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Thermal niches and climate change reshape marine invasion risk worldwide

Luis Enrique Angeles-Gonzalez [a], Tulio F. Villalobos-Guerrero [b], Manuel Alejandro Delgadillo-Nuño [c,d], Josymar Torrejón-Magallanes [e], Angel Escamilla-Aké [f,g], Fernando Díaz [a], Carlos Rosas [f,*]

[a] Laboratorio de Ecofisiología de Organismos Acuáticos, Departamento de Biotecnología Marina, Centro de Investigación Científica y de Educación Superior de Ensenada (CICESE), Carretera Ensenada–Tijuana #3918, Ensenada, Baja California, 22860, Mexico
[b] Departamento de Ecología Marina, Centro de Investigación Científica y de Educación Superior de Ensenada (CICESE), Ensenada, Baja California, 22860, Mexico
[c] Laboratorio de Arrecifes y Biodiversidad, Departamento de Ecología Marina, Centro de Investigación Científica y de Educación Superior de Ensenada (CICESE), Ensenada, Baja California, 22860, Mexico
[d] Laboratorio de Genómica Funcional, Departamento de Biotecnología Marina, Centro de Investigación Científica y de Educación Superior de Ensenada (CICESE), Ensenada, Baja California, 22860, Mexico
[e] Instituto Del Mar Del Perú, Esquina Gamarra y General Valle s/n, Chucuito, Callao, 07021, Peru
[f] Unidad Multidisciplinaria de Docencia e Investigación, Facultad de Ciencias, Universidad Nacional Autónoma de México (UNAM), Puerto de Abrigo, Sisal, Yucatán, 97356, Mexico
[g] Centro para El Desarrollo Educativo, Científico, Tecnológico y Ambiental (CEDECTYA A.C.), Calle 21, Dzidzantún, Yucatán, 97506, Mexico

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ABSTRACT

Marine biological invasions and climate change are two major drivers of biodiversity loss, yet their interactions remain poorly understood. Here, we used correlative ecological niche models (ENMs) to characterise the thermal niches of 80 globally invasive marine species and project their thermal suitability from 2020 to 2100 under multiple Shared Socioeconomic Pathway scenarios. Our models, based on Minimum Volume Ellipsoids fitted to sea surface and bottom temperatures, revealed substantial differences across species' thermal affinities. Tropical and subtropical invaders are projected to experience widespread declines in thermal suitability, suggesting that warming at low latitudes may approach their physiological thermal limits and redistribute thermally suitable conditions toward higher latitudes (25° to 35° N/S). Temperate species exhibited lower magnitudes of thermal suitability change, consistent with their broader thermal tolerances, although increases in thermal suitability at higher latitudes (50° to 60° N/S) suggest potential emerging invasion risks as polar barriers weaken. Climate change is expected to reshape marine invasion patterns by altering the spatial distribution of thermally suitable conditions, amplifying risks at mid-to-high latitudes while constraining some tropical invaders. While our findings provide a baseline for understanding thermal constraints on marine bioinvasions, caution is warranted: realised niches may underestimate species' full thermal tolerances, and key factors like biotic interactions, functional characteristics, and other environmental variables were not included. Nonetheless, thermal niches emerge as a strong predictor of potential invasion risk, identifying regions with high thermal suitability for invasive species and informing early detection and management strategies.

1. Introduction

Bioinvasions are non-native species that cause both significant ecological and socioeconomic harm upon colonising new areas and follow a gradual invasion process (transport, introduction, establishment, and spread), with potential impacts being incurred at every stage of the invasion process (Ricciardi, 2013; Glon et al., 2020). Invasive species are introduced through natural dispersal, such as wind and water currents, but more commonly through anthropogenic activities, which allow them to bypass the geographic or environmental barriers that defined their original distribution range (Molnar et al., 2008; Ricciardi, 2013; Alidoost Salimi et al., 2021). Most of these species fail to establish

* Corresponding author.
E-mail address: crv@ciencias.unam.mx (C. Rosas).

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sustainable populations, although a self-sustaining population is more likely to form when sufficient well-adapted individuals arrive in a suitable region (Liu et al., 2020).

The increasing frequency of invasive species introductions poses significant ecological challenges, particularly as human-related activities continue to drive an exponential rise in these events worldwide (Seebens et al., 2016; Heger et al., 2021; Mormul et al., 2022). Particularly in marine bioinvasions, the increase of non-native species has been driven mainly by ship ballast water discharge, aquarium and ornamental trades, biofouling, floating debris, and submerged artificial structures (e.g. drilling platforms, harbours, canals, and marinas) (Seebens et al., 2016; Lacoursière-Roussel et al., 2016; Geburzi and McCarthy, 2018; Hulme, 2021) with ballast water and biofouling primarily associated with mobile invertebrates and sessile fouling organisms (Carlton and Geller, 1993; Floerl and Inglis, 2005), and aquarium and ornamental trades mainly linked to reef fishes and other aquarium species (Padilla and Williams, 2004).

Marine bioinvasions can trigger significant alterations, displacing native species, changing community structure and food webs (Thomaz et al., 2015; David et al., 2017), modifying the surrounding environments (Peller and Altermatt, 2024) and even causing local extinctions (Dueñas et al., 2021). Moreover, they also represent economic impacts on human activities for both developing and developed countries (Marbuah et al., 2014; Epanchin-Niell, 2017; Hanley and Roberts, 2019; Zenni et al., 2021; Henry et al., 2023).

For invasive species to establish in a region, they must pass through ecological filters, both abiotic and biotic (Crowl et al., 2008). Abiotic variables often act as the first ecological filter to invasion, as successful establishment requires invaders to tolerate environmental stressors through physiological adjustments. Failure to do so prevents species persistence regardless of biotic interactions (Gerhardt and Collinge, 2007; Olyarnik et al., 2009; Kelley, 2014). Particularly, temperature is considered important as it establishes physiological limits on survival, growth and reproduction in ectothermic marine organisms, due to its direct effects on biochemical and cellular processes (Somero, 2010; Pörtner and Peck, 2010; Kelley, 2014), defining the environmental boundaries which allow populations to persist. Within these thermally suitable conditions, establishment success and local impacts are further shaped by biological mechanisms such as species interactions (e.g. competition, predation, and enemy release), positive facilitation, invader life-history and stress-tolerance traits, and post-introduction evolutionary processes (Papacostas et al., 2017). In addition, species distribution models have highlighted temperature as a key factor limiting the global distribution of marine species (Bosch et al., 2018; Angeles-Gonzalez et al., 2023; Meyer et al., 2024).

Beyond bioinvasions, climate change is also a major enhancer of biodiversity loss and an alteration driver. Although these two drivers are often analysed independently, evidence suggests they may interact synergistically, generating unforeseen and irreversible consequences for native communities (Mainka and Howard, 2010; Kernan, 2015).

Thus, a key pathway through which climate change may influence biological invasions is by altering transport and introduction mechanisms, notably through the removal of physical and thermal barriers to species dispersal, thereby promoting ecosystem disruption (Hellmann et al., 2008; Gallardo et al., 2016; Mahanes and Sorte, 2019). For instance, recent observations in temperate ecosystems indicate that the weakening of thermal barriers is facilitating the appearance of species associated with lower latitudes, suggesting that tropicalisation processes are underway (Zarzyczny et al., 2024). This process may also involve species identified as invasive (e.g., Johnson, 2015). Moreover, climate change may facilitate the establishment of new invasive species and modify the impacts and distributions of existing ones (Hellmann et al., 2008).

The expansion of non-native invasive species under changing climatic conditions is likely to generate novel ecological and socio-economic interactions, with outcomes that are difficult to predict but expected to be largely detrimental to native biodiversity, local economies, and human health. However, the current lack of a baseline for marine species poses a significant challenge for management and conservation efforts (Bradley et al., 2023).

To anticipate these risks, predictive tools are needed to forecast the potential distributions of invasive species under current and future climatic conditions. Correlative ecological niche models (ENMs) have become crucial tools for predicting the fundamental niche (FN) of bioinvasive species. The FN defines the environmental conditions where species can maintain populations without in-migration. Individuals outside these conditions typically fail to reproduce, thus limiting potential introductions. Ecologists have utilised ENMs to map suitable areas for potential invaders, thereby informing conservation and management strategies and helping to identify regions at risk (Loya-Cancino et al., 2023; Thuiller, 2024; Zhu et al., 2024; Liu et al., 2025; Ohanna et al., 2025).

Among available modelling approaches, the Minimum Volume Ellipsoid (MVE) has gained increasing attention for niche characterisation, particularly in studies focused on representing fundamental niches in environmental space. The MVE summarises niche structure by describing both the niche centroid and the dispersion of environmental conditions occupied by a species. The niche centrality hypothesis proposes that environmental conditions near the niche centroid are associated with higher fitness, whereas fitness decreases as conditions depart from this centre. Consistent with this expectation, distance from the MVE ellipsoid centre has been shown to be negatively related to fitness-related attributes such as population abundance and genetic variation (Osorio-Olvera et al., 2020b; Ángeles-González et al., 2021) (Fig. 1).

Thus, by examining thermal niches; a key factor in species' survival and spread, predictive models provide valuable insights into the global risks posed by invasive species for current and future scenarios. A worldwide perspective allows us to identify potential distribution patterns and redistributions and pinpoint areas of vulnerability. Here, we adopt a species-specific modelling approach that focuses on temperature as a common physiological constraint, given its fundamental role in setting limits to survival, performance, and persistence in marine ectotherms, and its function as a first-order ecological filter for potential establishment during biological invasions. In this study we modelled the realised thermal niches of 80 invasive species, generating over 3000 thermal suitability maps under current and future scenarios. This provides, to our knowledge, the first global marine-scale analysis of invasion risk explicitly based on species-level thermal niche modelling.

2. Materials and methods

2.1. Species selection

Species selection for modelling was based on online global databases and resources focused on marine invasive species. These included the Smithsonian Environmental Research Center's National Estuarine and Marine Exotic Species Information System (NEMESIS, Fofonoff et al., 2018), the Global Invasive Species Database (GISD, 2024), the World Register of Introduced Marine Species (Costello et al., 2024), and EncicloVida (CONABIO, 2024). The species set includes well-documented invasive species, as well as non-native and cryptogenic taxa with demonstrated establishment, spread, or recognised invasion risk under current or future environmental conditions. A total of 80 species were considered for modelling (Supplementary material 1 and 2). Information on species impacts and invasion pathways is provided in Supplementary material 2 (Table S1).

2.2. Environmental data

Environmental data were obtained from Bio-ORACLE v3.0, focusing on characterising the thermal niche of marine species. We extracted sea surface temperature layers (SSTmax, SSTmin, SSTmean) and sea bottom

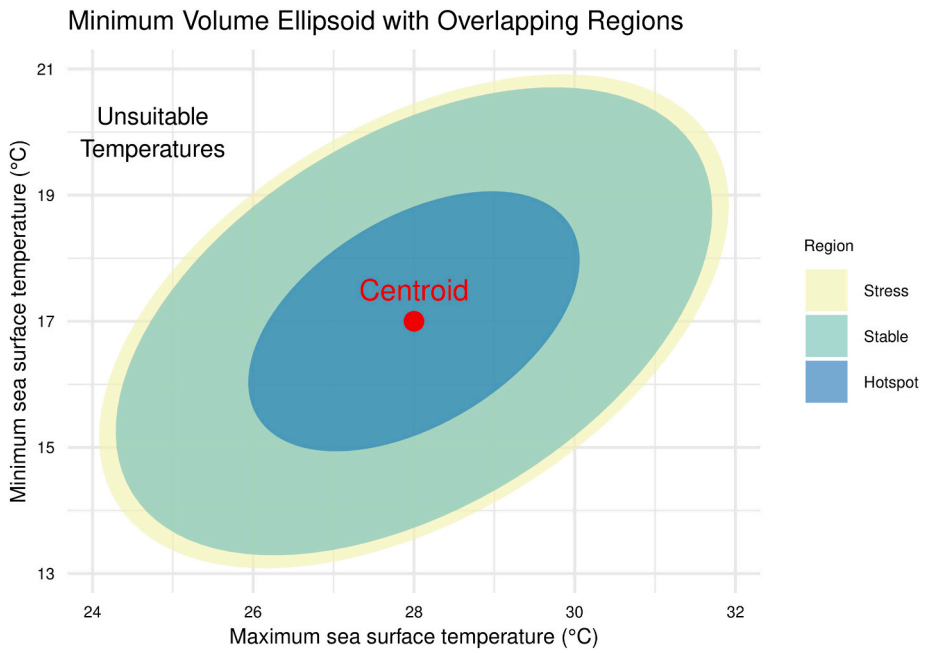

Fig. 1. Hypothetical thermal niche represented by a minimum volume ellipsoid (MVE) based on sea surface temperature extremes. The ellipsoid centre indicates optimal fitness conditions; thermal suitability decreases with distance from the centre, with areas outside the ellipsoid representing environments unsuitable for sustaining viable populations.

temperature layers (SBTmax, SBTmin, SBTmean) for the period 2010–2020, where SSTmax and SBTmax and SSTmin and SBTmin correspond to the maximum and minimum of the monthly mean temperatures, and SSTmean and SBTmean correspond to the multi-annual mean. For benthic variables, only minimum-depth layers were used; thus, bottom temperatures are estimated at the shallowest bathymetric portion of each grid cell (Assis et al., 2024).

Present-day temperature conditions in Bio-ORACLE are derived from monthly data produced by two pre-processed reanalysis products from the Copernicus Marine Environment Monitoring Service: the Global Ocean Physics Reanalysis and Forecast, and the Global Ocean Biogeochemistry Analysis and Forecast.

For future climate scenarios, we utilised environmental layers from Bio-ORACLE v3.0, which provides decadal-averaged marine data spanning 2000 to 2100. These datasets are based on outputs from multiple Earth System Models (ESMs) participating in the Coupled Model Intercomparison Project Phase 6 (CMIP6), encompassing Shared Socioeconomic Pathways (SSPs) such as SSP1-1.9, SSP1-2.6, SSP2-4.5, SSP3-7.0, and SSP5-8.5, where the suffix denotes the approximate radiative forcing, which quantifies the net energy imbalance imposed on the Earth's climate system, projected for the year 2100 (in W/m^2) (Meinshausen et al., 2020).

The environmental variables include physical, chemical, and biological parameters relevant to marine ecosystems. Minimum Bathymetry data were obtained from the General Bathymetric Chart of the Oceans (GEBCO), incorporated in Bio-ORACLE v3.0, offering cell-specific depth estimates. All layers are provided at a spatial resolution of approximately 5.5 km at the equator.

2.3. Occurrence records

Species occurrence data were obtained from multiple repositories, including OBIS, GBIF, and VertNet, using the R programming language (R Core Team, 2023). Data extraction was performed with the R packages *robis* (Provoost and Bosch, 2022), *rgbif* (Chamberlain et al., 2023), and *rvertnet* (Chamberlain, 2021), using the functions "occurrence", "occ_data", and "vertsearch", respectively.

The duplicate records were removed. Later, the occurrences falling in NA raster cells were relocated to the nearest valid cell within two pixels using the "points2nearestcell" function from *rSDM* (Rodriguez-Sanchez, 2024), addressing spatial mismatches caused by resolution differences near coastlines or land-sea boundaries. Occurrences still located on land after adjustment were excluded.

Subsequently, occurrences showing environmental values, particularly temperature, that were highly inconsistent with species tolerances were excluded. This was performed only when supporting evidence for viability under such extreme conditions was not found in reference sources (CONABIO, 2024; Fofonoff et al., 2018; GISD, 2024; Costello et al., 2024). This filtering step aimed to remove potential sink populations or erroneous records that could bias the modelling process (Sillero et al., 2021).

Lastly, to reduce spatial sampling bias commonly associated with online occurrence records, we applied a spatial thinning procedure using a 100 km threshold with the "thin" function from the R package *spThin* (Aiello-Lammens et al., 2015), running 1000 iterations per species. This step helped ensure a more even spatial representation of occurrences for subsequent modelling. Databases with 30 or more spatially filtered occurrences were retained for data exploration, model calibration, and projection.

Although dispersal abilities vary widely among taxa, the 100 km threshold was selected to balance bias reduction and to retain an acceptable sample size of occurrences. For ENMs based on Mahalanobis distance such as MVE, model robustness is driven by sample size and the treatment of error and bias (Etherington, 2021). A uniform thinning of 100 km ensured sample sizes where MVE performs well (>30 occurrences) and provides a consistent and reproducible approach that limits the loss of information arising from species-specific thinning schemes and avoids the time required to implement species-by-species filtering.

2.4. Calibration region

Environmental layers were cropped using the marine ecoregions proposed by Spalding et al. (2007), which are defined by biogeographic factors such as isolation, upwelling, freshwater influx, temperature regimes, and coastal complexity. For model calibration and thus cropping, we formulated an accessibility hypothesis based on historical dispersal

capacity, identifying areas where species may or may not have established viable populations (Barve et al., 2011).

For invasive species that recently arrived in novel areas, defining accessibility is particularly challenging. Hence, we considered regions as native, non-native, or cryptogenic using the framework of Fofonoff et al. (2018). For native regions, surrounding unsuitable ecoregions were included, whereas for non-native and cryptogenic regions, only ecoregions with recorded occurrences were retained for modelling.

2.5. Model calibration, and projection

2.5.1. Species classification

Species were classified into thermal affinity categories using minimum sea surface temperature (SSTmin), acknowledging that thermal barriers often follow latitudinal gradients. Median SSTmin values from occurrence records were calculated per species; those with ≥18 °C were classified as tropical–subtropical, and those with <18 °C as temperate (Kleypas et al., 1999). This threshold is consistent with ocean-front and matches biogeographic frameworks distinguishing tropical–subtropical from temperate regions (Spalding et al., 2007; Briggs and Bowen, 2012). We note however, that some species classified as temperate are eurythermal and also occur in tropical waters; thus, 18 °C is best regarded as an operational rather than absolute boundary. The thermal niche breadth was also calculated as the difference between SSTmax and SSTmin for each record, with median SST ranges computed per species and thermal category. Later a Mann–Whitney *U* test was used to compare the thermal niche breadth between species from tropical–subtropical and temperate zones.

2.5.2. Model calibration

Model calibration was performed using the ellipsoid_selection function in environmental space to fit MVEs encompassing 99% of the occurrence records, a threshold shown to maximise robustness of MVE-based models under moderate sample sizes and data error, while avoiding degradation under bias (Etherington, 2021). This procedure was implemented using the R package ntbox (Osorio-Olvera et al., 2020a) and repeated 20 times using a subsampling approach. In each iteration, 75% of the occurrence data was used for model training and 25% for testing. Each species was modelled independently using species-specific occurrence data. The use of a common modelling framework reflects a consistent focus on temperature as a physiological filter, rather than shared ecological requirements.

For each species, models were calibrated using all possible combinations of two or three environmental variables, including both surface and bottom temperatures. This resulted in 35 unique variable combinations (derived from six temperature layers), which were each evaluated across 20 subsampling iterations, yielding 700 models per species and 56,000 models in total across all species. The candidate environmental variables used to generate these combinations were SSTmax, SSTmin, SSTmean, SBTmax, SBTmin, and SBTmean. To assess overall model performance, the median value across the 20 iterations was calculated for each variable combination.

Models were first filtered based on performance thresholds. We excluded models that: (i) had pairwise collinearity ≥0.85 (ii) not statistically significant based on partial Receiver Operating Characteristic (pROC; $p > 0.05$); (iii) had omission rates of >0.10 (suggesting overfitting); (iii) had an Area Under the Curve (AUC) value of <0.7; or (iv) exhibited prevalence >0.5 (indicating overprediction). Among the remaining models, we prioritised those incorporating both maximum and minimum temperature variables, whether from surface or bottom layers over mean temperatures as thermal extremes more directly constrain species' physiological limits (Sunday et al., 2012; Pinsky et al., 2019).

Model selection followed a hierarchical approach based on omission rates: models with omission rates <0.05 were preferred; if unavailable, those with omission rates ≤0.075 or ≤0.10 were considered sequentially. From this subset, models with the highest AUC were selected.

2.5.3. Model projections

The selected models were projected globally using the "ellipsoidfit" function from the ntbox package (Osorio-Olvera et al., 2020a), generating thermal suitability maps with values from 1 (niche centroid) to 0 (outside the ellipsoid) for present and future climate scenarios, resulting in a total of 3920 thermal suitability maps, which are available at https://doi.org/10.6084/m9.figshare.30968881.

For the present-day scenario, individual species' thermal suitability maps were aggregated by calculating each map's median thermal suitability, allowing for the identification of regions with higher aggregations of environmental niche centroids and showing areas more susceptible to invasions under the niche centrality hypothesis. In addition, species thermal suitability maps were also categorised into tropical, subtropical, and temperate zones based on the established thermal classifications, and for each climate category across all scenarios and periods, median thermal suitability maps were generated. Changes in thermal suitability were assessed by computing differences between each future scenario and the present-day scenario within each thermal category.

Subsequently, we focused on regions shallower than 200 m, with difference maps masked using minimum bathymetry data to isolate shallow marine areas. Processed data were exported as CSV files, and latitudinal trends in thermal suitability gains and losses were visualised through line plots across different scenarios and periods (Fig. 2).

3. Results

3.1. Thermal niche patterns

Most species were found to be associated with temperate zones (n = 59), rather than the tropical-subtropical ones (n = 21) (Supplementary material 1). The results revealed substantial differences in thermal niche breadth among species dwelling in tropical, subtropical, and temperate waters. Temperate-dwelling species exhibited the widest thermal niches, with higher medians and greater variability. A Mann–Whitney *U* test was used to compare the thermal niche breadth between species from tropical–subtropical and temperate zones. The Mann–Whitney *U* test revealed a highly significant difference in thermal niche breadth between temperate and tropical–subtropical species ($U = 20$, n = 59 temperate vs. 21 tropical–subtropical, $p < 0.001$), indicating marked differences in their thermal niche breadth distributions (Fig. 3).

3.2. Calibration results and thermal suitability maps

The selected models exhibited a median omission rate of 0.01, with values ranging from 0.00 to 0.07 (interquartile range: 0.01 to 0.03). The median AUC was 0.94, with values ranging from 0.87 to 0.98 (interquartile range: 0.92 to 0.95), indicating overall high model performance (Supplementary material 3).

In the Caribbean Sea and the Gulf of Mexico, thermal suitability values were generally low to moderate (~0.1 to 0.3), with no extensive areas of high thermal suitability detected across the Caribbean islands or surrounding coasts. In the tropical Indo-Pacific, thermal suitability was predominantly low, with widespread areas exhibiting values below 0.2. At slightly higher latitudes, areas influenced by seasonal upwelling and major eastern boundary upwelling systems (EBUS), such as the Yucatán Peninsula, northwestern Africa, the Arabian Peninsula (Yemen and Oman), and western India displayed higher thermal suitability values (>0.2).

In the Northwest Atlantic, coastlines along the eastern United States (30 to 45°N) exhibited low to moderate thermal suitability (~0.1 to 0.25), particularly along the southeastern coast, while Canadian Atlantic coasts showed very low thermal suitability (<0.1). In the Northeast

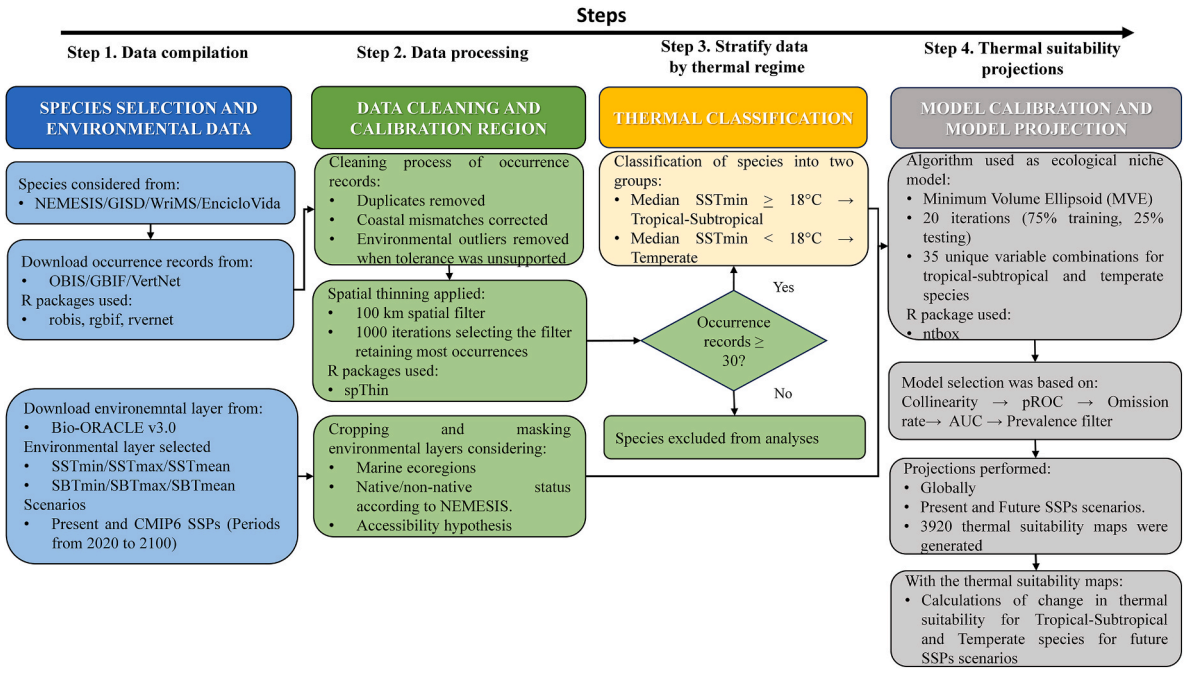

Fig. 2. Workflow illustrating data compilation, processing of occurrence records, stratification of species by thermal regime, and projection of thermal suitability under present and future climate scenarios, including downstream analyses.

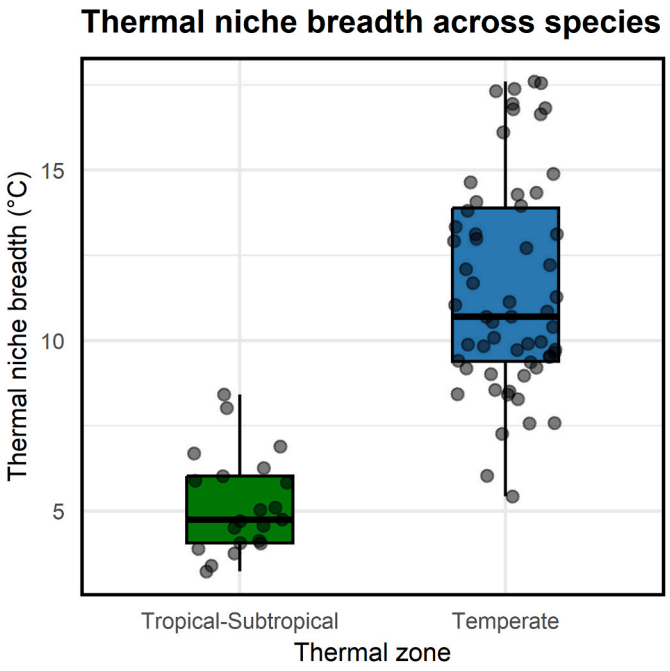

Fig. 3. Boxplots of thermal niche breadth (°C) across species classified as tropical-subtropical (green), and temperate (blue). Each point represents a species-level median SST range. Temperate species showed the widest thermal niches, followed by subtropical and tropical groups.

Atlantic, the British Isles, northern France, and the North Sea displayed moderate to high thermal suitability (0.2 to 0.4), while the Iberian Peninsula (Spain and Portugal) showed moderate values (~0.2 to 0.3). The Mediterranean Sea exhibited some of the highest thermal suitability values globally, with widespread areas reaching 0.35 to 0.42, particularly around Spain, France, Italy, Greece, and Turkey.

In the Northwest Pacific, coastal Japan, South Korea, and the East China Sea displayed high thermal suitability (0.35 to 0.4), whereas thermal suitability declined sharply further north along eastern Russia and Hokkaido (<0.1). Along the Northeast Pacific, the U.S. West Coast (California) and the Baja California Peninsula (Mexico) exhibited moderate thermal suitability (~0.25 to 0.3), with lower values (~0.1 to 0.2) toward northern California, Oregon, and Washington. Canadian Pacific coasts (British Columbia) displayed very low thermal suitability (<0.1).

In the Southwest Atlantic, southern Brazil and Uruguay showed moderate thermal suitability (~0.25 to 0.3), while Argentina's coast (Buenos Aires and Patagonia) exhibited lower values (~0.1 to 0.2), with lower values at higher latitudes. In the Southeast Atlantic, coastal Namibia and South Africa (Benguela Current region) showed low to moderate thermal suitability (~0.1 to 0.25), with slightly elevated values near coastal upwelling zones.

In the Southwest Pacific, eastern Australia (New South Wales and southern Queensland) exhibited moderate thermal suitability (~0.25 to 0.3), whereas southern Australia (Victoria, South Australia, Tasmania) showed lower values (~0.1 to 0.2). Along New Zealand's coast, particularly around the North Island, thermal suitability ranged from very low to low (<0.1 to 0.2). Finally, in the Southeast Pacific, northern and central Chile displayed low to moderate thermal suitability (~0.15 to 0.25), while southern Chile exhibited lower values (~0.1 to 0.15), with lower values at higher latitudes (Fig. 4).

3.3. *Latitudinal patterns of thermal suitability change across scenarios and years*

Projected changes in thermal suitability revealed distinct latitudinal patterns across tropical-subtropical and temperate-tolerant species under different emission scenarios and future years. In tropical-subtropical species, thermal suitability changes were relatively constrained across latitudes, with predominant decreases ranging from −0.2 to −0.5 across most areas, especially between 0° and 30°N. In contrast, moderate thermal suitability increases (up to +0.2) were detected mainly around southern tropical latitudes (~30°S) under higher emission scenarios (SSP4-6.0 and SSP5-8.5) and northern tropical latitudes (~30 °N), although the increases were lower (+0.1).

Temperate-tolerant species displayed smaller magnitudes of thermal suitability change overall, typically within the range of −0.1 to +0.1.

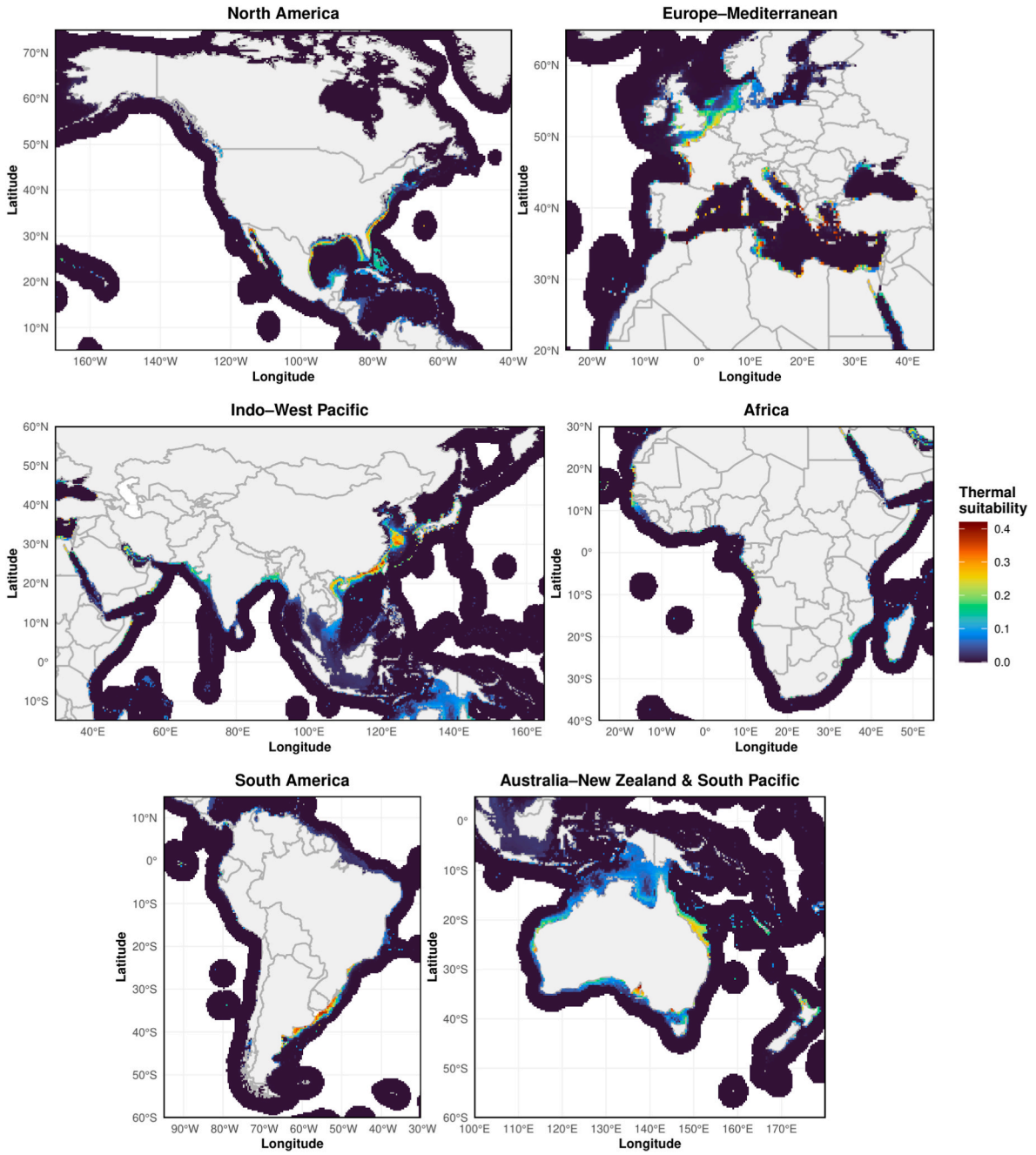

Fig. 4. Projected median thermal suitability for species under present-day conditions (2010–2020). Thermal suitability values range from 0 (low) to 0.42 (high), with warmer colours indicating higher thermal suitability. Elevated thermal suitability is observed in the Mediterranean Sea, the northwest Pacific, and parts of the eastern Pacific and western Atlantic.

Thermal suitability increases (~+0.05 to +0.1) were concentrated at higher temperate latitudes (45 to 60° N and S), whereas thermal suitability decreases (−0.05 to −0.1) occurred closer to 30 to 45 °N and S. Although the magnitude of change was lower compared to tropical and subtropical species, poleward shifts of thermally suitable areas were still apparent, particularly under SSP5-8.5 by 2090.

Overall, the magnitude and direction of thermal suitability change strongly depended on climatic affinity, with tropical species experiencing larger net decreases in thermal suitability, subtropical species exhibiting intermediate changes, and temperate species maintaining relatively stable thermal suitability values, with projected poleward shifts in the distribution of thermally suitable areas. In addition, minimal changes in thermal suitability were observed for all species under the lower warming scenarios (SSP1-1.9 and SSP1-2.6) (Fig. 5).

3.4. Spatial patterns of thermal suitability change

Thermal suitability patterns were generated for all climate change scenarios; however, we focus on the worst-case scenario (SSP5-8.5), citing other scenarios only when distinctive patterns are observed. Projected changes in thermal suitability under the SSP5-8.5 scenario revealed distinct patterns across tropical, subtropical, and temperate species. For tropical species, widespread decreases in thermal suitability dominated, with declines reaching up to −0.5 along the coasts of West Africa, Southeast Asia, northern Australia, Brazil, and the Caribbean. Positive changes were rare and localised, suggesting a broad reduction

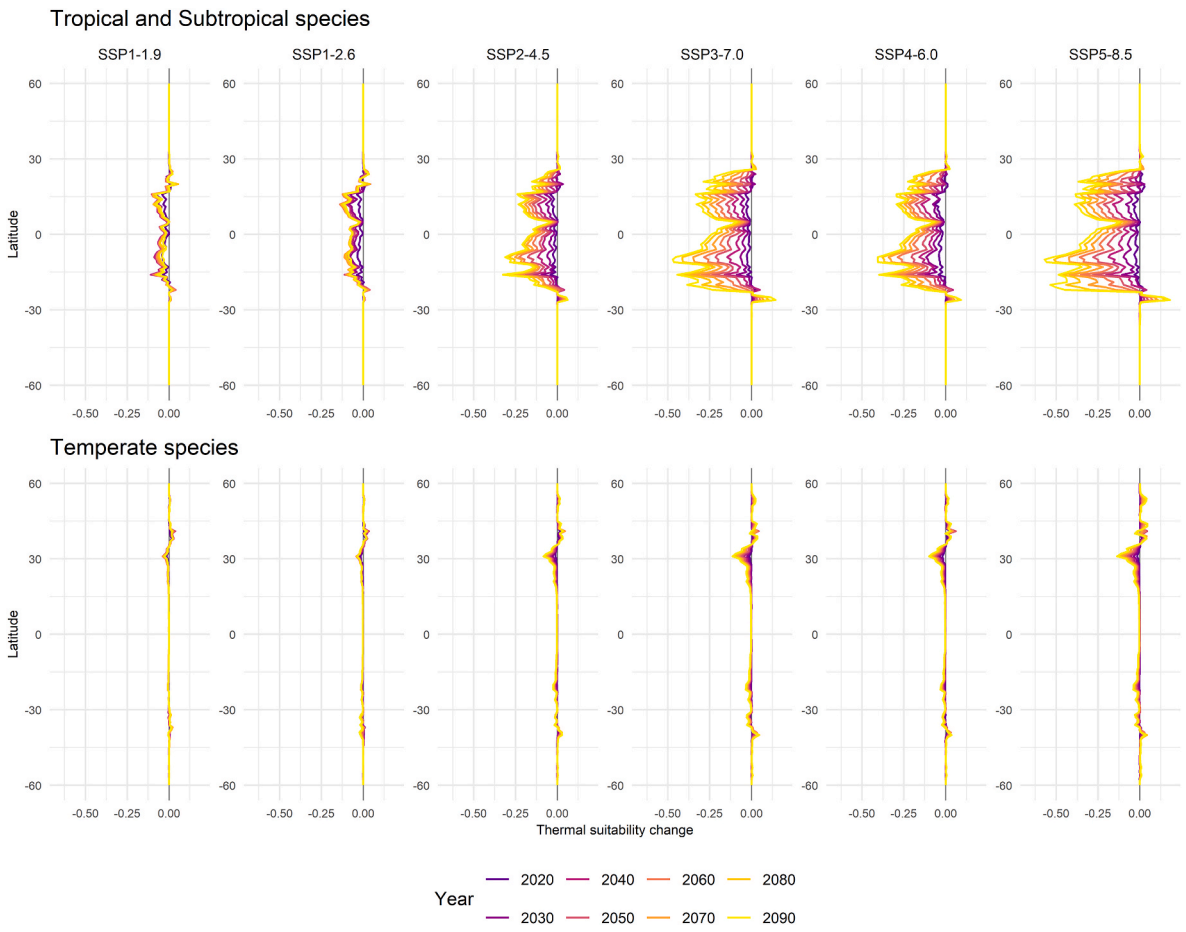

Fig. 5. Projected changes in thermal suitability for tropical-subtropical, and temperate species across six emission scenarios (SSP1-1.9 to SSP5-8.5) and future decades (2020–2090). Negative values (left) indicate decreases in thermal suitability, whereas positive values (right) indicate increases in thermal suitability. Lines represent decadal changes coloured from purple (2020) to yellow (2090), plotted by latitude.

in thermally suitable conditions for tropical species under extreme warming scenarios.

Interestingly, under intermediate warming scenarios (e.g., SSP2-4.5) and during the early stages of warming, some tropical and subtropical upwelling regions, such as Baja California and the Yucatán Peninsula, Mexico maintained relatively higher thermal suitability compared to surrounding areas. Although the thermal barrier associated with eastern boundary upwelling systems (EBUS) diminishes under warming, it continues to constrain the latitudinal extent of thermally suitable conditions for some subtropical and tropical species (Fig. 6).

Temperate species exhibited a more favourable pattern, with widespread increases in thermal suitability across higher latitudes. Increases (0.1 to 0.5) were observed along northeastern North America, northern Europe, northern Japan, southern Chile, and southern Australia. Decreases in thermal suitability (−0.1 to −0.3) were mainly confined to lower-latitude margins of current temperate distributions, indicating poleward shifts in the distribution of thermally suitable areas under future warming conditions (Fig. 7).

4. Discussion

4.1. Results interpretation

Temperature is a fundamental factor shaping species distributions and influencing invasion dynamics, particularly in the current climate crisis. Broad thermal tolerance has been recognised as a key predictor of invasion potential in marine ecosystems, with eurythermic species typically displaying greater establishment potential (Zerebecki and Sorte, 2011; Lenz et al., 2011; Bates et al., 2013; Liu et al., 2025). Such traits are commonly associated with organisms from temperate regions, where greater environmental variability may select for broader thermal ranges (Angilletta, 2009).

Consistent with these patterns, our results show that many of the analysed invasive species were classified as temperate-affinity, where thermal variability may favour broader tolerance ranges (Sunday et al., 2011). It should be noted, however, that the predominance of eurythermal species in our dataset may partly reflect the composition of species historically reported as invasive, rather than a deliberate selection bias. Although temperate-affinity species appear disproportionately represented among global invaders, this does not imply that all temperate taxa share equal invasion potential, and tropical species can also be highly successful invaders, as shown by cases such as the lionfish, *Pterois volitans* and *P. miles* (Loya-Cancino et al., 2023).

However, alternative, non-thermal explanations may also contribute to the lower number of reported invasions in tropical regions. Lower shipping intensity (Seebens et al., 2013) and reduced research effort (Drake and Lodge, 2004) in tropical ecosystems may partly explain the fewer reported invasions. High native biodiversity (Freestone et al., 2013) and relatively low human disturbance have also been proposed as potential bioinvasion barriers (Fine, 2002) although such elements were outside the scope of this work.

This pattern may help explain the greater potential invasion risk observed in temperate regions. At the same time, global patterns should be interpreted with caution, as reporting biases may underrepresent tropical invasions (Hughes et al., 2021). Nevertheless, broad thermal tolerance likely facilitates transport via fouling and ballast water,

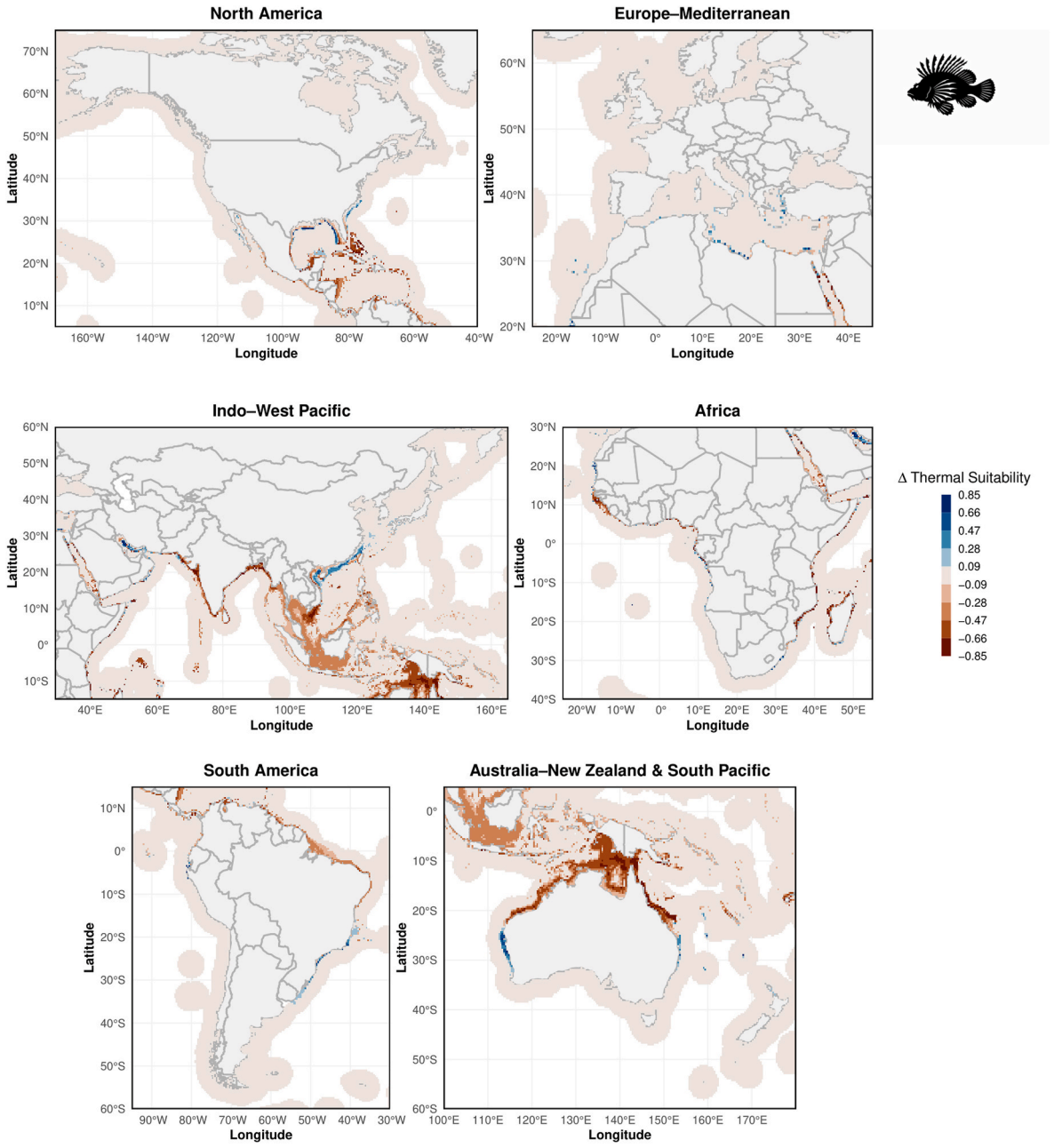

Fig. 6. Projected changes in coastal thermal suitability (Δ thermal suitability) for tropical–subtropical species under the high-emissions scenario SSP5-8.5 (2090–2100). Results are shown for six major oceanic regions: North America, South America, Europe–Mediterranean, Africa, Indo–West Pacific, and Australia–New Zealand & South Pacific. Additional scenarios and full-resolution maps are available in Figshare (https://doi.org/10.6084/m9.figshare.30968881).

increasing the likelihood of introduction into new areas with similar thermal conditions, and potentially favouring subsequent establishment and spread (Bates et al., 2013).

Indeed, human activities, particularly global shipping and aquaculture, play a significant role in facilitating marine bioinvasions. High shipping traffic and aquaculture operations in Southeast Asia and Western Europe contribute to elevated invasive species richness. Historical species introductions and increasing shipping traffic, aided by the Allee effect (a minimum population threshold for a species' successful establishment), coincide with high thermal suitability in northeastern North America and southwestern Australia (Ricciardi, 2013; Osorio-Olvera et al., 2019). In contrast, lower invasion potential due to extreme environmental conditions might occur in the Arctic and Southern Oceans, although climate change and ocean warming may alter these dynamics.

4.2. *Thermal suitability change interpretation*

The ENMs developed here project that tropical invasive species will experience widespread losses in climatic thermal suitability across their low latitude ranges under future warming scenarios. Rising temperatures at low latitudes may push these species beyond their physiological thermal limits. Our findings are consistent with previous modelling efforts for land organisms. Bellard et al. (2013) predicted declines in invasive species richness in equatorial regions for terrestrial taxa. This pattern is unsurprising, as tropical organisms, particularly marine species, often possess limited thermal safety margins, living near their upper thermal optima (Pinsky et al., 2019). Evidence suggests species adaptation to warmer conditions is less common than adaptation to colder environments, although exceptions exist in fast-reproducing taxa (Qu and Wiens, 2020). Consequently, some tropical species, which are

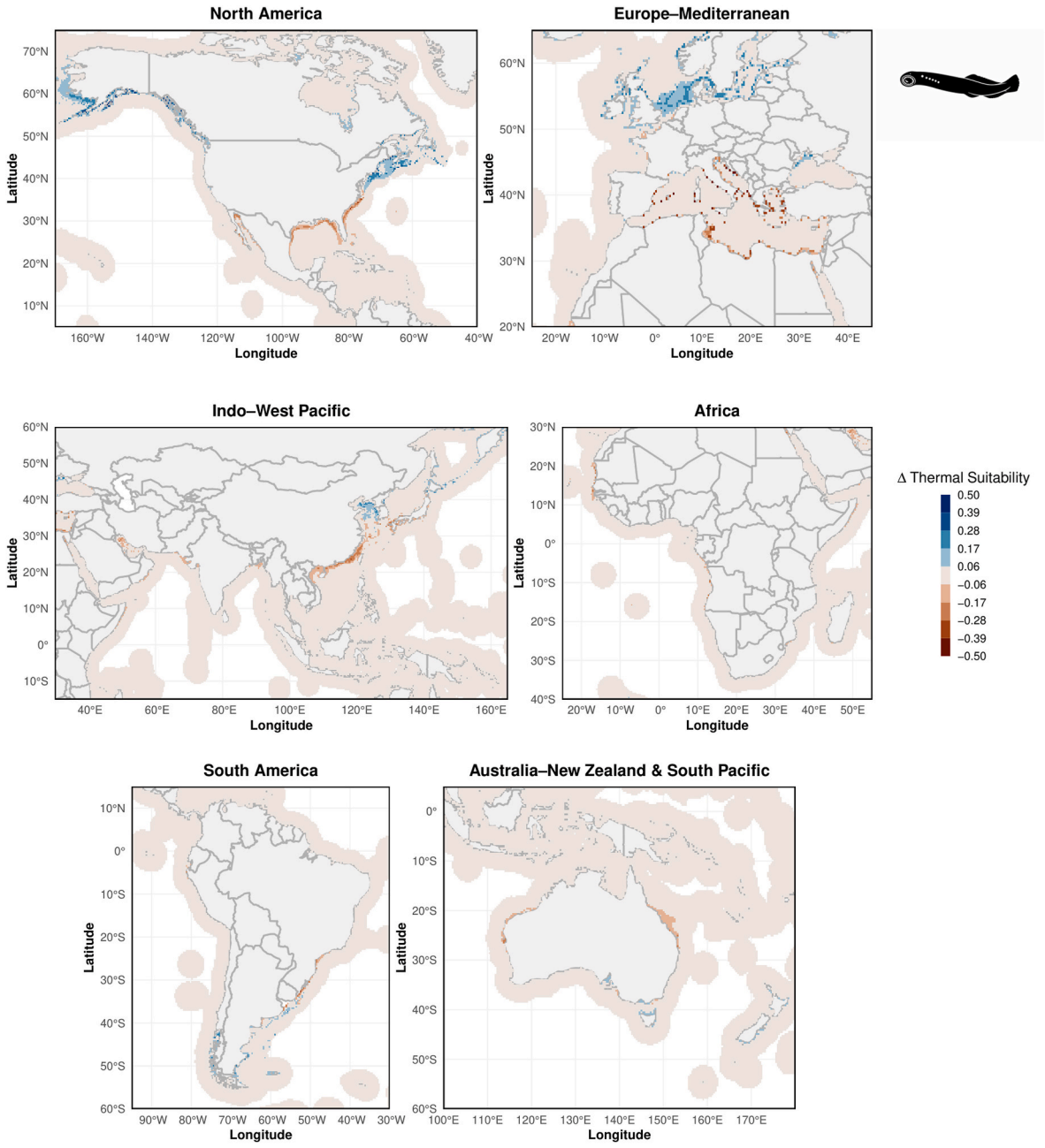

Fig. 7. Projected changes in coastal thermal suitability (Δ thermal suitability) for temperate species under the high-emissions scenario SSP5-8.5 (2090–2100). Results are shown by major oceanic regions: North America, South America, Europe–Mediterranean, Africa, Indo–West Pacific, and Australia–New Zealand & South Pacific. Additional scenarios and full-resolution maps are available in Figshare (https://doi.org/10.6084/m9.figshare.30968881).

adapted to a more thermally stable environment, have a more limited capacity to find thermally suitable regions, thus facing greater challenges in tolerating future warming (Downie et al., 2025).

Although warming is expected to weaken oceanographic barriers and promote tropicalisation (25° to 30° N and S) in heavily invaded regions, such as California (Sorte et al., 2010) or the Mediterranean Sea (Zarzyczny et al., 2024), some tropical and subtropical species may still struggle to persist under thermal conditions characteristic of higher latitudes. This pattern suggests the presence of a strong physiological filter, where winters exceeding the tolerance limits of non-native species result in high overwinter mortality and hinder successful establishment. Similar processes have been described in tropical systems, where winter conditions act as environmental barriers limiting thermal suitability at higher latitudes despite ongoing global warming (Angeles-Gonzalez et al., 2024; Downie et al., 2025) Nevertheless, our results suggest that tropical upwelling regions could provide localised thermal refugia under mild warming, potentially acting as aggregation zones and mitigating some impacts (Lourenço et al., 2016; Angeles-Gonzalez et al., 2024). From a management perspective, these regions may warrant increased attention, as their potential role as thermal refugia could also concentrate suitable conditions for both native and non-native species, highlighting the importance of targeted monitoring and early-detection strategies rather than assuming inherent resistance to biological invasions. Projected declines in thermal suitability for several high-risk invaders may also offer management opportunities, as declining thermal suitability in invaded areas could reduce competitiveness, although human transport may counterbalance these effects (Bellard et al., 2013).

Temperate species, in turn, exhibited only modest thermal suitability losses at lower latitudes, accompanied by small gains at higher latitudes (50° to 60° N and S) under future climate scenarios. This limited

response likely reflects the reduced benefits of warming for species already adapted to broad seasonal temperature variability and new constraints encountered near the poles, such as reduced area or photoperiod mismatches. As noted above, many temperate species are eurythermal (Zerebecki and Sorte, 2011; Lenz et al., 2011; Bates et al., 2013), which may confer greater resilience to warming and help explain the thermal suitability change patterns observed. However, it is important to consider that climate change could enhance potential invasion risks at higher latitudes by removing geographical barriers such as icecaps, allowing ships to transport new propagules into previously inaccessible regions (Mahanes and Sorte, 2019). As warming progresses, monitoring these emerging pathways will be crucial.

Our findings imply that climate change will not uniformly favour marine invasions but will instead generate distinct biogeographical patterns driven by species' thermal affinities and physiological limits. The data and correlative ENMs generated in the present study help to identify marine regions where thermal conditions are projected to become suitable for invasive species and to determine their thermal distribution, particularly concerning potential environmental barriers that may hinder their expansion (Zhu et al., 2024; Liu et al., 2025).

Additionally, this study demonstrates that ENMs are valuable tools for characterising changes in thermal suitability, guiding management strategies and identifying marine regions where thermal conditions are projected to remain or become favourable for invasive species, particularly when considered alongside known introduction pathways. Our results show that temperate regions with intense maritime traffic and long invasion histories (northeastern North America, Western Europe, and parts of southeastern Australia) represent areas where thermally suitable conditions coincide with high propagule pressure, suggesting elevated invasion potential.

However, these patterns need to be interpreted with caution, as they could reflect biases and uneven sampling efforts. Thus, ENMs should be used to support risk screening and prioritisation for monitoring and early detection, rather than to define absolute invasion risk. Indeed, identifying main transport routes with a potentially high non-native species introduction risk (Zhu et al., 2024), together with early detection and rapid response, remains essential to prevent and control marine bioinvasions (Reaser et al., 2020).

In this management context, early detection and rapid response are widely recognised as critical components of effective bioinvasion management (Reaser et al., 2020). In this context, the Convention on Biological Diversity (CBD), a global treaty adopted at the 1992 Earth Summit, recognises invasive alien species as a major threat to biodiversity. Under their Article 8(h), the CBD calls on Parties to prevent the introduction of, control, or eradicate invasive alien species (United Nations, 1992).

4.3. Data and models limitations

Results should be interpreted with caution. ENMs typically estimate the realised niche, a subset of the fundamental niche restricted by ecological interactions and biogeographic barriers. For invasive species, such biotic interactions may include ecological mechanisms such as competition with native species or predation pressure (Papacostas et al., 2017), as well as chemical interactions, including the release of allelopathic chemicals which can limit establishment success even under climatically suitable conditions. Thus, distributions may not fully reflect a species' full environmental tolerance. Biotic interactions are essential because they can hinder the success of invasive species.

In marine systems, such invasion restrictions are driven by ecological interactions, including competition with native species for space or resources and predation, which could stop the establishment of potential invasive species even under suitable environmental conditions (Papacostas et al., 2017). For instance, chemical interactions have been proposed as potential modifiers of invasion success; for example, chemical cues released by resident benthic organisms can negatively affect larval settlement and early performance of invasive sun corals (*Tubastraea* spp.), indicating chemically mediated biotic resistance in marine systems (Mizrahi et al., 2017). In addition, other environmental factors influence species distributions as well, such as pH, oxygen (Pörtner and Peck, 2010), and salinity (Paiva et al., 2018; D'Amen et al., 2023). Moreover, climate change may reveal currently unavailable portions of species' ecological niches (Chevalier et al., 2024), suggesting that some species may tolerate broader conditions than field observations indicate.

Another limitation of this study is the ecological heterogeneity of the invasive species considered. The analysed species encompass a wide range of life histories and functional strategies (e.g. sessile organisms, mobile predators), each of which is limited by distinct ecological requirements beyond temperature. Using a common modelling framework based only on temperature does not capture functional-group-specific limitations, such as substrate preference, trophic interactions, or dispersal capacity (Papacostas et al., 2017). Thus, the thermal suitability estimated in this work should be interpreted as a first physiological filter rather than as a measure of potential invasion success. For this reason, future studies integrating additional environmental variables, functional-group-specific approaches (Papacostas et al., 2017), or information on marine traffic (Seebens et al., 2013) would allow a more comprehensive assessment of invasion and climate change risk (e.g., Nyboer et al., 2019).

5. Conclusions

The findings from this study provide new insights into marine bioinvasions for researchers and conservation scientists. Unlike previous global syntheses, which typically relied on richness patterns or conceptual models, this study provides a species-level ENM approach with thousands of spatial projections. This offers a more detailed and quantitative foundation for anticipating marine invasion risks under climate change. These thermal niche models serve as baselines for comparative studies, supporting investigations into thermal tolerance patterns across taxa and regions helping identify potential hotspots where temperatures could allow an intensification of bioinvasion.

The projections presented here describe changes in thermally suitable conditions rather than habitat suitability or realised invasion outcomes. Despite this limitation, they are a robust first-order physiological constraint, relevant for anticipating invasion patterns under climate change. Expanding models to consider additional environmental variables and biotic interactions, alongside physiological data, could yield a more comprehensive understanding of species' responses to environmental stressors. Finally, better characterising human-mediated pathways remains crucial for anticipating future marine invasions and informing effective prevention and management strategies.

CRediT authorship contribution statement

Luis Enrique Angeles-Gonzalez: Writing – review & editing, Writing – original draft, Validation, Methodology, Formal analysis, Data curation, Conceptualization. **Tulio F. Villalobos-Guerrero:** Writing – review & editing, Writing – original draft, Data curation. **Manuel Alejandro Delgadillo-Nuño:** Writing – review & editing, Writing – original draft, Data curation. **Josymar Torrejón-Magallanes:** Writing – review & editing, Writing – original draft, Methodology. **Angel Escamilla-Aké:** Writing – review & editing, Writing – original draft, Data curation. **Fernando Díaz:** Writing – review & editing, Writing – original draft, Funding acquisition. **Carlos Rosas:** Writing – review & editing, Writing – original draft, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence

the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2026.107919.

Data availability

All scripts and data required to replicate the models are available on Figshare: https://doi.org/10.6084/m9.figshare.30968881.

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