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Reshuffling of Azorean Coastal Marine Biodiversity Amid Climate Change

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ABSTRACT

Aim: Climate change poses a challenge to the Azores' biodiversity, with consequences that remain unexplored. To shed light on the potential impacts of climate change, we have developed a large ensemble of species distribution models (SDMs) for species found in the coastal marine environments and examined their spatiotemporal turnover and stability.

Location: The Azorean archipelago.

Taxon: Coastal marine species (mammals, fish, turtles, seabirds, kelp forest and corals).

Methods: SDMs were fitted a large ensemble comprising 10 machine learning algorithms and a fivefold cross-validation resampling procedure, thus yielding a maximum number of 50 models fitted per species. These models were then utilised for projecting species distribution under different future scenarios. The projected distributions of the species were employed to assess changes in the stability of their ranges throughout the entire modelled period (2030–2100) and in their community compositions by examining changes in alpha diversity and beta diversity over 10-year periods.

Results: We show that under our model assumptions over 12% of the modelled units could lose suitable climate by the end of the century, with this number increasing up to 25% under a high carbon emissions scenario. Climate change refugia, which are areas of long-term species range stability, are expected to be mainly located in the coastal areas in the northernmost part of the archipelago. A substantial loss of suitable climate is anticipated for mammals and birds, which is likely to trigger a major loss of species on the islands of Santa Maria, São Miguel, Pico and Faial. For fish, the loss of suitable climates is less pronounced. However, climate change is expected to cause a major reshuffling of the pelagic fish assemblage, with important consequences for local fisheries on each island.

Main Conclusions: Our models provide insights into how climate change may alter the distribution of Azorean marine coastal species, offering important guidance for conservation and management efforts in these important North Atlantic ecosystems.

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1 | Introduction

The Azores is a volcanic archipelago located in the North Atlantic Ocean. It boasts a unique biodiversity shaped by convergent influences from Europe, America and Africa. Situated at the crossroads of these three continents, the Azores exhibit a blend of species that have arrived through various natural dispersal routes and mechanisms (Borges and Hortal 2009; Morton and Britton 2000). This convergence has resulted in a rich assemblage of plant and animal life found in a few other places on the planet. However, this extraordinary biodiversity faces a growing threat associated with climate change. While such effects have been examined across terrestrial ecosystems (Ferreira et al. 2016, 2019) and offshore marine zones (Calado et al. 2011), a comprehensive assessment of the expected impacts of climate change on coastal marine ecosystems is still missing.

The Azores' coastal marine ecosystems play a vital role in supporting local communities and sustaining the region's economy. For example, they provide crucial habitats for commercially valuable fish species, which support the local fishing industry (Carvalho, Edwards-Jones, and Isidro 2011). Additionally, the archipelago's coastal waters attract visitors from around the world for their exceptional biodiversity, offering opportunities for nature-based tourism and recreational activities like fishing, snorkelling, diving, as well as shark and whale watching (Bentz et al. 2014; Diogo and Pereira 2013; Queiroz, Guerreiro, and Ventura 2014; Silva 2015). The economic well-being of the Azorean community is thus intrinsically linked to the health and vitality of its coastal biodiversity.

Although ongoing climate change inevitably poses new challenges to the Azores' coastal marine biodiversity, the extent of its impacts is still poorly studied. Rising sea temperatures, increased storm intensity and changing oceanic currents can all lead to shifts in species distributions, alter ecological interactions and disrupt the delicate balance of these ecosystems (Poloczanska et al. 2013; Smale et al. 2019). Furthermore, ocean acidification resulting from the absorption of excess carbon dioxide by seawater poses a particular threat to the calcifying organisms and the intricate food webs within the Azorean marine ecosystems (Guinotte and Fabry 2008). To begin addressing these issues, we use the largest ensemble of species distribution models (SDMs) possibly developed for coastal marine environments to examine the potential effects of climate change scenarios on the persistence and potential redistribution of suitable environmental conditions for marine species of mammals, reptiles, fish (both pelagic and benthic), breeding birds, as well habitat suitability for corals and kelp. We ask the following: (1) How large is the proportion of species projected to lose suitable climate in the future? (2) How does the rate of loss of suitable climate compare across different taxonomic groups? (3) How will loss of climate suitability affect species turnover? All three questions were addressed considering Shared Socioeconomic Pathway (SSP) scenarios of future climate change with low (SSP1-1.9) and high (SSP5-8.5) carbon emissions.

2 | Materials and Methods

2.1 | Species Checklist and Occurrence

Our dataset was created through a three-step process. Firstly, we compiled a list of species inhabiting the coastal ecosystems of the Azores by conducting a spatial query within the coastal zone of each one of the nine islands of the archipelago, considering a 12-mile distance from the edge. Secondly, we verified the distribution of each species in coastal zones by consulting available checklists and experts. Thirdly, we removed any duplicate entries and filtered the list of species to retain only those with a minimum of 15 occurrences. The entire pipeline for creating the dataset was implemented using R v. 4.2.1. Each step is described in detail below.

In the first step, we generated the initial inventory of data for coastal species by querying recorded occurrences of all species within a 12-mile buffer along the coastlines of the seven islands comprising the Azorean archipelago. The buffer width was selected in accordance with the review process of the Network of Marine Protected Areas of the Azores (RAMPA), overseen by the Blue Azores programme (<https://www.blueazores.org/>), which aims to bolster marine biodiversity protection by delineating and enhancing protected areas. While the initial boundary was set to differentiate between coastal and offshore zones based on variations in scientific data, user groups and socio-economic factors, it was deemed appropriate to expand the buffer from the originally intended 6 to 12 miles. This extension addressed the resolution of environmental data (3 miles), the presence of species near the buffer edge and potential geolocation errors, thereby providing a more robust and comprehensive representation of coastal marine diversity. Species occurrence data were compiled from various repositories, including eBird (2021), GBIF.org (2023), OBIS (Halpin et al. 2009), BioTIME (Dornelas et al. 2018) and the Azores Portal of Biodiversity ('AZP'; Borges et al. 2010). Data from projects conducted in the Azores were also considered in our inventory (Azevedo and Barreiros 2019; Barcelos, Azevedo, and Barreiros 2022a, 2022b; Barcelos and Barreiros 2022; Luz et al. 2022; Neto et al. 2021). Morphotypes and genus-level identifications were discarded. This initial inventory resulted in a preliminary checklist of 4563 species.

In the second step, we focused on standardising taxonomic names and excluding species whose distribution did not encompass the coastal marine areas of the Azores. Initially, taxonomic names were standardised using the WORMS taxonomic dictionary (Horton et al. 2017). Subsequently, the resulting list underwent a comprehensive review conducted by specialists and cross-referenced with published taxonomic lists to ensure the exclusion of potentially misidentified or non-occurring species. To validate the accuracy of the list, algae species were reviewed by Andrea Zita Botelho and Manuela Parente Cardoso, marine invertebrates by Ana Costa and seabirds by Azucena Martin. We further eliminated duplicate entries based on geographic coordinates to ensure the accuracy of our data. Following the revisions, the final checklist comprised 2,779,112 spatial records of 1716 species representing 26 phyla.

Owing to extreme heterogeneity in the spatial representativeness of species distributions data across groups, in the final step, we opted to exclude species with less than 15 records within the 12-mile buffer. The application of this criterion resulted in the exclusion of 1394 species, leaving a final list with 323 species (see Data S1). The final checklist comprised 25 species of marine mammals, 239 species of fish, 4 species of turtles, 9 species of breeding seabirds, 2 species of kelps and 44 species of corals. Given the scarcity and incomplete nature of data for corals and kelps, we consolidated all coral and kelp species records, treating them as two distinct biogenic habitats (habitat forming species). That is, out of a pool of 323 species, we modelled the distribution for 277 species and 2 biogenic habitats.

2.2 | Data for Fitting Species Distribution Models

We used species occurrence data as spatial points with presence records only (i.e., without absence records), specifying locations where species were observed. We also used a set of environmental and climate variables obtained from BioORACLE V3.0 (Assis et al. 2024), which provides essential physical, chemical and biological GIS raster layers for surface and benthic marine realms with global extent and uniform resolution (0.05° resolution, approx. 5 km at the equator). The variables provided are presented as statistical summaries of weather data over time slices of 10-year intervals for a baseline period (2010–2020) and future periods (2030–2040, 2040–2050, 2050–2060, 2060–2070, 2070–2080, 2080–2090 and 2090–100). Projections of future climates involved two shared SSP scenarios, including the SSP1-1.9 and SSP5-8.5 corresponding to the lowest (best) and highest (worst) greenhouse gas emissions scenarios, respectively (Riahi et al. 2017). We examined collinearity among predictor variables using the variance inflation factor (VIF) metric and selected a reduced set of uncorrelated and ecologically relevant predictors through a stepwise procedure (Naimi et al. 2014) to avoid multicollinearity (Dormann et al. 2013). The values of the VIF and the results of the stepwise procedure have been included in the FigShare repository (see below). Specifically, we selected four variables including maximum temperature, phytoplankton, pH and salinity and used them as predictors in SDMs. The benthos raster layers were used to model benthic species, including corals, kelps and fish. The surface raster layers were used to model the distribution of all other species.

2.3 | Species Distribution Modelling

For each one of the species considered, we fitted SDMs (Peterson et al. 2012). We used 10 machine learning algorithms and a five-fold cross-validation resampling procedure, fitting a maximum of 50 models per species. SDMs were fitted for species with at least 15 presence records to avoid the effects of biases resulting from low sample size (Stockwell and Peterson 2002; Van Proosdij et al. 2016).

The extent of the study area can affect model results (Tessarolo et al. 2014; Thuiller et al. 2004), and this is particularly important when species–climate response curves are estimated with species distributions that fail to sample the full gradient where

the species are present (Araújo et al. 2019; Pearson et al. 2006). To address this issue, all species present in the coastal areas of the Azores were modelled including their reported occurrences across the entire North Atlantic, spanning latitudes from 15° to 65°N and longitudes from 4° to 54°W (see also Araújo et al. 2022). This broader geographical scope was crucial to better capture the full spectrum of environmental conditions for each species, thereby reducing the risk of underestimating species–environment response curves when projecting the impacts of environmental changes on species distributions, as suggested by previous research (Araújo et al. 2019; Thuiller et al. 2004).

Given that the available species distribution data contain presence-only records, we generated 1000 pseudo-absence points, which were used to represent the background set. The points were randomly sampled across the entire North Atlantic study area using the ‘background’ function from the ‘sdm’ package (Naimi and Araújo 2016). This method ensures that the pseudo-absence data capture the full spectrum of environmental conditions within the study area, thus better representing the environmental gradient for each species (Thuiller et al. 2004). Furthermore, the use of a consistent background dataset across all species reduces the risk of underestimating species–environment response curves and enhances the comparability of the models (Araújo et al. 2019).

The 10 machine learning algorithms used to develop SDMs were generalised linear model (‘GLM’, McCullagh 2019), classification and regression trees (CART, Breiman et al. 1984), boosted regression trees (BRT, Elith, Leathwick, and Hastie 2008), random forests (RF, Breiman 2001), multiple discriminant analysis (MDA, Hastie, Tibshirani, and Buja 1994), support vector machine (SVM, Vapnik 2000), multivariate adaptive regression spline (MARS, Friedman 1991), maximum entropy (Maxent, Phillips, Anderson, and Schapire 2006), domain (Carpenter, Gillison, and Winter 1993) and bioclimatic envelope (Busby 1991). Resampling by fivefold cross-validation was used to generate five replications of training and test datasets containing 70% and 30% of the total records, respectively (Fielding and Bell 1997). We then fitted 10 SDMs for each replication and evaluated them for their performance. We used the area under the curve (AUC) of the receiver operating characteristic (ROC) plot (Swets 1979) and the true skill statistic (TSS, Allouche, Tsoar, and Kadmon 2006) to estimate the predictive performance of models. AUC values under 0.5 indicate discrimination between observations and predictions worse than expected by chance; a score of 0.5 implies random discrimination; and a score of 1 indicates perfect discrimination. TSS is calculated as ‘sensitivity + specificity – 1’ and ranges from –1 to +1, where +1 indicates perfect agreement, a value of 0 implies agreement expected by chance and a value of less than 0 indicates agreement worse than chance.

2.4 | Ensemble Forecasting

For each species, we combined the outcome of the different models within an ensemble forecasting framework (Araújo and New 2007). Specifically, we estimated a consensus for each species across the baseline period by obtaining an AUC-weighted mean across all models (García et al. 2012). The models were

used to project the distribution of species into the future periods and then the outcomes of different models were combined using the same approach, representing a consensus SDM for different future scenarios. The resulting maps were reclassified into binomial maps indicating the presence or absence of the species using the 'lowest presence threshold' (LPT). The LPT was estimated for each species by selecting the lowest predicted value associated with any of the observed presence records, as described by Pearson et al. (2007). This approach can be interpreted ecologically as identifying pixels predicted to be at least as suitable as those where a species' presence has been recorded. The approach is conservative, identifying the smallest predicted area while maintaining zero omission errors in the training dataset.

All SDM and ensemble forecasting analysis was performed using the 'sdm' R package (Naimi and Araújo 2016). The large total number of replications and the sophisticated modelling workflow employed in this study made the computation expensive. Therefore, we used high-performance computing by adopting a parallelised procedure executed on an efficient supercomputer cluster based at the University of Évora (OBLIVION).

2.5 | Temporal Reshuffling of Marine Assemblages

Temporal reshuffling was assessed by monitoring changes in the estimated presence and absence of individual species over 10-year periods. Specifically, two currencies were examined: changes in alpha diversity and beta diversity. Alpha diversity, or species richness, was measured as the number of estimated species presences in the 0.05° gridded cells within each decade. This was calculated by stacking ensemble SDM projections for each species and decade, and summing the number of species present in each grid. The beta diversity was estimated by measuring the change in the estimated composition of the species within each grid cell over the successive decades. It was measured using the Sørensen index (Sorensen 1948), which calculates the similarity of species composition in a grid cell at two points in time as the ratio of the number of common and dissimilar species between the two time windows. Following Cardoso, Rigal, and Carvalho (2015), we also disaggregated beta diversity in terms of replacement and species richness components to assess whether compositional changes are attributable to rearrangements of co-existing species or to the local extinction of one or more species. Alpha and beta diversity were quantified using the 'divraster' R package (Mota et al. 2023).

Finally, we examined range stability throughout the entire modelled period (2030–2100). Areas projected to sustain the presence of the species across the entire period were classified as range retention refugia (Araújo et al. 2022), signifying their critical importance for species conservation in the face of climate change.

3 | Results

Overall, ensemble models showed good predictive performance across all biological groups ($AUC > 0.8$, see all the modelling results at <https://doi.org/10.6084/m9.figshare.25358638>).

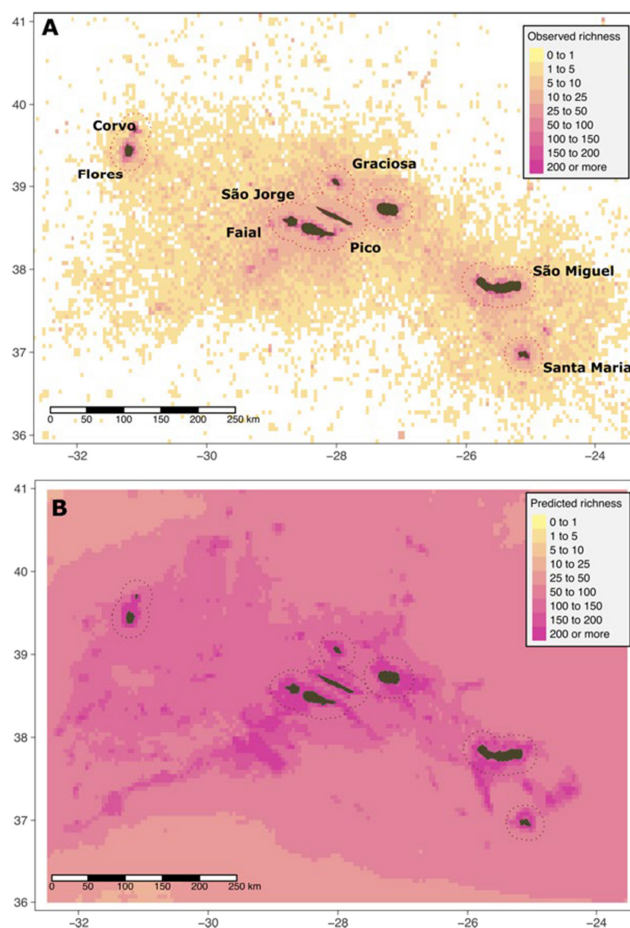


FIGURE 1 | Coastal marine diversity across the Azorean archipelago. (A) Observed species richness as calculated from existing occurrence records of sea birds, sea mammals, fishes, turtles and two biogenic habitats (kelps and corals). (B) Predicted species richness by stacking the ensemble forecasting of species distribution models. A coastal buffer of 12 miles is represented using dotted lines. Observed and predicted richness maps for each biological group considered are provided as Data S2 (Figures S2.1–S2.14).

Ensemble models largely capture the observed patterns of species richness in the Azores and offer predictions that extend beyond areas with high recorded concentrations of species (Figure 1). As expected, the highest number of co-occurring species is predicted for the coastal zones.

3.1 | How Large Is the Proportion of Species Projected to Lose Suitable Climate in the Future?

Projections estimate a decrease in the number of coastal marine species throughout the 21st century due to a reduction in suitable climatic conditions (suitable range) compared to the baseline period (Figure 2). The rate of loss of suitable areas for species is expected to differ depending on the emissions scenario (compare coloured bars in Figure 2A,B). Nevertheless, our projections indicate that by the year 2100, over 120 species in the coastal marine zones of the Azores archipelago could lose more than 50% of their suitable distribution areas.

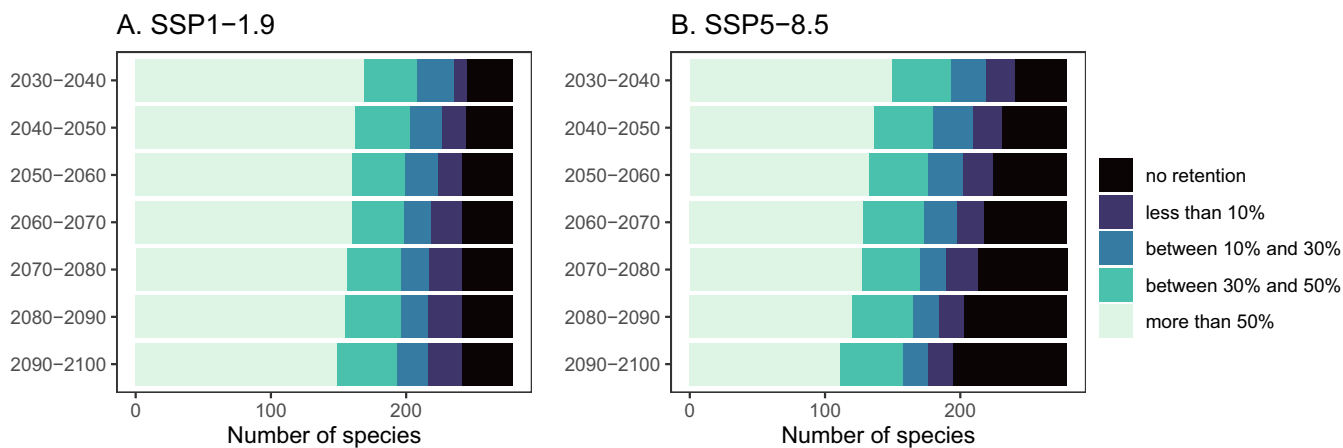


FIGURE 2 | Projected retention of the suitable climate range for marine species in the coastal marine Azores throughout the 21st century. The bars display the number of species falling into different classes based on the percentage of range retention forecasted in each decade. The black bars represent the number of species that would undergo complete loss of climate suitability within the 12-mile coastal buffer between decades under scenarios of low (A) and high (B) carbon emission scenarios. Further detailed information regarding the percentage of refugia retained by species in each decade and island is provided in Data S3 and S4.

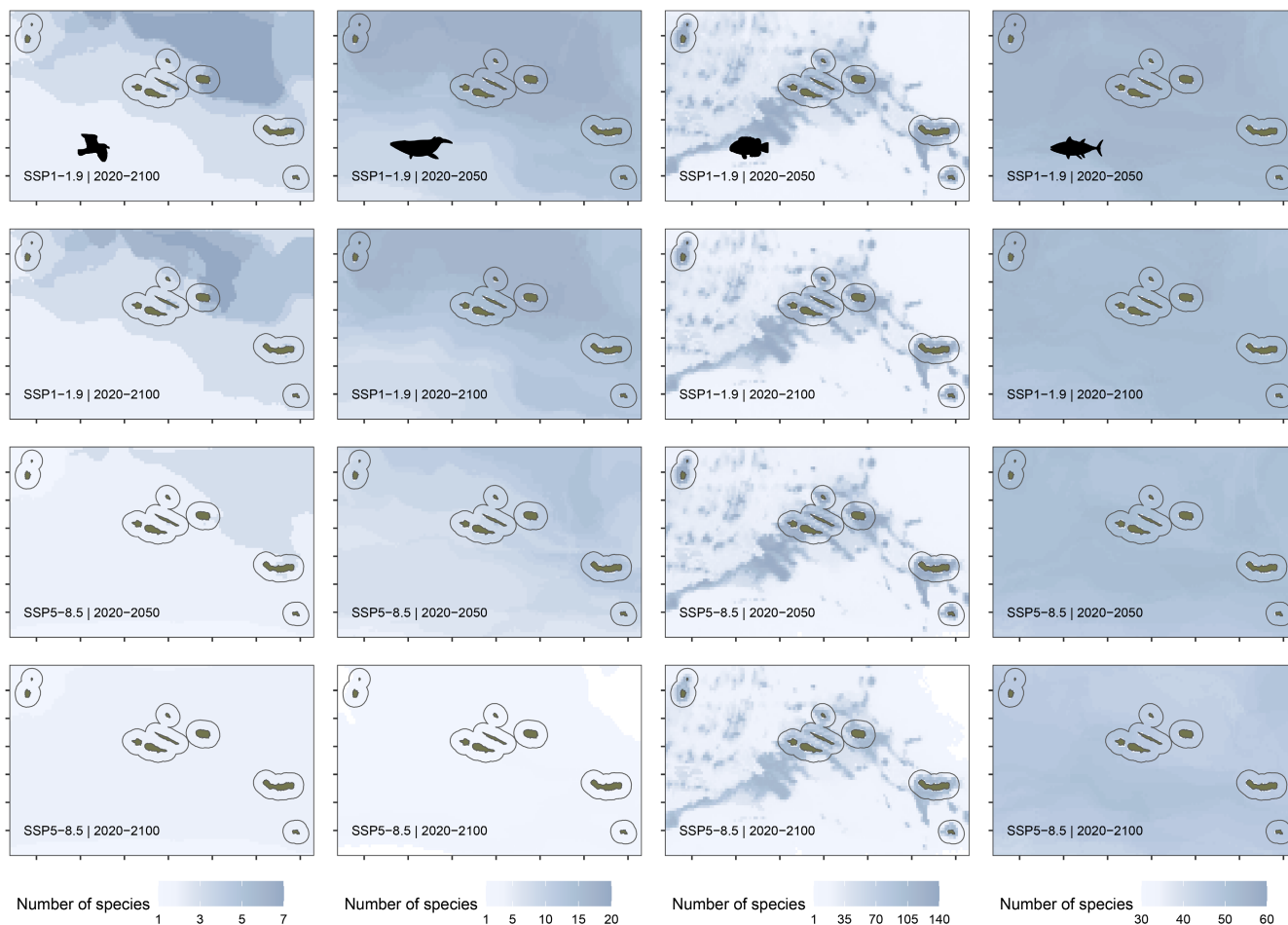


FIGURE 3 | Projected climate retention refugia for coastal marine assemblages of birds, mammals, benthic fish, and pelagic fish (left to right), from the mid (two top rows) to late 21st century (two bottom rows) under two climate change scenarios. Refugia are areas (grid cells) that are projected to remain suitable for at least one species until the middle or end of the century. Increased number of species with retained refugia is indicated by increased shades of grey. A coastal buffer of 12 miles is represented using black lines.

Under the low-carbon scenario (SSP1-1.9), changes in the retention of suitable areas would remain minimal over the century (Figure 2A). Climate change is projected to decrease

more than 90% of the suitable area for 18% of the modelled species (see purple and black bars in Figure 2A). Of this percentage, about 24 species are projected to lose the whole of their

suitable area in the Azores archipelago. In contrast, under the high emissions scenario (SSP5-8.5), the retention of suitable areas decreases from the beginning to the end of the century (Figure 2B). By the end of the century, the proportion of species expected to retain more than the 10% of their suitable area decreases from 55% in 2030–2040 to 40%. Indeed, over 80 species, including *Merluccius merluccius*, *Labrus bergylta* and *Symphurus nigrescens*, are projected to lose their suitable area completely within the 12-mile coastal buffers (black bars in Figure 2B). Refer to Data S3 and S4 for detailed information on the retention refugia per species, per island and per climate change scenario.

3.2 | How Does the Rate of Loss of Suitable Climate Compare Across Different Taxonomic Groups?

One approach to assess the impact of climate change on species distributions is to measure how much of current species distributions will remain climatically viable throughout a given time frame in the future. Such areas of range retention, or climate refugia, are critical for the persistence of species and for conservation planning. Across the Azorean archipelago, range retention areas are projected to shrink across a greater area and faster for seabirds and marine mammals than for benthic and pelagic fish (compare the changes in the blue zones in Figure 3). By 2100, the maximum number of bird species that will remain climatically viable within the 12-mile coastal buffer could range from 7 in SSP1-1.9 to 2 in SSP5-8-5. For marine mammals, the number of species that will remain climatically viable could decrease from 18 in SSP1-1.9 to 2 in SSP5-8-5 (refer to bottom panels in Figure 3).

In coastal marine environments (i.e., within the 12 miles of the coastline), benthic and pelagic fish are expected to maintain their refugia by 2100 (Columns 3 and 4 in Figure 3). However, the number of species able to retain their ranges in these areas may vary depending on the climate change scenario. For instance, the maximum number of benthic fish species that will remain climatically viable within the 12-mile coastal buffer could range from 133 in SSP1-1.9 to 115 in SSP5-8-5. For pelagic fish, the number of species that will remain climatically viable could decrease from 55 in SSP1-1.9 to 49 in SSP5-8-5.

3.3 | How Will Loss of Climate Suitability Affect Species Turnover?

Shifts in coastal marine species distributions will likely drive changes at the assemblage level. One approach to investigate changes is through the measurement of beta diversity through time. Analysis of beta diversity through time indicate changes in species richness more so than species replacement, as shown by the comparison of blue and yellow colours in the bar plots of Figure 4. The decline in climate suitability within coastal marine areas could lead to local extinctions of seabirds and mammals, with pronounced impacts in coastal communities near the islands of Santa Maria, São Miguel, Pico, Faial and Sao Jorge. This outcome is especially noticeable under the most extreme carbon scenario (SSP585), where most of these

species are anticipated to face local extinction by the mid-21st century (see Figure S2.15).

Furthermore, beta diversity calculations indicate alterations in species replacement rather than changes in species numbers are likely to be the primary drivers behind the reshuffling of fish communities (as illustrated by the comparison between the yellow and blue bars in Figure 4). The impact of distribution shifts on community reorganisation appears to be more pronounced for pelagic fish compared to benthic fish. This is indicated by the elevated levels of species turnover relative to overall beta diversity observed in across the islands.

4 | Discussion

Conservation planning and management must be tailored to account for the diverse responses of coastal marine species to climate change (Orgeret et al. 2022; Rilov et al. 2019). While climate change poses a global threat to marine biodiversity, the impact on diversity can differ significantly based on the specific sensitivities of each taxonomic group and the geographic characteristics of each part of the archipelago. It is crucial to incorporate these variances in conservation planning to effectively mitigate the adverse effects of climate change on coastal marine ecosystems (Poloczanska et al. 2013). To safeguard marine mammals effectively, conservation efforts should focus on prioritising the protection of climate refugia located in the northernmost coastal zones of the archipelago. Such an approach would protect potential migration pathways for larger species, like whales, facilitating their movement to areas with less exposure to adverse conditions (Fredston-Hermann, Gaines, and Halpern 2018).

Additionally, forecasting alterations in food webs resulting from fish species turnover could offer valuable insights for enhancing coastal marine fishery management on those islands of the archipelago anticipated to undergo significant species reshuffling. The reorganisation of assemblages due to climate-driven species replacement and loss is likely to modify existing food web dynamics and interaction intensities (Sydeman et al. 2015). These changes could redirect the flow of energy and carbon within ecosystems and potentially encourage the proliferation of pests and diseases (Bartley et al. 2019). Understanding these potential shifts is crucial for developing adaptive management strategies that can accommodate the evolving ecological seascape, thereby ensuring the sustainability and resilience of coastal marine resources and ecosystems (Kortsch et al. 2015). Therefore, incorporating models that consider biotic interactions, could complement understanding of the impacts of climate change on the coastal ecosystems of the Azores. By integrating biotic interactions into the models, we could gain deeper insights into the potential changes and challenges facing these environments, thereby enhancing our ability to devise effective conservation and management strategies.

Models and maps produced for future species ranges and retention refugia can offer crucial insights for the selection and design of networks of coastal marine protected areas (Araújo et al. 2022), along with various supplementary indicators of connectivity (Gouvêa et al. 2023) and vulnerability to both gradual and

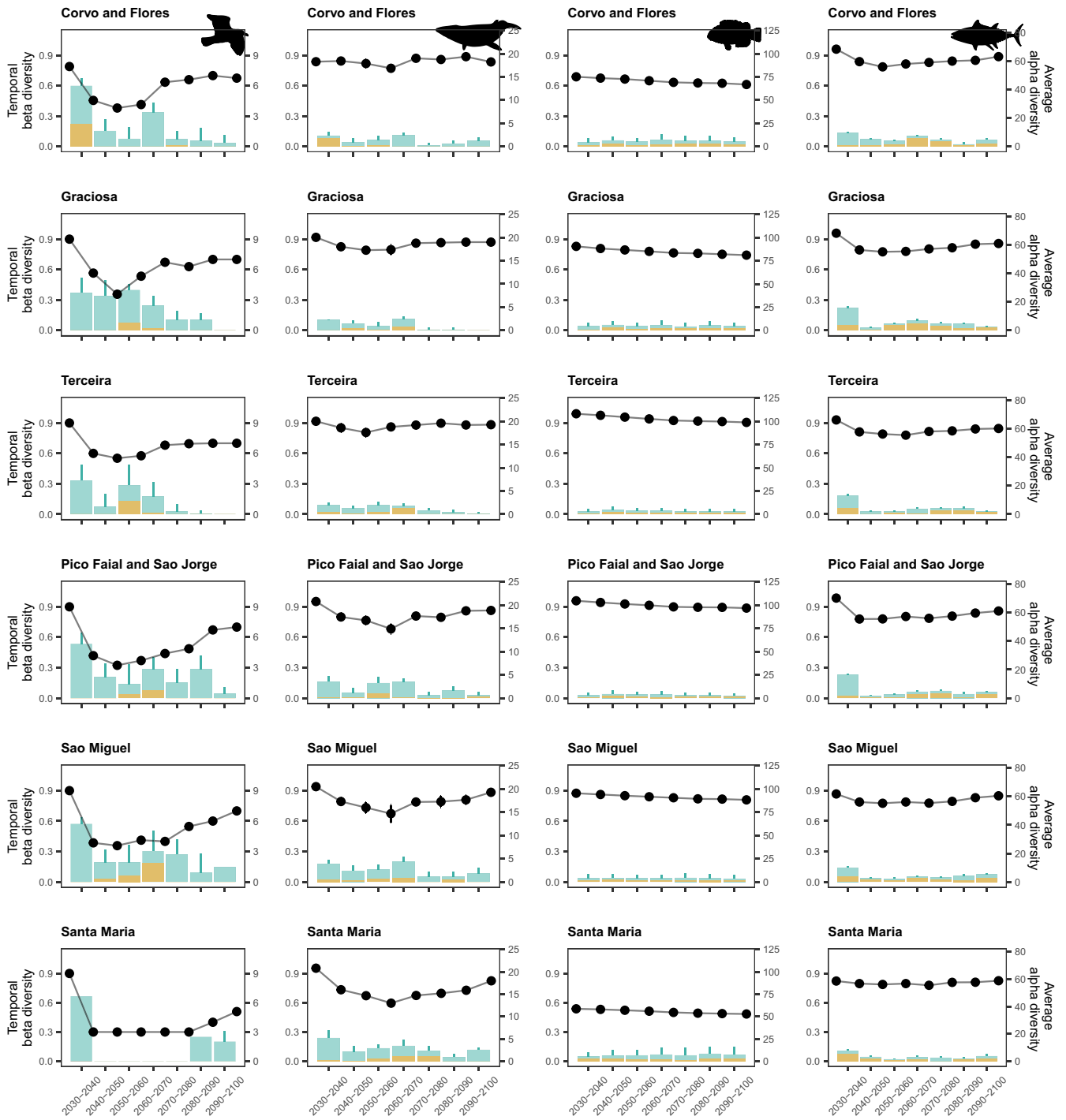


FIGURE 4 | Temporal beta diversity of coastal marine assemblages as driven by species loss and replacement. Blue bars represent beta diversity between decades (each bar represents the difference between a given decade and the decade preceding it). Yellow bars represent the fraction of the beta diversity that is associated with species replacement. Points represent the average alpha diversity (and standard deviation) found at each island in each decade. Temporal trends projected under the SSP1-19.

extreme climate changes (Buenafe et al. 2023; González-Trujillo et al. 2023). It is, however, important to bear in mind certain limitations inherent in our modelling approach. Firstly, the accuracy of our models is contingent upon the availability and density of occurrence records, which vary among species. This may potentially impact the reliability of predictions for those with sparse data. Secondly, our projections are based on specific climate scenarios and assumptions about future greenhouse gas emissions.

This introduces uncertainties regarding the precision of future predictions. Finally, by focusing solely on coastal marine species currently occurring in the Azores, our analysis did not account for the seasonal arrival or permanent encroachment of offshore and coastal species. Given the high functional connectedness of marine biodiversity (Albouy et al. 2019), an influx of species currently absent from the Azores, following warming of the ocean (Hastings et al. 2020), is almost guaranteed. The potential

displacement of marine faunas poses a dual-edged sword: on one hand, it introduces additional challenges for conserving native biodiversity, as some of the migrating species may compound the threats posed by climate change if, somehow, manage to outcompete native species (Alexander, Diez, and Levine 2015). On the other hand, it provides an opportunity to mitigate anticipated species losses by enabling the colonisation of species distributed in southerly regions, leading to the transformation of existing communities into new ones comprising species typically adapted to warmer waters (Lurgi, López, and Montoya 2012). Conducting a comprehensive evaluation of the redistribution and its implications for faunal biodiversity across the North Atlantic exceeds the scope of this study. However, such an assessment would be essential to gain a more complete understanding of the impacts of climate change on the biodiversity of the Azorean coasts.

This study provides new insights into how climate change will alter the distribution of Azorean coastal marine species. It unequivocally demonstrates the sensitivity of various taxonomic groups and islands to two distinct climate change scenarios and reveals the potential consequences for the species composition of coastal marine communities. Furthermore, it provides vital regional insight that will inform local climate change adaptation efforts. Particularly in the southern islands of the archipelago, where species redistribution is anticipated to be most significant, it is imperative for policymakers to focus on curbing over-exploitation and habitat degradation. This would help diminish the combined impacts of suboptimal natural resource management and climate change (Staudt et al. 2013). By engaging local communities in the conservation of habitats and species, this strategy not only enhances the resilience of marine ecosystems but also empowers communities, fostering a collaborative approach to environmental stewardship (Marques et al. 2013). Such an inclusive model of conservation would ensure that local knowledge and practices contribute to sustainable ecosystem management, thereby strengthening the overall effectiveness of climate adaptation measures.

Author Contributions

J.D.G.-T. and M.B.A. conceived the study. Environmental data layers were prepared by J.A. Species data collection was performed by J.D.G.-T. Analyses were implemented by J.D.G.-T. and B.N. The first draft of the manuscript was written by J.D.G.-T. and M.B.A. and all authors commented on subsequent versions of the manuscript. All authors read and approved the final manuscript.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The datasets analysed and generated in this study are available in the FigShare project page https://figshare.com/projects/Reshuffling_of_

[Azorean_coastal_marine_biodiversity_amid_climate_change/197941](https://doi.org/10.6084/m9.figshare.25358641) Occurrence data are available at <https://doi.org/10.6084/m9.figshare.25358641>. SDM outputs for every individual species are available at <https://doi.org/10.6084/m9.figshare.25358638>.

References

- Albouy, C., P. Archambault, W. Appeltans, et al. 2019. "The Marine Fish Food Web Is Globally Connected." *Nature Ecology & Evolution* 3, no. 8: 1153–1161. <https://doi.org/10.1038/s41559-019-0950-y>.
- Alexander, J. M., J. M. Diez, and J. M. Levine. 2015. "Novel Competitors Shape Species' Responses to Climate Change." *Nature* 525, no. 7570: 515–518. <https://doi.org/10.1038/nature14952>.
- 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>.
- Araujo, M., and M. New. 2007. "Ensemble Forecasting of Species Distributions." *Trends in Ecology & Evolution* 22, no. 1: 42–47. <https://doi.org/10.1016/j.tree.2006.09.010>.
- Araújo, M. B., R. P. Anderson, A. Márcia Barbosa, et al. 2019. "Standards for Distribution Models in Biodiversity Assessments." *Science Advances* 5, no. 1: eaat4858. <https://doi.org/10.1126/sciadv.aat4858>.
- Araújo, M. B., S. Antunes, E. Gonçalves, R. Oliveira, S. Santos, and I. Sousa Pinto. 2022. *Biodiversidade 2030: Nova Agenda Para a Conservação em Contexto de Alterações Climáticas*. Évora, Portugal: Universidade de Évora, Fundo Ambiental, Ministério do Ambiente e da Ação Climática.
- Assis, J., S. J. Fernández Bejarano, V. W. Salazar, et al. 2024. "Bio-ORACLE v3.0. Pushing Marine Data Layers to the CMIP6 Earth System Models of Climate Change Research." *Global Ecology and Biogeography* 33: e13813. <https://doi.org/10.1111/geb.13813>.
- Azevedo, J., and J. P. Barreiros. 2019. "Azores Cetaceans Updated Checklist." [Dataset]. <https://doi.org/10.15468/DMRKX9>.
- Barcelos, L., J. Azevedo, and J. P. Barreiros. 2022a. "Azores Actinopterygii Updated Checklist." [Dataset]. <https://doi.org/10.15468/GODGMQ>.
- Barcelos, L., J. Azevedo, and J. P. Barreiros. 2022b. "Azores Chondrichthyes Updated Checklist." [Dataset]. <https://doi.org/10.15468/DFQXWO>.
- Barcelos, L. M. D., and J. P. Barreiros. 2022. "Occurrences of Sea Turtles in Azores Archipelago." [Dataset]. <https://doi.org/10.15468/MZ8R7V>.
- Bartley, T. J., K. S. McCann, C. Bieg, et al. 2019. "Food Web Rewiring in a Changing World." *Nature Ecology & Evolution* 3, no. 3: 345–354. <https://doi.org/10.1038/s41559-018-0772-3>.
- Bentz, J., P. Dearden, E. Ritter, and H. Calado. 2014. "Shark Diving in the Azores: Challenge and Opportunity." *Tourism in Marine Environments* 10, no. 1: 71–83. <https://doi.org/10.3727/154427314X14056884441789>.
- Borges, P. A. V., R. Gabriel, A. M. Arroz, et al. 2010. "The Azorean Biodiversity Portal: An Internet Database for Regional Biodiversity Outreach." *Systematics and Biodiversity* 8, no. 4: 423–434. <https://doi.org/10.1080/14772000.2010.514306>.
- Borges, P. A. V., and J. Hortal. 2009. "Time, Area and Isolation: Factors Driving the Diversification of Azorean Arthropods." *Journal of Biogeography* 36, no. 1: 178–191. <https://doi.org/10.1111/j.1365-2699.2008.01980.x>.
- Breiman, L. 2001. "Random Forests." *Machine Learning* 45, no. 1: 5–32.
- Breiman, L., J. H. Friedman, R. A. Olshen, and C. J. Stone. 1984. *Classification and Regression Trees*. 1st ed. New York: Routledge. <https://doi.org/10.1201/9781315139470>.

- Buenafe, K. C. V., D. C. Dunn, J. D. Everett, et al. 2023. "A Metric-Based Framework for Climate-Smart Conservation Planning." *Ecological Applications* 33, no. 4: e2852. <https://doi.org/10.1002/eap.2852>.
- Busby, J. R. 1991. "BIOCLIM—A Bioclimate Analysis and Prediction System." In *Nature Conservation: Cost Effective Biological Surveys and Data Analysis*, edited by C. R. Margules and M. P. Austin, 64–68. Canberra: CSIRO.
- Calado, H., K. Ng, C. Lopes, and L. Paramio. 2011. "Introducing a Legal Management Instrument for Offshore Marine Protected Areas in the Azores—The Azores Marine Park." *Environmental Science & Policy* 14, no. 8: 1175–1187. <https://doi.org/10.1016/j.envsci.2011.09.001>.
- Cardoso, P., F. Rigal, and J. C. Carvalho. 2015. "BAT—Biodiversity Assessment Tools, an R Package for the Measurement and Estimation of Alpha and Beta Taxon, Phylogenetic and Functional Diversity." *Methods in Ecology and Evolution* 6, no. 2: 232–236. <https://doi.org/10.1111/2041-210X.12310>.
- Carpenter, G., A. N. Gillison, and J. Winter. 1993. "DOMAIN: A Flexible Modelling Procedure for Mapping Potential Distributions of Plants and Animals." *Biodiversity and Conservation* 2, no. 6: 667–680. <https://doi.org/10.1007/BF00051966>.
- Carvalho, N., G. Edwards-Jones, and E. Isidro. 2011. "Defining Scale in Fisheries: Small Versus Large-Scale Fishing Operations in the Azores." *Fisheries Research* 109, no. 2–3: 360–369. <https://doi.org/10.1016/j.fishres.2011.03.006>.
- Diogo, H., and J. G. Pereira. 2013. "Recreational Boat Fishing Pressure on Fish Communities of the Shelf and Shelf Break of Faial and Pico Islands (Azores Archipelago): Implications for Coastal Resource Management." *Acta Ichthyologica et Piscatoria* 43, no. 4: 267–276. <https://doi.org/10.3750/AIP2013.43.4.02>.
- Dormann, C. F., J. Elith, S. Bacher, et al. 2013. "Collinearity: A Review of Methods to Deal With It and a Simulation Study Evaluating Their Performance." *Ecography* 36, no. 1: 27–46. <https://doi.org/10.1111/j.1600-0587.2012.07348.x>.
- Dornelas, M., L. H. Antão, F. Moyes, et al. 2018. "BioTIME: A Database of Biodiversity Time Series for the Anthropocene." *Global Ecology and Biogeography* 27, no. 7: 760–786. <https://doi.org/10.1111/geb.12729>.
- 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>.
- Ferreira, M. T., P. Cardoso, P. A. V. Borges, R. Gabriel, E. B. De Azevedo, and R. B. Elias. 2019. "Implications of Climate Change to the Design of Protected Areas: The Case Study of Small Islands (Azores)." *PLoS One* 14, no. 6: e0218168. <https://doi.org/10.1371/journal.pone.0218168>.
- Ferreira, M. T., P. Cardoso, P. A. V. Borges, et al. 2016. "Effects of Climate Change on the Distribution of Indigenous Species in Oceanic Islands (Azores)." *Climatic Change* 138, no. 3–4: 603–615. <https://doi.org/10.1007/s10584-016-1754-6>.
- Fielding, A. H., and J. F. Bell. 1997. "A Review of Methods for the Assessment of Prediction Errors in Conservation Presence/Absence Models." *Environmental Conservation* 24, no. 1: 38–49. <https://doi.org/10.1017/S0376892997000088>.
- Fredston-Hermann, A., S. D. Gaines, and B. S. Halpern. 2018. "Biogeographic Constraints to Marine Conservation in a Changing Climate." *Annals of the New York Academy of Sciences* 1429, no. 1: 5–17. <https://doi.org/10.1111/nyas.13597>.
- Friedman, J. H. 1991. "Multivariate Adaptive Regression Splines." *Annals of Statistics* 19, no. 1: 1–67. <https://doi.org/10.1214/aos/1176347963>.
- Garcia, R. A., N. D. Burgess, M. Cabeza, C. Rahbek, and M. B. Araújo. 2012. "Exploring Consensus in 21st Century Projections of Climatically Suitable Areas for African Vertebrates." *Global Change Biology* 18, no. 4: 1253–1269. <https://doi.org/10.1111/j.1365-2486.2011.02605.x>.
- González-Trujillo, J. D., R. Roman-Cuesta, A. I. Muñoz-Castillo, C. H. Amaral, and M. B. Araújo. 2023. "Multiple Dimensions of Extreme Weather Events and Their Impacts on Biodiversity." *Climatic Change* 176: 155. <https://doi.org/10.1007/s10584-023-03622-0>.
- 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 of the United States of America* 120, no. 14: e2209637120. <https://doi.org/10.1073/pnas.2209637120>.
- Guinotte, J. M., and V. J. Fabry. 2008. "Ocean Acidification and Its Potential Effects on Marine Ecosystems." *Annals of the New York Academy of Sciences* 1134, no. 1: 320–342. <https://doi.org/10.1196/annals.1439.013>.
- Halpin, P., A. Read, E. Fujioka, et al. 2009. "OBIS-SEAMAP: The World Data Center for Marine Mammal, Sea Bird, and Sea Turtle Distributions." *Oceanography* 22, no. 2: 104–115. <https://doi.org/10.5670/oceanog.2009.42>.
- Hastie, T., R. Tibshirani, and A. Buja. 1994. "Flexible Discriminant Analysis by Optimal Scoring." *Journal of the American Statistical Association* 89, no. 428: 1255–1270. <https://doi.org/10.1080/01621459.1994.10476866>.
- Hastings, R. A., L. A. Rutterford, J. J. Freer, R. A. Collins, S. D. Simpson, and M. J. Genner. 2020. "Climate Change Drives Poleward Increases and Equatorward Declines in Marine Species." *Current Biology* 30, no. 8: 1572–1577.e2. <https://doi.org/10.1016/j.cub.2020.02.043>.
- Horton, T., S. Gofas, A. Kroh, et al. 2017. "Improving Nomenclatural Consistency: A Decade of Experience in the World Register of Marine Species." *European Journal of Taxonomy* 389: 1–24. <https://doi.org/10.5852/ejt.2017.389>.
- Kortsch, S., R. Primicerio, M. Fossheim, A. V. Dolgov, and M. Aschan. 2015. "Climate Change Alters the Structure of Arctic Marine Food Webs Due to Poleward Shifts of Boreal Generalists." *Proceedings of the Royal Society B: Biological Sciences* 282, no. 1814: 20151546. <https://doi.org/10.1098/rspb.2015.1546>.
- Lurgi, M., B. C. López, and J. M. Montoya. 2012. "Novel Communities From Climate Change." *Philosophical Transactions of the Royal Society, B: Biological Sciences* 367, no. 1605: 2913–2922. <https://doi.org/10.1098/rstb.2012.0238>.
- Luz, R., R. Cordeiro, A. Fonseca, and V. Gonçalves. 2022. "Cyanobacteria Checklist of the Azores Archipelago, Portugal." [Dataset]. <https://doi.org/10.15468/BFKTQO>.
- Marques, A. S., T. B. Ramos, S. Caeiro, and M. H. Costa. 2013. "Adaptive-Participative Sustainability Indicators in Marine Protected Areas: Design and Communication." *Ocean and Coastal Management* 72: 36–45. <https://doi.org/10.1016/j.ocecoaman.2011.07.007>.
- McCullagh, P. 2019. *Generalized Linear Models*. New York: Routledge.
- Morton, B. R., and J. C. Britton. 2000. "The Origins of the Coastal and Marine Flora and Fauna of the Azores." *Oceanography and Marine Biology* 38: 13–84.
- Mota, F. M. M., G. Alves-Ferreira, D. C. Talora, and N. M. Heming. 2023. "divraster: An R Package to Calculate Taxonomic, Functional and Phylogenetic Diversity From Rasters." *Ecography* 2023, no. 12: e06905. <https://doi.org/10.1111/ecog.06905>.
- Naimi, B., and M. B. Araújo. 2016. "sdm: A Reproducible and Extensible R Platform for Species Distribution Modelling." *Ecography* 39, no. 4: 368–375. <https://doi.org/10.1111/ecog.01881>.
- Naimi, B., N. A. S. Hamm, T. A. Groen, A. K. Skidmore, and A. G. Toxopeus. 2014. "Where Is Positional Uncertainty a Problem for Species Distribution Modelling?" *Ecography* 37, no. 2: 191–203. <https://doi.org/10.1111/j.1600-0587.2013.00205.x>.
- Neto, A. I., I. Moreu, E. F. Rosas-Alquicira, et al. 2021. "Marine Algal Flora of São Miguel Island, Azores." [Dataset]. <https://doi.org/10.15468/XTUZD3>.

- Orgeret, F., A. Thiebault, K. M. Kovacs, et al. 2022. "Climate Change Impacts on Seabirds and Marine Mammals: The Importance of Study Duration, Thermal Tolerance and Generation Time." *Ecology Letters* 25, no. 1: 218–239. <https://doi.org/10.1111/ele.13920>.
- Pearson, R. G., C. J. Raxworthy, M. Nakamura, and A. Townsend Peterson. 2007. "Predicting Species Distributions From Small Numbers of Occurrence Records: A Test Case Using Cryptic Geckos in Madagascar." *Journal of Biogeography* 34, no. 1: 102–117. <https://doi.org/10.1111/j.1365-2699.2006.01594.x>.
- Pearson, R. G., W. Thuiller, M. B. Araújo, et al. 2006. "Model-Based Uncertainty in Species Range Prediction." *Journal of Biogeography* 33, no. 10: 1704–1711. <https://doi.org/10.1111/j.1365-2699.2006.01460.x>.
- Peterson, A. T., J. Soberón, R. G. Pearson, et al. 2012. *Ecological Niches and Geographic Distributions*. Princeton: Princeton University Press. <https://doi.org/10.1515/9781400840670>.
- Phillips, S. J., R. P. Anderson, and R. E. Schapire. 2006. "Maximum Entropy Modeling of Species Geographic Distributions." *Ecological Modelling* 190, no. 3–4: 231–259. <https://doi.org/10.1016/j.ecolmodel.2005.03.026>.
- Poloczanska, E. S., C. J. Brown, W. J. Sydeman, et al. 2013. "Global Imprint of Climate Change on Marine Life." *Nature Climate Change* 3, no. 10: 919–925. <https://doi.org/10.1038/nclimate1958>.
- Queiroz, R. E., J. Guerreiro, and M. A. Ventura. 2014. "Demand of the Tourists Visiting Protected Areas in Small Oceanic Islands: The Azores Case-Study (Portugal)." *Environment, Development and Sustainability* 16, no. 5: 1119–1135. <https://doi.org/10.1007/s10668-014-9516-y>.
- Riahi, K., D. P. Van Vuuren, E. Kriegler, et al. 2017. "The Shared Socioeconomic Pathways and Their Energy, Land Use, and Greenhouse Gas Emissions Implications: An Overview." *Global Environmental Change* 42: 153–168. <https://doi.org/10.1016/j.gloenvcha.2016.05.009>.
- Rilov, G., A. D. Mazaris, V. Stelzenmüller, et al. 2019. "Adaptive Marine Conservation Planning in the Face of Climate Change: What Can We Learn From Physiological, Ecological and Genetic Studies?" *Global Ecology and Conservation* 17: e00566. <https://doi.org/10.1016/j.gecco.2019.e00566>.
- Silva, L. 2015. "How Ecotourism Works at the Community-Level: The Case of Whale-Watching in the Azores." *Current Issues in Tourism* 18, no. 3: 196–211. <https://doi.org/10.1080/13683500.2013.786027>.
- Smale, D. A., T. Wernberg, E. C. J. Oliver, et al. 2019. "Marine Heatwaves Threaten Global Biodiversity and the Provision of Ecosystem Services." *Nature Climate Change* 9, no. 4: 306–312. <https://doi.org/10.1038/s41558-019-0412-1>.
- Sorensen, T. 1948. "A Method of Establishing Groups of Equal Amplitude in Plant Sociology Based on Similarity of Species Content and Its Application to Analyses of the Vegetation on Danish Commons." *Biologiske Skrifter* 5: 1–34.
- Staudt, A., A. K. Leidner, J. Howard, et al. 2013. "The Added Complications of Climate Change: Understanding and Managing Biodiversity and Ecosystems." *Frontiers in Ecology and the Environment* 11, no. 9: 494–501. <https://doi.org/10.1890/120275>.
- Stockwell, D. R. B., and A. T. Peterson. 2002. "Effects of Sample Size on Accuracy of Species Distribution Models." *Ecological Modelling* 148, no. 1: 1–13. [https://doi.org/10.1016/S0304-3800\(01\)00388-X](https://doi.org/10.1016/S0304-3800(01)00388-X).
- Swets, J. A. 1979. "ROC Analysis Applied to the Evaluation of Medical Imaging Techniques." *Investigative Radiology* 14, no. 2: 109–121. <https://doi.org/10.1097/00004424-197903000-00002>.
- Sydeman, W. J., E. Poloczanska, T. E. Reed, and S. A. Thompson. 2015. "Climate Change and Marine Vertebrates." *Science* 350, no. 6262: 772–777. <https://doi.org/10.1126/science.aac9874>.
- 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., L. Brotons, M. B. Araújo, and S. Lavorel. 2004. "Effects of Restricting Environmental Range of Data to Project Current and Future Species Distributions." *Ecography* 27, no. 2: 165–172. <https://doi.org/10.1111/j.0906-7590.2004.03673.x>.
- Van Proosdij, A. S. J., M. S. M. Sosef, J. J. Wieringa, and N. Raes. 2016. "Minimum Required Number of Specimen Records to Develop Accurate Species Distribution Models." *Ecography* 39, no. 6: 542–552. <https://doi.org/10.1111/ecog.01509>.
- Vapnik, V. N. 2000. *The Nature of Statistical Learning Theory*. New York: Springer. <https://doi.org/10.1007/978-1-4757-3264-1>.

Supporting Information

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