



OPEN Predicting the range expansion of larger benthic foraminifera under earth's changing climate

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Larger benthic foraminifera (LBF) are major carbonate producers in shallow marine ecosystems and serve as sensitive indicators of environmental change on continental shelves. We developed and tested species distribution models for four peneroplid species (*Peneroplis planatus*, *P. pertusus*, *P. arietinus*, and *Coscinospira hemprichii*) using 355 occurrence records from the Arabian Gulf and 32 environmental variables to predict their range expansion under the current climate change and future scenarios. Beyond well-established temperature controls, our models identified iron concentration (68% of explained variance), light attenuation (21%), and dissolved oxygen (10%) as the primary environmental drivers of LBF distributions. The models achieved exceptional predictive accuracy with 92% Area Under the Receiver Operating Characteristic Curve (AUROC) for regional validation and 85% AUROC when extrapolated globally, demonstrating strong transferability across ocean basins. Climate change projections for 2100 predict significant westward range expansion, particularly into Atlantic Ocean regions previously unsuitable for these species. The projected expansion remains constrained within tropical and subtropical latitudes (50°N–50°S), indicating that temperature continues to impose fundamental limits to biogeographic dispersals. These findings reveal the importance of iron-supported symbiotic relationships in determining LBF distributions and suggest that climate-driven iron enrichment will increase LBF abundance and carbonate production in shallow marine systems worldwide, with significant implications for reef and shallow-water ecosystem structure, and global carbon cycling.

Climate change-induced ocean warming poses significant threats to marine ecosystems globally, with impacts extending from polar ice shelves to coastal waters^{1–3}. The increasing frequency and intensity of extreme events, such as marine heatwaves, further exacerbate the effects of rising ocean temperatures on marine biodiversity^{2,4}. These rapid alterations in ocean conditions underscore the urgent need to study and monitor environmental changes to understand their broader ecological impacts, particularly in regions experiencing accelerated warming.

Benthic foraminifera are single-celled eukaryotic organisms that inhabit diverse marine environments and play crucial roles in marine ecosystems^{5,6}. Their distribution and abundance are controlled by interactions between biotic and abiotic factors, creating diverse microhabitats that support specific foraminiferal assemblages^{7,8}. Among these, symbiont-bearing larger benthic foraminifera (LBF) are important contributors to carbonate production in shallow tropical and subtropical marine environments^{9,10}. These organisms face direct impacts from changes in their shallow-water habitats and can serve as valuable proxies for investigating climate change effects on marine biodiversity^{11–13}.

Understanding the ecological preferences and tolerances of LBF is crucial for their application as environmental indicators and for predicting their responses to future marine ecosystem changes^{11,12}. As major carbonate producers and ecosystem engineers, LBF represent ideal organisms for studying climate change impacts on shallow marine systems. Their symbiotic relationships with algal partners enable adaptation to environmental changes, while their calcification processes directly contribute to reef ecosystem structure and function.

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The relationship between climate change and LBF proliferation has been demonstrated during past warming events, most notably the Paleocene-Eocene Thermal Maximum (PETM). Scheibner and Speijer¹⁴ documented a three-stage carbonate platform evolution in the Tethyan realm during the early Paleogene, where coral-dominated platforms (Stage I) transitioned through a mixed coral-LBF stage (Stage II) to ultimately become LBF-dominated systems (Stage III) coinciding with the PETM. This transition occurred across 17 platform areas spanning the entire Tethys, demonstrating that climate-driven LBF expansion is a global phenomenon with precedent in Earth's history.

Traditionally, foraminiferal research has relied on sampling local areas to assess diversity and investigate differences among biofacies or communities^{15,16}. While this approach has provided valuable ecological insights, it is limited in spatial and temporal coverage, potentially leading to incomplete understanding of foraminiferal distributions and their roles in marine ecosystems across broader scales. These limitations are particularly problematic when attempting to predict responses to climate change, which operates at regional to global scales.

Species Distribution Models (SDMs) represent a powerful approach to overcome these limitations by enabling the exploration of entire ocean basins at high spatial and temporal resolutions^{17–19}. By integrating species occurrences with environmental data, SDMs can predict potential distributions across unsampled areas and project future distributions under climate change scenarios. Despite unique challenges posed by marine environments including dynamic oceanic processes, three-dimensional water column structure, and limited high-resolution environmental data^{20–22}, SDMs have gained increasing attention in marine research for understanding climate change effects on ecosystems^{23,24} and have been successfully applied to diverse organisms including plankton, benthic invertebrates, fish, and marine mammals^{25–28}.

In foraminiferal research, SDMs have proven valuable for investigating biogeography, ecology, and potential responses to environmental changes^{29–31}. These models provide frameworks for assessing potential impacts of environmental changes on foraminiferal communities, enabling development of predictive tools for ecosystem monitoring and environmental assessment, particularly in coral reef and shallow marine habitats^{32,33}.

We choose the Arabian/Persian Gulf as the ideal natural laboratory towards this research due to its well-defined environmental gradients, diverse marine habitats, and ongoing exposure to rapid environmental change^{34,35}. This shallow, semi-enclosed sea (average depth ca. 35 m, maximum depth > 100 m near the Strait of Hormuz) experiences extreme environmental conditions, making it particularly suitable for studying organism responses to environmental stress³⁶. The Gulf's unique characteristics represent a natural laboratory to predict how LBF may respond to future global ocean conditions.

We selected four peneroplid LBF species for this study: *Peneroplis planatus*, *Peneroplis pertusus*, *Peneroplis arietinus*, and *Coscinospira hemprichii*. These species were chosen because they: (1) are well-documented inhabitants of the Arabian Gulf with established ecological requirements, (2) represent important carbonate producers in shallow marine environments, (3) host symbiotic algae making them sensitive to environmental changes, and (4) are widely distributed in shallow-waters and have sufficient occurrence data for robust statistical modeling. These characteristics make them ideal indicators for studying climate change impacts on shallow marine ecosystems and for testing the broader applicability of our modeling approach to other LBF species globally.

Additionally, we used SDMs as a novel approach for habitat discovery and ecological niche inference for these LBF species. By modeling distributions using georeferenced occurrences and ecologically meaningful environmental variables (EMEVs), we generated habitat suitability maps providing insights into factors driving their distribution. We then projected these models under different Representative Concentration Pathways of the Intergovernmental Panel on Climate Change for 2050 and 2100 to assess potential responses to future environmental changes.

This study demonstrates the reliability and effectiveness of SDMs in understanding complex habitat features and future distributions of important marine organisms in the context of global climate change. Our approach aims to provide comprehensive understanding of foraminiferal ecology across broad spatial and temporal scales, ultimately facilitating application of these techniques to other areas of marine research.

Results

Model selection and performance

The forward stepwise selection procedure, applied to 32 initial environmental variables (Supplementary Table 1), identified three key EMEVs that significantly explain the distribution patterns of the studied LBF species: iron concentration (EMEV 20), diffuse attenuation coefficient (EMEV 2), and dissolved oxygen concentration (EMEV 17). The iterative selection process demonstrated the hierarchical importance of these variables in determining species habitat suitability.

In the first selection round, iron concentration alone emerged as the most critical environmental factor, accounting for 45.7% of the explained deviance ($D^2 = 0.457$, $\chi^2 = 92.123$, $df = 1$, $p = 8.15 \times 10^{-22}$). The addition of diffuse attenuation coefficient in the second round substantially improved model performance, increasing the explained deviance to 59.8% ($D^2 = 0.598$, $\chi^2 = 28.424$, $df = 1$, $p = 9.74 \times 10^{-8}$). The third round incorporated dissolved oxygen concentration, further enhancing the model's explanatory power to 66.5% ($D^2 = 0.665$, $\chi^2 = 13.598$, $df = 1$, $p = 2.26 \times 10^{-4}$). A fourth-round testing salinity addition yielded no significant improvement ($\chi^2 = 0.326$, $df = 1$, $p = 0.568$), confirming that the three-variable model captured the primary environmental drivers of LBF distribution (Table 1 and Supplementary Table 2).

The final model achieved a null deviance of 201.1, which was reduced to a residual deviance of 67.31 after incorporating the three key environmental variables. The model's Akaike Information Criterion (AIC) value of 75.31 indicates excellent goodness of fit, while maintaining appropriate model complexity. The modeling workflow (Supplementary Fig. 1) illustrates the two-phase approach used for model development and validation. Performance evaluation using the Area Under the Receiver Operating Characteristic Curve (AUROC)

Round	Variables	<i>n</i>	D ²	Chisq	df	<i>p</i>
1	EMEV 20	1	0.457	92.123	1	8.15E-22
2	EMEV 20 + EMEV 2	2	0.598	28.424	1	9.74E-08
3	EMEV 20 + EMEV 2 + EMEV 17	3	0.665	13.598	1	2.26E-04
4	EMEV 20 + EMEV 2 + EMEV 17 + EMEV 26	4	0.667	0.326	1	0.568

Table 1. Iterative model selection process showing the top-performing combinations of ecologically meaningful environmental variables (EMEVs) based on explained deviance (D^2), chi-squared statistic (Chisq), degrees of freedom (df), and *p*-values.

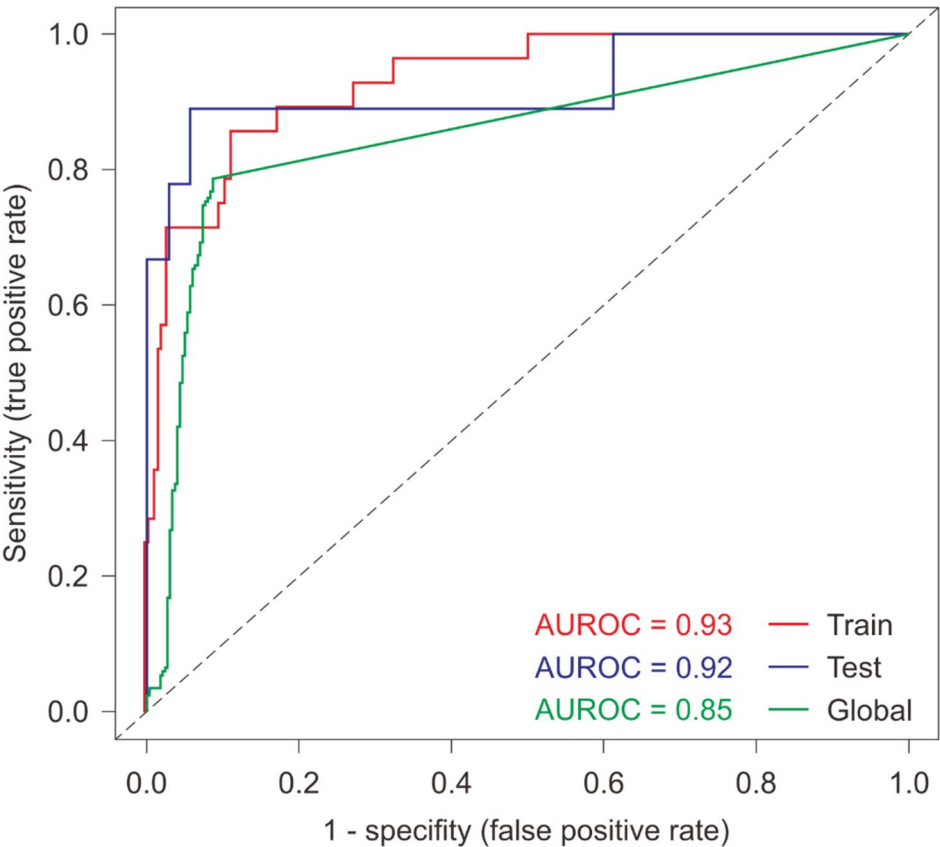


Fig. 1. Model performance evaluation using the area under the receiver operating characteristics (AUROC) for training, test, and global datasets.

demonstrated exceptional predictive accuracy: 93% for the training dataset (Arabian Gulf data used for model development), 92% for the independent test dataset (reserved Arabian Gulf data for validation), and 85% for the global validation dataset (worldwide occurrence records Fig. 1). The geographic distribution of training data showed good spatial coverage across the Arabian Gulf (Supplementary Fig. 2), with presence records concentrated along the western coastline where optimal environmental conditions occur.

Additional performance metrics confirmed the model's robustness across all evaluation datasets. Overall accuracy values were consistently high at 0.93, 0.92, and 0.90 for training, test, and global datasets, respectively (Table 2). Sensitivity (true positive rate) achieved perfect scores (1.0) for both training and test datasets, with 0.80 for the global dataset. Specificity (true negative rate) values were 0.86, 0.83, and 1.0 for the three datasets, respectively. The True Skill Statistic (TSS) values of 0.86, 0.83, and 0.80 for training, test, and global datasets demonstrate excellent discriminatory power while correcting for chance agreement.

Environmental variable contributions and spatial patterns

Analysis of the Fraction of Total Variation Accounted (FTVA) revealed the relative importance of each environmental variable in determining habitat suitability. Iron concentration dominated the model's predictive power, accounting for 68% of the habitat suitability index (HSI) variance among the three selected EMEVs. The HSI represents model predictions of environmental suitability on a scale from 0 (completely unsuitable) to 1 (optimal habitat). Diffuse attenuation coefficient contributed 21% of the explained variance, while dissolved

Metric	Train	Test	Global
Accuracy	0.93	0.92	0.90
Sensitivity	1.00	1.00	0.80
Specificity	0.86	0.83	1.00
TSS	0.86	0.83	0.80

Table 2. Model performance metrics (Accuracy, Sensitivity, Specificity, and True Skill Statistic: TSS) for the training, test, and global datasets, demonstrating the predictive power of the species distribution models.

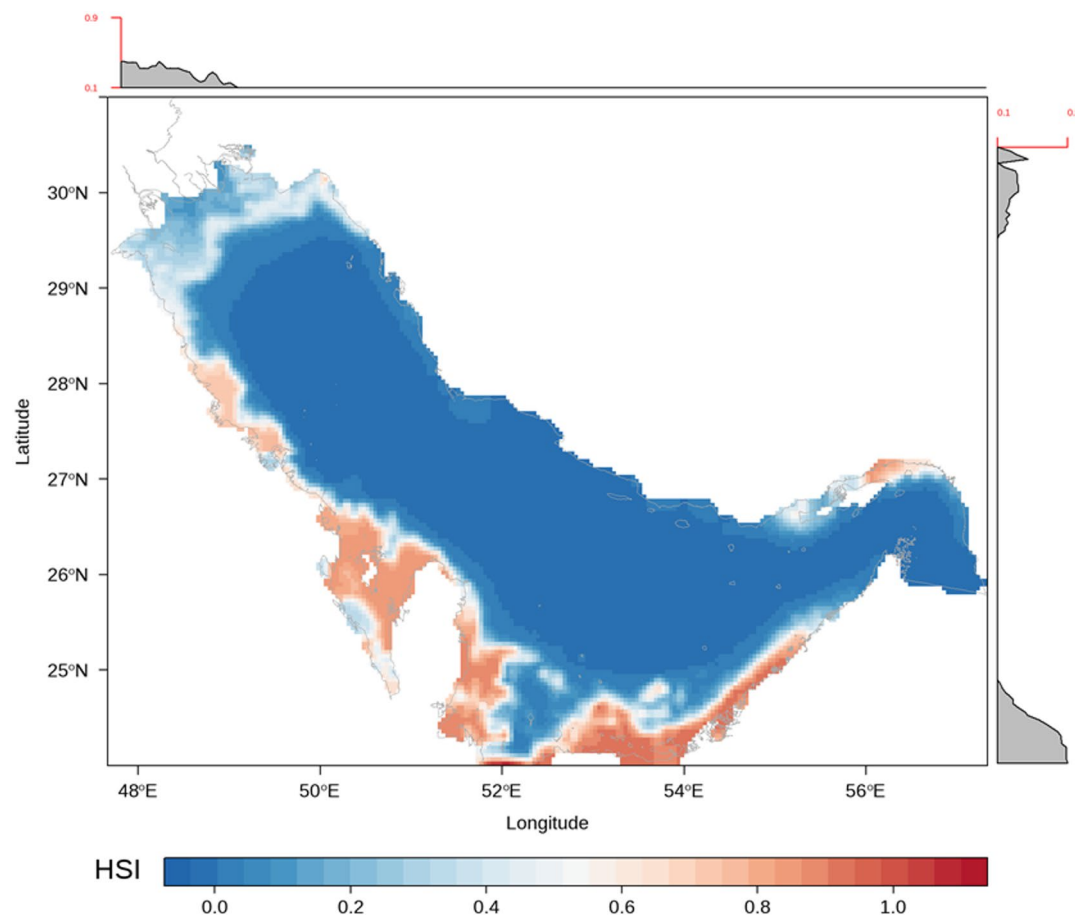


Fig. 2. Predicted habitat suitability for the four selected benthic foraminiferal species in the Arabian/Persian Gulf based on the final logistic regression model. Higher Habitat Suitability Index (HSI) values indicate more suitable environmental conditions for the species. Data processing and map generation were all done using R (version 4.4 : <https://cran.r-project.org/>).

oxygen concentration accounted for the remaining 10%. The spatial distribution of these environmental variables across the Arabian Gulf revealed distinct gradients that shape species distributions (Supplementary Fig. 3).

The model predictions provided distinct spatial patterns of habitat suitability within the Arabian Gulf region. Areas of optimal environmental conditions (HSI > 0.8) for the four LBF species were predominantly concentrated along the western coastline of the Arabian Gulf (Fig. 2, Supplementary Table 3). The most suitable continuous habitat extended from the Saudi Arabian Eastern Province city of Dammam southward to Salwa Bay, encompassing the entire coastline of Qatar and nearly the complete coastal stretch of the United Arab Emirates. Additional patches of suitable habitat were identified in the northern region near Jubail industrial city, just south of the Kuwait border.

Frequency of Occurrence Plot (FOP) analysis demonstrated unimodal relationships between the presence of the four target LBF species (*Peneroplis planatus*, *P. pertusus*, *P. arietinus*, and *Coscinospira hemprichii*) and their corresponding environmental requirements (Supplementary Fig. 4). FOP analysis showed the observed proportion of sampling points where species were present across different environmental value ranges. The occurrence patterns exhibited clear environmental optima for each of the three key variables, with species

presence peaking at intermediate values of iron concentration, diffuse attenuation, and dissolved oxygen at mean depth.

Global model extrapolation

The Arabian Gulf-trained model demonstrated excellent transferability when extrapolated to global scales, accurately predicting known species distributions worldwide with an AUROC of 85% (Fig. 1). The global predictions identified several distinct regions of climatically suitable habitat for the studied LBF species, providing validation of the model's biogeographic accuracy.

Predicted suitable habitats were identified within the Gulf of Mexico basin, including areas along the west Florida coastline, the Bahamas, southwest Cuba, and the Cayman Islands. In the Mediterranean Sea, the model predicted suitable conditions in several areas. In the Indo-Pacific region, suitable conditions were identified in parts of the Red Sea and Indian Ocean. Along the west African Atlantic coastline, extensive stretches of suitable habitat were identified from Guinea Bissau through Sierra Leone, Nigeria, Gabon, and the Democratic Republic of Congo. These predictions closely aligned with documented distributions of the target species from independent literature sources, confirming the model's global applicability^{31,37,46,67–70}.

The close correspondence between predicted and observed global distributions validated the ecological relevance of the three identified environmental drivers (iron concentration, light attenuation, and dissolved oxygen) beyond the Arabian Gulf training region. This successful extrapolation demonstrates that environmental relationships derived from regional studies can provide reliable predictions for global species distributions when based on EMEVs.

Future climate projections

Regional projections for the arabian gulf

Model projections under two climate scenarios (Representative Concentration Pathway 2.6 and 4.5) for two future time periods (2050 and 2100) showed minimal differentiation in the Arabian Gulf region (Supplementary Fig. 5). RCP scenarios represent different greenhouse gas emission pathways and associated climate forcing levels. However, detailed examination of the RCP 4.5 2100 scenario revealed subtle but notable geographical shifts in suitable habitat distribution.

Under the RCP 4.5 2100 scenario, the model predicted range expansion into deeper waters along the western flank of the Arabian Gulf (Fig. 3, Supplementary Table 3). Additional colonization was projected along the eastern coastal plains of the Iranian coastline and at both eastern and western coastlines near the Strait of Hormuz. These changes represent a longitudinal shift in species distribution patterns, with increased habitat suitability extending into previously unsuitable deeper water areas.

Specific depth analysis across monitoring stations revealed varying responses to future climate conditions (Supplementary Table 3). Western Arabian Gulf locations showed stable high suitability (HSI=0.8) near shorelines under both current and future scenarios. Eastern Arabian Gulf locations, currently showing minimal suitability (HSI=0), demonstrated substantial increases to HSI values of 0.8–0.9 under future scenarios, particularly in shallower waters (5–14 m depth). Southern Arabian Gulf stations maintained consistently high suitability near shorelines (HSI=0.9) across all scenarios.

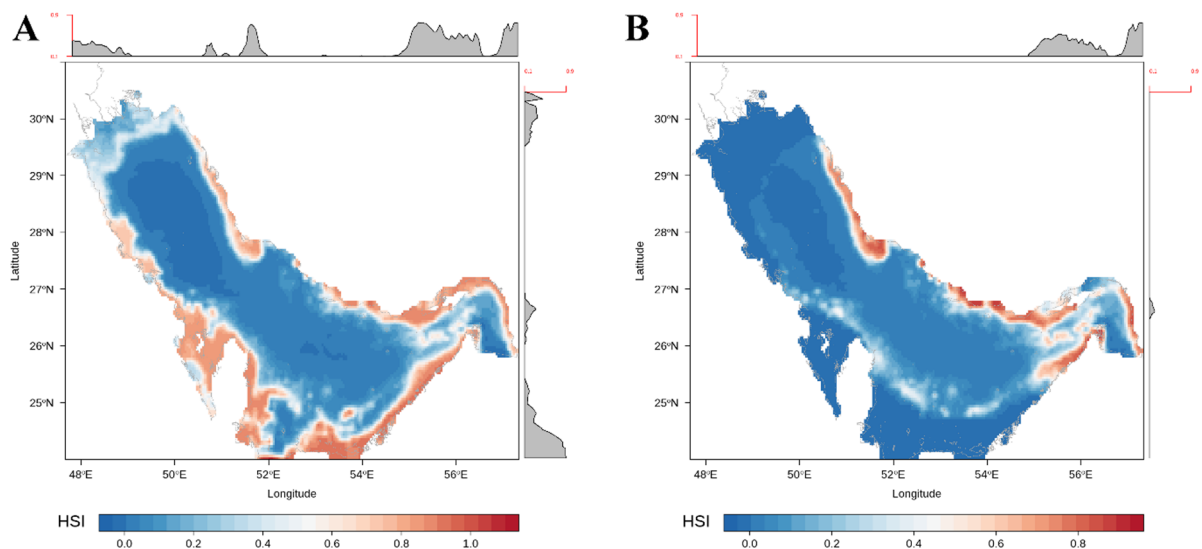


Fig. 3. Projected changes in the distribution of suitable habitats for the four selected benthic foraminiferal species in the Arabian/Persian Gulf under the RCP 4.5 climate change scenario for the year 2100. (A) Habitat Suitability Index (HSI) for 2100 (B) predicted habitat suitability difference in 2100 compared with current (see Fig. 2 above). Data processing and map generation were all done using R (version 4.4 : <https://cran.r-project.org/>).

Global climate projections

Global-scale projections for 2100 under RCP 4.5 with a conservative 2% increase in iron concentration demonstrated significant westward expansion of suitable LBF habitat (Fig. 4). The most pronounced changes occurred west of the prime meridian, with substantial increases in habitat suitability throughout the Atlantic Ocean basin (Supplementary Fig. 6).

Current global projections showed suitable habitat primarily concentrated between 50°N and 50°S latitude, with highest suitability east of the prime meridian (Fig. 4A). Future projections under RCP 4.5 with iron enrichment maintained this latitudinal constraint but showed marked longitudinal expansion (Fig. 4B). The difference analysis revealed substantial habitat gains in the Atlantic Ocean, Caribbean Sea, and parts of the eastern Pacific, while maintaining existing suitable areas in the Indo-Pacific region (Fig. 4C).

The projected expansion patterns suggested that LBF species will likely colonize new regions as ocean temperatures rise and iron availability increases. The expansion remained confined to tropical and subtropical latitudes, indicating that mean temperature of the water column continues to act as a limiting factor at higher latitudes despite improved iron availability. The marginal plots in Fig. 4 show clear increases in mean HSI values across both latitudinal and longitudinal gradients under future climate scenarios.

Discussion

Environmental controls on LBF distribution

Our findings fundamentally expand the current understanding of environmental controls on larger benthic foraminifera (LBF) distributions, revealing that iron concentration, light attenuation, and dissolved oxygen may play more critical roles than previously recognized. The prevailing paradigm has emphasized that symbiont-bearing foraminifera, particularly larger species like peneroplids, are primarily controlled by mean surface water temperature and the extension of the photic zone, with their latitudinal distributions largely determined by thermal constraints^{37,38}. While temperature undoubtedly remains important at biogeographic scales, our results demonstrate that within thermally suitable regions, other environmental factors become the primary determinants of habitat suitability and local distribution patterns.

The dominance of iron concentration in explaining 68% of habitat suitability variance has profound implications for understanding LBF ecology and predicting their responses to environmental change. Iron serves as a critical micronutrient that limits primary productivity across much of the global ocean³⁹, directly affecting the photosynthetic capacity of algal symbionts that LBF depend upon for energy and metabolic support^{40,41}. The strong relationship between iron availability and LBF distribution suggests that these organisms have evolved to occupy niches where iron supply can sustain productive symbiotic relationships, enabling them to thrive in oligotrophic tropical waters where other calcifying organisms may struggle.

The dominance of iron concentration in explaining LBF habitat suitability aligns with paleontological evidence from the PETM, when a global shift from coral-dominated to LBF-dominated carbonate platforms occurred¹⁴. During this period, rising temperatures pushed corals beyond their thermal tolerance limits, while enhanced continental weathering and runoff created eutrophic conditions that may have increased nutrient availability, allowing LBF to thrive in newly available ecological niches. This historical precedent supports our predictions that changing environmental conditions under future climate scenarios will drive LBF range expansion into regions where environmental stress may limit other carbonate producers.

The secondary importance of light attenuation (21% variance explained) aligns with the fundamental photosynthetic requirements of LBF-hosted symbionts. Diffuse attenuation coefficients integrate multiple factors affecting underwater light quality and quantity, including turbidity, water depth, and dissolved organic matter. The unimodal relationship observed between species occurrence and light attenuation suggests that LBF require sufficient light penetration for photosynthesis while potentially avoiding environments with excessive irradiance that could damage symbiotic algae^{42,43}. This finding supports previous laboratory studies demonstrating that LBF with symbionts require continuous light supply but perform optimally under moderate rather than maximum irradiance conditions^{44,45}.

Dissolved oxygen concentration, contributing 10% of explained variance, reflects the complex metabolic requirements of both LBF hosts and their symbionts. In sediment microhabitats, oxygen availability influences species depth distribution and tolerance of organic matter flux^{46,47}. The relationship between LBF occurrence and dissolved oxygen likely reflects their preference for well-oxygenated, oligotrophic environments where symbiotic photosynthesis can supplement host metabolism without interference from excessive organic matter decomposition or hypoxic stress.

Implications of iron enrichment for future distributions

The projected 2% increase in global iron concentrations by 2100, based on Hamilton et al.^{48,49} modeling of atmospheric soluble iron deposition changes under anthropogenic climate forcing, demonstrates significant potential for LBF range expansion under future climate scenarios. Hamilton et al.^{48,49} specifically projected that soluble iron deposition could increase by 63–95% in key ocean regions by 2100 under intermediate warming scenarios, making our 2% global average a highly conservative estimate. Enhanced iron delivery to marine systems through multiple pathways including increased wildfire frequency, expanded arid regions, and accelerated ice sheet melting^{49–54} will likely create more favorable conditions for symbiont-bearing LBF across broader geographic areas.

Iron enrichment effects extend beyond simple nutrient supplementation, fundamentally altering the thermal tolerance and ecological niche breadth of LBF species. Increased iron availability enhances the photosynthetic capacity of algal symbionts, enabling them to maintain productivity under elevated temperatures and potentially expanding the thermal niche that each species can inhabit^{40,41}. This symbiont-mediated thermal tolerance

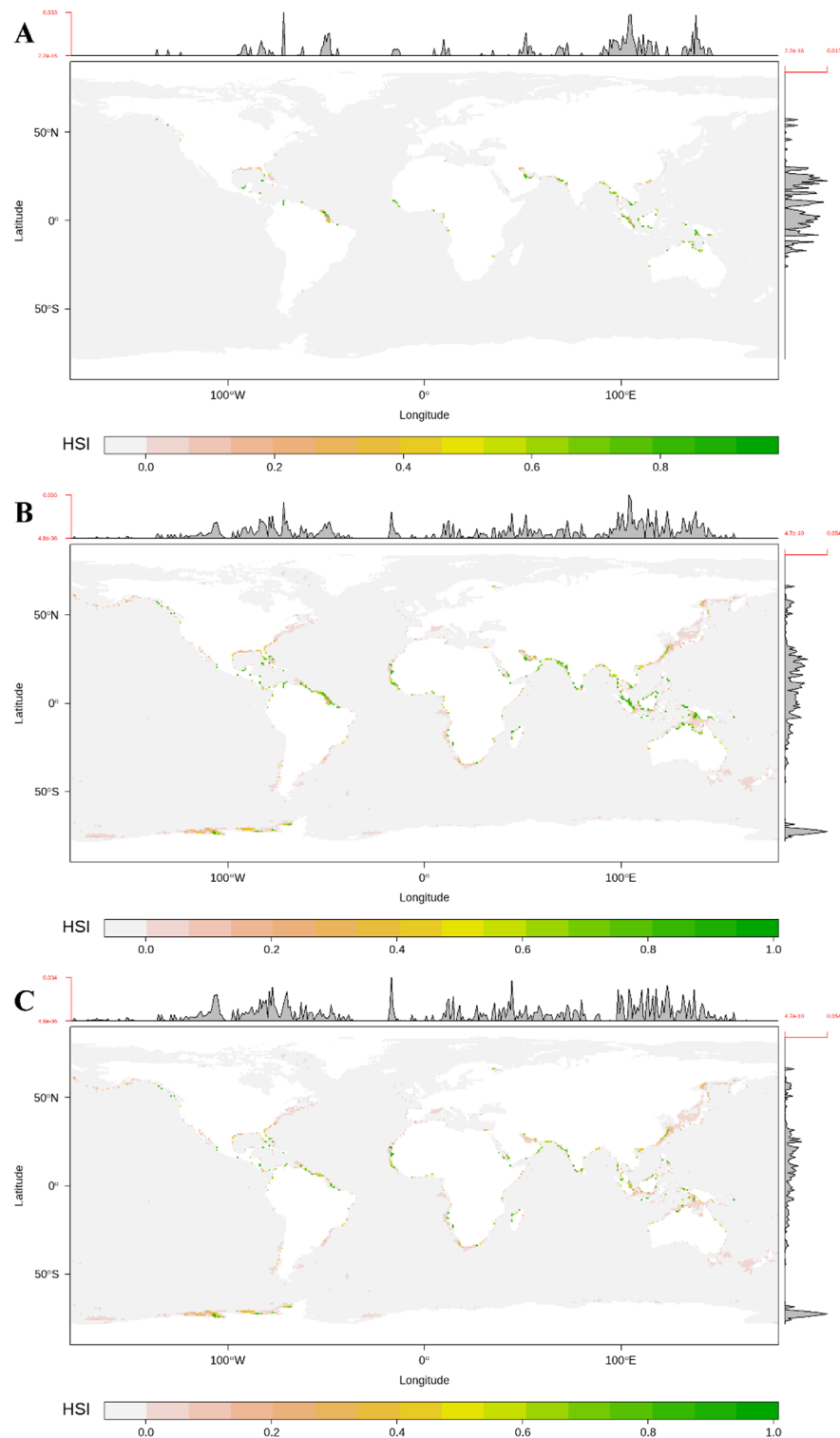


Fig. 4. Global extrapolation of the species distribution model. **(A)** Current predicted habitat suitability, **(B)** projected habitat suitability under the RCP 4.5 climate change scenario and a conservative 2% increase in seawater iron content by 2100, and **(C)** difference between current and future habitat suitability. The x-axis and y-axis marginal plots display mean Habitat Suitability Index (HSI) values. Data processing and map generation were all done using R (version 4.4 : <https://cran.r-project.org/>).

enhancement may explain why LBF showed relatively modest responses to temperature-only climate scenarios but demonstrated substantial range expansions when iron enrichment was incorporated into projections.

The projected westward expansion of suitable habitat, particularly into the Atlantic Ocean basins, represents a significant biogeographic shift with potential consequences for marine ecosystem structure and function. As LBF colonize new regions, they will likely become important contributors to local carbonate production and sediment composition. Given that LBF contribute up to 5% of global carbonate production, with individual species producing $0.3\text{--}2.7\text{ kg m}^{-2}\text{ yr}^{-1}$ in reef environments^{9,10}, their expansion could substantially alter carbonate budget dynamics in previously LBF-poor regions.

The maintenance of latitudinal constraints (50°N to 50°S) in future projections, despite iron enrichment, suggests that temperature continues to impose fundamental physiological limits on LBF distributions. This finding indicates that while iron availability may enhance local abundance and habitat suitability within thermally suitable regions, it cannot overcome the basic thermal requirements of LBF and their symbionts. The interaction between thermal tolerance and nutrient availability thus creates a complex biogeographic template that will shape future marine ecosystem responses to climate change.

Symbiotic relationships and adaptive capacity

The environmental variables identified by our models reflect the integrated requirements of both LBF hosts and their diverse symbiotic partners, highlighting the importance of these relationships in determining species responses to environmental change. The evolutionary significance of microbial assemblages in LBF extends beyond simple metabolic support, encompassing complex biochemical interactions that enable adaptation to diverse environmental conditions^{40,41}. Different symbiont communities confer varying degrees of thermal tolerance, nutrient efficiency, depth distribution and stress resistance, suggesting that LBF with appropriate symbiotic partnerships will be better positioned to exploit expanding habitat opportunities under climate change.

The specific environmental requirements revealed by our models may reflect the selective pressures that have shaped LBF-symbiont associations over evolutionary time. Iron limitation has likely been a persistent challenge in tropical oligotrophic waters, favoring LBF lineages that evolved efficient iron acquisition and utilization strategies through their symbiotic partnerships. Similarly, the optimization for intermediate light levels and well-oxygenated conditions suggests that successful LBF-symbiont associations have evolved to balance photosynthetic efficiency with protection from photodamage and oxidative stress.

The capacity for LBF to host multiple algal species within individual tests provides potential resilience against environmental change through symbiont shuffling or switching^{42,43}. As environmental conditions shift under climate change, LBF may be able to selectively favor symbiont communities that are better adapted to new conditions, providing a mechanism for rapid acclimation that could facilitate range expansion into previously unsuitable habitats. This symbiotic flexibility may explain the relatively optimistic projections for LBF under future climate scenarios compared to other calcifying marine organisms.

Paleontological context and future evolutionary responses

The projected responses of LBF to climate change scenarios find strong support in the paleontological record, particularly during past warming events such as the Paleocene-Eocene Thermal Maximum (PETM). During this period of rapid global warming approximately 56 million years ago, LBF demonstrated remarkable adaptability, with genera such as *Nummulites* and *Alveolina* expanding their geographic ranges into higher latitudes and diversifying rapidly as climatic conditions became more favorable^{55,56}. The PETM fossil record also documents the dominance of LBF as carbonate producers during warm climate periods, suggesting that similar ecological shifts may occur under future warming scenarios.

The long evolutionary history of Peneroplidae, spanning from the Cenomanian stage to the present and surviving multiple mass extinction events including the Cretaceous-Paleocene boundary and Eocene-Oligocene cooling⁵⁷, demonstrates the inherent resilience of this group to environmental change. This evolutionary persistence, combined with their demonstrated thermal tolerance and symbiotic flexibility, suggests that peneroplid LBF are well-positioned to not only survive but potentially thrive under projected climate change scenarios.

The integration of paleontological evidence with modern species distribution modeling provides a powerful framework for understanding potential future evolutionary responses. Past episodes of LBF proliferation during warm periods were commonly accompanied by increased speciation rates and morphological innovation, suggesting that future climate warming may be able to trigger similar evolutionary radiations. The identification of iron availability as a key environmental driver provides new insights into the mechanisms underlying these evolutionary patterns and suggests that future iron enrichment may accelerate LBF diversification and dispersal.

Model limitations and future research directions

While our SDM approach provides valuable insights into LBF distributions and climate change responses, several limitations must be acknowledged. The assumption of species-environment equilibrium may not hold during periods of rapid environmental change, potentially leading to overprediction of suitable habitat in areas where dispersal limitation or ecological lag effects prevent immediate colonization^{58,59}. Additionally, the static nature of our models does not account for potential evolutionary adaptation or symbiont community shifts that may alter species-environment relationships over the projection timeframes.

The coarse resolution of some environmental predictors, particularly iron concentration and primary productivity datasets, may not fully capture the fine-scale variability that influences LBF distributions in coastal and shallow water environments^{60,61}. Future modeling efforts would benefit from integration of high-resolution in situ measurements and remote sensing products to better constrain the drivers of LBF habitat suitability.

The development of dynamic models that incorporate dispersal processes, population dynamics, and symbiont community evolution would provide more realistic projections of species responses to climate change.

The uniform application of iron enrichment across global projections, while necessary given current data limitations, likely oversimplifies the complex spatial and temporal patterns of iron delivery to marine systems. Regional climate models with explicit representation of dust transport, wildfire emissions, and ice-derived iron sources would enable more spatially explicit projections of LBF range shifts. Similarly, the incorporation of ocean acidification effects, which may interact with iron availability and temperature to influence LBF calcification rates, represents an important area for future research.

Broader implications for marine ecosystem function

The projected expansion and increased dominance of LBF under future climate scenarios carry significant implications for marine ecosystem structure and function. As prolific carbonate producers and ecosystem engineers, LBF contribute substantially to reef framework construction, sediment production, and three-dimensional habitat complexity^{62–64}. Their increased abundance may help compensate for coral reef degradation in some regions, providing alternative sources of structural complexity and carbonate production as coral cover declines due to bleaching and ocean acidification.

This potential transition from coral-dominated to LBF-dominated systems has strong paleontological precedent during the PETM, when rising temperatures triggered coral reef disappearance and proliferation of more thermally tolerant LBF across the Tethyan realm¹⁴. Enhanced continental weathering and eutrophication during this period coincided with significant LBF diversification and the establishment of LBF-dominated carbonate platforms^{14,55}. However, the functional equivalence between LBF and coral reefs remains uncertain, particularly regarding critical ecosystem services such as coastal protection, fisheries support, tourism value, and biodiversity maintenance⁶⁵. The ecological consequences of this shift will likely vary regionally depending on local environmental conditions and ecosystem context.

Beyond structural changes, the biogeochemical implications of expanded LBF distributions extend to nutrient cycling, sediment transport, and food web dynamics. Range expansion into previously LBF-poor regions may fundamentally alter benthic-pelagic coupling processes, potentially reshaping entire marine ecosystems. Understanding these cascading effects will be important for predicting the full consequences of climate-driven LBF proliferation and the broader reorganization of shallow marine carbonate systems under changing environmental conditions.

Conclusions

This study demonstrates that species distribution modeling effectively predicts larger benthic foraminifera (LBF) distributions across multiple spatial scales, revealing that iron concentration (68% variance explained), light attenuation (21%), and dissolved oxygen (10%) control habitat suitability more than previously recognized. These findings expand our understanding of environmental controls beyond traditional temperature-focused models and highlight the critical role of micronutrient availability and symbiotic relationships in determining LBF distributions. Global model validation achieved 85% accuracy when extrapolated from Arabian Gulf training data to worldwide distributions, demonstrating strong transferability across diverse ocean basins.

Climate projections under Representative Concentration Pathway 4.5 scenarios predict significant westward LBF range expansion by 2100, particularly into Atlantic Ocean regions previously unsuitable for these organisms. The projected expansion remains constrained to tropical and subtropical latitudes (50°N–50°S), indicating that temperature continues to impose fundamental biogeographic limits. Enhanced atmospheric iron deposition under climate warming, projected to increase by 63–95% in key ocean regions, will likely drive increased LBF abundance and carbonate production in shallow marine systems globally.

As major carbonate producers contributing up to 5% of global carbonate production, expanding LBF populations will significantly influence marine carbonate budgets and ecosystem structure. This modeling framework provides a useful tool for predicting marine ecosystem responses to climate change and can be applied to other calcifying organisms. The approach demonstrates how LBF can serve as effective proxies for understanding environmental changes in shallow marine systems and supports broader ecosystem assessment under changing climate conditions.

Methods

Study area

The Arabian/Persian Gulf served as the primary study region for initial model development and validation. This semi-enclosed marginal sea, extending from the Indian Ocean, provides an ideal natural laboratory characterized by well-defined environmental gradients and diverse marine habitats^{34,35}. The Gulf is relatively shallow with an average depth of 35 m and maximum depth exceeding 100 m near the Strait of Hormuz³⁶. Its unique oceanographic characteristics including extreme temperature variations, high salinity, and variable nutrient conditions make it particularly suitable for studying organism responses to environmental stress and climate change scenarios.

The photic zone encompasses most of the Gulf except for limited areas along the Iranian coast, providing optimal conditions for symbiont-bearing LBF³⁶. The distribution of key environmental variables across the region (Supplementary Fig. 3) reveals distinct gradients that influence species distributions. Following initial model development and validation in the Arabian Gulf, we projected the trained models onto global oceans to assess habitat suitability and predict species distributions under current and future climate scenarios.

Species occurrence data

We compiled occurrence data for four larger benthic foraminifera (LBF) species (*Peneroplis planatus*, *P. pertusus*, *P. arietinus*, and *Coscinospira hemprichii*) from three distinct sources to ensure comprehensive spatial coverage and robust model training. The first source comprised distributional data compiled from benthic foraminiferal studies documenting species occurrences throughout the Arabian Gulf^{66–69} (Supplementary Table 4, Supplementary Fig. 2). This Arabian Gulf dataset included 355 georeferenced sampling locations providing high-resolution regional coverage. The second source consisted of published global occurrence records for target species⁷⁰, providing broad-scale biogeographic context and validation data for model extrapolation. The third source included supplementary distributional records from both published literature and verified taxonomic databases⁷¹, expanding global coverage for model validation (Supplementary Table 5).

The Arabian Gulf dataset (355 locations) was randomly partitioned using a 90/10 split to create independent training and testing datasets. The training dataset (90%, $n = 320$) was used for model calibration and parameter estimation, while the test dataset (10%, $n = 35$) was reserved for independent model validation. The test dataset deliberately included sparse data from the eastern Arabian Gulf (Iranian coast) to evaluate model robustness across environmental gradients. The combined global dataset from sources two and three served as an independent validation dataset for assessing model transferability and extrapolation accuracy beyond the training region. This partitioning strategy ensures rigorous model evaluation across multiple spatial scales while maintaining independence between training and validation datasets (Supplementary Fig. 1).

Environmental predictor variables

We selected ecologically meaningful environmental variables (EMEVs) from the BIO-ORACLE^{72,73} and MARSPEC⁷⁴ databases, accessed through the 'sdmpredictors' R package⁷⁵. EMEVs represent environmental parameters with direct ecological relevance to LBF physiology and habitat requirements. Present-day environmental conditions were based on monthly averages spanning 2000–2014 using Bio-ORACLE version 2 datasets.

The initial variable pool included 32 EMEVs representing key oceanographic parameters: sea surface and bottom temperature, salinity, nutrient concentrations (nitrate, phosphate, silicate), chlorophyll-*a*, current velocity, phytoplankton biomass, primary productivity, iron concentration, and light attenuation coefficients (Supplementary Table 1). These variables were selected based on their ecological relevance to LBF physiology, symbiont requirements, and habitat preferences.

We modeled future species distributions under two Representative Concentration Pathways (RCPs) established by the Intergovernmental Panel on Climate Change, representing different greenhouse gas emission scenarios and associated climate forcing levels. RCP 2.6 represents a stringent mitigation scenario that requires carbon dioxide emissions to peak by 2020 and decline to zero by 2100, likely maintaining global temperature rise below 2 °C by 2100. RCP 4.5 represents a moderate mitigation scenario that projects carbon dioxide emissions peaking around 2040 with subsequent stabilization, resulting in global temperature rise between 2 °C and 3 °C by 2100. We selected these scenarios because they represent policy-relevant pathways under current climate agreements, providing realistic bounds for near-term climate planning. RCP 8.5 was excluded as it represents an increasingly unlikely high-emission scenario given recent policy developments and renewable energy adoption trends.

For future projections, we applied a conservative 2% increase in seawater iron concentration above current levels by 2100 under RCP 4.5. This approach is directly informed by Hamilton et al.⁴⁸, who modeled the impact of atmospheric soluble iron deposition changes on ocean biogeochemical cycles under anthropogenic climate forcing. Their projections indicate that soluble iron deposition could increase by 63–95% in the Southern Ocean by 2100 under intermediate warming scenarios (RCP 4.5), with increases expected globally due to enhanced wildfire frequency, expanded arid regions, and accelerated ice sheet melting^{48–54}. Given these literature projections of iron deposition increases, our 2% global average represents a conservative modeling assumption, ensuring that our projections err on the side of caution while still incorporating the documented trend toward iron enrichment under climate warming. The iron increase was applied uniformly across model projections, acknowledging that regional variations exist but lacking sufficient spatial resolution in current projections to implement geographically explicit changes. This approach provides a first-order approximation of iron enrichment effects while maintaining model consistency.

Model development

We employed a maximum-likelihood interpretation of maximum entropy modeling using infinitely weighted logistic regression for model fitting^{76,77}. The modeling approach comprised two sequential phases (Supplementary Fig. 1). In the first phase, we developed initial models using known species distributions in the well-characterized Arabian Gulf basin, followed by rigorous validation using independent test data. The second phase involved spatial extrapolation of validated models to global extent^{78,79}, enabling prediction of suitable habitats worldwide.

We implemented a forward stepwise selection procedure to identify the most informative EMEVs while avoiding model overfitting. Beginning with individual variable assessment, we iteratively added variables based on significance testing ($p < 0.001$) and improvement in explained deviance (D^2). Model selection continued until additional variables failed to provide statistically significant improvement ($p > 0.05$). Environmental variable values were extracted at species occurrence locations using appropriate buffer zones to account for spatial uncertainty in georeferencing. The selection process was guided by statistical performance metrics rather than priori ecological assumptions, ensuring objective identification of the most predictive environmental factors.

Model evaluation and performance assessment

Model performance was evaluated using multiple complementary metrics addressing different aspects of predictive accuracy. For threshold-independent assessment, we used the Area Under the Receiver Operating Characteristic Curve (AUROC), which measures discriminatory ability across all threshold values, with values >0.7 indicating good performance and >0.9 indicating excellent performance⁸⁰.

For threshold-dependent metrics, we used a threshold of 0.5 for binary classification and calculated overall accuracy (proportion of correctly classified presence and absence predictions), sensitivity or true positive rate (proportion of actual presences correctly predicted), specificity or true negative rate (proportion of actual absences correctly predicted), and the True Skill Statistic ($TSS = \text{Sensitivity} + \text{Specificity} - 1$), which provides a balanced measure correcting for chance agreement^{81,82}.

We employed 10-fold cross-validation to assess model stability and reduce overfitting bias. Performance metrics were calculated across all validation folds to provide robust estimates of model accuracy. Model transferability was evaluated by comparing predictions against independent global occurrence data, assessing how well Arabian Gulf-trained models predict species distributions in other ocean basins.

Statistical analysis environment

All analyses were conducted in R statistical computing language (version 4.1.1)⁸³. Key packages included: tidymodels and tidyverse for data manipulation^{84,85}, MIAnaxent for maximum entropy modeling⁸⁶, sf and raster for spatial data processing^{87,88}, and sdmpredictors for environmental data access⁷⁵. Complete analytical workflows and R scripts are provided via the Zenodo repository [<https://doi.org/10.5281/zenodo.18547233>]. All maps included in the study and as supplementary materials are generated using custom reproducible code provided in the repository using R statistical software (version 4.4 : <https://cran.r-project.org/>).

Model assumptions and limitations

Our logistic regression models assume: (1) species are in equilibrium with their environment, (2) distributions are primarily determined by selected EMEVs, and (3) species-environment relationships remain static over projection timeframes^{89,90}. We acknowledge that occurrence data may contain sampling biases, environmental layers contain uncertainties (particularly in data-sparse regions), and future climate scenarios carry inherent uncertainties regarding greenhouse gas emissions and climate system responses^{91–94}.

Data and code availability

All data used in this study including all R-scripts and environmental layers for the various modeling routines are readily available and provided via the Zenodo repository [<https://doi.org/10.5281/zenodo.18547233>].

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References

- Smale, D. A. et al. Marine heatwaves threaten global biodiversity and the provision of ecosystem services. *Nat. Clim. Change*. **9**, 306–312 (2019).
- Oliver, E. C. et al. Longer and more frequent marine heatwaves over the past century. *Nat. Commun.* **9**, 1–12 (2018).
- Holbrook, N. J. et al. Keeping pace with marine heatwaves. *Nat. Rev. Earth Environ.* **1**, 482–493 (2020).
- Bates, A. E. et al. Defining and observing stages of climate-mediated range shifts in marine systems. *Glob. Environ. Change* **26**, 27–38 (2014).
- Gooday, A. et al. Historical records of coastal eutrophication-induced hypoxia. *Biogeosciences* **6**, 1707–1745 (2009).
- Murray, J. W. *Ecology and Applications of Benthic Foraminifera* (Cambridge university, 2006).
- Jorissen, F., de Stigter, H. C. & Widmark, J. G. A conceptual model explaining benthic foraminiferal microhabitats. *Mar. Micropaleontol.* **26**, 3–15 (1995).
- Schönfeld, J. et al. The FOBIMO (FORaminiferal Bio-MONitoring) initiative—towards a standardised protocol for soft-bottom benthic foraminiferal monitoring studies. *Mar. Micropaleontol.* **94**, 1–13 (2012).
- Langer, M. Assessing the contribution of foraminiferal protists to global ocean carbonate production. *J. Eukaryot. Microbiol.* **55**, 163–169 (2008).
- Doo, S. S., Hamylton, S., Finfer, J. & Byrne, M. Spatial and temporal variation in reef-scale carbonate storage of large benthic foraminifera: A case study on One Tree Reef. *Coral Reefs* **36**, 293–303 (2017).
- Murray, J. W. *Ecology and Palaeoecology of Benthic Foraminifera* (Routledge, 2014).
- Gooday, A. J. & Jorissen, F. J. Benthic foraminiferal biogeography: Controls on global distribution patterns in deep-water settings. *Annu. Rev. Mar. Sci.* **4**, 237–262 (2012).
- Debenay, J. P. A *Guide to 1,000 Foraminifera from Southwestern Pacific: New Caledonia* (IRD Editions, 2012).
- Scheibner, C. & Speijer, R. Late Paleocene–early Eocene Tethyan carbonate platform evolution—A response to long- and short-term paleoclimatic change. *Earth Sci. Rev.* **90**, 71–102 (2008).
- Frontalini, F. et al. Benthic foraminiferal assemblages and biotopes in a coastal lake: the case study of Lake Varano (southern Italy). *Acta Protozool.* **52**, 4 (2013).
- Martins, M. V. A. et al. Foraminiferal biotopes and their distribution control in Ria de Aveiro (Portugal): A multiproxy approach. *Environ. Monit. Assess.* **186**, 8875–8897 (2014).
- Rushton, S., Ormerod, S. J. & Kerby, G. New paradigms for modelling species distributions? *J. Appl. Ecol.* **41**, 193–200 (2004).
- Sánchez-Cordero, V., Cirelli, V., Munguia, M. & Sarkar, S. Place prioritization for biodiversity content using species ecological niche modeling. *Biodiversity Informatics* **2**, (2005).
- Vaughan, I. P. & Ormerod, S. J. Improving the quality of distribution models for conservation by addressing shortcomings in the field collection of training data. *Conserv. Biol.* **17**, 1601–1611 (2003).
- Dambach, J. & Rödder, D. Applications and future challenges in marine species distribution modeling. *Aquat. Conserv.* **21**, 92–100 (2011).
- Robinson, N. M., Nelson, W. A., Costello, M. J., Sutherland, J. E. & Lundquist, C. J. A systematic review of marine-based species distribution models (SDMs) with recommendations for best practice. *Front. Mar. Sci.* **4**, 421 (2017).

22. Bedia, J., Herrera, S. & Gutiérrez, J. M. Dangers of using global bioclimatic datasets for ecological niche modeling. Limitations for future climate projections. *Glob. Planet Change*. **107**, 1–12 (2013).
23. Robinson, L. et al. Pushing the limits in marine species distribution modelling: lessons from the land present challenges and opportunities. *Glob. Ecol. Biogeogr.* **20**, 789–802 (2011).
24. Melo-Merino, S. M., Reyes-Bonilla, H. & Lira-Noriega, A. Ecological niche models and species distribution models in marine environments: A literature review and spatial analysis of evidence. *Ecol. Model.* **415**, 108837 (2020).
25. Reiss, H., Cunze, S., König, K., Neumann, H. & Kröncke, I. Species distribution modelling of marine benthos: A North Sea case study. *Mar. Ecol. Prog. Ser.* **442**, 71–86 (2011).
26. Saupe, E. E. et al. Macroevolutionary consequences of profound climate change on niche evolution in marine molluscs over the past three million years. *Proc. R. Soc. B Biol. Sci.* **281**, 20141995 (2014).
27. Bentlage, B., Peterson, A. T., Barve, N. & Cartwright, P. Plumbing the depths: Extending ecological niche modelling and species distribution modelling in three dimensions. *Glob. Ecol. Biogeogr.* **22**, 952–961 (2013).
28. Chefaoui, R. M. & Serrão, E. A. Accounting for uncertainty in predictions of a marine species: integrating population genetics to verify past distributions. *Ecol. Model.* **359**, 229–239 (2017).
29. Langer, M. R., Weinmann, A. E., Lötters, S. & Rödder, D. Strangers in paradise: modeling the biogeographic range expansion of the foraminifera *Amphistegina* in the Mediterranean Sea. *J. Foraminif. Res.* **42**, 234–244 (2012).
30. Weinmann, A. E., Rödder, D., Lötters, S. & Langer, M. R. Heading for new shores: Projecting marine distribution ranges of selected larger foraminifera. *PLoS One* **8**, e62182 (2013).
31. Langer, M. R., Weinmann, A. E., Lötters, S., Bernhard, J. M. & Rödder, D. Climate-driven range extension of *Amphistegina* (Protista, Foraminifera): Models of current and predicted future ranges. *PLoS One* **8**, e54443 (2013).
32. Guisan, A. et al. Predicting species distributions for conservation decisions. *Ecology Lett.* **16**, 1424–1435 (2013).
33. Schmidt, C. et al. Extremely heat tolerant photo-symbiosis in a shallow marine benthic foraminifera. *Sci. Rep.* **6**, 30930 (2016).
34. Reynolds, R. M. Physical oceanography of the Gulf, Strait of Hormuz, and the Gulf of Oman—Results from the Mt Mitchell expedition. *Mar. Pollut. Bull.* **27**, 35–59 (1993).
35. Purser, B. H. & Seibold, E. The principal environmental factors influencing Holocene sedimentation and diagenesis in the Persian Gulf. In *The Persian Gulf* (ed. Purser, B. H.) 1–9 (Springer, 1973).
36. Beech, M. et al. The fish fauna of Abu Dhabi emirate. *Marine Atlas Abu Dhabi* 158–183 (2004).
37. Langer, M. R. & Hottinger, L. Biogeography of selected “larger” foraminifera. *Micropaleontology* **46**, 105–126 (2000).
38. Hollaus, S. & Hottinger, L. Temperature dependence of endosymbiotic relationships? Evidence from the depth range of Mediterranean *Amphistegina lessonii* (Foraminifera) truncated by the thermocline. *Eclogae Geol. Helv.* **90**, 591–598 (1997).
39. Tagliabue, A. et al. The integral role of iron in ocean biogeochemistry. *Nature* **543**, 51–59 (2017).
40. Prazeres, M. & Renema, W. Evolutionary significance of the microbial assemblages of large benthic Foraminifera. *Biol. Rev.* **94**, 828–848 (2019).
41. Prazeres, M., Uthicke, S. & Pandolfi, J. M. Ocean acidification induces biochemical and morphological changes in the calcification process of large benthic foraminifera. *Proc. R. Soc. B Biol. Sci.* **282**, 20142782–20142782 (2015).
42. Lee, J. J. Algal symbiosis in larger foraminifera. *Symbiosis* (2006).
43. Lee, J. J. & Hallock, P. Algal symbiosis as the driving force in the evolution of larger foraminifera a. *Ann. N. Y. Acad. Sci.* **503**, 330–347 (1987).
44. Hallock, P. Light dependence in *Amphistegina*. *J. Foraminif. Res.* **11**, 40 (1981).
45. Lintner, M., Lintner, B., Schagerl, M., Wanek, W. & Heinz, P. The change in metabolic activity of a large benthic foraminifera as a function of light supply. *Sci. Rep.* **13**, 8240 (2023).
46. Murray, J. W. The niche of benthic foraminifera, critical thresholds and proxies. *Mar. Micropaleontol.* **41**, 1–7 (2001).
47. Pielou, E. C. & others. *Ecological Diversity*. vol. 165 Wiley New York, (1975).
48. S Hamilton, D. et al. Impact of Changes to the Atmospheric Soluble Iron Deposition Flux on Ocean Biogeochemical Cycles in the Anthropocene. *Glob. Biogeochem. Cycles*. **34**, e2019GB006448 (2020).
49. Mahowald, N. M. et al. Atmospheric iron deposition: global distribution, variability, and human perturbations. *Annual Rev. Mar. Sci.* **1**, 245–278 (2009).
50. Hamilton, D. S. et al. Improved methodologies for earth system modelling of atmospheric soluble iron and observation comparisons using the mechanism of intermediate complexity for modelling iron (MIMI v1. 0). *Geosci. Model Dev.* **12**, 3835–3862 (2019).
51. Wadham, J. L. et al. The potential role of the Antarctic Ice Sheet in global biogeochemical cycles. *Earth Environ. Sci. Trans. R. Soc. Edinb.* **104**, 55–67 (2013).
52. Ito, A. et al. Pyrogenic iron: The missing link to high iron solubility in aerosols. *Sci. Adv.* **5**, eaau7671 (2019).
53. Hopwood, M. J., Cantoni, C., Clarke, J. S., Cozzi, S. & Achterberg, E. P. The heterogeneous nature of Fe delivery from melting icebergs. *Geochem. Perspect. Lett.* **3**, 200–209 (2017).
54. Lauderdale, J. M., Braakman, R., Forget, G., Dutkiewicz, S. & Follows, M. J. Microbial feedbacks optimize ocean iron availability. *Proceedings of the National Academy of Sciences* **117**, 4842–4849 (2020).
55. Scheibner, C., Speijer, R. & Marzouk, A. Turnover of larger foraminifera during the Paleocene-Eocene Thermal Maximum and paleoclimatic control on the evolution of platform ecosystems. *Geology* **33**, 493–496 (2005).
56. Cotton, L. J. Nordic Nummulites: an unusual occurrence of Nummulites planatus from Jyske Rev, Danish North Sea. *Micropaleontology* **69** (4–5) (2023).
57. Yasuhara, M., Doi, H., Wei, C.-L., Danovaro, R. & Myhre, S. E. Biodiversity–ecosystem functioning relationships in long-term time series and palaeoecological records: Deep sea as a test bed. *Philos. Trans. R. Soc. B Biol. Sci.* **371**, 20150282 (2016).
58. Araújo, M. B. & Guisan, A. Five (or so) challenges for species distribution modelling. *J. Biogeogr.* **33**, 1677–1688 (2006).
59. Heikkinen, R. K., Marmion, M. & Luoto, M. Does the interpolation accuracy of species distribution models come at the expense of transferability? *Ecography* **35**, 276–288 (2012).
60. Phillips, S. J. et al. Sample selection bias and presence-only distribution models: Implications for background and pseudo-absence data. *Ecol. Appl.* **19**, 181–197 (2009).
61. Syfert, M. M., Smith, M. J. & Coomes, D. A. The effects of sampling bias and model complexity on the predictive performance of MaxEnt species distribution models. *PLoS One* **8**, e55158 (2013).
62. Burt, J. et al. Insights from extreme coral reefs in a changing world. *Coral Reefs* **39**, 495–507 (2020).
63. Narayan, G. R. et al. Response of large benthic foraminifera to climate and local changes: Implications for future carbonate production. *Sedimentology* **69**, 121–161 (2022).
64. Doo, S. S., Fujita, K., Byrne, M. & Uthicke, S. Fate of calcifying tropical symbiont-bearing large benthic foraminifera: Living sands in a changing ocean. *Biol. Bull.* **226**, 169–186 (2014).
65. Edinger, E. N. et al. Normal coral growth rates on dying reefs: Are coral growth rates good indicators of reef health? *Mar. Pollut. Bull.* **40**, 404–425 (2000).
66. Amao, A. O. & Kaminski, M. A. A new foraminiferal species *Pseudotriloculina Hottingeri* N. Sp. from the Arabian Gulf. *J. Foraminif. Res.* **47**, 366–371 (2017).
67. Amao, A. O., Kaminski, M. A. & Setoyama, E. Diversity of foraminifera in a shallow restricted lagoon in Bahrain. *Micropaleontology* **62**, 197–211 (2016).
68. Amao, A. O. et al. Distribution of benthic foraminifera along the Iranian coast. *Marine Biodiversity* **1–14** (2018).

69. Amao, A. O. et al. A baseline investigation of benthic foraminifera in relation to marine sediments parameters in western parts of the Arabian Gulf. *Mar. Pollut. Bull.* **146**, 751–766 (2019).
70. Förderer, M., Rödder, D. & Langer, M. R. Patterns of species richness and the center of diversity in modern Indo-Pacific larger foraminifera. *Sci. Rep.* **8**, 1–9 (2018).
71. WoRMS Editorial Board. *World Register of Marine Species (WoRMS)* (WoRMS Editorial Board, 2020).
72. Assis, J. et al. Bio-ORACLE v2.0: Extending marine data layers for bioclimatic modelling. *Glob. Ecol. Biogeogr.* **27**, 277–284 (2018).
73. Tyberghein, L. et al. Bio-ORACLE: a global environmental dataset for marine species distribution modelling. *Glob. Ecol. Biogeogr.* **21**, 272–281 (2012).
74. Sbrocco, E. J. & Barber, P. H. MARSPEC: Ocean climate layers for marine spatial ecology: Ecological Archives E094-086. *Ecology* **94**, 979–979 (2013).
75. Bosch, S. *SdmPredictors: Species Distribution Modelling Predictor Datasets*. (2020).
76. Halvorsen, R., Mazzoni, S., Bryn, A. & Bakkestuen, V. Opportunities for improved distribution modelling practice via a strict maximum likelihood interpretation of MaxEnt. *Ecography* **38**, 172–183 (2015).
77. Halvorsen, R. A strict maximum likelihood explanation of MaxEnt, and some implications for distribution modelling. *Sommerfeltia* **36**, 1–132 (2013).
78. Merow, C., Smith, M. J. & Silander, J. A. Jr A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. *Ecography* **36**, 1058–1069 (2013).
79. Morales, N. S., Fernández, I. C. & Baca-González, V. MaxEnt's parameter configuration and small samples: Are we paying attention to recommendations? A systematic review. *PeerJ* **5**, e3093 (2017).
80. Pearce, J. & Ferrier, S. Evaluating the predictive performance of habitat models developed using logistic regression. *Ecol. Model.* **133**, 225–245 (2000).
81. Allouche, O., Tsoar, A. & Kadmon, R. Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). *J. Appl. Ecol.* **43**, 1223–1232 (2006).
82. Fielding, A. H. & Bell, J. F. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environ. Conserv.* **24**, 38–49 (1997).
83. R Core Team. *R: A Language and Environment for Statistical Computing* (R Foundation for Statistical Computing, 2025).
84. Kuhn, M. & Wickham, H. *Tidymodels: Easily Install and Load the Tidymodels Packages*. (2021). <https://www.tidymodels.org>
85. Wickham, H. et al. "Welcome to the tidyverse." *J. Open Source Softw.* **4**(43), 1686. <https://doi.org/10.21105/joss.01686> (2019).
86. Vollerling, J., Halvorsen, R. & Mazzoni, S. The MIAMaxent R package: Variable transformation and model selection for species distribution models. *Ecol. Evol.* **9**, 12051–12068 (2019).
87. Pebesma, E. Simple Features for R: Standardized support for spatial vector data. *R J.* **10**(1), 439–446. <https://doi.org/10.32614/RJ-2018-009> (2018).
88. Hijmans, R. J. *Raster: Geographic Data Analysis and Modeling*. <http://10.32614/CRAN.package.raster> (2020).
89. Guisan, A., Thuiller, W. & Zimmermann, N. E. *Habitat Suitability and Distribution Models: With Applications in R* (Cambridge University Press, 2017).
90. Elith, J. & Leathwick, J. R. Species distribution models: ecological explanation and prediction across space and time. *Annu. Rev. Ecol. Evol. Syst.* **40**, 677–697 (2009).
91. Pearman, P. B., Guisan, A., Broennimann, O. & Randin, C. F. Niche dynamics in space and time. *Trends Ecol. Evol.* **23**, 149–158 (2008).
92. Fourcade, Y., Engler, J. O., Rödder, D. & Secondi, J. Mapping species distributions with MAXENT using a geographically biased sample of presence data: A performance assessment of methods for correcting sampling bias. *PLoS One* **9**, e97122 (2014).
93. Wenger, S. J. & Olden, J. D. Assessing transferability of ecological models: An underappreciated aspect of statistical validation. *Methods Ecol. Evol.* **3**, 260–267 (2012).
94. Pachauri, R. K. et al. Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. (2014).

Author contributions

A.O.A. and F.F. conceptualized the study, conducted the investigation, curated the data, developed the methodology, performed formal data analysis, and wrote the original draft. M.K., L.C., K.A. and I.A. contributed to formal data analysis and writing the original draft.

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Declarations

Competing interests

The authors declare no competing interests.

Additional information

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