

Proximity to freshwater and seagrass availability mediate the impacts of climate change on the distribution of the West Indian manatee

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Abstract

How climate change alters persistence and distribution of endangered species is an urgent question in current ecological research. However, many species distribution models do not consider consumers in the context of their resources. The distribution and survival of the West Indian manatee (*Trichechus manatus*), listed as a Vulnerable species on the IUCN Red List, critically depend on seagrass resources and freshwater sources for drinking. We parameterized Maxent models with Bio-ORACLE environmental layers, freshwater proximity data, and modelled seagrass distance layers, to determine manatee and seagrass distributions under future climate change scenarios. We used two plausible IPCC Representative Concentration Pathways (RCP45 and RCP26, respectively) for the year 2050. The model fits had high accuracies and predicted a marked decline in seagrass coverage (RCP26: -1.9%, RCP45: -6%), coinciding with declines in manatee ranges (RCP26: -9%, RCP45: -11.8%). We

also found that over 94% of the projected manatee distribution for all scenarios fell within the seagrass distribution. The analysis showed a decline in seagrass coverage to significantly impact manatee distributions, since the distance to seagrass ecological layer contributed significantly to manatee distributions, along with distance to freshwater sources. Our findings suggest that manatees will lose substantial range due to future climate change, but the extent and direction of this change will be mediated by the degree of warming and its impact on the resources manatees depend on.

Introduction

Developing accurate predictions on how species will respond to climate change are pivotal to effectively conserving global biodiversity (Hughes, 2000; Walther et al., 2002; Burrows et al., 2011; Urban, 2015; Urban et al., 2016; Bryndum-Buchholz et al., 2019). Some species can adapt to thermal changes and the associated impacts through migratory movements, often in the poleward direction (Parmesan et al., 1999; Parmesan & Yohe, 2003; Fowler et al., 2018; Hastings et al., 2020; Osland & Feher, 2020; Pryor et al., 2022; Vaissi, 2022). However, many organisms have limited dispersal abilities and cannot react rapidly enough to changing environmental conditions (Parmesan et al., 1999; Intergovernmental Panel On Climate Change (IPCC), 2023a). Although organisms will also rely on the dispersal abilities of their main resources, the coupled responses of mobile consumers and their sedentary resources to climate change are poorly understood (Dawson et al., 2011). This oversight is significant because climate-induced shifts in the distribution of key resources strongly influence the distribution of their consumers (Carroll et al., 2017).

Currently, over 51% of marine mammals' core habitat is identified as 'at risk' from anthropogenic impacts and climate change (Avila et al., 2018), with the most at risk species occurring in coastal areas (Schipper et al., 2008; Albouy et al., 2017; Davidson & Dulvy, 2017). The West Indian manatee (*Trichechus manatus*), hereafter referred to as manatee, is one of the four living species in the order Sirenia, comprising manatees and dugongs. Manatees

Keywords:

climate change impacts, consumer-resource associations, habitat suitability, species distribution modelling, *Trichechus manatus*

ARTICLE INFO

Manuscript type: Article

Article History

Received: 19 July 2023

Received in revised form: 10 October 2023

Accepted: 10 December 2023

Available online: 23 February 2024

Handling Editor: Ana Carolina Meirelles

Citation:

Deeks, E., Kratina, P., Normande, I., Cerqueira, A. S., & Dawson, T. (2024). Proximity to freshwater and seagrass availability mediate the impacts of climate change on the distribution of the West Indian manatee. *Latin American Journal of Aquatic Mammals*, 19(1), 15-31. <https://doi.org/10.5597/lajam00321>

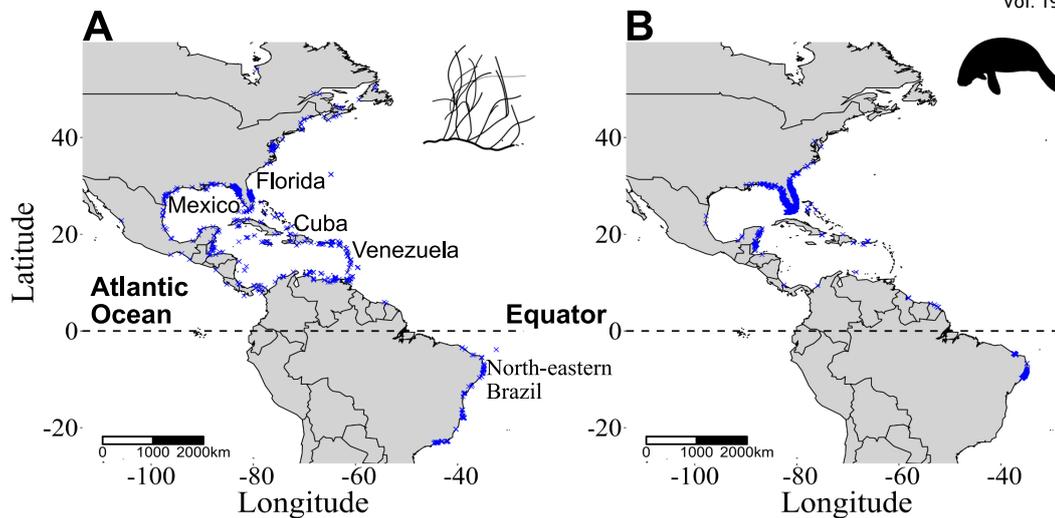


Figure 1. Occurrence data points (blue crosses) for the seagrass Maxent model (A) and the West Indian manatee (*Trichechus manatus*) Maxent model (B) inputs. The Equator is shown in the dotted line.

are opportunistic, fully aquatic herbivores (Best, 1981). They consume approximately 8% of their total body weight each day on aquatic plants such as seagrass and macroalgae, mostly in shallow waters (Best, 1981; Spiegelberger & Ganslosser, 2005; Reich & Worthy, 2006). The coastal distribution of this endangered consumer coincides closely with sources of freshwater for hydration (Lefebvre et al., 2001; de Meirelles et al., 2018; Vilaça et al., 2019; Favero et al., 2020). Many of the coastal habitats utilised by the manatee are negatively impacted by anthropogenic activities and climate change (Short et al., 2006; Ceccherelli et al., 2007; Figueiredo et al., 2008; Copertino et al., 2016).

Seagrasses are a staple food source for the manatee (Domning, 1981, 2001; Reich & Worthy, 2006; Edwards, 2013). The loss of seagrass from manatee and dugong habitats is problematic as it has the potential to result in the mortality of the associated populations (Marsh et al., 2022). For instance, in southern Hervey Bay (Australia), 7% of the dugong population stranded from emaciation following seagrass loss after an extreme weather event (Preen & Marsh, 1995). Manatee populations in Florida sustained an estimated 17% loss in 2013 due to a 60% loss of their seagrass resources (Gobler & Sunda, 2012). Yet, we still know very little about how the distribution of manatees and their freshwater and seagrass resources will change under climate change (Favero et al., 2020; Marsh et al., 2022).

Species distribution modelling (SDM) is a method used widely in the marine realm to predict species distributions based on their relationship with environmental variables (Osborne et al., 2001; Kozak et al., 2008; Waltari & Guralnick, 2009). Many species distribution models of marine species use oceanographic environmental variables, obtained from *in situ* sampling, remote sensing, and ocean models (Pendleton et al., 2020). Physiographic variables, such as depth, distance to the coast, and slope are also commonly used in SDMs (Panigada et al., 2008; Melo-Merino et al., 2020; Warwick-Evans et al., 2022). However, these models often overlook consumer-resource interactions under climate changes (Gregg et al., 2013; Kissling & Schleuning, 2015; Silber et al., 2017; Pendleton et al., 2020; Åkesson et al., 2021), typically focusing on projected oceanographic variables (Thuiller et al., 2004; Dawson et al., 2011; Urban et al., 2016).

Manatee conservation efforts require understanding the spatial ecology of manatees under climate change (Langtimm et al.,

2011; Favero et al., 2020; Marsh et al., 2022). In this study, we used a series of environmental variables, along with proximity to freshwater sources, and modelled future seagrass distributions to examine how climate change will impact manatee distributions for the year 2050. We looked at low (RCP26) and mid-range (RCP45) emission scenarios for the year 2050. The modelled seagrass layers were derived from projected seagrass climate change models. We hypothesise that the relative suitability of manatee distributions would decline under future climate change scenarios in response to the reduction of their key resources.

Methods

To determine the distributional changes of both manatee consumers and their main seagrass resources under different climate change scenarios, the four main methodological steps were used. (i) We first assembled the present distribution data for manatees and seagrass (Fig. 1); (ii) we then assembled environmental layers for present day and future IPCC Representative Concentration Pathways (RCP26 and RCP45) climate change scenarios. In the next step (iii), we modelled resource (seagrass) availability layers for the manatees (Fig. 2), and finally (iv) we constructed and fitted distribution models using the Maxent software (version 1.3-14) in the dismo package (Phillips et al., 2017; Hijmans et al., 2023) in RStudio version 4.2.3 (R Core Team, 2023) for present and future climate change scenarios of seagrass and manatee distributions.

2.1 Compiling distributional data for manatees and seagrass

Our study focused on the entire known range of the manatee (Lefebvre et al., 2001; Fig. 1). Seagrass occurrence data for this entire study region were obtained from the UN Environment World Conservation Monitoring Centre's Global Distribution of Seagrasses dataset (UNEP-WCMC & Short, 2021). We did not use a specific species of seagrass, as manatees typically eat all the seagrass species in their range (Marsh et al., 2022). West Indian manatee presence data were obtained from the Global Biodiversity Information Facility (GBIF.Org, 2023), GBIF Occurrence Download <https://doi.org/10.15468/dl.m85pu4> using the 'rgbif' R package (Chamberlain et al., 2022) in RStudio version 4.2.3 (R Core Team, 2023).

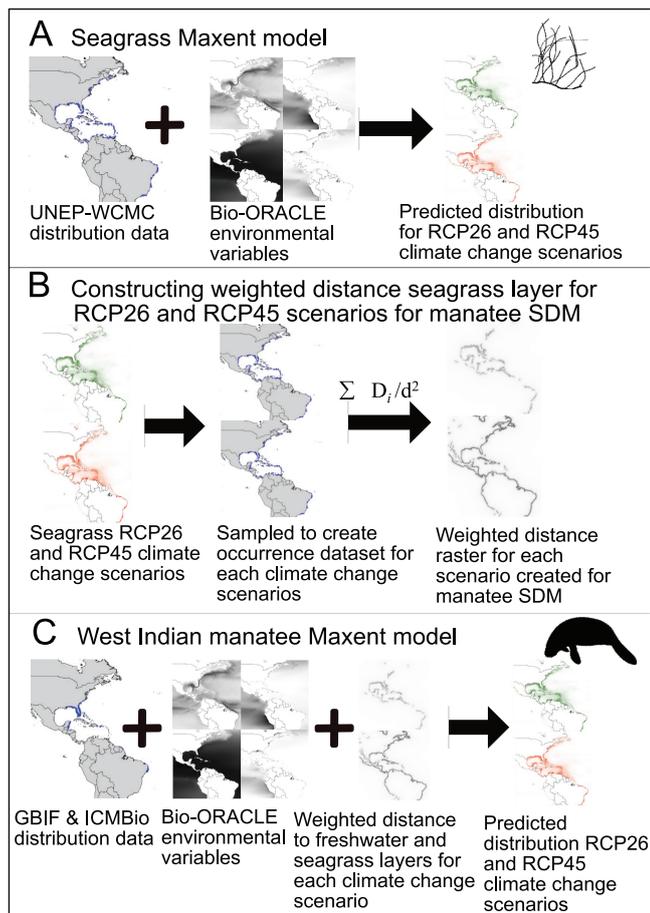


Figure 2. Schematic illustration of the methodology used to incorporate the weighted distance seagrass layers into the West Indian manatee (*Trichechus manatus*) Maxent model. A. Seagrass distribution data from the UN Environment World Conservation Monitoring Centre's Global Distribution (UNEP-WCMC) database, along with Bio-ORACLE environmental variables, were utilised to model seagrass distributions under low (RCP26) and moderate (RCP45) climate change scenarios using Maxent modelling. B. The modelled seagrass distributions, specific to each climate change scenario, were used to create a weighted distance raster. This allowed for an assessment of how resources under climate change impact manatee distributions. C. Finally, Global Biodiversity Information Facility (GBIF) and manatee telemetry data from the ICMBio Brazil, along with Bio-ORACLE environmental variables, the weighted distance to freshwater, and weighted distance to seagrass (under both climate change scenarios), were included as inputs to model manatee distributions under climate change.

Very few records were available for the distributional range of the manatee in Brazil, thus the GBIF occurrence dataset was further supplemented with occurrence data from the Chico Mendes Institute for Biodiversity Conservation (ICMBio), who obtained tracking data over a 10-year period from 38 West Indian manatees. The study involved the tracking of wild and captive-rehabilitated manatees using satellite devices provided by Telonics and NORTRONIC/FMA. To capture the manatees, nets were deployed from a boat, and following a health assessment and tagging process, the manatees were released at the same location where they were initially captured. Captive-rehabilitated manatees were tagged prior to their release, as described in Normande et al. (2016). The tagging procedure employed a peduncle belt, a 1.5-meter flexible tether, and a floating transmitter

Table 1. Environmental variables used in Maxent modelling of seagrasses. The model output was used to determine the relative impact of the distribution of seagrass resources on West Indian manatees (*Trichechus manatus*) in current and future (2040-2050) RCP26 and RCP45 scenarios.

Environmental variables	Units	Type of layer	Future RCP26 and RCP45 layer available
Calcite	Mol.m ⁻³	Mean surface layer	N
Current velocity	m.s ⁻¹	Mean surface layer	Y
Iron	μmol.m ⁻³	Mean surface layer	N
Nitrate	Mol.m ⁻³	Mean surface layer	N
pH	-	Mean surface layer	N
Salinity	PSS	Mean surface layer	Y
Sea surface temperature	°C	Mean surface layer	Y
Silicate	Mol.m ⁻³	Mean surface layer	N

(Reid et al., 1991). Although incorporating telemetry data into our study introduced the risk of potential bias of the SDMs, previous research has shown that telemetry data supplemented with non-GPS tracking datasets (in our case, much of the GBIF database) can overcome these biases and, overall, the effects are negligible (O'Toole et al., 2021).

Occurrence records of manatees were spatially filtered, and duplicates removed using the 'CoordinateCleaner' from the R package 'rgbif'. Occurrence data collected prior to the year 2000 were removed from the occurrence dataset because the present day environmental variables were generated and averaged over the years 2000-2014 (Assis et al., 2018). We recognise the importance of accounting for spatial autocorrelation in the context of species distributions. While spatial autocorrelation does exist in species distributions, its primary effect is on model fit statistics, and does not fundamentally compromise the core relationships between species and their environment (Pearson & Dawson, 2003; Pearson & Dawson, 2004). In any case, to limit spatial autocorrelation, all occurrence records within the 9.2 km grid-cells were aggregated within the same grid-cell to create a single 'presence' data point.

2.2 Compiling environmental layers for present day and future climate change scenarios

Mean surface layers of the present (2000-2014) and near-future (2040-2050) environmental variables that are hypothesized to influence seagrass (Table 1) and manatee (Table 2) distributions were extracted from the Bio-ORACLE v2.0 database (Assis et al., 2018). The Bio-ORACLE projected future environmental variables were limited to sea surface temperature (°C), salinity (PSS), and current velocity (m.s⁻¹). For the manatee models, seagrass distance (explained further in the next section) was also used as an explanatory variable. Other environmental variables used in the model projections were included due to their importance to the associated species distributions. Where there was no future projections for some of the environmental variables (Tables 1, 2), we used the current data (Sill & Dawson, 2021). Whilst it is recognised that some of these variables will change in the future,

Table 2. Environmental and ecological variables used in Maxent modelling of the West Indian manatee (*Trichechus manatus*) for current and future RCP26 and RCP45 scenarios. The model variable inputs included environmental variables from the Bio-ORACLE v2 database, modelled seagrass weighted distance layers for both climate change scenarios, and weighted distance to freshwater sources.

Environmental variables	Units	Type of layer	Future RCP26 and RCP45 layer available
Salinity	PSS	Mean surface layer	Y
Primary prod	g.m-3.day ⁻¹	Mean surface layer	N
Phosphate	Mol.m ⁻³	Mean surface layer	N
Sea surface temperature	°C	Mean surface layer	Y
Seagrass distance	-	Weighted distance layer (including RCP26 and RCP45 projections)	Y
River distance	-	Weighted distance layer	N
Current velocity	m.s ⁻¹	Mean surface layer	Y

our assumption is that spatial variation of this data at local to regional scales will remain similar to present conditions by the year 2050; this is further expanded on in the discussion. The resolution for all layers used in the Maxent model was 5 arcmin (approximately 9.2 km at the Equator).

Multicollinearity of the input variables was tested using the 'removeCollinearity' function with the 'spearmen' method from the 'virtualspecies' package in R (Leroy et al., 2016). Environmental variables with a collinearity coefficient of $r > 0.7$ (Dormann et al., 2013; Merow et al., 2013), and a variable inflation factor of < 4 were removed from the models (Graham, 2003). This resulted in eight variables used in the seagrass SDM (Table 1) and seven variables used in the manatee SDMs (Table 2).

The Intergovernmental Panel on Climate Change (IPCC, 2015) established four representative concentration pathways (RCPs), which ranged from low emission scenarios: RCP26, to the highest emissions scenario: RCP85. The four RCPs (RCP26, RCP45, RCP60, RCP85) represent the full range of possible radioactive forcing values (IPCC, 2023b). Two well-recognized climate scenarios, for years 2050 and 2100, are available in the Bio-ORACLE database (Tyberghein et al., 2012; Assis et al., 2018). We selected to model consumer and resources for the near future (year 2050) and compare the two most plausible RCP scenarios: the low (RCP26) and a mid-range (RCP45) emissions scenario (Riahi et al., 2011; Hausfather & Peters, 2020), expanded on in the discussion.

2.3 Modelling seagrass availability layers for the manatee

For each climate change scenario from the seagrass Maxent models, we constructed weighted distance input variables, which were inputted into the manatee Maxent model. These variables were constructed based on the output of the seagrass Maxent model for each climate change scenario (Fig. 2). We sampled points within the projected distribution of the seagrass Maxent models to create a pseudo distribution occurrence dataset based on low and moderate emission climate change scenarios. This was achieved using the 'generate random point' function within the ArcGIS® Pro 3.0 software by ESRI (2023). The resulting

dataset contained the same number of distribution points as the initial baseline seagrass occurrence dataset described in Methods 2.1 (Fig. 1; UNEP-WCMC & Short, 2021). Subsequently, we created a weighted distance layer for the present-day baseline, as well as the future low and moderate emission climate change scenarios. This allowed us to project the manatee SDM onto the future climate change scenarios for seagrass (Fig. 2). The methodology employed to generate the weighted distance layer was consistent with that used for the weighted distance to freshwater layer, which is described in detail below (Fig. 2).

We constructed weighted distance layers, using proximity to freshwater and seagrass, for the manatee SDM. The freshwater layer was not projected into future climate change scenarios, unlike the seagrass layer. To create the freshwater distance layer, we utilised the hydrosheds data (Lehner et al., 2008). The weighted distance layers were generated using the 'distance allocation' function in ArcGIS Pro, which calculated the distance of each pixel to the nearest seagrass or freshwater source. In this calculation, we employed inverse distance squared weighted interpolation to assign higher importance to cells closest to freshwater and seagrass resources. This approach resulted in a stronger gradient, where the distance value would diminish quickly – which was relevant given the gridded input cells of the environmental variables were relatively large (9 km²).

Each grid cell at the centre of a defined radius (30 km²) was defined as the sum of the total distance to the source of the other grid cells in the radius divided by the distance squared. Cells at the outer edge of the radius had less influence on the calculation. The following function was executed in the 'raster calculator' after implementing the distance allocation function in ArcGIS Pro:

$$\sum \frac{D_i}{d^2}$$

where D is the source of freshwater or seagrass, and d is the distance from raster cell to freshwater or seagrass source.

2.4 Maxent models for present and future climate change scenarios for seagrass and manatee distributions

Given the limited availability of comprehensive absence data for manatees, primarily due to their elusive nature (Castelblanco-Martínez et al., 2018), we opted to employ the most accurate presence-only model, Maxent (Phillips, 2009; Phillips et al., 2017). In order to obtain the most robust model and the least overfitted model predictions, we used the ENMeval 2.0 package which gave optimal model settings given our data (Muscarella et al., 2014). The two parameters tuned using ENMeval() were the regularization multiplier and the feature classes; default settings were used for the rest of the model. For the manatee and seagrass SDMs, the regularization multiplier was 0.5 for both, and the feature classes were set as 'LQHPT' and 'LQHP', respectively. We split our distribution data for both species models into 75% training and 25% testing (Phillips, 2008). The maximum number of background points was set to 10,000 and run over 1,000 iterations. Ten replicates (10-fold cross-validation) were executed to evaluate the averaged results, which was used as the basis for the further analysis (McCullagh & Nelder, 1989). Jackknife analyses were performed to determine the relative importance of the environmental variables to manatee and

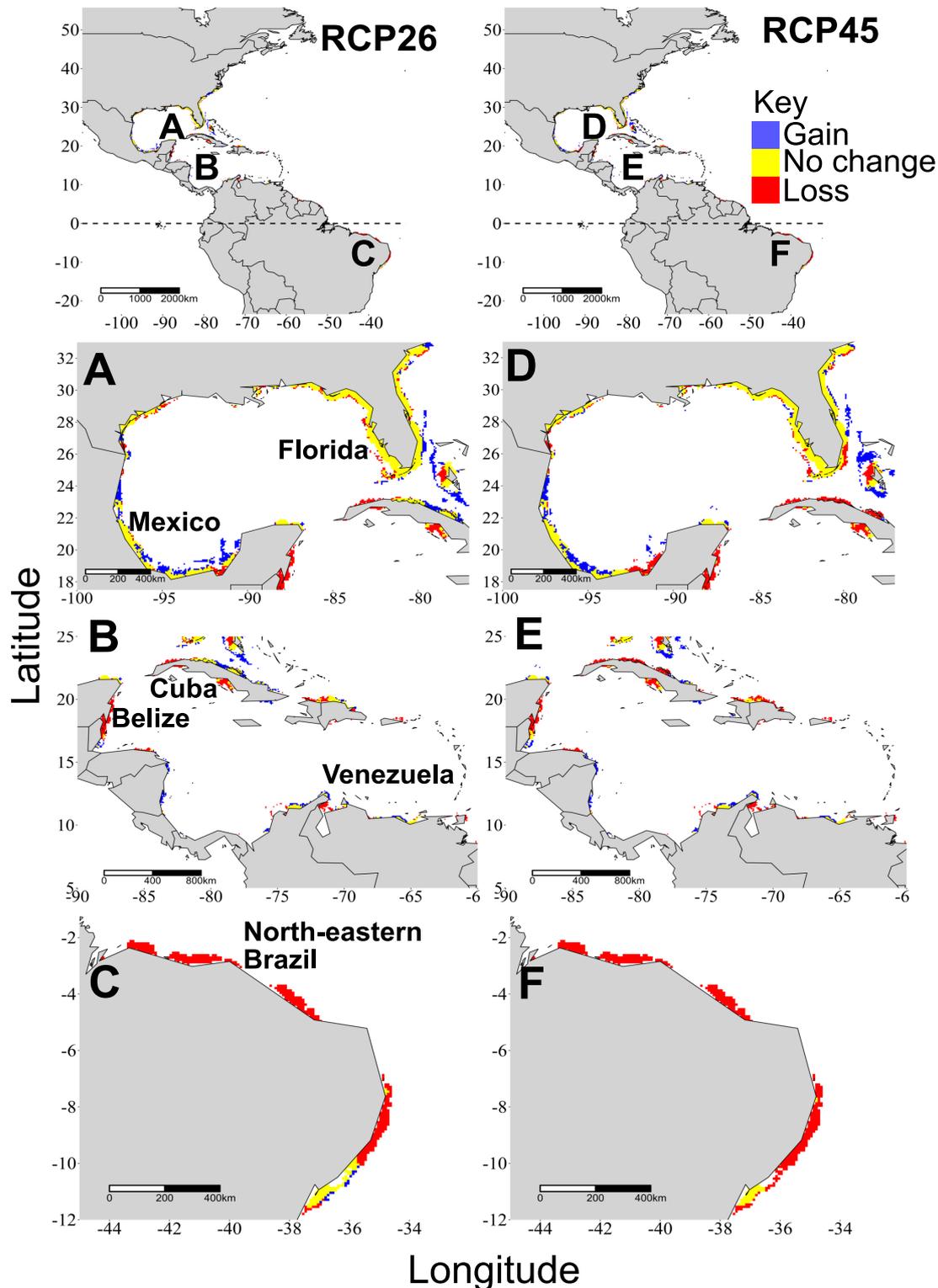


Figure 3. Change in habitat suitability for the West Indian manatee (*Trichechus manatus*) under present-day conditions and two climate change scenarios (mid-range RCP45 and low RCP26) across its range. Outputs were generated from Maxent modelling. The upper two panels display the complete Maxent output, with letters indicating the corresponding regions shown in the lower three rows. Model outputs for the RCP26 scenario in 2050 for A) the Gulf of Mexico region, B) Caribbean region, and C) northeastern Brazil region. Model outputs for the RCP45 scenario in 2050 for D) the Gulf of Mexico region, E) Caribbean region, and F) northeastern Brazil region.

Table 3. Net changes in predicted habitat suitability, measured in terms of overall area (km²) and percentage change, from present day to the year 2050. Maxent models include the West Indian manatee (*Trichechus manatus*) and seagrass, under high (RCP45) and low (RCP26) emission climate change scenarios. The projected distributions were generated from parameterized Maxent models specific to each species.

Maxent model	Area change compared with present day (km ²)	Area loss (%)
Manatee RCP26	-27,407	9
Manatee RCP45	-64,222	11.8
Seagrass RCP26	-72,071	1.9
Seagrass RCP45	-230,249	6

seagrass distributions (Supplementary Material Figs S1, S2) and stepwise removal of variables was carried out. The continuous Boyce Index (CBI) (Hirzel et al., 2006), which is considered the most appropriate metric for assessing model predictions applied to presence-only datasets (Manzoor et al., 2018), was used with the 'ecospat' package (Di Cola et al., 2017). The area under the Receiver Operator Curve (AUC) was used to evaluate model performance (Lobo et al., 2008; Merow et al., 2013). The AUC values ranged between 0.5 and 1, with 0.5 indicating a model performance no better than random, and 1.0 indicating a well fit model (Swets, 1988; Merow et al., 2013).

The models trained and tested on the current scenario (2010-2015) were subsequently projected onto the corresponding set of environmental variables representing the future mid-century period (2040-2050). These environmental variables encompassed temperature, salinity, current velocity, and, specifically for the manatee SDM, seagrass (see methodology section 2.3 for further details). Other environmental variables that could not be projected to future scenarios were kept the same and included in the models.

The continuous output of the Maxent models was converted to binary maps of suitable and unsuitable areas for all species and scenarios using thresholding, which aims to give a statistically optimal cut-off value for better estimates of the impacts of climate change on species ranges (Liu et al., 2005, 2013; Hijmans et al., 2023). The habitat threshold values, as determined using the 'threshold' function in the dismo package (Hijmans et al., 2023), were 0.38 for manatees and 0.19 for seagrass, with the specific threshold calculation method optimised for balancing sensitivity and specificity in the binary classification models. We calculated the percent contribution of each environmental variable during the training of the Maxent model. The programme identified the environmental variables important for fitting the model by incrementally adjusting the coefficients of individual features. The resulting gain is attributed to the corresponding environmental variables, which are then expressed as percentages (Phillips, 2006). The permutation importance of each variable was calculated through randomly shuffling its values in the training data and observing the resulting decrease in training accuracy, presented as a percentage (Phillips, 2006). Both metrics of the Maxent models were calculated through the Maxent modelling software. All analyses were conducted in the RStudio programming language (R Core Team, 2023), except for Methods 2.4: creation of ecological layers, which was implemented in ArcGIS Pro (ESRI, 2023).

Results

The receiver operator curve (ROC) values revealed high predictive performance of the training and test datasets for both the manatee and seagrass Maxent models, with all area under the curve (AUC) values exceeding 0.95 (Supplementary Material Table S1). The CBI values for manatees (0.916) and seagrass (0.989) both also indicated robust model performance.

The projected distribution of manatees, both in the present and future scenarios, exhibited concentration around specific regions such as the Florida peninsula, the northeast coast of Brazil, and the Gulf of Mexico. Patchy distributions were also observed in Mexico, Belize, and French Guiana (Fig. 3). Regarding seagrass distributions, a continuous association was observed with coastlines spanning from North America, Mexico, and Venezuela. There was a slight interruption in the distribution around the states of Amapá and Pará in Brazil before resuming along the northeast coast of Brazil (Fig. 4 C, F). Notably, over 94% of the manatee distribution across all scenarios fell within the projected seagrass distribution (Table 4).

Projection of the Maxent models to the year 2050 showed significant spatial declines in seagrass suitable habitat compared to present day conditions. The estimated declines in seagrass suitable habitat were -1.9% under the RCP26 scenario and -6% under the RCP45 scenario (Table 3). The largest projected gain in habitat suitability for the manatee, under both climate change scenarios, were concentrated in the most northerly regions, specifically around Mexico and Florida (Fig. 3 A, D). Conversely, areas near the Equator, such as Brazil, had the largest projected loss in suitable habitat. Countries like Belize, despite their geographical proximity to favourable habitats such as Florida, were projected to have large areas of habitat loss (Fig. 3 B, E). Despite an overall decline in habitat suitability coverage for both species under both climate change scenarios, the manatee distribution exhibited a closer overlap with the seagrass distribution under the moderate emission scenario compared to the low emissions scenario and the baseline conditions (Table 4).

The ecological distance layers from freshwater and seagrass resources, along with phosphate concentrations, were found to be the top three variables explaining the habitat suitability of the manatee, with relative contributions of 41.7%, 36.4% and 7.4%, respectively (Fig. 5). The model indicated that the highest probability of manatee habitat suitability was within a range of 20-60 weighted distance squares from freshwater and 50-150 weighted distance squares from seagrass (Fig. 6). Notably, suitable habitat was found at greater distances from food sources than freshwater sources. Values beyond these ranges showed a significant decline in predicted habitat suitability. The maximum probability of manatee habitat suitability was within phosphate concentrations 0 - 0.15 mol.m⁻³ (Fig. 6). The other examined environmental variables, such as sea surface temperature, had a relatively lesser impact on determining manatee habitat suitability (Fig. 5).

Iron concentration was the most important environmental variable for seagrass distributions, with a relative contribution of 64.4% (Fig. 5). The presence of seagrass was predominantly predicted in areas with iron concentrations up to 0.005 µmol.m⁻³

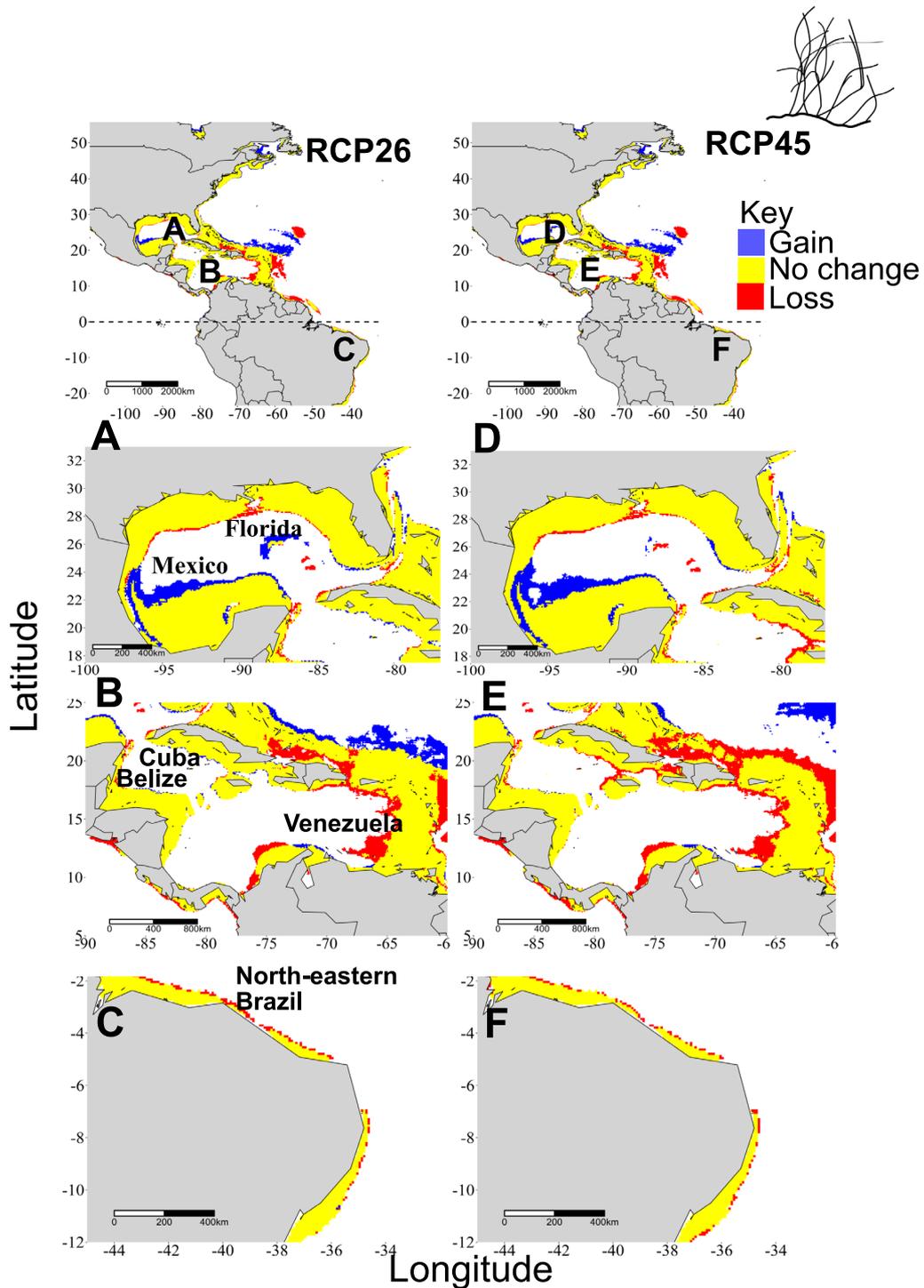


Figure 4. Change in habitat suitability for seagrass under present-day conditions and two climate change scenarios (mid-range RCP45 and low RCP26) across its range. Outputs were generated from Maxent modelling. The upper two panels display the complete Maxent output, with numbers indicating the corresponding regions shown in the lower three rows. Model outputs for the RCP26 scenario in 2050 for A) the Gulf of Mexico region, B) Caribbean region, and C) northeastern Brazil region. Model outputs for the RCP45 scenario in 2050 for D) the Gulf of Mexico region, E) Caribbean region, and F) northeastern Brazil region.

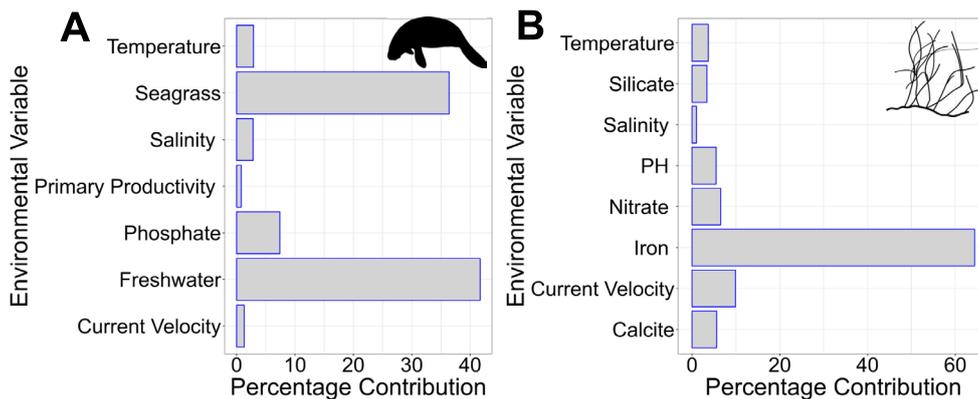


Figure 5. The percentage contribution of environmental variables to the species habitat suitability as predicted by the Maxent model. A) Percent contribution of environmental variables to the West Indian manatee. B) Percent contribution to the seagrass distribution.

(Fig. 7). Other environmental factors, including current velocity, pH, nitrate, and silicate, contributed less to seagrass distributions, explaining 9.9%, 6.5%, 5.5% and 3.4% of the seagrass distributions, respectively (Fig. 5). Environmental variables were within ranges of 25 - 35 mol.m⁻³, 8 - 9, 1 - 1.3 m.s⁻¹ and 20 - 75 mol.m⁻³, respectively (Fig. 7).

Discussion

Our study has demonstrated that by 2050, as climate change continues to progress, global habitat suitability for manatees is expected to diminish significantly (RCP26: -9%, RCP45: -11.8%). The AUC values of the Maxent models exhibited minimal variation across the 10 replicates (Supplementary Material Table S1), indicating consistent and robust model performance (Wang et al., 2010). The projected decline in the manatee population is most pronounced in tropical regions, specifically in Belize, Cuba and notably, Brazil. Additionally, we observed a poleward shift towards more northern regions, such as Florida and Mexico, where manatees are projected to gain suitable habitat. In contrast to earlier assumptions that suggested rising sea levels and increased water temperatures would facilitate manatee range expansion (Marsh et al., 2017), our findings indicate that the effects of climate change on the ecological parameters influencing manatee distributions, such as seagrass, puts a more nuanced perspective on the matter.

Seagrass was the second most important variable for predicting manatee habitat suitability. We found that over 94% of the manatee distribution for all scenarios fell within the seagrass distribution, and this association tightened under higher emission climate change scenarios. Similar to manatees, the greatest seagrass loss is projected to occur in tropical regions (Fig. 4), with seagrass distributions shifting poleward under future climate change (Assis et al., 2017; Repolho et al., 2017; Duarte et al., 2018). These findings align with evidence of seagrass declines in tropical areas such as Belize (Short et al., 2006; Gaston et al., 2009), Brazil (Pitanga et al., 2012; Copertino et al., 2016), and Cuba (Thorhaug et al., 2017), although the specific causes of these declines have not been directly linked to climate change.

The extent to which seagrass losses will impact manatee

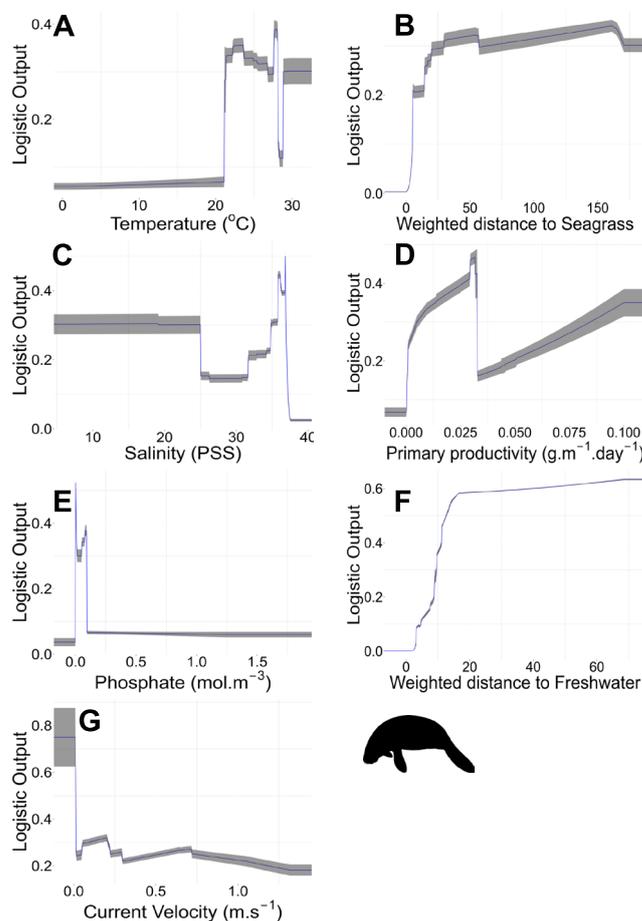


Figure 6. Response curves of West Indian manatee to individual environmental variables, as predicted by the Maxent model. The response curves depict the nonlinear relationship between the logistic prediction (species presence probability) and each environmental predictor variable based on the species occurrence data. A) temperature (°C), B) weighted distance to seagrass, C) salinity (PSS), D) primary production(g.m⁻¹.day⁻¹), E) phosphate (mol.m⁻³), F) weighted distance to freshwater, G) current velocity (m.s⁻¹). It is important to note that the weighted distance layers work counter-intuitively, with higher values indicating closer proximity to the respective sources. The grey bar indicates the standard deviation from the mean, which is represented by the blue line.

distributions can vary as there is variation in manatee diets across their range. Stable isotope analysis revealed manatees in Belize and Puerto Rico feed predominantly on seagrass, while in Florida, there is greater regional variation in their resources (Alves-Stanley et al., 2010). Similarly, in Brazil, manatees consume mostly algae in the state of Paraíba, while those in Alagoas consume more seagrass (Borges et al., 2008). All of the seagrass species listed as Near-Threatened, Vulnerable, and Endangered in the IUCN Red List Category are continuing to decline (Short et al., 2011). As seagrass distributions decline, manatees will either need to relocate along with the resource or adapt their feeding habits to encompass a wider variety of resources (Edwards, 2013). It is plausible that manatee populations with more specialised diets, in tropical regions, and with limited alternative food sources face greater climate change risks than their subtropical counterparts.

Understanding how species distributions will change under climate change is challenging for many reasons. Chief among these challenges is the scarcity of data that enables us to project future environmental conditions reliably (Urban et al., 2016). This can lead to uncertainties in predicting species extinction risk (Thuiller et al., 2004). We included in the models some environmental variables for which future projections were unavailable, similar to studies by Sill & Dawson (2021). We assumed that the spatial variation in these variables at local and regional scales at present day would be similar to the variation in 2050. For example, studies suggested iron (Lauderdale et al., 2020) and phosphate (Deng et al., 2022) will not undergo significant changes as a direct result of climate change. We also expect pH to change by 2050 due to ocean acidification, but more so at higher latitudes due to colder waters and lower carbonate saturation levels (Orr et al., 2005; Andersson et al., 2008) as opposed to lower latitudes, where our study was based. Furthermore, the variables provide important environment context for shaping the distribution of the associated species. Notably, freshwater availability, a critical environmental parameter for manatees (Favero et al., 2020), could not be projected into the future. Nevertheless, based on the permutation importance (Supplementary Material Fig. S3), variable importance (Fig. 5), and jackknife analysis (Supplementary Material Fig. S1), its exclusion from the model would have compromised the accuracy of the manatee distribution projections. As for the other unprojected variables, except for phosphate and freshwater for manatees, and iron for seagrass, their contributions were relatively modest in shaping the model output. However, jackknife tests indicated that including these variables in the model still enhanced the modelling output (Supplementary Material Figs S1, S2). In either scenario, their contribution, while beneficial, did not significantly impact the overall model output.

As this study aims to provide practical information for conservation practitioners, we selected to model consumer and resources for the near future (year 2050). We did not extend our projections to the year 2100 since conservation strategies typically operate at relatively short-term timelines, seldom spanning more than a few decades (Rose et al., 2019, 2020). Longer-term projections are more relevant to global environmental policies discussions (Rosa et al., 2020; Craddock-Henry et al., 2021), which was beyond the scope of this study. As discussed, our decision to incorporate certain environmental variables for which future

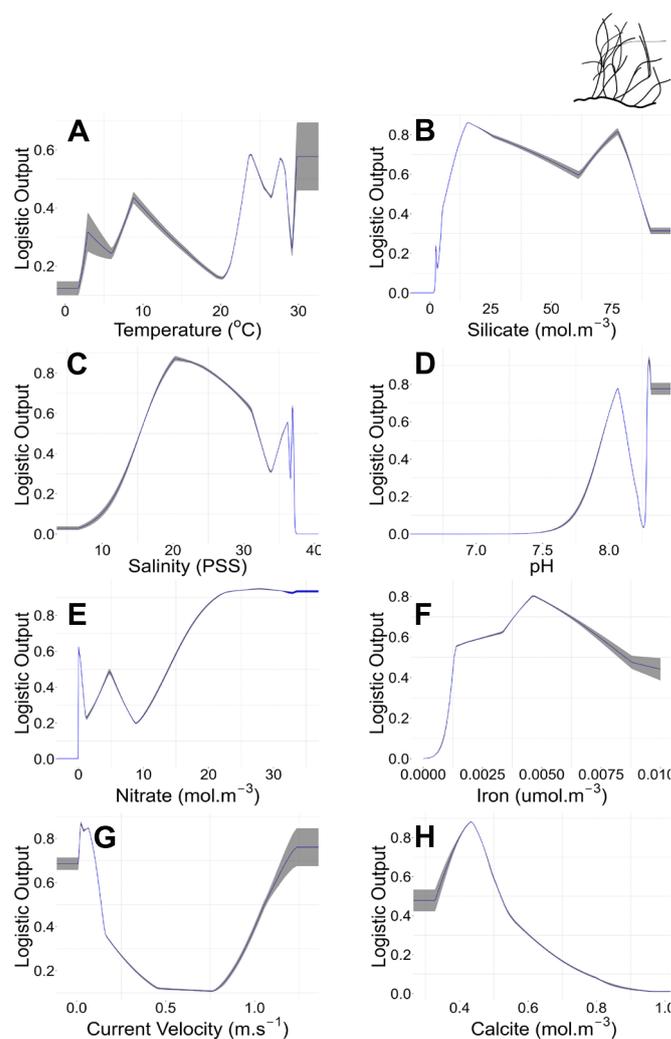


Figure 7. Response curves of seagrass to individual environmental variables, as predicted by the Maxent model. The response curves depict the nonlinear relationship between the logistic prediction (species presence probability) and each environmental predictor variable based on the species occurrence data. A) temperature ($^{\circ}\text{C}$), B) silicate (mol.m^{-3}), C) salinity (PSS), D) pH, E) nitrate (mol.m^{-3}), F) iron ($\mu\text{mol.m}^{-3}$), G) current velocity (m.s^{-1}), H) calcite (mol.m^{-3}). The grey area indicates the standard deviation from the mean, which is represented by the blue line.

projections were unavailable (Tables 1, 2) assumed that these variables would remain relatively stable at local and regional scales by 2050. However, extending this assumption to 2100 would be unwarranted, given the likelihood of environmental changes. Therefore, we opted to model up to the year 2050 only, which allowed us to include ecologically relevant parameters and ultimately have a more informed species distribution.

We opted to compare two emission scenarios, the low (RCP26) and one of the mid-range (RCP45) scenarios (Riahi et al., 2011; Hausfather & Peters, 2020). However, the use of the different RCP scenarios for modelling future climate change is a subject of scientific debate. The recent 27th United Nations climate change summit has called into question the international commitment to limiting global temperature rise to 2°C , a level closely aligned with the RCP26 scenario. Following the COP21 Paris Agreement (UNFCCC, 2018), policy development and lack of progress on meeting necessary emission reduction targets will make this

Table 3. The total projected area (km²) of suitable habitat for seagrass and the West Indian manatee (*Trichechus manatus*) in present day, as well as under high (RCP45) and low (RCP26) climate change scenarios for the year 2050. The last column illustrates the degree of overlap between the predicted distributions of West Indian manatee and seagrass.

Maxent model	Seagrass (km ²)	Manatee (km ²)	Manatee overlap with seagrass (km ²)	Manatee overlap with seagrass (%)
Present day	4062875	334135	314097	94
RCP26	3990804	305728	291918	95.4
RCP45	3832626	269913	261257	96.7

mitigation pathway challenging, but not unfeasible (Millar et al., 2017; IPCC, 2023b). Recent assessments of future climate projections suggest global temperature rises of 2.8 °C, which is more consistent with the RCP45 pathway (Hausfather & Peters, 2020). While RCP45 and RCP 60 scenarios had similar climate trajectories up until the mid-21st century, we opted for the former scenario because it has slightly higher global temperature increases (0.9 °C) than the RCP 6.0 scenario (0.8 °C) relative to the baseline (1996-2005; Nazarenko et al., 2015). The mid-range scenarios only significantly diverge in mean surface air temperatures at around 2070 (Nazarenko et al., 2015). The high RCP85 emissions scenario was not examined due to its perceived unrealistic nature (Riahi et al., 2011; Murphy, 2019), reflecting a return to coal resources that does not align with the 21st century global energy landscape (Ritchie & Dowlatabadi, 2017). Our choice of the RCP26 and RCP45 future scenarios aligns with the range highlighted in the most recent IPCC AR6 Synthesis Report on Climate Change 2023.

The most important environmental variable for the seagrass SDM suitability and distribution was iron concentration. Iron is a critical nutrient for primary production since it is required for synthesising photosynthetic pigments and the functioning of the enzyme rubisco (Winder & Nishio, 1995). It is ultimately an essential factor for seagrass growth as it increases the chlorophyll *a* concentration in seagrass leaves and enhances growth (Duarte et al., 1995). Yet, iron is commonly a limiting factor in marine tropical environments (Duarte et al., 1995; Coale et al., 1996; Sterner et al., 2004; Anton et al., 2018), especially in shallow, carbonated waters where seagrasses typically grow (Marbà et al., 2022). Our findings underscore the significance of iron concentrations as a key determinant for seagrass distribution.

Sea surface temperature had relatively little importance to the predictions of seagrass distributions, likely due to the range of sea surface temperature of the study region and the fact that our analysis did not include local adaptations of seagrass nor a seasonal component. The thermal range of seagrasses predicted by the model was between 21 and 28 °C, which is similar to the range for optimal growth (23 – 32 °C) predicted from other studies (Lee et al., 2007). However, the poleward dispersion of seagrasses suggests in the tropics they are nearing their maximal thermal tolerances (Marbà et al., 2022).

The two climate change scenarios chosen for this study require active mitigation efforts to meet their designated targets (Murphy, 2019). In the absence of any mitigation measures, the potential for habitat loss is far greater. However, managing and

mitigating the impacts of climate change on manatees present significant challenges due to limited research and monitoring, leading to uncertainty about effective management strategies (Gulland et al., 2022). A substantial portion of resources for many manatee populations exists outside of protected areas, such as the Colombian-Caribbean populations, where 89% of manatee habitat is located beyond marine protected areas (Castelblanco-Martínez et al., 2015). Tropical seagrasses, despite being highly vulnerable to climate change (Tulloch et al., 2020), have few restoration initiatives compared with temperate regions (Thorhaug et al., 2020). Urgent conservation efforts are needed for the declining tropical and subtropical meadows (Unsworth et al., 2014, 2019). For this to be effective, legislative planning and policy frameworks that mitigate multiple pressures are required (Duarte et al., 2018).

Manatees, especially those in small populations in low-income countries, are highly vulnerable to climate change (Marsh et al., 2017). In Brazil, the isolation of manatees from other populations has led to high genetic differentiation, making them a priority for conservation efforts (Luna et al., 2012; Lima et al., 2021). Unfortunately, our study suggests that climate change could drastically reduce suitable habitats for northeastern Brazil's 1,100 manatees (approximately, Alves et al., 2015). Despite robust rehabilitation programmes for these depleted populations (Normande et al., 2016; Attademo et al., 2022), the vulnerability of manatees to strandings and habitat loss remains a concern that needs to be addressed (Domning, 1981; Parente et al., 2004; de Meirelles, 2008; de Meirelles et al., 2018). Another pressing issue is the loss of manatee habitat suitability in Belize, which disrupts migratory links between Mexico and Central American manatee populations (Nourisson et al., 2011; Castelblanco-Martínez et al., 2012). To ensure genetic connectivity among declining manatee populations, it is crucial to prioritise the establishment of safe passages between river systems through the sea (Satizábal et al., 2012; Debrot et al., 2023). Belize is particularly important for doing this, as it is a stronghold for manatees in the Caribbean (O'Shea & Salisbury, 1991; Morales-Vela et al., 2000).

Previous studies have suggested that populations of manatees in Florida are highly vulnerable to climate change (Albouy et al., 2020). However, our study indicates that Florida may provide potential habitat gains for manatees. Additionally, the Gulf of Mexico, despite much of the coastline not being traditionally considered part of the manatee's range, is projected to gain suitable habitat (Hieb et al., 2017). It is important to note that this perspective is limited, and further research is needed to address existing knowledge gaps. Many factors impacting the manatees realised niche were not considered in the Maxent model used in our study, including the effects of human activities (Crain et al., 2008). Future studies should take into account regional threats to specific manatee populations, such as the impacts of harmful algal blooms on seagrasses in Florida (Griffith & Gobler, 2020; Marsh et al., 2022) and seasonal behaviors of different populations. For instance, seeking warm water refuge in winter, which strongly influences manatee distributions in Florida (Runge et al., 2007), whereas manatees in tropical areas such as Brazil and Mexico show different seasonality patterns (Olivera-Gómez & Mellink, 2005; Favero et al., 2020). Populations in Venezuela and Colombia are subject to negative interactions with fishermen

and hunting (Castelblanco-Martínez et al., 2009; Herrera-Trujillo & Trujillo, 2017), while watercraft collisions from tourism pose a greater threat to manatee survival in Belize and Florida (Morales-Vela et al., 2000; Galves et al., 2023). Although these factors were outside the scope of this study, they should be considered in future research to develop more precise management plans in vulnerable areas.

We found that the distributional shifts for manatees were notably stronger toward northern regions such as Mexico and Florida, moving away from equatorial areas such as Brazil, compared to the shifts observed for their seagrass resources. Other studies show that different trophic levels can have different sensitivities, resistance, and recovery from climate change. How the reshuffling of ecological communities under climate change will transcend different trophic levels is still unclear (Vad et al., 2023; Voigt et al., 2003). We propose a potential workflow for including projected climate change layers for ecological niche modelling of species within the context of their resources and consumers using the methodology described for seagrass (Fig. 2). This would advance our understanding of biotic interactions and how we can expect them to change under future climate change. This provides a more realistic methodological consideration to species distribution modelling under climate change scenarios.

In conclusion, the projected poleward movement and reduction in the distribution of seagrasses over the next three decades due to climate change, and the consequential decline of the West Indian manatee distribution highlight the critical need to consider biotic interactions in large scale distribution modelling. Furthermore, our model projections of loss in habitat suitability under climate change are likely conservative, as they do not include the substantial human impacts on both manatee and seagrass habitats. Therefore, comprehensive conservation efforts must address both climate-related challenges and anthropogenic influences to secure a sustainable future for West Indian manatees and their critical habitats at both regional and global scales.

Acknowledgments

ED is supported by a studentship awarded by the Natural Environment Research Council (Grant Number NE/S007229/1). IN is supported by an International Visiting Ph.D. studentship granted by Brazilian National Council for Scientific and Technological Development - CNPq.

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Supplementary material

Table S1. Maxent model training and test AUC values over the 10 replicates ran for seagrass and manatee models.

Figure S1. Jackknife results from a Maxent model for the Antillean manatee (*Trichechus manatus manatus*)

Figure S2. Jackknife results from Maxent model for seagrass

Figure S3. The permutation importance of environmental variables to the species habitat suitability as predicted by the Maxent model. A) permutation importance of environmental variables to the West Indian manatee. B) permutation importance to the seagrass distribution.