

RESEARCH ARTICLE

Global diversity patterns of larger benthic foraminifera under future climate change

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Abstract

Global warming threatens the viability of tropical coral reefs and associated marine calcifiers, including symbiont-bearing larger benthic foraminifera (LBF). The impacts of current climate change on LBF are debated because they were particularly diverse and abundant during past warm periods. Studies on the responses of selected LBF species to changing environmental conditions reveal varying results. Based on a comprehensive review of the scientific literature on LBF species occurrences, we applied species distribution modeling using Maxent to estimate present-day and future species richness patterns on a global scale for the time periods 2040–2050 and 2090–2100. For our future projections, we focus on Representative Concentration Pathway 6.0 from the Intergovernmental Panel on Climate Change, which projects mean surface temperature changes of +2.2°C by the year 2100. Our results suggest that species richness in the Central Indo-Pacific is two to three times higher than in the Bahamian ecoregion, which we have identified as the present-day center of LBF diversity in the Atlantic. Our future predictions project a dramatic temperature-driven decline in low-latitude species richness and an increasing widening bimodal latitudinal pattern of species diversity. While the central Indo-Pacific, now the stronghold of LBF diversity, is expected to be most pushed outside of the currently realized niches of most species, refugia may be largely preserved in the Atlantic. LBF species will face large-scale non-analogous climatic conditions compared to currently realized climate space in the near future, as reflected in the extensive areas of extrapolation, particularly in the Indo-Pacific. Our study supports hypotheses that species richness and biogeographic patterns of LBF will fundamentally change under future climate conditions, possibly initiating a faunal turnover by the late 21st century.

KEYWORDS

climate change, coral reefs, Coral Triangle, global warming, larger benthic foraminifera, marine biodiversity, species distribution modeling

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1 | INTRODUCTION

Despite the 2016 Paris Agreement to aim for keeping global average temperatures below 2°C above pre-industrial levels and implementing measures to limit the increase to 1.5°C, the trend toward global warming continues unabated (IPCC, 2021; Schwalm et al., 2020). The ambitious target would only be achievable with drastic and prompt emissions cuts, which are considered unlikely to happen in due time (IPCC, 2021; Raftery et al., 2017).

Even moderate climate change will lead to rising sea surface temperatures (SSTs) and a fundamental and irreversible ecological transformation of the world's oceans including increased extinction rates and shifting of species distribution ranges (Hoegh-Guldberg & Bruno, 2010; IPCC, 2021; Jones & Cheung, 2015; Pachauri, 2014; Price et al., 2019). The loss in species richness may occur abruptly, will impact marine ecosystem functioning, and will have noticeable consequences for humanity (Cardinale et al., 2012; Doney et al., 2012; Hoegh-Guldberg & Bruno, 2010; Hughes et al., 2017; Magnan et al., 2021). Warm-water coral reefs are among the most diverse ecosystems but also severely threatened by climate change, pollution, and direct damage (Burke et al., 2011; Lough et al., 2018; Spalding & Brown, 2015). Forecasts are bleak, expecting the rates of reef degradation exceeding the ones of reef accretion (Pandolfi et al., 2011; Spalding & Brown, 2015). This will result in global habitat loss and an equatorial retraction of reef area (Couce et al., 2013; Freeman et al., 2013).

Symbiont-bearing larger benthic foraminifera (LBF) are ubiquitous components in modern coral reefs, prolific carbonate producers and contribute substantially to reef accretion and substrate stability (Fujita et al., 2016; Hohenegger, 2006; Langer, 2008; Langer et al., 1997). Their distribution and abundance are mainly controlled by evolutionary history and environmental factors such as SST, nutrient availability, photosynthetically available radiation, substrate type, and water energy (Fujita et al., 2014; Girard et al., 2022; Hallock, 1984, 1999; Langer & Hottinger, 2000; Renema, 2018; Renema et al., 2008; Schmidt et al., 2016).

Previous analyses on biogeographic patterns of modern LBF have mainly focused on the Indo-Pacific (Adams, 1983; Belasky, 1996; Förderer et al., 2018; Langer & Hottinger, 2000; Renema, 2007; Renema et al., 2008). They have shown that LBF diversity highly correlates with that of corals and other tropical marine shallow-water taxa, and peaks in the world's most biodiverse marine ecoregion, the Western Coral Triangle (Förderer et al., 2018; Hoeksema, 2007; Veron et al., 2011).

The marine fauna of the Atlantic Ocean is much less diverse and substantially different from that in the Indo-Pacific (Paulay, 1997; Veron et al., 2015). This also applies for LBF, as several taxa are considerably species poor in the Atlantic compared to their counterparts in the Indo-Pacific (Hallock, 1999; Hottinger, 2001; Langer & Hottinger, 2000). Generally, Atlantic tropical marine biodiversity is considered highest in the Caribbean where coral reefs are most extensive (Burke et al., 2011; Roberts et al., 2002; Tittensor et al., 2010). However, it remains difficult to delineate a center of

richness in the tropical Atlantic since studies have been highly localized and coverage of taxonomic and biogeographic research is considered still insufficient (Hoeksema et al., 2017; Miloslavich et al., 2010, 2011). Previous studies on LBF indicate that present-day high-rank taxon diversity peaks all along the Antillean arc and within the Brazilian province, and is low in the northern Gulf of Mexico and along the northern South American shelf, where coastal waters are nutrient rich due to upwelling and the presence of large river deltas (Weinmann, 2009; Weinmann & Langer, 2010).

Future scenarios for selected LBF taxa and the fossil record indicate that LBF might gain importance as carbonate producers and reef framework builders due to global warming as it was the case during periods with higher average global temperatures (Goldbeck & Langer, 2009; Hallock, 2000; Scheibner & Speijer, 2008; Weinmann et al., 2013). However, ocean warming may not only promote range shifts of LBF to higher latitudes, but also lead to decreasing abundances and range retraction for certain LBF taxa in lower latitudes (Weinmann et al., 2013). Over the past years, multiple studies have been investigating responses of the most common LBF species to different environmental stressors through *in vitro* experiments and *in vivo* observations, but the results are ambiguous (review in Hohenegger et al., 2022; Narayan et al., 2022).

Here, we compile and analyze an extensive data set of more than 4.700 occurrence records of LBF morphospecies, covering virtually all occupied marine biogeographic regions. We project species distribution models (SDMs) onto different IPCC climate change scenarios to uncover present-day and future LBF species richness patterns. This enabled us to identify present-day and future centers of LBF species richness, previously unknown areas of potential high diversity, and the global-scale impacts of projected climate change on LBF biogeographic patterns.

2 | MATERIALS AND METHODS

2.1 | Species records and environmental data

A number of 4.762 occurrence records were included for establishing the species richness maps (Table S1). These were obtained for 74 LBF species with at least five reported occurrence records. In total, we identified 105 species of LBF (Table S2). The investigated sample sites cover a latitudinal range between 45°N and 33°S (Figure 1a). The data set was compiled based on primary data and records obtained from 212 scientific publications (List S1). Primary data are from field studies conducted by the authors, revisions of material, and micropaleontological collection visits. For our study, we followed the morphospecies concept, since the vast majority of studies included in our analysis are based on this well-established approach. To ensure a robust taxonomic framework, all literature sources have been critically reevaluated and species were synonymized by the authors if appropriate, since species-level taxonomy may vary from author and subsequently affects biogeography. Synonymizing requested that species were adequately illustrated and key features

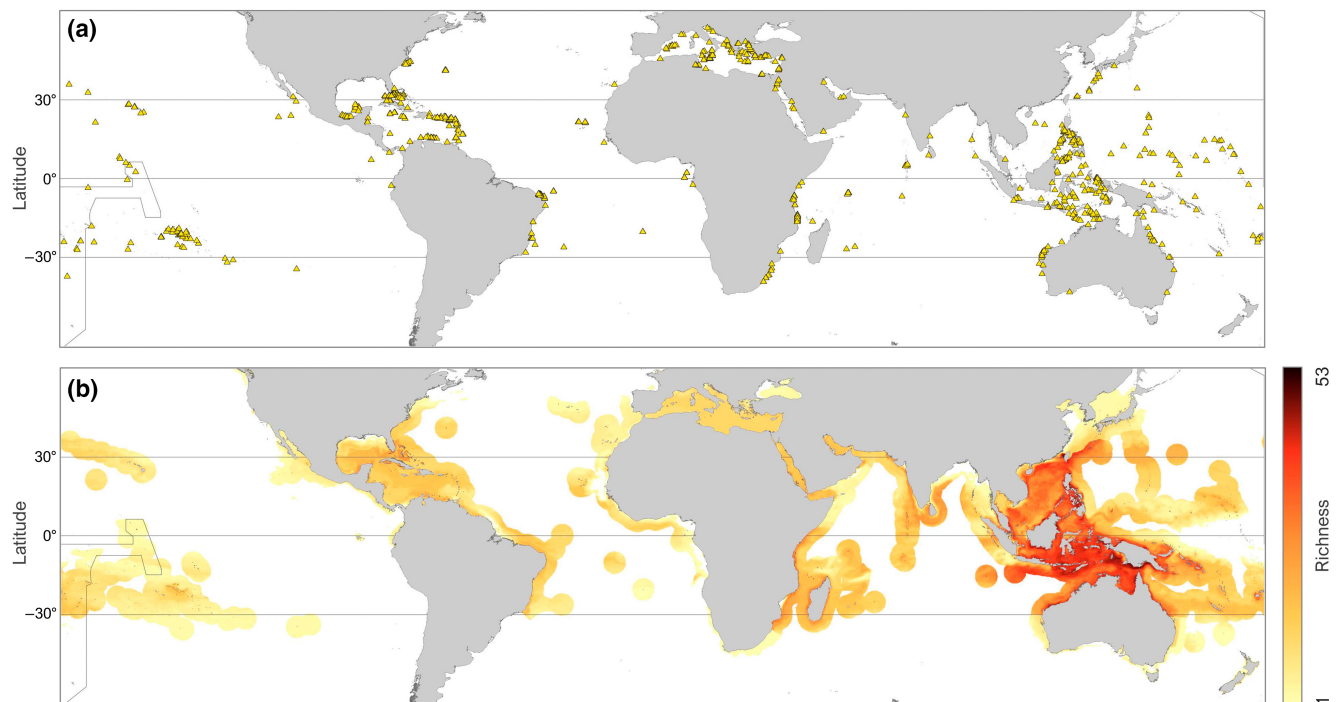


FIGURE 1 Maps showing (a) the geographic point data set (yellow triangles) used for species distribution model (SDM) and (b) predicted present-day global larger benthic foraminifera species richness based on SDM output using a set of marine data layers (Table S3) as environmental variables. Note that locations presented in (a) can have multiple species records

were clearly recognizable or were as such in previous studies of the respective author. Ambiguous species and generic records were not included. Collection visits to the Natural History Museum in Geneva (Switzerland) and the Naturalis Biodiversity Center in Leiden (Netherlands) allowed studying original material including type specimens.

In case locality information was not provided in the literature as coordinates, they had to be drawn from locality descriptions and georeferenced using Google Earth. The total data set includes species-level records covering the full range of habitats occupied by modern LBF within a general depth range down to the limits of the photic zone (<150m), while the vast majority of records were recorded in depths up to 30m (Figure S1).

It is important to emphasize that, while our study represents one of the most comprehensive data compilations available to date, it does not claim to cover all extant LBF species, nor does it provide complete distribution data of all species included.

Present-day and future climate projection data sets including 33 layers of limiting temperature-, chemical-, and nutrient-related environmental parameters (Table S3) were obtained from Bio-ORACLE for Representative Concentration Pathway (RCP) scenarios 2.6, 4.5, 6.0, and 8.5 for the time periods 2040–2050 and 2090–2100 (Assis et al., 2017; Tyberghein et al., 2012). Present-day variables were derived from remote sensing (e.g., SSTs) and interpolation of on ground measurements (e.g., chemical variables). The four RCPs are based on the IPCC's Coupled Model Intercomparison Project (CMIP) 5 model for climate scenarios and describe different pathways of greenhouse gas emissions. While the most stringent emissions scenario

(RCP2.6) appears no longer feasible, the RCP4.5 and RCP6.0 scenarios most likely frame the possible future of the oceans (Hausfather & Peters, 2020; IPCC, 2021). Although previous analyses have concluded a stronger tendency toward the worst-case scenario RCP8.5 (Combal & Fischer, 2016; Schwalm et al., 2020), according to the actual report of the IPCC, the uncertainty over future temperature change had narrowed with both the prior best- and worst-case scenarios having now become less relevant (IPCC, 2021). For our future projections, we focus on the RCP6.0 scenario which assumes that annual emissions will increase moderately from current levels with a mean global temperature increase of 1.3°C by 2046–2065 and 2.2°C by 2081–2100 relative to 1986–2005, primarily due to population growth capped at 10 billion while per capita emissions remain constant (IPCC, 2013). Due to the high dimensionality of predictors, we used a principal component analysis to archive a lower dimensionality and to remove likely redundancies.

2.2 | Computation of SDMs

SDMs were computed using Maxent v. 3.4.4 (Phillips et al., 2006, 2017), which is one of the most used correlative SDM software (Srivastava et al., 2019). Additionally, the R-packages raster (Hijmans, 2016), dismo (Hijmans et al., 2017), and ENMeval (Muscarella et al., 2014) were used for further processing in R 4.0.

To restrict the prediction of the species ranges on areas where LBF are generally distributed and to avoid excessive interpolation and extrapolation, we used layers of the Marine Ecoregions of the

World (MEOW) biogeographic classification as defined by Spalding et al. (2007) as a mask for SDM training and subsequent projection. MEOW is a global hierarchical classification system of coastal zones based on taxonomic configurations, influenced by evolutionary history, patterns of dispersal, and isolation (Spalding et al., 2007). It classifies the world's nearshore areas into 12 distinct marine realms, that are further differentiated into 62 marine provinces which are, in turn, split into 232 ecoregions.

For each species, we identified those ecoregions in which the species is currently present and used them as environmental background. As several settings can be used for fine tuning of Maxent models, we followed Warren and Seifert (2011) and tested several combinations of regularization multipliers (from 0.5 to 2.5 in 0.1 steps, 5 and 10) and feature classes (L, LP, LQ, LH, LT, LQP, LQH, LQT, LPH, LPT, LHT, LQPT, LQHT, LPHT, LQPHT; L = Linear, P = Product, Q = Quadratic, H = Hinge, T = Threshold). As first performance filter, we selected only SDMs with an AUCTest above 0.7 (AUC = area under the ROC curve; Elith & Graham, 2009; Lobo et al., 2008; Phillips & Dudík, 2008), wherein a bootstrap approach with a 80% data split for model training and 20% used for model testing was performed for model evaluation. Subsequently, we computed based on the raw predictions the corrected Akaike information criterion (AICc; Warren & Seifert, 2011) for each 25 replicates of each combination of settings. The optimal settings per species were determined by the lowest average AICc over the replicates.

Using the best fitting model settings determined via AICc, the final models were computed based on 100 replicates using the same bootstrap approach for evaluation, and projected on the full geographic range in cloglog format, which estimates the probability of presence for the target species ranging between 0 and 1 (Phillips et al., 2017). The 10 percentile training omission cloglog threshold was set as threshold for presence-absence.

Potential extrapolation errors were quantified using MESS (Multivariate Environmental Similarity Surfaces; Elith et al., 2010). In these areas, predictions should be treated with caution as they require extrapolation beyond the environmental training range of the models. To estimate the environmental buffering capacity of the habitats by distributional shifts in depth, we extracted for each grid cell with a maximum depth of 150m the annual maximum SSTs and the maximum temperatures at the minimal, median, and maximum depth within occupied biomes. The relative differences in temperatures were plotted against depth to illustrate the environmental capacities at each site, and against latitude to illustrate the differences between tropical and temperate regions. Furthermore, we quantified those areas exceeding a maximum SST of 31°C under current and RCP 6.0 conditions to quantify the amount of likely limiting conditions.

The SDM output was subsequently used for creating area and line charts in Microsoft Excel to visualize richness gradients for LBF in a 1° resolution over latitudinal grid space.

Unlike our previous publication on Indo-Pacific LBF species diversity (Förderer et al., 2018), we focused solely on modeling and did not implement buffered point data of rare species with fewer

than five occurrence records. This is to ensure comparability with our future projections.

Richness maps representing present-day and future scenarios were created by overlaying individual presence-absence maps of LBF species as predicted by Maxent. Data for creating maps and richness gradients were processed in R (<https://cran.r-project.org/>) and Microsoft Excel.

The maps were illustrated using QGIS (3.14) and projected onto the WGS 1984 PDC Mercator coordinate system. The maps have a spatial resolution of 2.5-arcminutes, equivalent to about 4.5 km at the equator. The georeferenced landscape is a 1:10 m scale and was obtained from Natural Earth free vector and raster map data.

3 | RESULTS

3.1 | Documented LBF species diversity and distribution

All definitions of marine realms, provinces, and ecoregions in this publication correspond to those defined by Spalding et al. (2007).

In total, we identified 105 species of LBF belonging to six families and two orders of foraminifera (Table S2). Of all identified species, at least 12 species are circumtropic, the majority of them belonging to the order Miliolida. A number of 63 species are reported only from the Indo-Pacific and 22 species appear endemic to the Atlantic. Most of the 17 species recorded in the Mediterranean are members of the circumtropic group (10 species) or are shared with either the Indo-Pacific (6 species) or the Atlantic Ocean (1 species).

According to our literature research, the latitudinal range of LBF spans at least from 45°N in the Mediterranean Sea to 34°S at the coast of New South Wales (Australia; Figure 1a; Table S1). The widest latitudinal range in both directions is covered by members of the Peneroplidae, order Miliolida (Table S1). Among the Peneroplidae, the non-striate genus *Laevipeneroplis* is particularly diverse in the western tropical Atlantic as is the soritid chlorophyte-symbiont-bearing sub-family of the Archaiasinae.

The diatom-bearing Rotaliida are more diverse in the Indo-Pacific with one family, the Calcarinidae, being a unique and characteristic feature of the Indo-Pacific LBF fauna.

Analyzing own additional material from Sao Tomé and Príncipe revealed the presence of a few small specimens of *Operculina* sp. (Figure S2), thereby representing the first documented record of this genus in the eastern tropical Atlantic. The Sao Tomé species' features very much resemble the figures of Caribbean *Operculina* specimens illustrated by McCulloch (1981), and we therefore tentatively synonymized our identifications. Future studies are needed to determine if it is a separate species or belongs to a circumtropic species that is also present in the Indo-Pacific.

Of the 105 species identified, a relatively large proportion (31 species) is considered rare, as they were reported in few publications or localities only. These rare taxa could not be included in the SDM analyses due to the small number (<5) of occurrence records.

3.2 | Species distribution models

We established SDMs using Maxent to assess present-day and future patterns of LBF species richness. For the present-day richness patterns, we present two different models. The first one is based on a set of different environmental variables including water chemistry and nutrition-related variables (Figure 1b; Table S3), and the second one (Figure 2a) is based solely on SST and salinity-related variables to allow direct comparison with our future SDM projections for the time periods 2040–2050 and 2090–2100 (Figure 2b,c; Figures S3–S5).

3.3 | Present-day LBF species richness pattern

As environmental variables used in our present-day SDM (Figure 1b), we generated PCAs based on 33 marine nutrition and other abiotic

layers from Bio-ORACLE for ecological modeling in Maxent (Table S3). PC1 is mainly driven by salinity, phosphate, photosynthetically available radiation, and temperature-related variables capturing 32.3% of the total variance, PC2 is mainly driven by temperature, chlorophyll, and nitrate-related variables (21.6% of the total variance), PC3 is mainly driven by phosphate variables (13.9% of the total variance), and PC4 by nitrate variables (7.6% of the total variance). The remaining PCs 5, 6, and 7 together explain 11.2% of the total variance.

The evaluation of the variable contribution implies that for most of the species PC3 had the highest explanatory power (Table S4), indicating that nutrient concentration was deemed the most useful parameter.

The average performance of the Maxent models is considered significantly better than random (mean AUCtest = 0.855, median AUCtest = 0.861, range AUCtest = 0.657–0.996; Table S4).

Projected species richness ranges from one to a maximum of 53 species (Figure 1b). The most species-rich areas are located

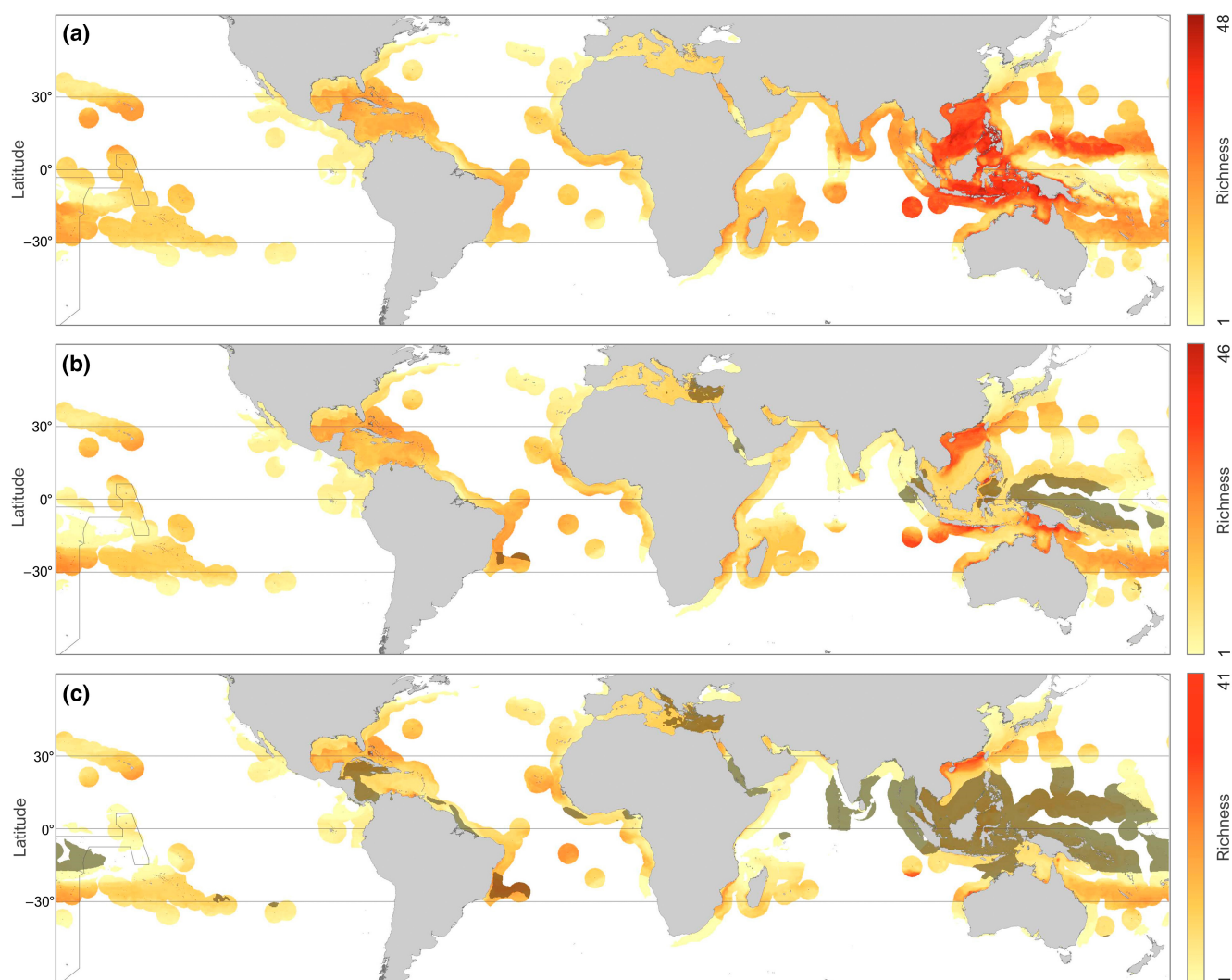


FIGURE 2 Predicted global larger benthic foraminifera species richness as per species distribution model output using sea surface temperature and salinity as environmental variables for modeling under (a) present-day and (b, c) future climate conditions for time periods 2040–2050 (b) and 2090–2100 (c) under Representative Concentration Pathway 6.0 scenario. Areas where projections are less reliable (Multivariate Environmental Similarity Surfaces) are indicated in gray shades.

in the Western Coral Triangle and Sahul Shelf provinces of the Central Indo-Pacific biogeographic realm. There is a steeper decline in richness toward the eastern Pacific margin than to the western Indian Ocean. Maximum richness (12 species) in the eastern Pacific is not reached in the tropical zones but in the Gulf of California (Cortezian ecoregion) that is part of the Temperate North Pacific realm. In the Western Indian Ocean, the coastlines of Kenia, Tanzania, and the Mozambique Channel are predicted to have up to 32 LBF species.

In the Atlantic, the highest richness (28 species; Figure 1b) is projected for the northern part of the tropical northwestern Atlantic province. There, the largest area of high richness is shown for the Bahamian ecoregion, more precisely the Bahama Banks that represent extensive shallow-water submerged carbonate platforms around the Bahama archipelago. Similar high near-coastal richness is also projected for the northern Greater Antilles ecoregion (southern Cuban coast), parts of the southern Gulf of Mexico, the Floridian and the Southern Caribbean ecoregions.

In the Mediterranean Sea, species richness is distributed quite homogeneously. The highest richness (16 species) is predicted to occur in the Gulf of Iskenderun that is part of the Levantine Sea ecoregion in the northeastern Mediterranean.

When compared per latitude, the Indo-Pacific has a more unimodal latitudinal gradient and markedly higher maximum species richness than the Atlantic between 30°N and 50°S (Figure S6).

3.4 | Temperature- and salinity-based SDMs

For establishing the climate data SDMs (Figure 2; Figures S3–S5), we used a set of SST- and salinity-related environmental variables (Table S5).

Of the 74 species included, temperature-related variables contributed more to the distribution of the majority (42 species) and salinity-related variables contributed more to the distribution of 32 species, indicating that temperature had a slightly greater effect on future distribution patterns than salinity (Table S5).

The average performance of the Maxent models is considered significantly better than random (mean AUCtest = 0.802, median AUCtest = 0.814, range AUCtest = 0.476–0.992; Table S5).

3.5 | Present-day species richness pattern

The resulting richness pattern (Figure 2a) is essentially consistent with the full-environmental data model (Figure 1b) but shows a somewhat less differentiated pattern in most regions. Maximum richness also peaked in the Western Coral Triangle ecoregion but is lower (48 species) than in the full-environmental data model (53 species), and less focused. The Atlantic overall appears richer, as does the Central and Eastern Pacific. One major difference is noticed for the East Caroline Islands ecoregion in the Tropical Northwestern Pacific province that appears markedly species richer than in the

full-environmental data model. To ensure comparability with our future projections, we did not create a hybrid map by merging the rare species as separate layers with the SDM, as we did for our Indo-Pacific analysis (Förderer et al., 2018). Therefore, the Philippines, from which several rare species are reported (e.g., McCulloch, 1977), do not stand out as the bull's eye of species diversity.

3.6 | Species richness patterns under projected environmental change

Comparison of the latitudinal gradient patterns of SST and salinity-based SDMs for today and the periods 2040–2050 and 2090–2100 under the RCP6.0 scenario shows reduced maximum richness per latitude and an increasingly sharp and widening bimodal pattern for the future (Figure 3). Future species richness in low latitudes, particularly between 10°N and the equator, could be reduced by more than a half by the time period 2090–2100.

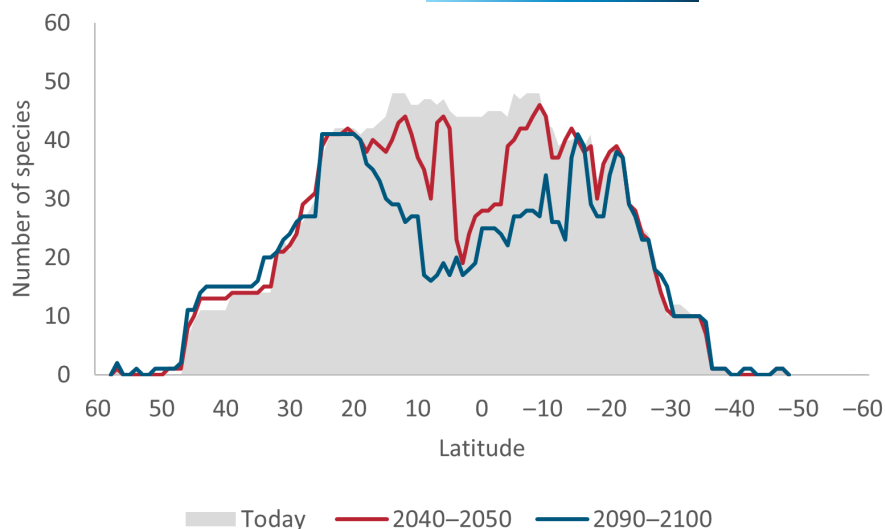
In the Indo-Pacific, the models show a progressing severe reduction in species richness in almost all regions of low latitude (Figure 2b,c), and a distinctive bimodal latitudinal pattern (Figures S7 and S8). Latitudes 20°N to 15°S are broadly and particularly affected and richness is reduced in general. Zones of higher species richness are dwindling and being pushed to the margins, for example, toward the Southern China ecoregion in the North and the Northwest Australian Shelf and Tropical Southwestern Pacific provinces in the South. Regions above latitudes 20°N and below 15°S generally exhibit less net loss of species richness.

In the Atlantic, on the contrary, bimodality also strengthens (i.e., reduced richness at low latitude), but maximum species richness slightly increases, particularly in the southern hemisphere (Figures S9 and S10). However, a reduction of potential species richness is also predicted for low latitudes between 10°N and just below 0°S, for example, affecting the North Brazil Shelf province and the Eastern Caribbean ecoregion. Zones of higher richness are also being largely pushed to the margins in the Western Atlantic: to the Bahamian, the Floridian, and the Southern Gulf of Mexico ecoregions in the North and the Eastern Brazil and Trinidad and Martin Vaz Islands ecoregions in the South. In contrast, the St. Helena and Ascension Islands province in the Central Tropical Atlantic and the West African Transition province in the Eastern Tropical Atlantic are predicted to become progressively species richer. Also, in the Mediterranean Sea, the models show a westward progression of enrichment.

By the time period 2040–2050, SST conditions move out of the current training range for regions in the Central Indo-Pacific, as reflected by the MESS areas indicative for less reliable model projection due to extrapolation beyond the training ranges (Figure 2b). This is particularly the case for the Eastern Coral Triangle province, and elsewhere like in the eastern Mediterranean, a smaller part of the Southern Red Sea, Eastern Brazil, and the Aegean and Levantine Sea.

The extent of areas requiring extrapolation into novel conditions increases by the time period 2090–2100 and then cover almost entirely the lower latitude zones in the Central Indo-Pacific from the

FIGURE 3 Global latitudinal maximum richness gradients based on species distribution model output (present-day and future Representative Concentration Pathway 6.0 scenario) with use of temperature- and salinity-related variables for computing



Philippines to the Sahul Shelf, the Western Indian Ocean around India and the Maldives, large part of the Southern Red Sea, the eastern and central Mediterranean, the Southern and Southwestern Caribbean, and Eastern Brazil. Large proportions in those areas show a strong increase in grid cells exceeding a SST of 31°C in the future (Figures S11–S14). The quantification of possible buffering effects by shifting distributions toward higher depths indicates that the buffering capacities at the vast majority of sites range between 0 and 3°C (Figure S14). On a latitudinal gradient, the buffering capacities are lowest in tropical regions and highest in northern latitudes (Figure S14).

The SDMs projected onto the remaining RCP scenarios (RCP2.6, RCP4.5, and RCP8.5) returned qualitatively identical results with severe reduction of species richness in the Central Indo-Pacific, the Atlantic being less affected, and an increase in areas of uncertainty with time, most extensively for the worst-case scenario RCP8.5 (Figures S3–S5).

4 | DISCUSSION

Using global-scale modeling on LBF for the first time, we found a potentially severe reduction of species richness under future climate change conditions, particularly in the central Indo-Pacific that represents today's diversity stronghold of LBF. The trophic level was found to be most influential on present-day biogeographic distribution, closely followed by salinity and temperature. Using only salinity- and temperature-related variables, future projections were more so driven by temperature. Potential buffering capacities by distributional changes in deeper habitats were rather restricted to a few °C and lowest in the tropics. However, we cannot exclude buffering effects of fine-scale microclimatic pockets, which may be underestimated given the broad-scale environmental variables used herein (Bachman et al., 2022). Furthermore, the spatial resolution of our environmental predictors may affect our results. Present-day SST in BioOracle is derived from remote sensing and represents on-spot measurements that are capable to capture also comparatively fine-scale differences within their spatial resolution. However, we

acknowledge that very small-scale patterns such as tidal ponds or small, shallow lagoons may not be as accurately captured due to the spatial resolution of the data set. Given the global scale of our analysis, this may affect only very small portions of our study area. On the other hand, with rising SST also, these shallow parts will have a higher temperature which will likely show a linear response with the broader scale SST making our predictors qualitatively suitable as the derived thresholds will scale up equally in the future.

4.1 | Present-day biogeographic patterns

Our study to date represents the most comprehensive data compilation on LBF species' identities and biogeographic distributions in the world's oceans. According to our SDMs, species diversity is markedly higher in the Indo-Pacific than in the Atlantic Ocean and today's highest species richness is found in the Indo-Pacific's Western Coral Triangle province (Figure 1b). This is in alignment with biogeographic analyses on other tropical shallow-water taxa (e.g., Roberts et al., 2002; Sanciangco et al., 2013; Tittensor et al., 2010), and was discussed in detail in our previous analysis on Indo-Pacific LBF species richness (Förderer et al., 2018). The discrepancy in tropical marine diversity between the Atlantic and the Indo-Pacific oceans is largely attributed to historic events and geological processes (Keith et al., 2013; Leprieur et al., 2015; Pellissier et al., 2014; Renema et al., 2008).

Previous biogeographic analyses on Atlantic LBF diversity were limited to high-rank taxonomy and found diversity to be highest along the Antillean arc and off the Brazilian coast (10–12 genera; Weinmann, 2009; Weinmann & Langer, 2010). Our SDMs now primarily identify the northern part of the Caribbean Sea (i.e., the Bahamian ecoregion) as the most likely center of richness (28 species), also considering the extent of suitable area. This suggests that the most species-rich areas in the Indo-Pacific would have about twice as many LBF species as those in the Atlantic (Figure 1b; Figure S6). However, since we could only include species with at least five reported occurrence records in our modeling, a considerable number of rare species (about 30% of all identified) is not

represented. Considering that the majority of the rare species is reported from the Indo-Pacific, it is more likely that the disparity is closer to three to one (Table S2). Yet, while the majority of LBF taxa is more diverse in the Indo-Pacific, this does not apply to chlorophyte-bearing miliolid taxa as the Archaiasinae and *Laevipeneroplis* spp. (Hallock & Peebles, 1993; Table S2). Chlorophyte-bearing taxa are rare in the Indo-Pacific but are a typical element of the Caribbean LBF fauna where they are reportedly thriving in a wide range of shallow habitats and environmental conditions (Amergian et al., 2022; Hallock & Peebles, 1993; Langer & Hottinger, 2000; Prazeres & Renema, 2019). They are largely absent from the eastern Atlantic and most of the species reported from eastern Atlantic localities are globally distributed (Fajemila & Langer, 2017). This may indicate limited eastward dispersal. However, the eastern Atlantic LBF fauna is still not well studied, and our SDMs suggest that conditions would allow for higher species richness regionally (i.e., West African Transition province; 20 species at maximum). Our finding of some small specimens of *Operculina* sp. (Figure S2) in material from Sao Tomé and Príncipe also indicates underreporting of eastern Atlantic LBF diversity. The genus *Operculina* is very common and locally abundant in nearshore sediments in the central Indo-Pacific and western Indian Ocean (Langer & Hottinger, 2000). It was present in the Caribbean region during the Upper Eocene and the Oligocene (Cushman, 1930) but it has been rarely reported in modern samples: from three localities in the Caribbean (McCulloch, 1981) and from Brazil (Lévy et al., 1995). However, the presence of modern *Operculina* spp. in the Atlantic Ocean has been widely questioned (Cushman, 1930; Langer & Hottinger, 2000), presumably because of its scarceness, small size, and the lack of photographic images. Small specimens of *Operculina* may not only be easily overlooked, but also confounded with immature specimens of *Heterostegina depressa*, a globally distributed nummulitid. Our record of *Operculina* sp. now confirms its existence in the Atlantic Ocean and further represents the first record from the eastern tropical Atlantic.

4.2 | Future patterns

Our future projections suggest a potential dramatic reduction of LBF species richness, particularly in today's diversity stronghold—the central Indo-Pacific (Figure 2b,c). Both temperature and salinity shape future richness patterns of LBF, with temperature having a slightly stronger influence. Temperature is known to be a primarily limiting parameter for LBF distribution (Langer & Hottinger, 2000) with combined elevated temperature and salinity levels showing synergistic effects on survival and function of LBF (Kenigsberg et al., 2022). Although our modeling shows an increase in areas of uncertainty for the future, our results are in line with projections of dramatic biodiversity losses in the Coral Triangle ecoregion and the general redistribution of marine biodiversity (Couce et al., 2013; Molinos et al., 2015). The tremendous loss of suitable shallow-water habitat in the central Indo-Pacific will be difficult to offset by the potential gain of new suitable coastal areas from sea-level rise and the shifting of tropical

climate zones toward higher latitudes (Hallock, 2005). Potential refugia for Indo-Pacific LBF are located primarily in the northern South China Sea, the Northwest Australian Shelf, and the Southern Tropical Pacific, indicating a progressive “splitting” of the center of diversity (Figure 2b,c). Our SDMs further indicate that as early as by time period 2040–2050, LBF will be confronted with completely novel conditions in low-latitude regions in the Central Indo-Pacific, and in parts of the eastern Mediterranean, the southern Red Sea, and South Brazil (Figure 2b; Lotterhos et al., 2021). By 2040–2050, there are also still some isolated “pockets” in the Philippine islands where high species richness could be maintained. However, this becomes very uncertain for time period 2090–2100, where large proportions of the diversity hotspots exceed a SST of 31°C.

While our models predict an eradication of the center of marine tropical biodiversity in the central Indo-Pacific, a large portion of high diversity areas in the Atlantic could be spared and might even show an increase in species richness (Figures S9 and S10). This is in alignment with projected global coral reef suitability that shows a marked temperature-driven decline in the future, particularly for the central Indo-Pacific and less so for the Atlantic and marginal environments (Couce et al., 2013). Our models are also consistent with future projections for planktonic foraminiferal diversity that show a substantial loss of species richness at low latitudes, resulting in a pronounced bimodal latitudinal pattern (Yasuhara et al., 2020).

The emerging widening and deepening of the species richness gap in low latitudes according to our future SDMs (Figures S7–S9) supports the hypothesis that the general bimodal pattern of the latitudinal marine biodiversity gradient is driven by equatorial temperatures being beyond the upper physiological thermal tolerances of species (Chaudhary et al., 2016, 2017; Yasuhara et al., 2020). An increase in bimodality and increasing habitat fragmentation in low latitudes could lead to disruption of genetic connectivity among LBF populations (Choo et al., 2020).

Range expansions of tropical LBF species to higher latitudes on the other hand will, in turn, impact native biota and carbonate production, resulting in substantial changes in ecosystem function (Mouanga & Langer, 2014).

Multiple laboratory and field studies have analyzed responses of selected LBF species to changing environmental conditions (review in Narayan et al., 2022). This includes elevated nutrient levels (e.g., El Kateb et al., 2018; Prazeres et al., 2016; Schmidt et al., 2011) as well as thermal and salinity tolerances of LBF species (e.g., Kenigsberg et al., 2022; Pinko et al., 2020; Prazeres et al., 2016, 2017; Schmidt et al., 2016; Stühr et al., 2017, 2021; Titelboim et al., 2019).

The results suggest mixed potential responses to climate change. Some studies reported broad tolerances or even positive effects on LBF species to elevated temperatures (Stühr et al., 2017; Weinmann & Langer, 2017) or nutrients (Akther et al., 2020; Schmidt et al., 2011). Others show that, at least above a certain tolerance threshold, vitality decreases (e.g., Pinko et al., 2020). Nevertheless, survivorship declines with combined stressors (Kenigsberg et al., 2022; Prazeres et al., 2017; Schmidt et al., 2014; Stühr et al., 2017, 2021) and long-term exposure to temperatures above 31°C (Doo et al., 2014;

Narayan et al., 2022; Stühr et al., 2017). Given the RCP 6.0 storyline, our analyses suggest that SST in large proportions especially of the species richest areas in the Indo-Pacific may be beyond this threshold. Next to latitudinal range shifts, some species may also respond by shifting their distribution to deeper habitats counterbalancing the warming trends. However, assessing the thermal buffering capacities in these areas our results suggest that only a limited potential of a few °C do exist even if the species shift their distributions toward deeper habitats (Figure S14).

The reactions to changing environmental conditions are not only species specific, but also vary intra-specifically depending on adaptations to local habitat conditions (Choo et al., 2020; Prazeres et al., 2016, 2021; Weinmann & Langer, 2017). Species populations being regularly exposed to fluctuating conditions have shown to be less sensitive than those living in stable environments (Prazeres et al., 2016). Research of potential acclimatization capacities of LBF has so far been limited to the most abundant and widespread taxa because of their important role as carbonate producers. Thus, tolerance ranges of the vast majority of LBF species remain unknown, and only limited conclusions can be drawn about future patterns of species richness.

Our sensitivity analyses suggest that the environmental buffering capacities by shifting distributions toward deeper habitats within the general occurrence of the species is limited, especially in the most species-rich areas in the tropics. For the vast majority of LBF taxa, depth ranges are poorly known and most observations come from rather shallow study sites with a depth range between 0 and 30 m. This likely reflects the accessible depth range by scuba diving. Even if species are able to shift their distributions to deeper habitats, light intensities will also be lower further reducing the habitat quality at these sites.

Larger benthic foraminifera diversification and carbonate production have been closely linked to ocean climatic conditions throughout Earth's history (BouDagher-Fadel, 2008). After the devastating Cretaceous-Paleogene boundary (KPB) mass extinction, by which LBF were severely affected and over 80% of all LBF species disappeared, the group diversified and started to develop larger and more complex tests again during the Paleogene (BouDagher-Fadel, 2008). These developments were initiated and driven by several hyperthermal events of which the Paleocene Eocene Thermal Maximum (PETM; 56 Mya) is the most widely known (Whidden & Jones, 2012).

The PETM was a global greenhouse warming event caused by a massive release of carbon dioxide and other greenhouse gases into the atmosphere within less than 20 ka (Keller et al., 2018; McNerney & Wing, 2011). During this time, SSTs in low latitudes were raised by 4–5°C, resulting in 33–34°C warm tropical waters in the early Eocene (Tripathi et al., 2003) and a widening of the tropical reef zone to higher latitudes (Scheibner & Speijer, 2008). While the PETM triggered a massive decline in deep-water benthic foraminifera (Keller et al., 2018; Thomas, 1998), it is not considered a major extinction event for other taxa, including LBF (Keller et al., 2018; Scheibner et al., 2005; Speijer et al., 2012).

However, it did also lead to faunal turnover in LBF (Hottinger & Schaub, 1960; Scheibner et al., 2005), reflected primarily in the onset of species diversification, but also in the initial disappearance and later

replacement of taxa (Hottinger, 1998; Orue-Etxebarria et al., 2001; Whidden & Jones, 2012). Especially affected at the onset of the PETM were taxa that were highly-adapted to oligotrophic conditions that were then replaced by moderately adapted successors (Scheibner & Speijer, 2008; Scheibner et al., 2005). Similar observations have been made for other hyperthermal events of the Paleogene: a pattern of an increase in the number of last occurrences of LBF species followed by an increase in the number of first occurrences (Whidden & Jones, 2012). This suggests that the overall increase in species diversity during the Paleogene was due to faunal turnover and driven by the overall warming trend as well as available ecological space following extinctions (Hallock, 2005; Whidden & Jones, 2012).

The PETM is often used in climate research to understand what environmental changes might occur as a result of current man-made climate change and when those changes might happen (Keller et al., 2018). However, it is difficult to estimate upcoming ecological and biological changes based on what happened during the PETM because today's warming is much faster (Keller et al., 2018). Actual carbon dioxide emissions to the atmosphere are 9–10 times higher than emissions during the PETM, making today's warming trend the fastest of any climate event since the extinction of non-avian dinosaurs (Gingerich, 2019). While the PETM lasted about 170 ka, we do not know yet how long the actual unabated warming trend will last and which one of the IPCC's scenarios will come closest to reality. Another factor of uncertainty in the impact on modern organisms is that current climate change starts from a cooler baseline than at the onset of the PETM, when warm and generally ice-free conditions prevailed, indicating that taxa during the PETM were better adapted to elevated temperatures (Scheibner & Speijer, 2008). Our modeling results support the assumption that a PETM-like faunal response is a kind of best-case scenario and we are more likely heading toward a KPB-like mass extinction (Keller et al., 2018).

Current IPCC reports (IPCC, 2021, 2022), studies on LBF tolerances to multiple stressors (review in Narayan et al., 2022), and the similarity of our modeling analyses to those of other tropical marine taxa (e.g., Couce et al., 2013; Molinos et al., 2015; Yasuhara et al., 2020) suggest a bleak future for marine calcifiers altogether. Although LBF have shorter lifespans and faster generation cycles than, for examples, corals and may adapt more quickly, it is uncertain whether their adaptive capacity can keep up with the pace of current climate and environmental change (Lotterhos et al., 2021).

Modeling alone cannot account for all parameters that affect a species' distribution and survivability in the face of climate change (e.g., altered substrates; Girard et al., 2022). However, in combination with the fossil record and field and laboratory analyses, it is a helpful tool to gain insight into a possible future.

We conclude that global biogeographic patterns of LBF are expected to undergo fundamental changes including loss of species in the course of climate change. Fragmentation of habitat and separation of populations might drive parapatric speciation in the Indo-Pacific in the aftermath of extinction (Leprieur et al., 2015).

This first global-scale modeling approach highlights the need to gain more knowledge about species-specific tolerances and how

LBF species may be able to adapt to changing conditions. Further research and a better understanding of both aspects are key to anticipating the impacts of climate change on LBF worldwide.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Dryad at <http://doi.org/10.5061/dryad.pnvx0k6rq>. The related software is being published at Zenodo: <https://doi.org/10.5281/zenodo.7292770>. Additional information is available from the corresponding author upon reasonable request.

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