Functioning Relative to Native Foundation Species." *Marine Biology* 167, no. 6: 81. https://doi.org/10.1007/s00227-020-03689-8.

Nguyen, H. M., P. J. Ralph, L. Marín-Guirao, M. Pernice, and G. Procaccini. 2021. "Seagrasses in an Era of Ocean Warming: A Review." *Biological Reviews* 96, no. 5: 2009–2030. https://doi.org/10.1111/brv.12736.

Nordlund, L. M., E. L. Jackson, M. Nakaoka, J. Samper-Villarreal, P. Beca-Carretero, and J. C. Creed. 2018. "Seagrass Ecosystem Services – What's Next?" *Marine Pollution Bulletin* 134, no. April: 145–151. https://doi.org/10.1016/j.marpolbul.2017.09.014.

Pansini, A., G. La Manna, F. Pinna, P. Stipcich, and G. Ceccherelli. 2021. "Trait Gradients Inform Predictions of Seagrass Meadows Changes to Future Warming." *Scientific Reports* 11, no. 1: 18107. https://doi.org/10.1038/s41598-021-97611-x.

Pereda-Briones, L., E. Infantes, A. Orfila, F. Tomas, and J. Terrados. 2018. "Dispersal of Seagrass Propagules: Interaction Between Hydrodynamics and Substratum Type." *Marine Ecology Progress Series* 593: 47–59. https://doi.org/10.3354/meps12518.

Peterson, A. T., and M. B. Araujo. 2012. "Uses and Misuses of Bioclimatic Envelope Modeling." *Ecology* 93, no. 1: 1527–1539. https://doi.org/10.1890/11-1930.1.

Pilczynska, J., S. Cocito, J. Boavida, et al. 2019. "Genetic Diversity Increases With Depth in Red Gorgonian Populations of the Mediterranean Sea and the Atlantic Ocean." *PeerJ* 2019, no. 5: 1–18. https://doi.org/10.7717/peerj.6794.

Poloczanska, E. S., M. T. Burrows, C. J. Brown, et al. 2016. "Responses of Marine Organisms to Climate Change Across Oceans." *Frontiers in Marine Science* 3. https://doi.org/10.3389/fmars.2016.00062.

Purvaja, R., R. S. Robin, D. Ganguly, et al. 2018. "Seagrass Meadows as Proxy for Assessment of Ecosystem Health." *Ocean and Coastal Management* 159: 34–45. https://doi.org/10.1016/j.ocecoaman.2017.11.026.

Roberts, D. R., V. Bahn, S. Ciuti, et al. 2017. "Cross-Validation Strategies for Data With Temporal, Spatial, Hierarchical, or Phylogenetic Structure." *Ecography* 40, no. 8: 913–929. https://doi.org/10.1111/ecog.02881.

Sanderson, B. M., B. C. O'Neill, and C. Tebaldi. 2016. "What Would It Take to Achieve the Paris Temperature Targets?" *Geophysical Research Letters* 43, no. 13: 7133–7142. https://doi.org/10.1002/2016GL069563.

Segurado, P., M. B. Araújo, and W. E. Kunin. 2006. "Consequences of Spatial Autocorrelation for Niche-Based Models." *Journal of Applied Ecology* 43, no. 3: 433–444. https://doi.org/10.1111/j.1365-2664.2006.01162.x.

Senay, S. D., S. P. Worner, and T. Ikeda. 2013. "Novel Three-Step Pseudo-Absence Selection Technique for Improved Species Distribution Modelling." *PLoS One* 8, no. 8: e71218. https://doi.org/10.1371/journal.pone.0071218.

Short, F., T. Carruthers, W. Dennison, and M. Waycott. 2007. "Global Seagrass Distribution and Diversity: A Bioregional Model." *Journal of Experimental Marine Biology and Ecology* 350, no. 1–2: 3–20. https://doi.org/10.1016/j.jembe.2007.06.012.

Short, F. T., and C. P. McRoy. 1984. "Nitrogen Uptake by Leaves and Roots of the Seagrass Zostera Marina L." *Botanica Marina* 27, no. 12: 547–556. https://doi.org/10.1515/botm.1984.27.12.547.

Short, F. T., R. G. Coles, and C. A. Short. 2001. *Introduction. Global Seagrass Research Methods*. Amsterdam: Elsevier.

Spalding, M. D., H. E. Fox, G. R. Allen, et al. 2007b. "Marine Ecoregions of the World: A Bioregionalization of Coastal and Shelf Areas." *Bioscience* 57, no. 7: 573–583. https://doi.org/10.1641/B570707.

Spalding, M. D., H. E. Fox, G. R. Allen, et al. 2007a. "Marine Ecoregions." *Climate Change 2013 - The Physical Science Basis* 57, no. 7: 1–30. https://www.cambridge.org/core/product/identifier/CBO9781107415324A009/type/book_part.

Strydom, S., K. Murray, S. Wilson, et al. 2020. "Too Hot to Handle: Unprecedented Seagrass Death Driven by Marine Heatwave in a World Heritage Area." *Global Change Biology* 26, no. 6: 3525–3538. https://doi.org/10.1111/gcb.15065.

Taheri, S., B. Naimi, C. Rahbek, and M. B. Araújo. 2021. "Improvements in Reports of Species Redistribution Under Climate Change Are Required." *Science Advances* 7, no. 15: ABE1110. https://doi.org/10.1126/SCIADV.ABE1110.

Tang, K. H. D., and T. Hadibarata. 2022. "Seagrass Meadows Under the Changing Climate: A Review of the Impacts of Climate Stressors." *Research in Ecology* 4, no. 1: 27–36. https://doi.org/10.30564/re.v4i1.4363.

Teagle, H., and D. A. Smale. 2018. "Climate-Driven Substitution of Habitat-Forming Species Leads to Reduced Biodiversity Within a Temperate Marine Community." *Diversity and Distributions* 24, no. 10: 1367–1380. https://doi.org/10.1111/ddi.12775.

Tessarolo, G., T. F. Rangel, M. B. Araújo, and J. Hortal. 2014. "Uncertainty Associated With Survey Design in Species Distribution Models." *Diversity and Distributions* 20, no. 11: 1258–1269. https://doi.org/10.1111/ddi.12236.

Thuiller, W., S. Lavorel, M. B. Araújo, M. T. Sykes, and I. C. Prentice. 2005. "Climate Change Threats to Plant Diversity in Europe." *Proceedings of the National Academy of Sciences of the United States of America* 102, no. 23: 8245–8250. https://doi.org/10.1073/pnas.0409902102.

UNEP-WCMC, S. F. 2021. *Global Distribution of Seagrasses (Version 7.1). Seventh Update to the Data Layer Used in Green and Short (2003).*

Cambridge, UK: UN Environment World Conservation Monitoring Centre. https://data.unep-wcmc.org/datasets/7.

Valavi, R., J. Elith, J. J. Lahoz-Monfort, and G. Guillera-Arroita. 2019. "blockCV: An r Package for Generating Spatially or Environmentally Separated Folds for k-Fold Cross-Validation of Species Distribution Models." *Methods in Ecology and Evolution* 10, no. 2: 225–232. https://doi.org/10.1111/2041-210X.13107.

Valavi, R., G. Guillera-Arroita, J. J. Lahoz-Monfort, and J. Elith. 2022. "Predictive Performance of Presence-Only Species Distribution Models: A Benchmark Study With Reproducible Code." *Ecological Monographs* 92, no. 1: 1486. https://doi.org/10.1002/ecm.1486.

van Katwijk, M. M., A. Thorhaug, N. Marbà, et al. 2016. "Global Analysis of Seagrass Restoration: The Importance of Large-Scale Planting." *Journal of Applied Ecology* 53, no. 2: 567–578. https://doi.org/10.1111/1365-2664.12562.

Viana, I. G., R. Siriwardane-de Zoysa, D. A. Willette, and L. G. Gillis. 2019. "Exploring How Non-native Seagrass Species Could Provide Essential Ecosystems Services: A Perspective on the Highly Invasive Seagrass Halophila Stipulacea in the Caribbean Sea." *Biological Invasions* 21, no. 5: 1461–1472. https://doi.org/10.1007/s10530-019-01924-y.

Vignali, S., A. G. Barras, R. Arlettaz, and V. Braunisch. 2020. "SDMtune: An R Package to Tune and Evaluate Species Distribution Models." *Ecology and Evolution* 10, no. 20: 11488–11506. https://doi.org/10.1002/ece3.6786.

Villero, D., M. Pla, D. Camps, J. Ruiz-Olmo, and L. Brotons. 2017. "Integrating Species Distribution Modelling Into Decision-Making to Inform Conservation Actions." *Biodiversity and Conservation* 26, no. 2: 251–271. https://doi.org/10.1007/s10531-016-1243-2.

Waycott, M., C. M. Duarte, T. J. B. Carruthers, et al. 2009. "Accelerating Loss of Seagrasses Across the Globe Threatens Coastal Ecosystems." *Proceedings of the National Academy of Sciences of the United States of America* 106, no. 30: 12377–12381. https://doi.org/10.1073/pnas.0905620106.

Wenger, S. J., and J. D. Olden. 2012. "Assessing Transferability of Ecological Models: An Underappreciated Aspect of Statistical Validation." *Methods in Ecology and Evolution* 3, no. 2: 260–267. https://doi.org/10.1111/j.2041-210X.2011.00170.x.

Zurell, D., J. Franklin, C. König, et al. 2020. "A Standard Protocol for Reporting Species Distribution Models." *Ecography* 43, no. 9: 1261–1277. https://doi.org/10.1111/ecog.04960.

Supporting Information

Additional supporting information can be found online in the Supporting Information section.