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Can upwelling regions be potential thermal refugia for marine fishes during climate warming?

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ABSTRACT

Species are expected to migrate to higher latitudes as warming intensifies due to anthropogenic climate change since physiological mechanisms have been adapted to maximize fitness under specific temperatures. However, literature suggests that upwellings could act as thermal refugia under climate warming protecting marine ecosystem diversity. This research aimed to predict the effects of climate warming on commercial and non-commercial fish species reported in official Mexican documents (>200 species) based on their thermal niche to observe if upwellings can act as potential thermal refugia. Present (2000–2014) and Representative Concentration Pathway (6.0 and 8.5) scenarios (2040–2050 and 2090–2100) have been considered for this work. Current and future suitability patterns, species distribution, richness, and turnover were calculated using the minimum volume ellipsoids as algorithm. The results in this study highlight that beyond migration to higher latitudes, upwelling regions could protect marine fishes, although the mechanism differed between the innate characteristics of upwellings. Most modeled species (primarily tropical fishes) found refuge in the tropical upwelling in Northern Yucatan. However, the highest warming scenario overwhelmed this region. In contrast, the Baja California region lies within the Eastern Boundary Upwelling Systems. While the area experiences an increase in suitability, the northern regions have a higher upwelling intensity acting as environmental barriers for many tropical species. Conversely, in the southern regions where upwelling is weaker, species tend to congregate and persist even during elevated warming, according to the turnover analysis. These findings suggest that tropicalization in higher latitudes may not be as straightforward as previously assumed. Nevertheless, climate change affects numerous ecosystem features, such as trophic relationships, phenology, and other environmental variables not considered here. In addition, uncertainty still exists about the assumption of increasing intensity of upwelling systems.

1. Introduction

Anthropogenic climate change (CC) effect on marine ecosystems has been thoroughly studied to understand and predict its potential impacts (Doney et al., 2012). Literature suggests that CC could provoke synergistic environmental effects, usually impacting marine organisms negatively (Doney et al., 2012; Pörtner, 2010; Pörtner and Peck, 2010). Although various environmental stressors may synergistically impact marine organisms, literature has predominantly focused on the effects of thermal stress. This is because evidence shows that temperature can affect organisms at a biogeographical scale, making it a crucial factor to study (Cheung et al., 2013; Fredston et al., 2021; Payne et al., 2016, 2021; Poloczanska et al., 2013, 2016).

Moreover, a sizeable theoretical framework has been developed

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around temperature and how physiological mechanisms co-define animal thermal niches (TN - Pörtner et al., 2017). The available quantity of temperature data, either with satellites, buoys or by hydrodynamic models, has allowed the biogeographical impacts of climate warming worldwide to be addressed. For instance, organism distribution shifts are consistent with ocean surface temperature changes (Poloczanska et al., 2013). Further evidence has shown that alterations in the composition and abundance of global fishery catches could be associated with temperature changes (Cheung et al., 2013; Doubleday et al., 2016).

Species distribution has been modeled to predict potential redistribution changes that CC may cause (Angeles-Gonzalez et al., 2023; Cheung et al., 2009, 2011; Cisneros-Montemayor et al., 2020). Usually, most works have highlighted latitudinal changes in distribution or migration to deeper waters. Although latitudinal shifts are generally the main conclusion of most studies, literature also suggests the potential role of upwelling regions as climatic refugia for marine populations (Angeles-Gonzalez et al., 2017; Ángeles-González et al., 2021b; Dixon et al., 2022; Glynn, 1996; Lourenço et al., 2016; Rodriguez-Ruano et al., 2023). In the context of the present research study, climatic refugia are regions where the majority of the species stay or retreat to endure changing climatic conditions (Keppel et al., 2012; Lourenço et al., 2016; Monsarrat et al., 2019) – in this case, temperature increases due CC.

Coastal upwelling transports cold water from deep ocean waters to the surface. Upwelling intensity and length dictate whether regional environmental conditions vary temporarily or permanently from neighboring regions. Upwellings also supply cold water that is not directly linked to climate, which can decouple warming regions from global CC (Lourenço et al., 2016) – a desired characteristic in regions with the potential of being climate refugia (Keppel et al., 2012). Some studies propose that upwelling regions worldwide may strengthen due to CC, since stronger wind patterns will be generated due to higher land-sea pressure differences (Bakun et al., 2015 - Bakun hypothesis). The previous process could provide some degree of protection to coastal upwelling ecosystems against temperature increases (García-Reyes et al., 2023). However, there is ongoing controversy surrounding the possibility of an increase in upwelling intensity due to the uncertainty in predictions of upwelling ecosystems (Du et al., 2023; García-Reyes et al., 2023; Lluch-Cota et al., 2014). Nevertheless, upwelling ecosystems could potentially serve as climate refugia if they continue offering colder environments than the surrounding waters at least at short term.

At regional level, few studies have aimed to evaluate the vulnerability of fishery resources to CC in Mexico. However, bioclimatic models for 128 marine species predicted a substantial decrease in catches in the Yucatan Peninsula (YP) in Mexico (Cisneros-Montemayor et al., 2020). Nevertheless, no direct evidence was found that upwellings could mitigate warming effects. Other studies in Mexico have dealt with the potential use of upwelling regions as buffer zones (Angeles-Gonzalez et al., 2017, 2023; Ángeles-González et al., 2021b). For instance, Angeles-Gonzalez et al. (2023) modeled potential changes in thermal habitat based on thermal physiological data, finding that the YP upwelling regions, Western Baja California Peninsula (WBCP), and the Gulf of California might act as climate refugia.

On the other hand, the species temperature-driven migration possibility into upwelling zones may be uncertain, since these areas experience strong environmental fluctuations (Chavez and Messié, 2009; Kämpf and Chapman, 2016). Such fluctuations may present difficulties, particularly for tropical species adapted to thrive in warm, steady conditions (Pörtner and Farrell, 2008; Somero, 2010). For example, environmental fluctuations in the Gulf of California driven by changes in wind direction cause seasonal changes in species composition (Ángeles-González et al., 2021c; Lluch-Cota et al., 2007; Sánchez-Velasco et al., 2009).

Based on the literature, the present study aims at two main objectives: (1) predict warming effects due to CC in Mexican marine fishes based on a TN characterization using correlative ecological niche models (ENMs). The ENM approach intends to estimate the fundamental niche (set of all environmental values that permit a species to exist – in this case, a TN); (2) observe if upwelling regions act as potential climate refugia under CC, protecting the marine ecosystem diversity. Mexico is a good case study, given that many oceanic processes like upwellings occur throughout the country (Lara-Lara et al., 2008; Salas de León and Monreal-Gómez, 2005).

2. Material and methods

2.1. Study region

Mexico's Territorial Sea and Exclusive Economic Zone (MEEZ) spans 3,149,920 km^2, with 2,320,380 km^2 corresponding to the Pacific Ocean, 829,540 km^2 to the Gulf of Mexico and the Caribbean Sea (De la Lanza-Espino, 2004). The country's coastline, excluding the islands, measures 11,122 km, with 7828 km along the Pacific and Gulf of California and 3294 km along the Gulf of Mexico and the Caribbean Sea (DOF, 2018). In coastal upwelling ecosystems, the wind carries subsurface water to the surface by forcing surface water to move offshore. Sub-superficial waters usually have lower temperatures, creating a colder habitat than the regions around them (Kämpf and Chapman, 2016). Therefore, the present research deals with four significant upwelling areas: (1) Northern YP; (2) Gulf of Tehuantepec; (3) Gulf of California; and (4) WBCP (Fig. 1) (Salas de León and Monreal-Gómez, 2005).

Seasonal upwelling takes place during the spring and summer in the YP, which occurs when the Yucatan current strengthens and pushes waters from the intermediate layer (about 250 m deep) from the Caribbean Sea towards the Gulf of Mexico. As a result of friction with the continental slope, a topographic upwelling is created, which lowers the temperatures in the region and spreads over the continental shelf – more noticeable in Northern YP (Enriquez et al., 2013, 2013, 2013; Salas de León and Monreal-Gómez, 2005) keeping the surface temperatures at about 23–28 °C throughout the year (Angeles-Gonzalez et al., 2017).

From May to October, the Gulf of Tehuantepec experiences a meteorological phenomenon: the "Tehuantepec winds." These strong winds come from the Northern Gulf of Mexico and cross the isthmus towards the Gulf of Tehuantepec, exceeding 20 m/s. As a result, southward water drag leads to significant offshore upwellings, causing a decrease in surface temperature as much as ~8 °C (surrounding waters are about 24–30 °C) with minimum temperatures found at 150 km offshore (Barton et al., 1993). When these winds weaken, surface water starts to warm again (Lara-Lara et al., 2008; Salas de León and Monreal-Gómez, 2005).

The Gulf of California experiences upwellings due to changes in its wind patterns influenced by the surrounding mountain chains. During summer, southeastern winds cause upwellings along the western shores of the Gulf (although it has been argued that it corresponds to a weak upwelling due to weak winds and deeper thermocline – Lluch-Cota, 2000), while in winter, northwestern winds result in upwellings in the eastern coast, creating a very dynamic ecosystem (Lluch-Cota et al., 2010; Salas de León and Monreal-Gómez, 2005) with significant variation in temperature in the scale of about 15 °C (~15–30 °C).

Finally, upwellings are triggered in the WBCP by northeastern spring and summer winds that run parallel to the coastline (corresponding to the California current system). This Eastern boundary upwelling system (EBUS) facilitates offshore water mass movement, inducing a cooling effect (López-Aviles et al., 2024). Upwelling intensity is higher in the northern and central segments of the WBCP (Salas de León and Monreal-Gómez, 2005; Zaytsev et al., 2003), with temperatures from MODIS-Aqua sensors showing a range from 15 to 19 °C. This phenomenon diminishes towards lower latitudes (<27 °N), with temperatures ranging from 20 to 28 °C. The bottom topography and coastal orientation have been identified as influential factors in intensifying upwelling in lower latitudes (Zaytsev et al., 2003), although evidence suggests that wind curl patterns also contribute to generating upwellings in the

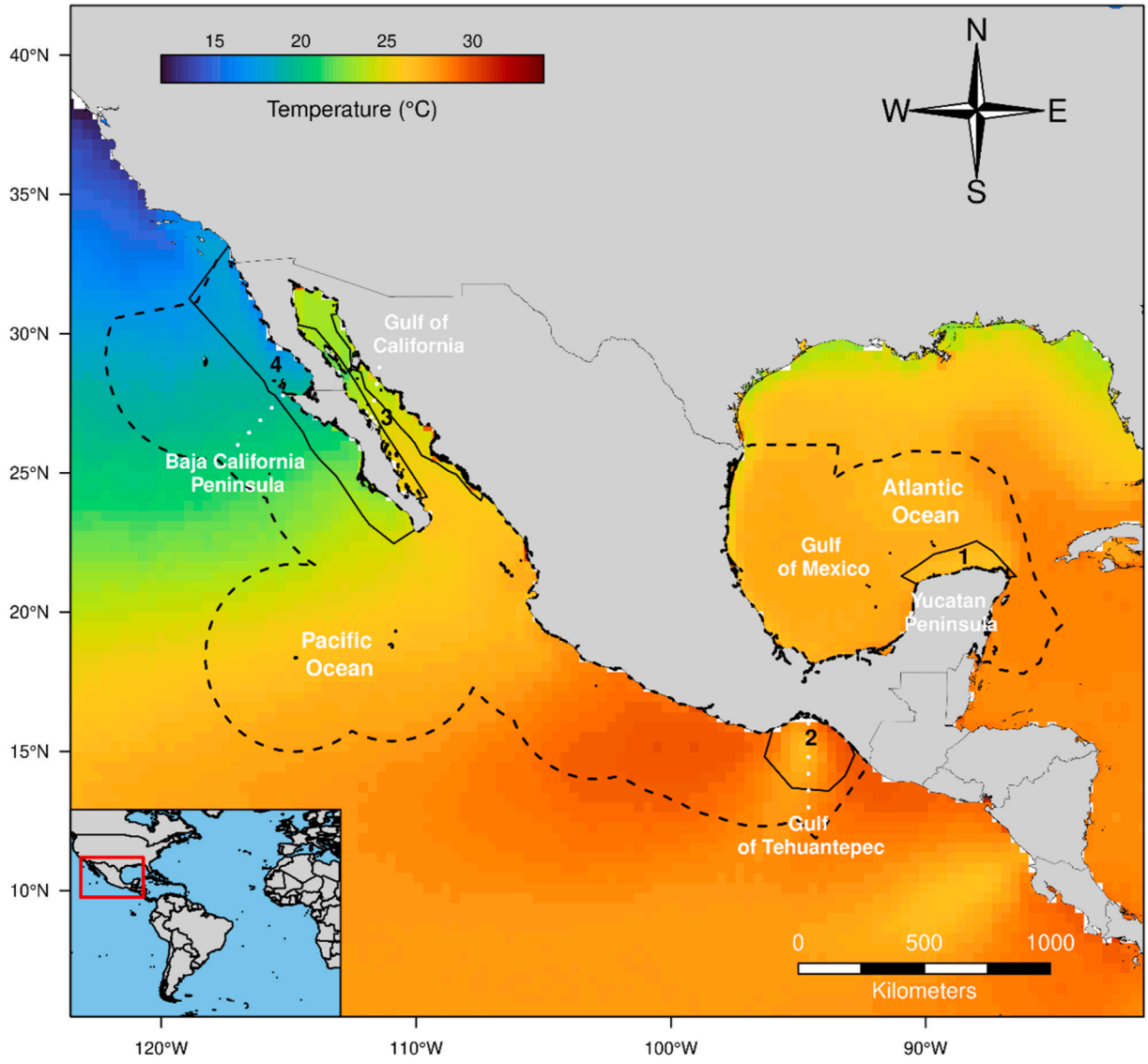

Fig. 1. Average sea-surface temperature for the period 2019–2023. The delineated line indicates the Mexican exclusive economic zone. The major upwelling regions are shown as follows: (**1**) Northern Yucatan Peninsula; (**2**) Gulf of Tehuantepec; (**3**) Gulf of California; and (**4**) Western Baja California Peninsula. Data were obtained from the sensor MODIS-Aqua (https://oceancolor.gsfc.nasa.gov/).

Southern WBCP extent (López-Aviles et al., 2024).

2.2. Environmental data

Bio-ORACLE v2.2 dataset was used to download sea surface temperatures (SST): maximum, mean, minimum and range of sea surface temperatures (SSTmax, SSTmean, SSTmin, and SSTran, respectively) for current (2000–2014) and 2040–2050 and 2090–2100 periods under Representative Concentration Pathways (RCP) 6.0 and 8.5 scenarios (https://www.bio-oracle.org/) (Assis et al., 2017) were considered. The future scenarios from Bio-ORACLE v2.2 were obtained by averaging the Community Climate System Model 4 (CCSM4), Hadley Centre Global Environmental Model 2 (HadGEM2-ES), and Model for Interdisciplinary Research on Climate (MIROC5) (see Assis et al., 2017 for details). The RCP 6.0 and RCP 8.5 projection scenarios assume the most severe warming from all RCP with a temperature increase of ~1 °C from 2040 to 2050 and ~3 °C from 2090 to 2100. The most extreme scenarios were selected since the aim was to identify the most vulnerable regions and potential climate refugia in Mexico. Bathymetry data from MARSPEC (Sbrocco and Barber, 2013) was also downloaded. It is important to mention that the same bathymetric layer was used for current and future scenarios. The environmental layers had a 9 × 9 km resolution per pixel at the Equator. Figures of the environmental layer are added in supplementary material 1 (Figs. S1, S2, S3, S4, and S5).

2.3. Species selection

Species selection for modeling was based on the Mexican Official Federal documents "Carta Nacional Pesquera" (CNP) published from 2017 to 2023 – a document that provides precise and up-to-date information on where, when, and how much fishing is allowed for commercial aquatic species fished in Mexico in addition to the bycatch which may not have commercial importance (DOF, 2023, 2022, 2017). Fish species of both commercial and non-commercial importance were selected.

During the selection process, any taxonomy names no longer accepted or wrongly spelled were corrected using as a reference the World Register of Marine Species (WoRMS - https://www.marinespecies.org/), which provides "an authoritative and comprehensive list of names of marine organisms". This situation is important since species

misidentification may produce inaccurate biological and ecological information (Bortolus, 2008) and could potentially setback the correct development of effective policies for ecosystem protection (Knowlton, 2000; Lima et al., 2017). In total, 384 species were identified in Mexican federal documents, with 266 being fishes (Supplementary Material 2).

2.4. Occurrence data

Species records were downloaded from the repositories: Ocean Biodiversity Information System (OBIS), Global Biodiversity Information Facility (GBIF), and VertNet using the packages "*robis*" (Provoost and Bosch, 2022), "*rgbif*" (Chamberlain et al., 2023) and "*rvertnet*" (Chamberlain, 2021) from the programming language R (R Core Team, 2023), respectively. The species records were curated by removing duplicate and inland records. Furthermore, occurrences associated with environmental outliers were visually screened; if the values were too atypical from the bulk of the data, they were deleted (Simoes et al., 2020).

Oversampling biases are also problematic in online repositories since they can alter TN calculations. To reduce this problem, first, only one occurrence was considered per pixel. Later, a spatial filtering was applied by using the "*thin*" function from the R package "*spThin*" (Aiello-Lammens et al., 2015). No universally accepted distance exists for spatial thinning. Therefore, three databases were created for each species using a different thinning distance of 0 km (i.e., one occurrence per pixel), 50 km, and 100 km.

The study also used exploratory plots to visualize surface temperature data for the pooled species group. Species occurrences were overlaid on environmental variables, and data was extracted, averaged, and stored in a data frame for later visualization. Only species with 30 occurrences or more were considered. Exploratory figures were also done for each species individually to visualize their TN and stored in Figshare due to the high number of figures (https://doi.org/10.6084/m9.figshare.24257542).

2.5. Algorithm of the correlative ecological niche models

The minimum volume ellipsoid (MVE) algorithm was used to represent the species fundamental niche. This algorithm was selected because empirical and theoretical works assume that fundamental niches have convex shapes (Jiménez et al., 2019); moreover, the distance to the center of an ellipsoid has been shown to be negatively related to fitness attributes, such as population abundance and genetic variation (Altamiranda-Saavedra et al., 2020; Ángeles-González et al., 2021a; Ochoa-Zavala et al., 2022; Osorio-Olvera et al., 2020b). The MVE is a multivariate estimator that builds ellipsoids spanning a predetermined percentage of observations, predicting a centroid and scattering of the data (Van Aelst and Rousseeuw, 2009). The centroid and total volume of the ellipsoids are represented by the combination of non-optimal environmental factors ($\boldsymbol{x} = [x_1, x_2, \ldots, x_n]$) and optimal centroid ($\boldsymbol{\mu} = [\mu_1, \mu_2, \ldots, \mu_n]$) where the highest suitability occurs. The suitability function of an ellipsoid depends on the Mahalanobis Distance equation:

$$d_M(\boldsymbol{x},\boldsymbol{\mu}) = (\boldsymbol{x}-\boldsymbol{\mu})^T \sum^{-1} (\boldsymbol{x}-\boldsymbol{\mu}) \quad \text{(Eq. 1)}$$

where $\sum$ is a covariance matrix. Finally, the suitability of x is computed as:

$$S(\boldsymbol{x}) = \exp\left(-\frac{1}{2}\, d_M(\boldsymbol{x},\boldsymbol{\mu})\right) \quad \text{(Eq. 2)}$$

2.5.1. Models calibration

Databases with equal or greater than 30 occurrences after spatial filtering were considered for model calibration and projection. The temperature values associated with each species occurrence were extracted; posteriorly, a Pearson's correlation (function "*cor*" in base R) analysis was used to eliminate variables with a correlation greater than 0.8. The variables were deleted according to a hierarchical order as follows: SSTmax, SSTmin, SSTmean, and SSTran. This hierarchical order was considered given that species inhabiting tropical regions have shown to be highly sensitive to warming temperatures (Pörtner and Farrell, 2008; Somero, 2010). In addition, prioritizing SSTmin allows us to consider temperature variations present in the upwelling systems and indirectly consider SSTran. Our model projections did not consider only surface environmental models or bathymetry incorporating only SSTran, as these models tended to overextend species potential distribution or exhibit instability under CC projections. In total, 22530 models were considered in this work.

After the correlation analysis, environmental layers were cropped according to a calibration region which consisted in a buffer of 500 km around species occurrences. This region is meant to represent an accessibility hypothesis, i.e., areas explored by the species, whether they have been able to settle or not (Owens et al., 2013). Ten thousand environmental random background points were extracted from the calibration region. To use an MVE, the background data is not mandatory, but it is necessary to estimate the partial receiver operating characteristic curve (pROC) and the area under the curve (AUC) of the ROC (Osorio-Olvera et al., 2020a). Thus, 10,000 background points were deemed helpful in characterizing the calibration region.

For model calibration, the function "ellipsoid_selection" from the "*ntbox*" R package (Osorio-Olvera et al., 2020a) was used under the stratified selection criteria with a repeated subsampling (10 times), where 75% of the occurrences were used to train the MVEs, while the remaining 25% was employed as test data. For the MVE 97.5% of the data was considered. This inclusion percentage has been shown to characterize the niche at sample sizes of 30 correctly, improves MVEs when erroneous occurrences registered are about $\leq$ 20%, and does not perform worse at any level of bias (Etherington, 2021).

Models that did not have statistical significance -according to the pROC analysis ($P > 0.05$) had omission rates of more than 0.10 (Peterson et al., 2008), or AUC of less than 0.6 were removed. From the remaining models, consideration was given to those with an omission rate equal to or less than 0.025. If none met these criteria, the threshold was incrementally raised, first to 0.05, then to 0.075, and finally up to 0.1, halting the process upon reaching an acceptable omission rate. Following this iteration, the model with the highest AUC value was selected. Priority was given to models with three or more variables, enabling a more accurate description of the multidimensional TN, which is particularly important in highly dynamic systems such as upwellings. Bi-dimensional models were considered if obtaining three-dimensional models was not feasible due to correlation or if none passed the calibration process. No projection was made if the models did not meet the selection criteria.

2.5.2. Suitability maps, richness, and species turnover

The selected models for each species were projected with the "*ellipsoidfit*" function from the "*ntbox*" package to the MEEZ for present (2000–2014) and future scenarios (RCP 6.0 and 8.5, period 2040–2050 and 2090–2100, respectively). There is evidence that ellipsoidal structures would indicate the regions where fitness is optimized (Ángeles-González et al., 2021a; Osorio-Olvera et al., 2019, 2020b) (Fig. 2). Thus, regions with higher proportions of species' optimal fitness were located through an overall suitability map, which was created by averaging suitability maps of all species. In this case, values of 1 would indicate maximum performance (i.e., niche centroid) and 0 unviable environments (outside the ellipsoids). Subtraction between present suitability maps and RCP scenarios were also done to identify regions which gained or lost suitability.

The suitability maps for each species were transformed into presence-absence maps by binarizing it where pixels with values of "1" represent presence and "0" absence. The threshold value for a model is

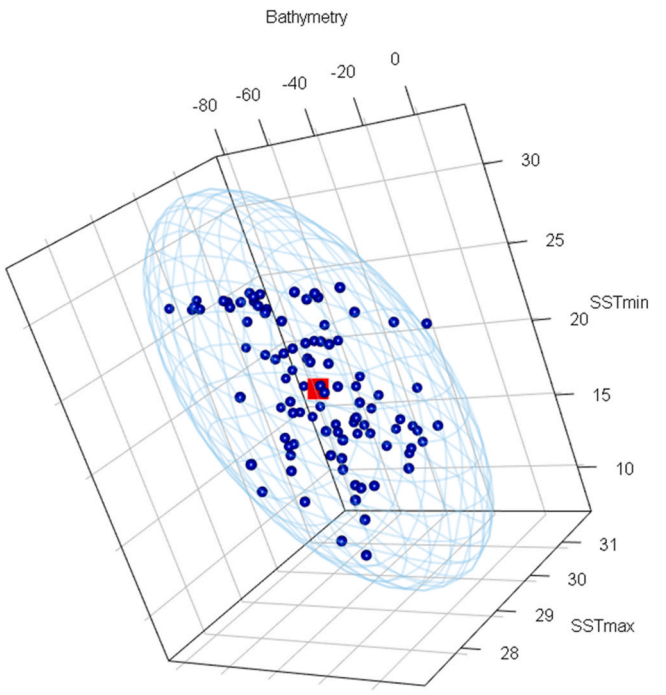

Fig. 2. An example of a three-dimensional ecological niche obtained from a minimum volume ellipsoid defined by three variables (bathymetry, minimum temperature [SSTmin], and maximum temperature [SSTmax]). The estimated centroid is presented in red and consists of environmental combinations where fitness would be hypothetically higher. This ellipsoid corresponds to the species Bothus robinsi. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

usually determined based on the intended model application (Peterson, 2006). If all occurrence data is considered, overly broad predictions can be made. To avoid this situation, an alternative approach is to select a threshold value that includes a certain percentage of presence records (Peterson et al., 2011). Thus, a suitability value was chosen that excluded the 2.5% of training presences with unusual environmental combinations (similar to the approach used for the MVEs).

The taxonomic richness and its changes under CC scenarios were calculated by summing-up the binary maps; i.e., presence-absence maps. Finally, the species turnover was calculated for all scenarios using the Jaccard distance index in base R (function *"dist"*). The Jaccard distance index represents the proportion of the total species pool shared by the two communities given by the following formula:

$$d(i,j) = \frac{b+c}{a+b+c} \Rightarrow 1 - sim\,(i,j) \qquad \text{(Eq. 3)}$$

Where a is the species shared per pixel in time i (present scenario) and j (future scenario) represented as 1; b is the species present in pixel i (1) but not j (0); c is the species present in pixel j but not i. These differences were spatially projected to locate regions with higher species turnover (Fig. 2).

3. Results

Based on environmental data linked to species occurrences, the majority of fishes documented in the CNP are observed within the SSTmax of 28–29 °C, 20–22 °C for SSTmin, and 25–26 °C for SSTmean, indicating a high dominance of tropical species. These species predominantly inhabit regions with temperature variations from 7 to 8 °C (Fig. 3).

For model projections, 242, 222, and 194 species from databases filtered at 0, 50, and 100 km were selected, respectively. The most selected models considered bathymetry, SSTmax, and SSTmin (532 models), followed by bathymetry and SSTmax (38 models), and bathymetry, SSTmax, and SSTran (37 models). (Supplementary material 1, Fig. S6). For most species, the selected ENMs have acceptable levels of omission rates (~0.06) and AUC (>0.9) (Supplementary material 1, Fig. S7). The average suitability and species richness maps show a species cluster in the Central and Southern WBCP and Northern YP regions under warming scenarios (Fig. 4 - Supplementary material 1, Figs. S8 and S9).

Species in WBCP congregate mainly in the south. At latitudes above 28 °N, low temperatures create a barrier for certain tropical species, like those of Lutjanidae genera (e.g., *Lutjanus guttatus*, *L. inermis*, L. *novemfasciatus*, *L. peru*, and *L. viridis* - https://doi.org/10.6084/m9.figshare.24257542). For example, *L. inermis* thrives in regions with warm temperatures from 25 to 30 °C (Fig. 5), which are not found in higher latitudes, even in warming scenarios. However, some species may overcome this environmental barrier (as seen with *Scomber japonicus* - https://doi.org/10.6084/m9.figshare.24257542).

Similarly, suitability subtraction maps indicate that not all upwellings enhance suitability uniformly. During all warming scenarios, suitability decreased in the Southwestern Gulf of Mexico, Caribbean, and Pacific, both in the Gulf of Tehuantepec and Gulf of Baja California. Conversely, a temperature rise of 2 °C increased suitability in Northern YP (+0.3) and Southwestern BCP (+0.1). A suitability reduction was observed in Northern YP away from the upwelling influence (offshore). Further temperature increase under the RCP 8.5 scenario in 2090–2100 (~3 °C) reduced species suitability even in YP upwelling (−0.4). In contrast, all the WBCPs increase in suitability (+0.1 to 0.3) (Fig. 6 and Supplementary material 1 Figs. S8 and S9).

Richness change patterns follow similar trends, where temperature rises could increase the upwelling region richness may increase in the upwelling of the YP (+25) although an offshore reduction exists. Further thermal stress in the RCP 8.5 (2090–2100) changes this pattern (−20 in richness - Fig. 6, Supplementary material 1, Figs. S8 and S9). In contrast, an overall increase in richness occurs in the WBCP (+25 to 50). For the turnover analysis, both Northern YP and Southern WBCP act as a buffer area in species composition since values do not exceed 0.20 in all scenarios. A significant increase in species turnover was observed in the northern offshore regions in the YP due to species loss across most of Mexico in all scenarios, which ranged from 0.3 to 0.6 under the RCP 8.5 scenario (2090–2100). In the northern regions of the WBCP, changes were observed in species composition due to new species arriving from lower latitudes (Fig. 6 – Supplementary material 1, Figs. S10 and S11).

4. Discussion

Even though a direct abundance measurement was not considered, MVEs may reflect important population fitness parameters, such as abundance and genetic diversity (Ángeles-González et al., 2021a; Ochoa-Zavala et al., 2022; Osorio-Olvera et al., 2020b). Based on this, Mexico's most vulnerable regions to temperature increases are the Caribbean, Western regions of the YP and the Pacific, and the Gulf of California. These results partially agree with Cisneros-Montemayor et al. (2020), who noticed that fishery catches could significantly decrease in YP and the Caribbean. However, they find no evidence that the upwelling region at the north of YP can mitigate the decline in catches. They also observe potential increases in fishery yields in the central and southern regions of the Pacific.

ENM projections are subjected to the environmental models used, which add uncertainty and variation to predictions (Peterson et al., 2018). Thus, differences between our findings and Cisneros et al. (2021) may be due to disparities in the hydrodynamic models used (see Cisneros-Montemayor et al., 2020). In the present study models with higher resolution were used (0.08° × 0.08° compared to 0.5° × 0.5°), which might have influenced the outcomes. Cisneros-Montemayor et al. (2020) suggested that higher-resolution models could generate more precise

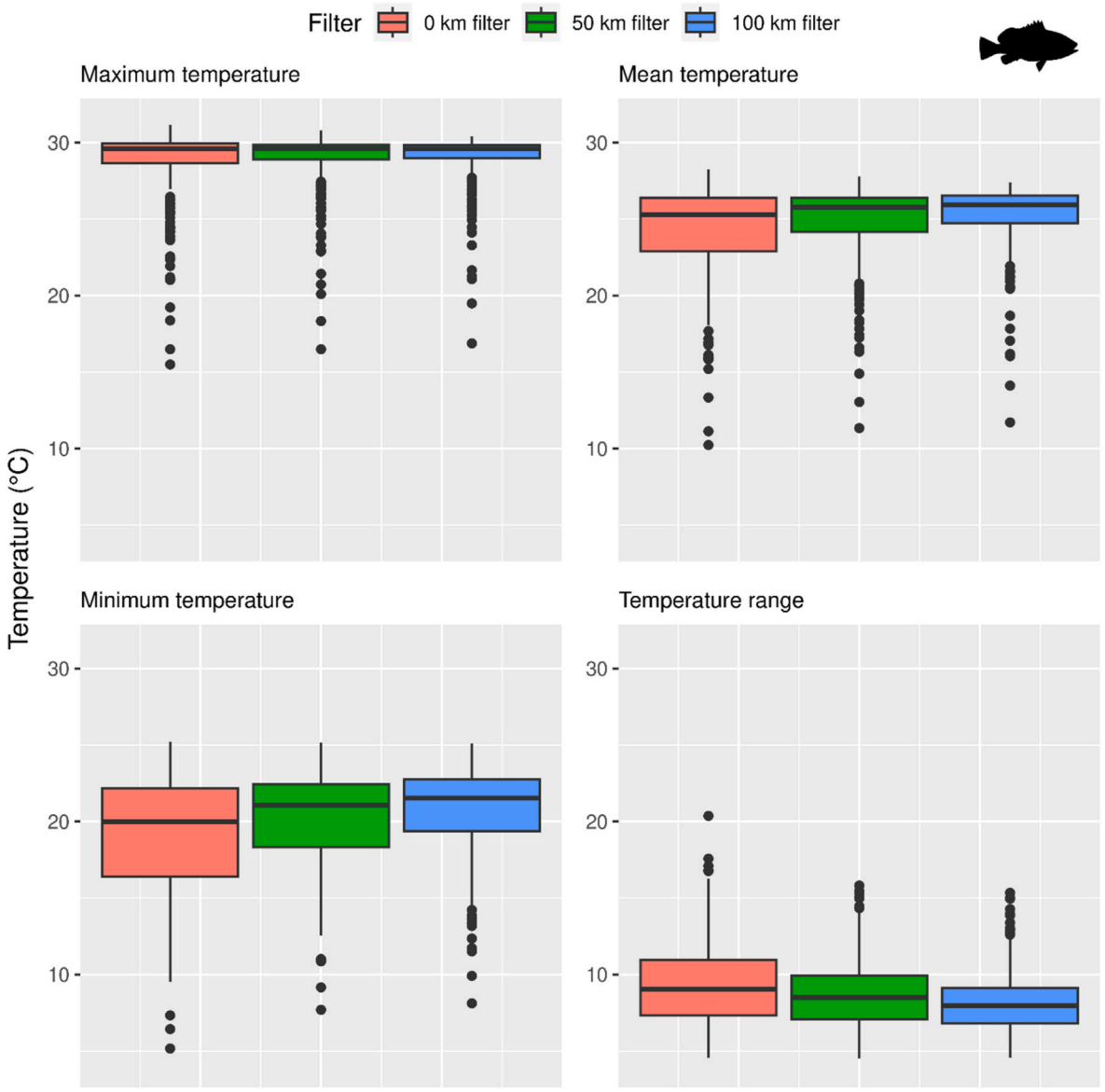

Fig. 3. Boxplots representing the average values of maximum, minimum, mean, and range of temperatures where fish species of the Carta Nacional Pesquera are observed for the databases spatially filtered by 0 (one occurrence per pixel), 50, and 100 km filter.

results for the scales at which fisheries operate in Mexico. Likely, environmental layers used in here could better characterize coastal upwelling. However, considerable uncertainty still exists on the effects of upwelling regions in CC scenarios (see the caveat section).

The results in this study show that Northern YP and WBCP can potentially be thermal refuge zones, although significant differences in response need to be noted. Discussions of CC and warming have mainly focused on species redistribution to higher latitudes or greater depths; however, such assumptions could mask other potential responses. For example, in Benguela's upwelling system, fifty percent of the species have migrated toward the Equator in South Africa and Namibia with species moving to shallower waters (Poloczanska et al., 2016), such patterns are similar to our predictions for Northern YP. Lourenço et al. (2016) discovered that due to warming, the alga *Fucus guiryi* disappeared from non-upwelling coasts but thrived near upwelling centers. The Peruvian Current System simulations and sightings have shown that *Scomber japonicus* may conglomerate near the EBUS under El Niño and CC scenarios (Torrejón-Magallanes et al., 2021), meanwhile, in YP, fishing data suggest that *Octopus maya* may conglomerate at the upwelling region under thermal anomalies (Angeles-Gonzalez et al., 2017).

In the Holocene, both the Gulf of Panama and the Gulf of Chiriqui had comparable calcium-carbonate accumulation rates. However, seasonal upwelling in the Gulf of Panama hindered reef development. Today, seasonal upwelling in the Gulf of Panama mitigates thermal stress from CC, resulting in higher carbonate production than in the Gulf of Chiriqui (Rodriguez-Ruano et al., 2023). Our observations in YP upwelling region aligned with initial expectations and the literature above, suggesting that upwelling ecosystems can serve as buffer zones against CC. However, patterns differed in the WBCP region.

Intensified upwelling in the northern areas of the WBCP characterized by lower temperatures acted as an environmental barrier for many tropical species reported by the CNP (e.g., family Lutjanide), challenging the generalized notion of tropicalization (Zarzyczny et al., 2023). EBUS are ecosystems with strong seasonality and lower temperatures (Bograd et al., 2023; Chavez and Messié, 2009), which contrasts with warm and stable tropical ecosystems. If species have developed behavioral and physiological mechanisms to optimize fitness across a range of temperatures, strictly tropical species may find their distribution limited between the western Pacific in Mexico and the central and northern regions of the WBCP.

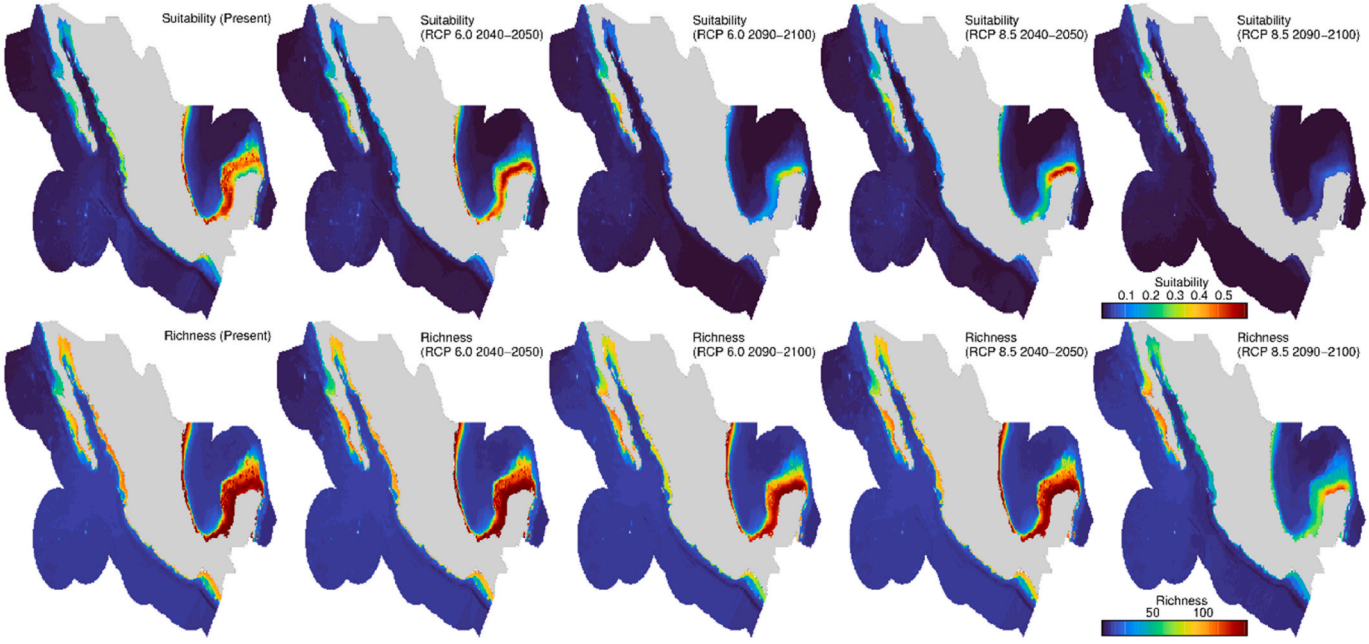

Fig. 4. Average suitability (top row – i.e., where ellipsoid centroids converge more) and species richness (bottom row – number of species) for marine fishes under various climate change scenarios for databases with a 50 km spatial filter.

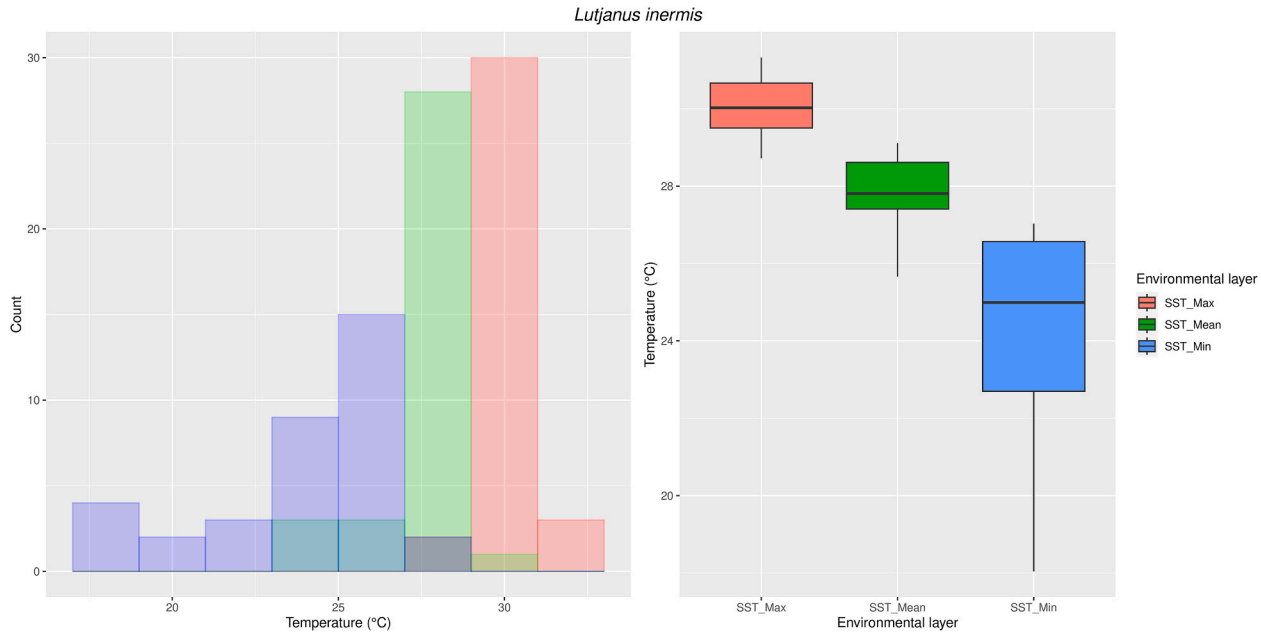

Fig. 5. Histograms and boxplots representing the maximum (SSTmax), mean (SSTmean), and minimum temperatures (SSTmin) where *Lutjanus inermis* are found based on occurrence databases and environmental layers used for model calibration. The 50 km spatial filter database was used for this figure.

In contrast, non-tropical species like *Scomber japonicus* can tolerate the low temperatures in the northern areas of WBCP, benefiting from higher upwelling intensity shown by increased suitability and higher turnover in the northern region. Thus, the importance of considering species-specific adaptation to native conditions should be highlighted when predicting future patterns and assessing the viability of upwelling zones as thermal refugia. The CNP species, composed mostly of tropical species, congregate in the Southern WBCP, where the temperatures are higher and the upwelling influence is weaker. This region provides protection to tropical species, explaining the increase in suitability richness, and lower turnover. Similarly, this pattern is observed in YP upwelling; however, under the most extreme scenarios (RCP 8.5, 2090–2100), the YP becomes overwhelmed, indicating that thermal refugia can be surpassed by warming effects (Dixon et al., 2022; McWhorter et al., 2022).

No evidence has been found that either the Gulf of Tehuantepec or the Gulf of California had a mitigating effect on warming. This lack of effect could be due to specific factors. For example, upwelling in the Gulf of Tehuantepec occurs mainly offshore at great depths (Barton et al., 1993), while most of the species documented in the CNP inhabit coastal regions. For the Gulf of California, strong seasonality (±15 °C) causes changes in species composition and abundance (Ángeles-González et al., 2021c; Sánchez-Velasco et al., 2009; Solana-Arellano et al., 2023) and they may not be favorable for tropical species (Pörtner and Farrell, 2008;

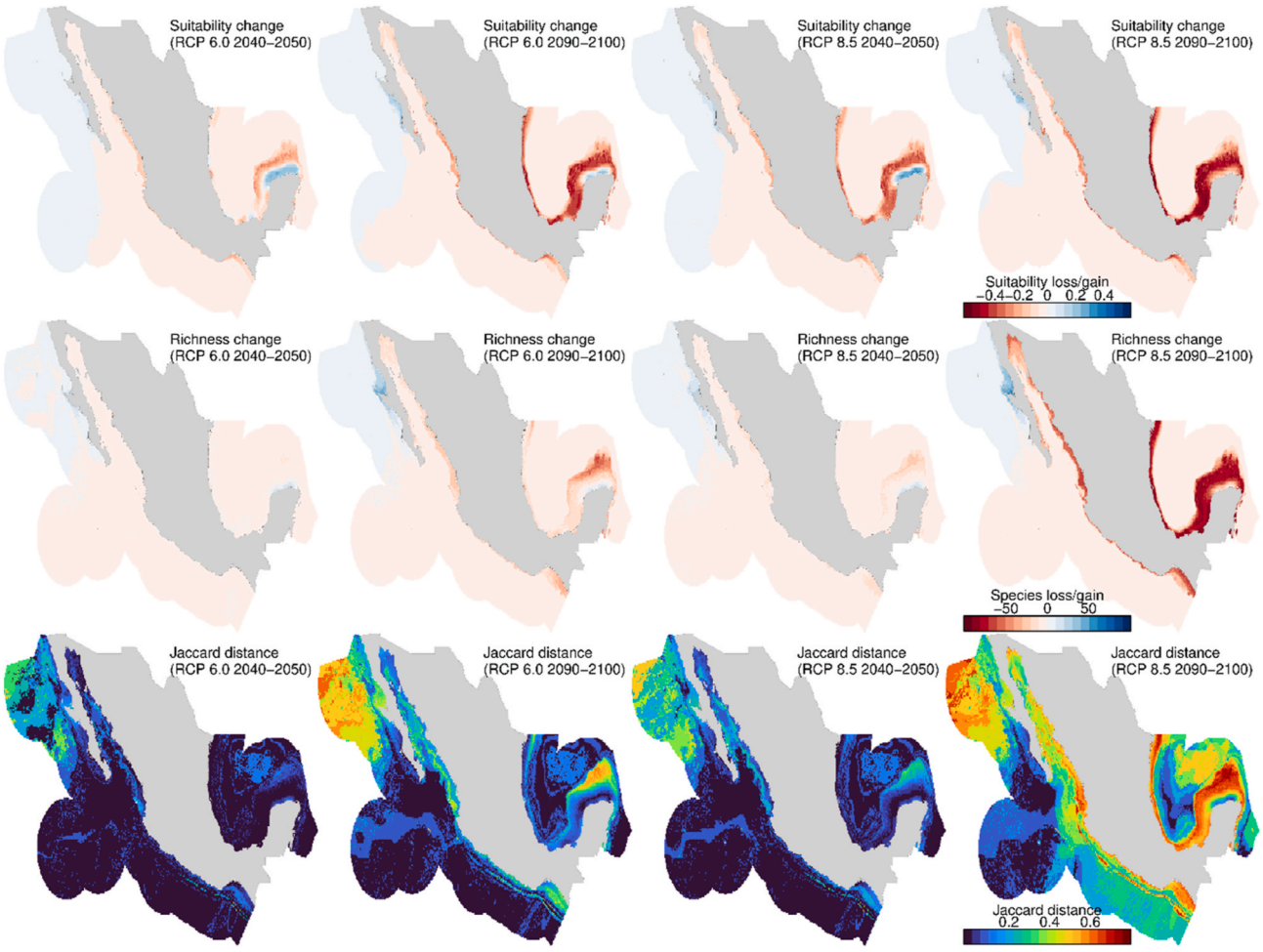

Fig. 6. Changes in marine species suitability (top row), species richness (middle row), and spatial-temporal turnover of marine fishes (bottom row) under various climate change scenarios for databases with a 50 km spatial filter.

Somero, 2010). Angeles-Gonzalez et al. (2023) suggested that the Gulf of California could act as a thermal refugia, but they only considered the mean temperature and failed to account for the high-temperature seasonality.

These findings indicate that certain upwellings could offer favorable climate conditions for species in a warming scenario allowing them to survive. However, it is important to consider species-specific adaptations to thermal variation. For instance, coral reefs adapted to tropical climates benefit from the tropical upwelling in the Gulf of Panama (Rodriguez-Ruano et al., 2023). Thus, tropical species may not be able to fully utilize EBUS as thermal refuges; in contrast, tropical upwellings could serve as thermal refuges for tropical species, promoting biodiversity conservation helping avoid local extinction, preserve genetic diversity, and potentially support range expansion through adaptive processes (Lourenço et al., 2016).

Finally, defining upwelling areas as conservation spots is a complex balancing act that involves weighing ecological benefits against economic and social costs. Upwelling zones are among the most productive fishing grounds in the world. Therefore, restrictions on fishing activities within these regions may lead to a reduction in the accessible areas for commercial fisheries to operate and significantly affect catch volumes of many marine species – a key protein source for many coastal communities, potentially impacting food security and economy (Allison et al., 2009; Escamilla-Aké et al., 2024). On the other hand, in the longer term, considering upwelling areas as conservation spots could help in the recovery of stocks when overfishing takes place.

This recovery can potentially lead to more stable marine populations, which can be sustainably harvested in the future, potentially leading to more consistent yields and less variability in fish population sizes year-to-year. The success of such measures depends largely on the specific regulations implemented, management strategy effectiveness, and stakeholders' ability to adapt to changes (Berkes, 2010; Pomeroy and Douvere, 2008). Incorporating adaptive strategies and robust engagement is required to address the needs and concerns of all parties affected, particularly fishing communities whose livelihoods and food security might be impacted.

4.1. Caveats

Considering that CC is projected to impact not only the temperatures but also numerous ecosystem features is very important, such as trophic relationships and phenology of processes related to life histories or species habitats. For example, pollution, sea-level rise, and many other factors further impact marine organisms in Mexico (Martínez-Arroyo et al., 2011). The CC may also decrease oxygen concentrations and increase CO_2, acidifying the oceans (Feely et al., 2008); these processes would reduce the energetic budget of marine species and their TN (Doney et al., 2012; Pörtner and Peck, 2010).

In addition, the prediction of oceanographic processes under CC scenarios is a complex task that introduces a significant amount of uncertainty for upwelling ecosystems, since recent evidence challenges Bakun hypothesis. The increase in surface ocean heat gain results in increased stratification, implying that greater wind energy is required to bring deep waters to the surface. Uncertainty still exists in wind speed

trends, as observations and global circulation models yield inconsistent results (Du et al., 2023; García-Reyes et al., 2015; Lluch-Cota et al., 2014). Indeed, observations and predictions for the California Current system indicate an upwelling weakening, but evidence is still inconclusive (Du et al., 2023; García-Reyes et al., 2023). This situation may benefit tropical species by facilitating northward migration, allowing tropical species to migrate to higher latitudes. However, it underscores the need for further study of the CC potential effects on these ecosystems, particularly because ENMs are dependent on such predictions.

5. Conclusion

The present study highlighted the potential use of upwelling regions as climate refugia via climate warming effect mitigation by acting as an "oasis" under environmental pressure. The EBUS in the WBCP and the upwelling north of YP may be important regions for conservation; however, regions of intense upwelling like the EBUS could act as environmental barriers for many tropical species increasing the known complexity of responses of marine species to warming. Future studies could use a pool of tropical, subtropical, and temperate species to compare the EBUS effects on fishes' redistribution. In addition, future studies could also search for evidence of such changes; literature, data recompilation, or fossil records could shed light on this assumption. This information could help us to validate or refute our hypothesis. This work only accounted for a TN, which must be considered an incomplete reconstruction of the niche. Notwithstanding these concerns, if the hypothesis is viable, CC studies would benefit from developing more analyses in upwelling regions, particularly by conservation biologists and decision-makers.

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CRediT authorship contribution statement

Luis Enrique Angeles-Gonzalez: Writing – review & editing, Writing – original draft, Software, Data curation, Conceptualization. **Josymar Torrejón-Magallanes:** Writing – review & editing, Writing – original draft, Software. **Angel Escamilla-Aké:** Writing – review & editing, Writing – original draft. **Luis Osorio-Olvera:** Writing – review & editing, Writing – original draft, Software, Formal analysis, Conceptualization. **Otilio Avendaño:** Writing – review & editing, Writing – original draft, Data curation. **Fernando Díaz:** Writing – review & editing, Writing – original draft, Conceptualization. **Carlos Rosas:** Writing – review & editing, Writing – original draft, Conceptualization.

Declaration of competing interest

The authors report no potential competing interests.

Data availability

All data and codes necessary for result replication can be accessed at https://doi.org/10.6084/m9.figshare.24257542.

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Appendix A. Supplementary data

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