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RESEARCH ARTICLE

Acidification and deoxygenation matter in assessing redistribution of global cold-water coral biodiversity induced by climate change

Shuaishuai Liu,[1,2,3] Bingqing Xiao,[1,2,3,4] Ákos Bede-Fazekas,[5,6] Stefano Mammola,[7,8] Jorge García Molinos,[9] Jamie M. Kass,[10,11] Jorge Assis,[12,13] Chen Lin,[1,2,3] Junmei Qu,[1,2,3] Hongwei Huang,[1,2,3] Qiang Lin,[1,2,3,15*] Zhixin Zhang [1,2,3,14,15*]

[1]State Key Laboratory of Tropical Oceanography, Guangdong Provincial Key Laboratory of Applied Marine Biology, South China Sea Institute of Oceanology, Chinese Academy of Sciences, Guangzhou, China; [2]Marine Biodiversity and Ecological Evolution Research Center, South China Sea Institute of Oceanology, Guangzhou, People's Republic of China; [3]University of Chinese Academy of Sciences, Beijing, People's Republic of China; [4]College of Life Science and Technology, Jinan University, Guangzhou, China; [5]Institute of Ecology and Botany, HUN-REN Centre for Ecological Research, Vácrátót, Hungary; [6]Department of Environmental and Landscape Geography, Institute of Geography and Earth Sciences, ELTE Eötvös Loránd University, Budapest, Hungary; [7]Molecular Ecology Group (MEG), Water Research Institute (IRSA), National Research Council (CNR), Verbania, Italy; [8]Finnish Museum of Natural History, University of Helsinki, Helsinki, Finland; [9]Arctic Research Center, Hokkaido University, Sapporo, Japan; [10]Graduate School of Life Sciences, Tohoku University, Miyagi, Japan; [11]Advanced Institute for Marine Ecosystem Change (WPI-AIMEC), Tohoku University, Sendai, Japan; [12]Centre of Marine Sciences, University of Algarve, Faro, Portugal; [13]Faculty of Bioscience and Aquaculture, Nord Universitet, Bodø, Norway; [14]Global Ocean and Climate Research Center, South China Sea Institute of Oceanology, Guangzhou, People's Republic of China; [15]Sanya Institute of Ocean Eco-Environmental Engineering, Sanya, People's Republic of China

Abstract

The ocean is undergoing significant changes, including warming, acidification, and deoxygenation, which pose great challenges to marine biodiversity. However, most models projecting the impacts of climate change on marine species overlook predictor variables critically meaningful for species' ecologies such as pH and dissolved oxygen. The recent release of high-resolution projections of different future climate-change scenarios offers the opportunity to explore species redistribution under multiple threats beyond ocean warming. Accordingly, we conducted a global comparative analysis to study the impact of incorporating predictor variables describing pH and dissolved oxygen into marine species distribution models. We used models trained for 268 cold-water coral species to project potential future distributions for different climate and dispersal scenarios over different time periods. We found that, irrespective of scenario or period, models using pH and dissolved oxygen projected 11.5–21.4% higher impacts of climate change than those without them. For instance, by the end of the century under a high emission scenario, models including pH and oxygen projected an average range contraction of 48.2% for cold-water corals under a no-dispersal scenario, compared with a 26.8% contraction projected by models excluding these two predictors. Given the substantial differences in the predicted distribution patterns and the biological importance of these variables, we highlight that researchers should consider more diverse sets of predictor variables when predicting future range shifts for marine biodiversity assessments under climate change.

In the marine environment, the effects of climate change are expressed principally through ocean warming, acidification, deoxygenation, and shifts in hydrodynamic regimes. These changes are predicted to drive a global redistribution of biodiversity with major ecological, socioeconomic, and governance implications (e.g., García Molinos et al. 2016; Pinsky

*Correspondence: linqiang@scsio.ac.cn; zxzhang@scsio.ac.cn

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Shuaishuai Liu and Bingqing Xiao contributed equally to this work.

et al. 2018; Lenoir et al. 2020). Therefore, a better understanding of species' distributional dynamics under climate change is urgently needed. This is particularly true for marine species, as they are shifting their distributions comparatively much faster than terrestrial ones (Lenoir et al. 2020). This can be attributed to the fact that geographic distributions of marine ectotherms tend to fill their physiological thermal tolerances more closely (Sunday et al. 2012), and because the ocean offers a thermally more homogenous and less fragmented environment than on land, resulting in narrower thermal safety margins and faster range shift rates of marine species (Pinsky et al. 2019).

Species distribution models (SDMs) correlate species' distributional data and environmental predictors to predict species habitat suitability in space and/or time (Guisan et al. 2017). Despite being one of the most widely used tools to predict species' range shifts in response to climate change (Araújo et al. 2019), applications of SDMs in the marine realm are far behind those of the terrestrial realm mainly because of the comparatively greater challenges in acquiring data on marine environments and species' distributions (Robinson et al. 2011; Melo-Merino et al. 2020). However, the number of SDM studies focusing on marine species has increased exponentially in recent years as open data on species distributions and marine environmental layers are becoming widely available.

Despite the significant body of work on the application of marine SDMs for species conservation and management (e.g., Robinson et al. 2011), most studies still use a reduced number of common environmental predictor variables often related to temperature (e.g., Qu et al. 2023; Chen et al. 2024). Although useful, this practice may fail to adequately capture the wide range of environmental variables driving marine species' redistributions under climate change (e.g., Doney et al. 2012). Besides ocean warming, climate change is altering ocean chemistry through processes such as acidification and deoxygenation. By the end of this century under a high-emission scenario, global ocean oxygen levels are projected to decline by 3.45% (Bopp et al. 2013), nearly three-quarters of the ocean will experience deoxygenation (Gong et al. 2021), and global surface ocean pH is anticipated to drop by 0.3 units, indicating significant ocean acidification (IPCC 2021). A growing body of evidence supports that ocean acidification and deoxygenation have important consequences for marine life and are recognized as important contributing factors to past mass extinction events (Gruber 2011; Sampaio et al. 2021). However, very few SDM studies to date have incorporated these two important predictors when exploring redistribution dynamics of marine species under climate change.

The increasing availability of newly released high-resolution datasets, such as Bio-ORACLE version 3.0 (Assis et al. 2024), provides an opportunity to explore the redistribution of marine biodiversity under multiple threats, including ocean warming, acidification, and deoxygenation. Accordingly, we used cold-water corals as case-study organisms to develop SDMs, incorporating and excluding predictors for pH and oxygen, to quantify differences in their projected future redistributions. We selected cold-water corals for several reasons. First, they are important marine habitat engineers that are highly susceptible to the impacts of climate change (Roberts et al. 2016; Tong et al. 2023; Fragkopoulou et al. 2025), including ocean warming (Brooke et al. 2013), ocean acidification (Roberts et al. 2006), and deoxygenation (Portilho-Ramos et al. 2022). Second, cold-water corals typically inhabit deep waters, which are experiencing dramatic chemical and physical changes that are expected to accelerate in the future (Sweetman et al. 2017; Brito-Morales et al. 2020). Third, a high-quality distribution dataset for cold-water corals is publicly available (Balogh et al. 2023).

To address this knowledge gap, we first carried out a literature review to determine how frequently pH and oxygen have been accounted for in studies projecting the redistribution of marine species under climate change. Then, we conducted a global comparative analysis to test the impact of incorporating pH and dissolved oxygen into marine SDMs while controlling for the number of predictors. We trained models for 268 cold-water coral species and projected their potential future distributions under multiple climate and dispersal scenarios across different time horizons. We hypothesized that models accounting for pH and oxygen should project more serious impacts of climate change (e.g., greater extirpations and larger redistributions) than models without them.

Materials and methods

Literature review

To estimate the quantity and type of predictors used by SDM studies analyzing the redistribution of marine species under climate change, we conducted a literature search on the Web of Science (April 23, 2025) using the following search string:

TS = ("marine" OR "ocean" OR "sea") AND TS = ("Species distribution model*" OR "Ecological niche model*" OR "Bioclimatic envelope model*" OR "Bioclimate envelope model*" OR "Climate envelope model*" OR "Niche model*" OR "Distribution model*" OR "Habitat suitability model*" OR "Correlative model*") AND TS = ("climate change" OR "climate warming" OR "global warming") AND TS = ("range*" OR "distribution*").

We focused the search on peer-reviewed research articles (i.e., we excluded literature reviews, opinion papers, gray literature, and book chapters) published between January 1, 1980 and December 31, 2024.

We made a first screening of the title and abstract of the initial retrieved set of articles ($n = 1674$) against the following inclusion criteria: papers had to (1) use SDMs for (2) prediction of marine species distributions (3) using marine predictors (e.g., papers modeling intertidal species using terrestrial

predictors did not qualify). We applied an inclusive screening by retaining articles that met the three criteria as well as those in doubt (i.e., where the title and abstract information was not specific or complete enough to verify the criteria). This resulted in a preliminary subset of 689 articles retained for full text revision. Subsequently, we screened the full-text of the remaining papers to ensure that all three inclusion criteria were strictly met, resulting in a final set of 516 studies retained for data extraction (Supporting Information Table S1 and Fig. S1). For each of these papers, we extracted the publication year, study extent, target taxa, predictors used for model development, and the broad modeling approach used in each study (i.e., correlative or mechanistic). We also defined the geographic extent for each study according to one of the following three standards given in order of preference: (1) reported coordinates in terms of longitude and latitude, (2) marine ecoregions at the province level as delineated by Spalding et al. (2007), and (3) Food and Agriculture Organization Fishing Areas (available at https://www.fao.org/fishery/en/area/search).

Species list and distribution data

We retrieved occurrence records from the global distribution dataset of cold-water corals provided by Balogh et al. (2023). This dataset includes quality-controlled geographical distributions of cold-water coral species from online biodiversity repositories and peer-reviewed publications (*see* details in Balogh et al. 2023). To minimize the adverse effect of sampling bias on model fitting, we filtered occurrence records for each cold-water coral species by keeping one occurrence per 3-arcmin (~ 5.5 km at the equator) grid cell (e.g., Zhang et al. 2024a), matching the spatial resolution of marine predictors for model development (Assis et al. 2024). Given that the discrimination ability of a SDM is closely correlated with sample size, we only considered species with over 30 occurrence records (e.g., Wisz et al. 2008). After completing these data filtering procedures, a total of 47,573 occurrence records for 268 cold-water coral species were retained for analysis, with an average (± SD) of 177 (± 268) occurrences per species (minimum: 30 records, maximum: 2461 records; Supporting Information Table S2 and Fig. S2).

Marine predictors

Cold-water corals grow slowly and typically exhibit long lifespans (e.g., Sigwart et al. 2025). Moreover, corals are susceptible to changes in a variety of marine environmental conditions including temperature (Frieler et al. 2013), salinity (Coles and Jokiel 2018), current velocity (Kumagai et al. 2018), pH (Anthony et al. 2008), and dissolved oxygen (Alderdice et al. 2022). Therefore, for each of the five environmental variables, we extracted the maximum and minimum monthly values observed over the period 2000–2010 from the BIO-ORACLE version 3.0 database (Assis et al. 2024). We considered these values because species' physiological performances are typically determined by extreme conditions (e.g., Zhang et al. 2021). Apart from the marine environmental predictors, we also considered two topographical predictors from BIO-ORACLE, bathymetry and terrain ruggedness index, due to their important roles in determining the distributions of cold-water corals (Tong et al. 2023). Collinearity among predictors was assessed via pairwise Pearson's correlation coefficients using a threshold of $|r| > 0.7$ for variable reduction (Dormann et al. 2013) (Supporting Information Fig. S3). Among highly correlated pairs of predictors, we considered the most biologically meaningful one according to evidence from the literature (*see* Supporting Information Table S3 for details). As a result, we considered a final set of seven predictors: water depth, terrain ruggedness index, maximum temperature, minimum salinity, minimum current velocity, minimum dissolved oxygen, and minimum pH. We then developed SDMs with two predictor variable sets: (1) all seven predictors, and (2) with five predictors leaving out pH and oxygen.

With respect to future projections of marine environmental predictors, we considered two shared socioeconomic pathways (SSPs; SSP2-4.5 and SSP5-8.5) for two future time-periods (2040–2050 and 2090–2100). We retrieved future data layers from the BIO-ORACLE database, which are based on an ensemble of 11 CMIP6 Earth System Models (*see* details in Assis et al. 2024).

Model development

To build SDMs, we selected the maximum entropy model MaxEnt 3.4.3, a presence-background machine-learning algorithm with tunable complexity parameters (Phillips et al. 2017). MaxEnt often outperforms other modeling algorithms in comparative studies and hence is widely used in SDM studies (e.g., Melo-Merino et al. 2020). For each species, we sampled 10,000 random background points within 1000 km buffers around occurrence records that define the study extent (Zhang et al. 2024b, 2025). Following best practices (e.g., Araújo et al. 2019), we optimized the complexity of MaxEnt models by exploring different combinations of feature classes that determine flexibility of model fit (linear [L], quadratic [Q], and hinge [H]) and regularization multiplier parameters that penalize model complexity using the *ENMeval* package version 2.0.5 (Kass et al. 2021). We fitted a total of 32 candidate models with different parameter combinations (four feature class combinations: L, LQ, LQH, and H; and eight regularization multipliers ranging from 0.5 to 4.0 at an interval of 0.5).

Here, we aimed to compare models with different numbers of predictor variables (i.e., seven vs. five predictors), but as the addition of predictor variables to a model can inflate model performance even when they have little relevance for the species (Fourcade et al. 2018), we chose an information criterion approach to model selection. We used the Akaike Information Criterion corrected for small sample sizes (AICc) to select models, which measures goodness-of-fit while applying a

penalty for additional model parameters (Warren and Seifert 2011), thus enabling the comparison of models built with predictor sets that have different numbers of predictors (Kass et al. 2020). The penalty in AICc leads to higher values for models with added predictors that do not improve model performance (lower AICc means better fit). Thus, even with this penalty, if models with pH and oxygen still have lower AICc than models without these predictors, we can say that their addition improved model fit even with the increase in model complexity. We followed the widely accepted "rule of thumb" for model selection (Burnham and Anderson 2002), which considers two or more models to have similar support when the difference with the lowest AICc value (ΔAICc) is less than or equal to 2 units, while greater differences indicate stronger support for the lowest AICc model (Burnham and Anderson 2002).

However, information criterion approaches to model selection do not consider the results of cross-validation, which is used to determine model performance on withheld data and can assess model transferability if spatial or temporal blocking is used (Roberts et al. 2017). Therefore, selecting models using AICc may not result in models with good transferability (Low et al. 2021), but cross-validation results for selected models can be evaluated to determine performance on withheld data (Kass et al. 2020). As information criterion metrics are only calculated on the full training data, we also assessed whether the selected optimal models performed well on withheld data using spatial block cross-validation. Specifically, we used the "block" approach in *ENMeval* R package, which involves splitting the occurrence and background data into four spatial blocks containing an approximately equal number of occurrence records, then iteratively building a model on three blocks and evaluating it on the withheld block. For each iteration, we measured model performance using the continuous Boyce Index (CBI), which was developed specifically for presence-background models (Hirzel et al. 2006) and measures model calibration (i.e., how well model predictions correlate with the observed proportions of occupied sites). All model predictions, including those during cross-validation, were clamped to restrict non-analog values to the extremes of the training data (default in *ENMeval*). High environmental similarity between training and validating datasets generally leads to better predictive performance. As models that include pH and oxygen predictors are more likely to encounter environmental conditions in the spatially blocked validation dataset that differ from those represented in the training dataset, we expect that our spatial cross-validation results for these models should show lower performance than for models without these predictors.

To assess the significance of the observed values of these metrics to random data, we built 100 null models based on the parameter settings for each empirical model, evaluated the null models on the same withheld data as the empirical models, and compared CBI values to null distributions (Bohl et al. 2019)—we report the resulting *p*-values and effect sizes for this analysis. We also determined the predictor importance of pH and oxygen in models with those variables via a permutation approach with 10 repetitions. In brief, for each variable, we (1) randomly permutated its values while keeping other variables unchanged, (2) made predictions using this modified dataset, and (3) computed the Pearson correlation coefficient (r) between these predictions and the reference predictions. We quantified variable importance as $1 - r$. Our modeling process is documented following the OPMAP protocol (Zurell et al. 2020) (*see* Supporting Information Table S4 for details).

We converted the continuous habitat suitability predictions into binary maps using the lowest 10 percentile of model predictions for species' occurrence records as thresholds (e.g., Zhang et al. 2021, 2025). We then quantified the similarity in predictions between the two types of models using two metrics: Schoener's D for continuous predictions and the Jaccard similarity coefficient for binary predictions. Given the vital role of species dispersal in range shifts under climate change, we projected species redistribution dynamics under two dispersal scenarios: no-dispersal scenario (i.e., coral species will not colonize areas with newly suitable conditions in the future) and unlimited-dispersal scenario (i.e., coral species will colonize any area with newly suitable conditions within their study extent in the future) (Guisan et al. 2017). We calculated the percentage of range size change for coral species under climate change using the following formula:

$$\text{Range size change} = \left(\text{Area}_{\text{future}} - \text{Area}_{\text{present}}\right)/\text{Area}_{\text{present}} \times 100\%$$

where positive/negative range size change values indicate that corals will expand/contract their geographical ranges in the future. Range size change is always null or negative under the no-dispersal scenario, whereas under the unlimited-dispersal scenario it can also be positive (contractions < expansions).

For each coral species, we also measured the extent of extrapolation (i.e., projecting habitat suitability to novel environmental space) between present-day reference environments and future environments by calculating multivariate environmental similarity surfaces (MESS; Elith et al. 2010) using the *mess* function in the *dismo* R package (Hijmans et al. 2024). The MESS maps indicate the level of similarity between a focal predictor set (here, future conditions) and a reference one (here, current conditions used for training models), with positive/negative values indicating increasingly similar/dissimilar environmental conditions, and the values are determined by the most extreme predictor in the set (Elith et al. 2010). We hypothesize that future predictor sets including pH and oxygen should have a higher proportion of negative MESS values compared to datasets without these two variables.

In addition to model selection based on information criterion approaches, we conducted a sensitivity analysis by selecting models using a 10% omission rate and CBI value (*see* details in Zhang et al. 2025). The main results were consistent

across selection criteria (Supporting Information Tables S5–S7), suggesting that our findings are insensitive to the choice of model selection criteria.

Results

Literature review

According to our literature review, a total of 516 papers published between 1980 and 2024 used SDMs to predict the redistribution of marine species under future climate change (Fig. 1 and Supporting Information Fig. S1). These studies showed strong geographical and taxonomic biases, with most papers concentrated in the northern Atlantic and western Pacific (Fig. 1a) and largely focused on marine fish species (Fig. 1b). Among these studies, 78.7% ($n = 406$) considered neither pH nor oxygen, whereas 14.5% ($n = 75$) used either pH or oxygen, and only 6.8% ($n = 35$) considered both predictors (Fig. 1c). These results indicate that pH and oxygen are largely overlooked when estimating the redistribution of marine species under climate change.

Comparison of model performance and range size

Of the 268 cold-water coral species, the model including pH and oxygen was selected as best model (ΔAICc > 2) for 165 species (61.6%), while the model without those two predictors was selected for 55 species (20.5%). We found no support for the selection of either model (ΔAICc < 2) for the remaining 48 species (17.9%) (Supporting Information Table S2). Both models showed relatively high validation CBI values, though models with pH and oxygen had values that were significantly lower on average (0.727 ± 0.150) than those of the models without them (0.733 ± 0.156), indicating a greater challenge to make predictions for new conditions (two-sided paired Wilcoxon signed rank tests, $V = 20{,}180$, $p < 0.05$; Supporting Information Table S2 and Fig. S4). For most species (75% of models with pH and oxygen, and 73.9% for models without pH and oxygen), both model types performed significantly better than null models for validation CBI (with $p < 0.05$). For nearly all species (93.3%), both model types had effect sizes higher than 0. However, models with pH and oxygen predictors did not have significantly higher effect sizes for validation CBI (Wilcoxon paired signed rank test, $V = 16{,}572$, $p > 0.1$). Whereas depth and maximum sea surface temperature had consistently the highest overall relative importance, well above the rest of predictors for both types of models, the importance of minimum pH and oxygen in the models varied greatly across species (Supporting Information Fig. S5).

The two types of distribution models predicted different suitable range sizes. As expected, models without pH and oxygen predicted significantly larger (two-sided paired Wilcoxon signed rank tests, $V = 21{,}752$, $p < 0.01$) suitable range areas ($4.707 \times 10^6 \pm 1.248 \times 10^7$ km^2) than the models with these variables ($4.618 \times 10^6 \pm 1.244 \times 10^7$ km^2) (Supporting Information Table S8 and Fig. S6). This result suggests that pH and oxygen exhibit constraining effects on cold-water coral distributions and indirectly shows the utility of adding these two variables. Although species richness values predicted by the two types of SDMs were overall highly correlated at the global scale (Pearson's $r = 0.920$, $p < 0.001$) (Fig. 2, Supporting Information Figs. S7 and S8), differences in the predicted spatial distribution patterns of individual coral species between the two models, with an average Schoener's D value of 0.863 ± 0.068 and Jaccard similarity coefficient value of 0.738 ± 0.125 (Supporting Information Table S8), resulted in different predicted species richness in approximately one-third (32.3%) of the regions with differences in local grid cell richness varying from −39 to 26 (Fig. 2). Nonetheless, both models identified coral diversity hotspots (i.e., top 1% of the most species-rich grid cells) with overall consistency (Jaccard similarity coefficient = 0.811), showing the highest coral diversity in the Caribbean Sea, the Gulf of Mexico, and the Coral Triangle (Supporting Information Figs. S7, S9, and S10).

Redistribution under climate change

As expected, the percentage of negative MESS values was significantly higher in datasets with pH and oxygen than the corresponding datasets without them (Supporting Information Fig. S11), and SDMs with pH and oxygen consistently predicted greater range losses of cold-water species for all scenarios and periods tested (Fig. 3, Table 1, and Supporting Information Table S9 and Fig. S12). Regardless of dispersal assumptions, the magnitude of these changes and the differences between the two models increased significantly with higher emission scenarios and time, ranging from minimums of $-12.2 \pm 41.8\%$ (with pH and oxygen) and $-0.7 \pm 25.3\%$ (without pH and oxygen) under SSP2-4.5 and unlimited-dispersal by 2040–2050 to a maximum of $-48.2 \pm 40.0\%$ (with pH and oxygen) and $-16.8 \pm 29.3\%$ (without pH and oxygen) under SSP5-8.5 and no-dispersal by the end of the century (Table 1). Overall, our results suggest that SDMs with pH and oxygen predicted on average 16.8% greater range loss under climate change than those that did not account for pH and oxygen (Table 1). With respect to spatial changes in coral richness under climate change, the two types of SDMs projected a profound richness decrease in the Coral Triangle, while models without pH and oxygen projected comparatively lower impacts of climate change on cold-water corals in several regions including the Caribbean Sea and the Gulf of Mexico (Fig. 4 and Supporting Information Figs. S13–S15).

Discussion

Despite the sensitivity of many marine species towards changes in seawater pH and oxygen, these variables have been largely unaccounted for by studies assessing climate-driven range shifts of marine organisms using SDMs. Our results

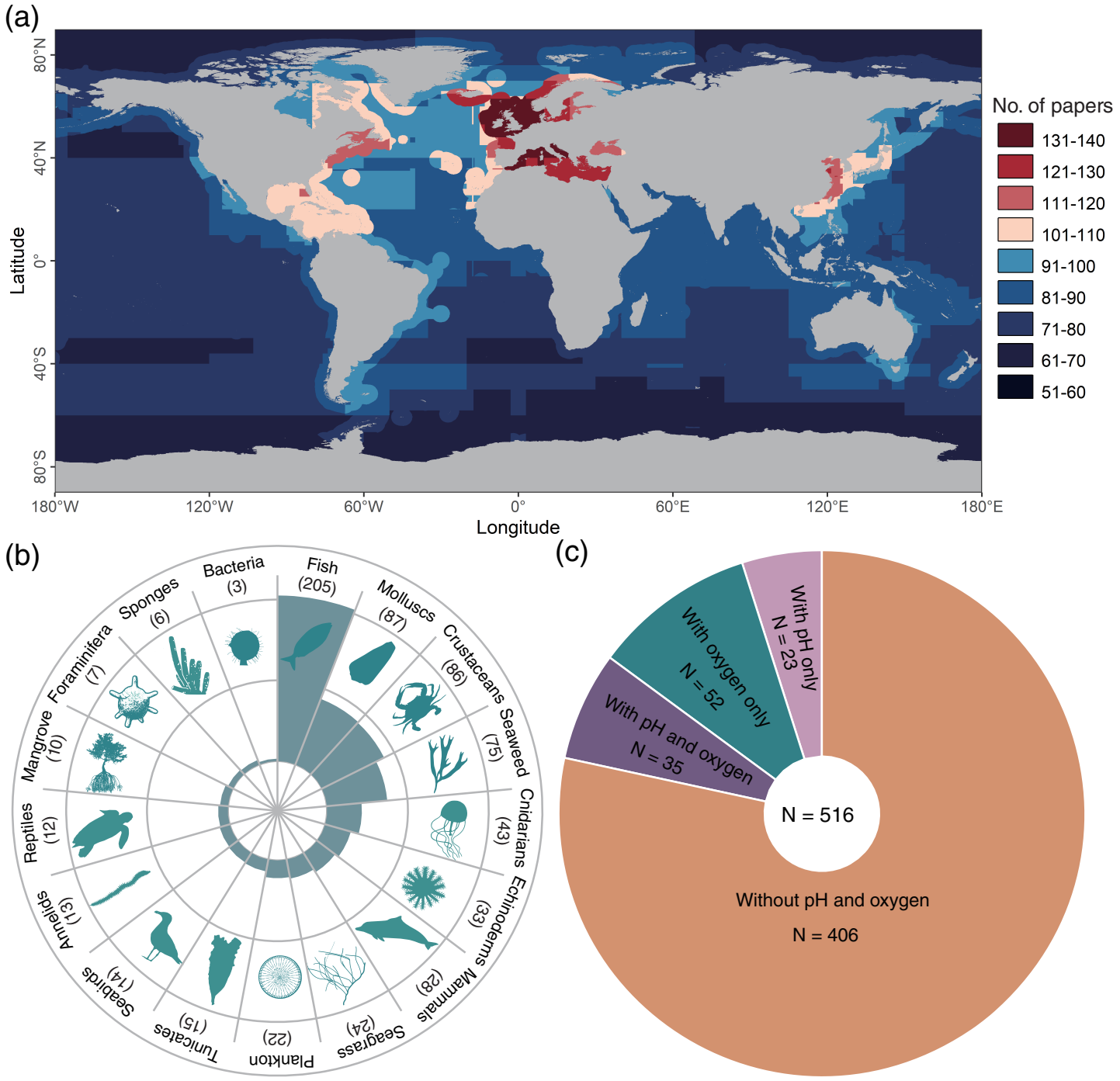

Fig. 1. Results of the literature review on papers modeling redistribution dynamics of marine species under climate change using species distribution models (SDMs). (**a**) Geographic and (**b**) taxonomic distributions of relevant published SDM studies. (**c**) Number of studies accounting for acidification and/or deoxygenation. In panel (**b**), numbers in parentheses indicate the number of papers for each taxonomic group, and the silhouettes were sourced from PhyloPic (http://phylopic.org). *See* Supporting Information Fig. S1 for detailed information about the literature review.

show that, irrespective of scenario, timeframe, or dispersal assumption, models including pH and dissolved oxygen predicted substantially stronger climate change impacts and yielded spatial distributions that diverged markedly from models excluding these variables. These findings demonstrate that the choice of predictors critically shapes biodiversity forecasts, underscoring the need for careful model construction in climate change research. Importantly, by showing that key

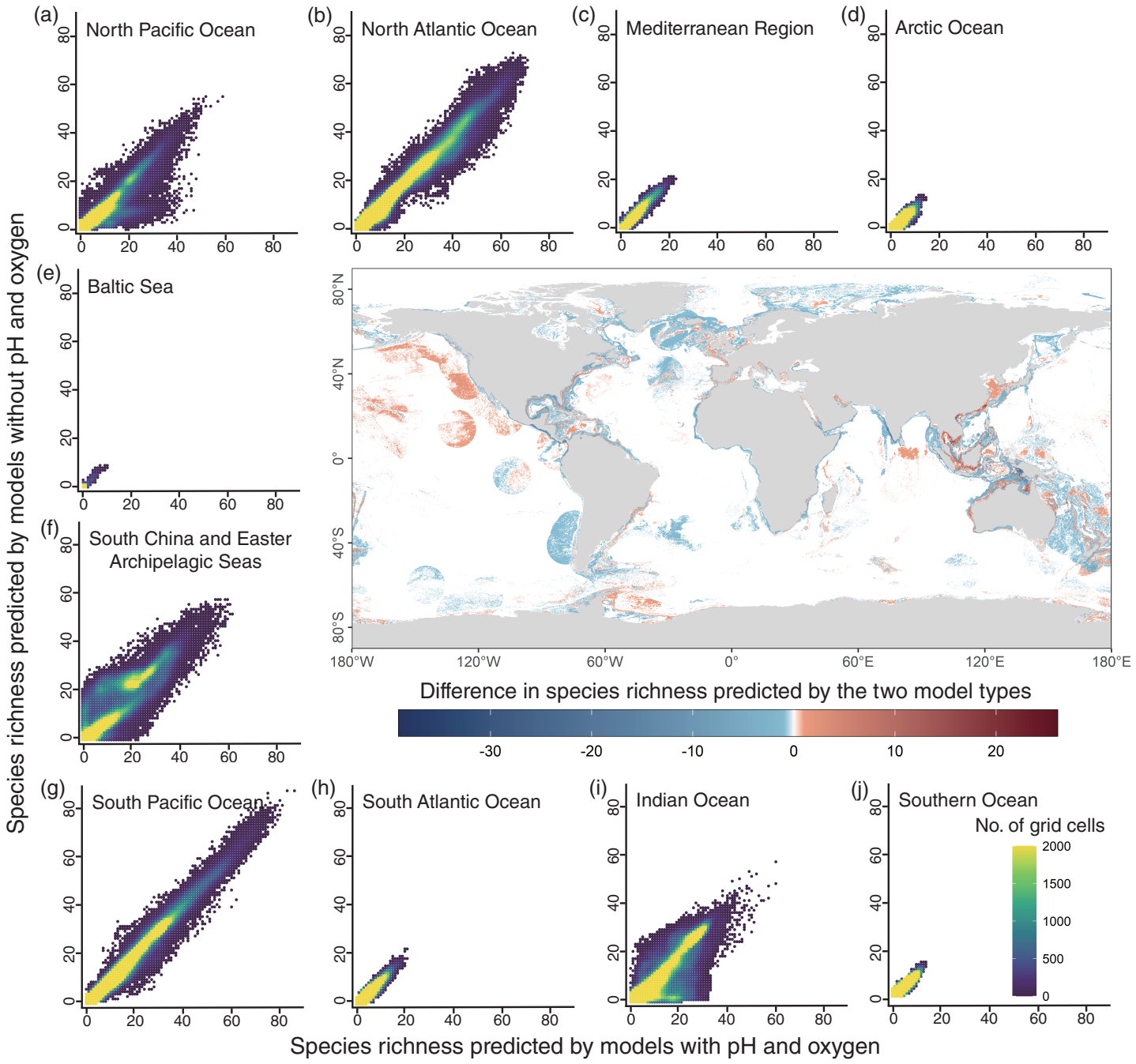

Fig. 2. Species richness estimates for cold-water corals made using species distribution models with and without pH and oxygen predictors. (**a**–**j**) Correlation between regional species richness estimated using models with (*x*-axis) and without (*y*-axis) pH and oxygen predictors for specific oceans and seas (*see* Supporting Information Fig. S10 for a global map showing their geographic distribution). In panels (**a**–**j**), the color represents the number of grid cells exhibiting a given combination of species richness estimates derived from the two types of models. The map shows the global difference in species richness predicted by the two types of models. Areas with positive (reddish)/negative (bluish) values represent higher/lower richness predicted by models with pH and oxygen. *See* Supporting Information Fig. S7 for species richness estimates made using the two types of models.

environmental stressors such as ocean acidification and deoxygenation drastically alter projected outcomes, our study emphasizes that relying on limited predictor sets risks underestimating extinction risks and misidentifying future refugia. We therefore advocate for the systematic inclusion of biologically meaningful variables, tailored to the focal taxa, to improve the robustness of biodiversity assessments. Such refined predictions are vital for informing conservation

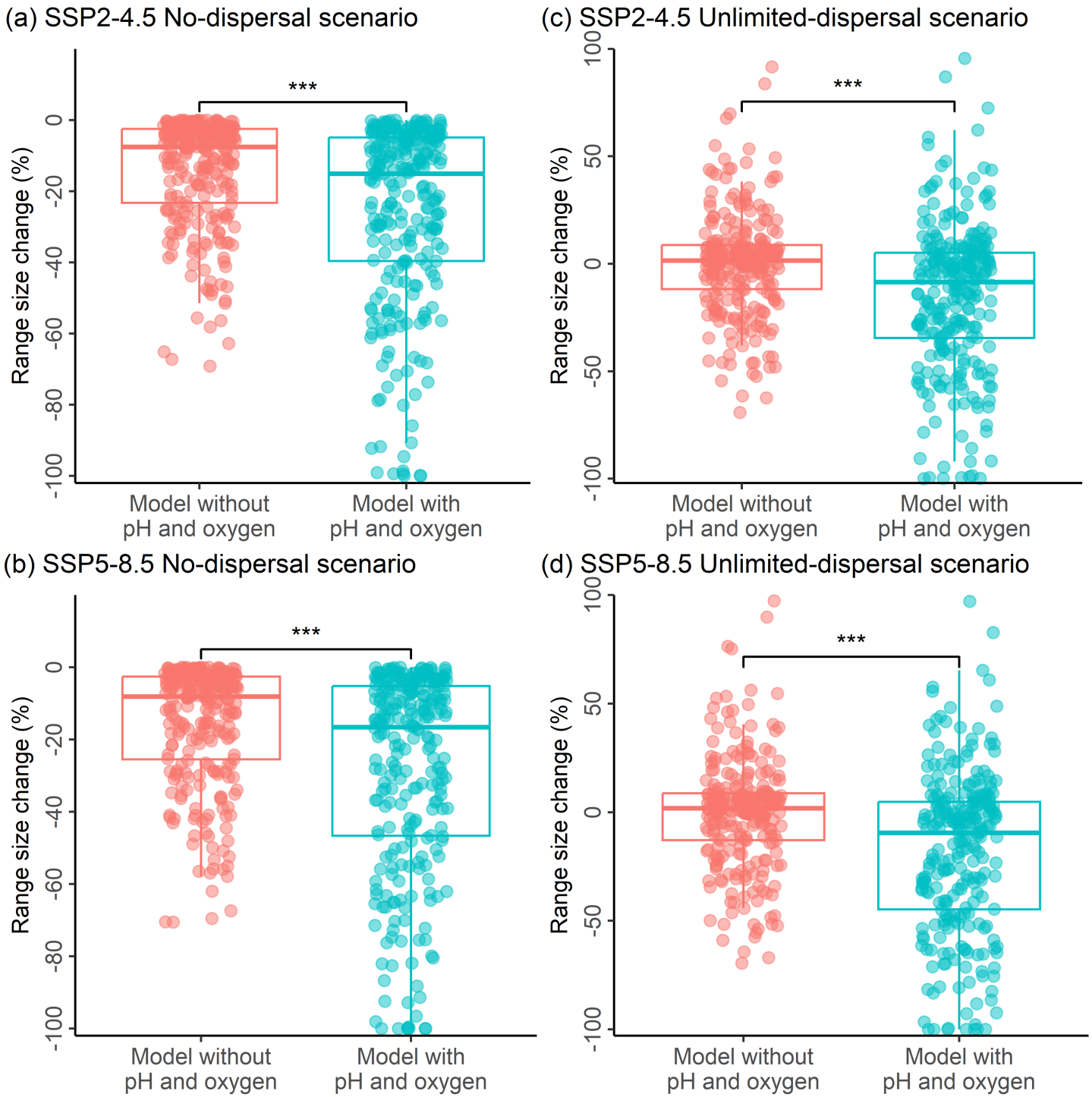

Fig. 3. Range size change of cold-water coral species projected by species distribution models with and without pH and oxygen predictors for the years 2040–2050. Results shown for SSP2-4.5 and SSP5-8.5 under "no-dispersal" scenarios (**a**, **b**), and SSP2-4.5 and SSP5-8.5 under unlimited-dispersal scenarios (**c**, **d**). Asterisks (***) indicate $p < 0.001$. *See* Supporting Information Fig. S12 for range-size change for the years 2090–2100.

planning, identifying climate refugia, and prioritizing management interventions, thereby supporting more effective strategies to safeguard vulnerable marine ecosystems in a rapidly changing ocean.

Acidification and deoxygenation matter for marine species

Temperature is one of the most important predictors determining the geographical distributions of marine species. For instance, among a set of relevant predictors including oxygen

Table 1. Future range size change of cold-water coral species projected by species distribution models with and without pH and oxygen predictors. SSP refers to Shared Socioeconomic Pathways developed by the Intergovernmental Panel on Climate Change (IPCC). Values expressed as average ± SD.

		No-dispersal scenario		Unlimited-dispersal scenario	
SSP	Future time	Models with pH and oxygen	Models without pH and oxygen	Models with pH and oxygen	Models without pH and oxygen
SSP2-4.5	2040–2050	−25.7 ± 25.6%	−14.2 ± 15.3%	−12.2 ± 41.8%	0.7 ± 25.3%
SSP5-8.5	2040–2050	−28.6 ± 28.1%	−15.4 ± 16.8%	−14.8 ± 45.4%	0.1 ± 27.3%
SSP2-4.5	2090–2100	−38.5 ± 34.4%	−20.0 ± 22.2%	−19.9 ± 64.5%	1.2 ± 37.3%
SSP5-8.5	2090–2100	−48.2 ± 40.0%	−26.8 ± 29.3%	−20.4 ± 118.6%	−0.2 ± 51.7%

concentrations, Tittensor et al. (2010) found that temperature was the only predictor highly correlated with species richness across all 13 taxonomic groups analyzed. Reflecting this perceived importance, our literature review found that 95.7% ($n = 494$) of marine SDM papers published over the last 45 years used exclusively temperature. However, this result may also partly reflect a bias in the type of environmental variables that are most frequently measured. Temperature data is widely available, easy to obtain, and often used as a proxy for a range of ecological processes. In contrast, other potentially important factors—such as the acidification and deoxygenation discussed here, but also nutrient availability, ocean currents, habitat complexity, and biotic interactions—are more challenging to quantify on broad spatial scales and are thus less frequently included in global biodiversity models. Although temperature is inarguably a key variable driving marine species' ranges, the perceived dominance of temperature in shaping marine species distributions may be, at least in part, conditioned by data availability and methodological convenience.

Ignoring some of these important marine predictors when assessing species' vulnerability to climate change might produce misleading outputs. For instance, McHenry et al. (2019) used SDMs to project range shifts of 125 marine species in the US Northeast Shelf. They found that, compared with models considering only seawater temperature (surface and bottom) and topographic predictors, models additionally accounting for salinity and sea surface height exhibited better predictive performance and projected greater climate change impacts. The predictive performance of distribution models is closely associated with the number of predictors (Naas et al. 2024; Soley-Guardia et al. 2024), and increasing this number can improve model performance irrespective of the actual biological relevance of those predictors (Fourcade et al. 2018; Santini et al. 2021), so approaches like AIC that directly penalize the addition of variables are crucial when comparing variable sets of different sizes. In our study, models with pH and oxygen predictors had higher performance via AICc for most species, though spatial cross-validation showed that difficulties in transferring to new environmental conditions led these models to also have slightly, though significantly, lower validation CBI values. Furthermore, although we evaluated relative model performance via CBI to select models with optimal complexity settings, new metrics to measure model performance have been proposed (e.g., Jiménez and Soberón 2020; Somodi et al. 2024), so we encourage researchers to compare approaches to assess model performance.

We showed that forecasts of future range shifts for marine organisms projected by models incorporating pH and oxygen led to much higher differences than projections for models lacking these variables. This reflects the relatively high importance of pH and oxygen variables in the models (Supporting Information Fig. S5), suggesting models incorporating the two predictors may reproduce more realistically biological responses than those without them, perhaps in combination with the effect of the greater extent of extrapolation for predictions from these models (Supporting Information Fig. S11). We nonetheless note that the correlative nature of SDMs does not imply causation and further studies are required to clarify these possibilities—including, for example, laboratory-based ecophysiological tests to evaluate the physiological impacts of these limiting factors, alongside mechanistic models of future species redistributions (e.g., Kearney and Porter 2009). In any case, given that the majority of previous SDM studies have largely overlooked pH and oxygen (Fig. 1c) and the substantial differences in geographic distribution patterns predicted when accounting for these variables in SDMs, we encourage scientists to incorporate a greater number of ecologically relevant marine predictors, particularly those expected to change most due to climate change. Providing more realistic projections of species' redistributions under future climate change will help to prioritize conservation efforts. Meanwhile, we acknowledge that models of future marine pH and oxygen concentrations are subject to higher uncertainties than those for temperature, which will propagate into larger uncertainties in model predictions (Bopp et al. 2013; Frölicher et al. 2016). We highlight the importance of quantifying different sources of uncertainties in future projections of ocean physical and chemical variables and the urgent need to improve accuracy of Earth system models.

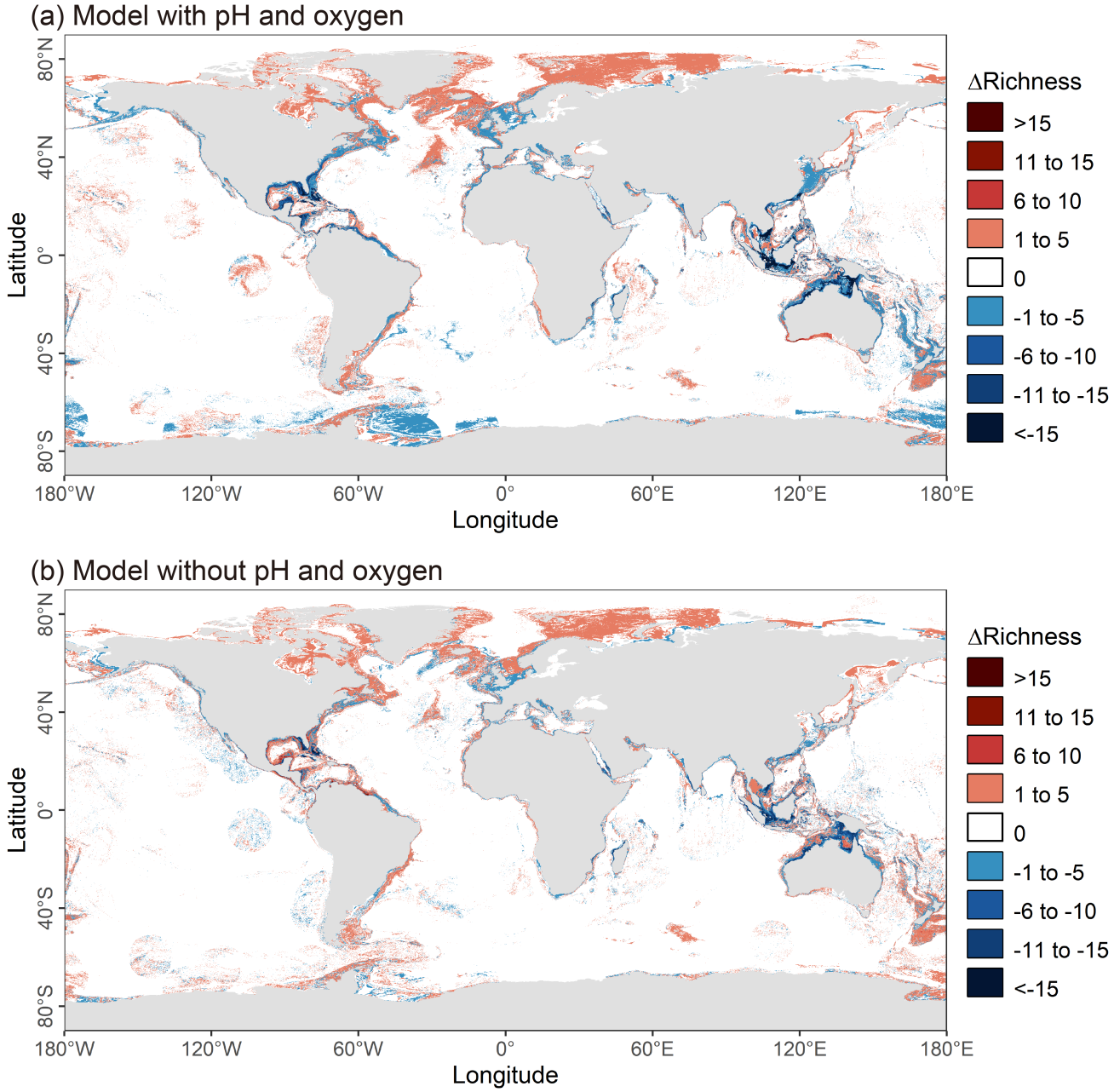

Fig. 4. Projected changes in richness of cold-water coral species under the SSP5-8.5 scenario for the years 2040–2050 using species distribution models with (**a**) and without (**b**) pH and oxygen predictors. *See* Supporting Information Fig. S13–S15 for richness changes for other scenarios and future time periods.

Given the differences in our predictions for models with similar discrimination performance, we warn against the common practice of justifying the choice of predictors for model training based solely on the performance metrics (Fourcade et al. 2018). Regardless of the relatively high performance of models with and without pH and oxygen predictors according to their validation CBI values (means of 0.727 and 0.733, respectively; Supporting Information Fig. S4), the model with pH and oxygen showed significantly larger range contractions with climate change (Fig. 3, Table 1, and Supporting Information Fig. S12). As we also found that non-analog conditions were more prevalent with the predictor set including pH and oxygen, this means models built with these predictor sets extrapolated more, which increases the uncertainty of the predictions (Elith et al. 2010; Soley-Guardia et al. 2024). Therefore, we advocate for caution when selecting predictor sets for

SDMs that are used for transferring to non-analog conditions, suggest the use of diagnostic visualizations like the MESS map to identify regions of prediction uncertainty and the predictor variables that drive non-analog conditions at local scales.

The recent availability of comprehensive datasets provides a variety of predictors (e.g., Bio-ORACLE version 3.0) associated with the multiple threats posed by climate change to global oceans (e.g., warming, acidification, deoxygenation, and eutrophication) at high resolution for present and future periods under alternative scenarios (Assis et al. 2024), which should allow for more robust predictions of ecological responses to climate change. Based on our results, we encourage researchers to consider the use of diverse predictor sets like these to incorporate a wider range of driving factors (and associated threats) when developing marine SDMs for biodiversity assessment under climate change. Moreover, we encourage the development and expansion of existing open databases by incorporating marine microclimate data, which can help avoid overpredictions of range shifts (e.g., Maclean and Early 2023), as well as more ecologically meaningful predictors (e.g., sediment types and extreme climate events such as heatwaves). Such efforts would greatly improve our predictions of range shifts for marine species under climate change. We also acknowledge that the incorporation of other factors and additional knowledge into distribution models, such as physiological tolerance (Zhang et al. 2024b), genetic variation (Chen et al. 2024), biotic interactions (Zhang et al. 2024a; Qu et al. 2025), species traits (Comte et al. 2024), and dispersal capacity (Shipley et al. 2022) is also needed to improve future range predictions. For example, our literature review showed that just 11.0% (57 out of the 516 papers reviewed) of the identified published papers used mechanistic SDMs in marine research. Although mechanistic models can significantly improve the reliability of dynamic range estimates by accounting explicitly for the physiological constraints of the environment on species performance (e.g., Kearney and Porter 2009; Mammola et al. 2021), the life-history information required to build these models is still extremely scarce for most marine species.

Implications for future SDM applications to marine biodiversity

Two practical suggestions for marine biodiversity assessment under climate change emerge from our results. Firstly, the choice of predictors matters. Different predictor combinations resulted in large differences in model predictions, highlighting the importance of selecting ecologically relevant predictors in SDM studies (e.g., Petitpierre et al. 2017; Fourcade et al. 2018; Soley-Guardia et al. 2024). Secondly, we encourage researchers to account for available environmental predictors that are known to have more proximal effects on marine species when modeling their future redistributions. This is in line with previous findings for the terrestrial realm: predictor choice has a great influence on model performance and prediction uncertainty (e.g., Synes and Osborne 2011), while the incorporation of additional, ecologically relevant predictors could improve the accuracy of SDMs (e.g., Stewart et al. 2021).

Improved projections of future species distribution shifts are required to better inform conservation planning and adaptive management of marine resources (Fuchs et al. 2026). For example, the importance of considering the effects of climate change when designing marine protected areas to be robust against a range of future impacts is increasingly recognized (e.g., Olsen et al. 2018; Hoppit et al. 2022; Fuchs et al. 2026). Similarly, the transboundary movement of species driven by climate change poses a growing challenge for the equitable and sustainable management of global fisheries (e.g., Pinsky et al. 2018), requiring proactive and adaptive management reforms that account for shifting productivity and shifting distributions (e.g., Free et al. 2020). Based on our findings, we suggest that including ecological meaningful predictors for marine SDMs is one important way to improve our projections of marine species redistribution under climate change. Our study demonstrates that incorporating acidification and deoxygenation into marine SDMs substantially improved model accuracy for a majority of the species modeled which, based on existing evidence on the ecological importance of these variables to corals, suggest an implicit improved ecological realism of their distribution projections under climate change. Models relying solely on temperature predictors risk underestimating species' vulnerability and misrepresenting future habitat shifts. The observed shifts in species distributions and spatial habitat patterns highlight the complex responses of marine biodiversity to multiple environmental stressors. Integrating a broader suite of predictors will enhance the capacity of biodiversity forecasts to inform conservation planning and adaptive management in a rapidly changing ocean. These findings underscore the urgent need for comprehensive modeling approaches to support effective biodiversity conservation under future climate scenarios.

Author Contributions

Shuaishuai Liu: Writing – original draft, data curation, investigation, writing – review and editing. Bingqing Xiao: Writing – original draft, data curation, investigation, writing – review and editing. Ákos Bede-Fazekas: Conceptualization, methodology, writing – original draft. Stefano Mammola: Methodology, writing – original draft. Jorge García Molinos: Methodology, writing – original draft. Jamie M. Kass: Methodology, writing – original draft. Jorge Assis: Methodology, writing – original draft. Chen Lin: Data curation, methodology. Junmei Qu: Data curation. Hongwei Huang: Data curation. Qiang Lin: Conceptualization, supervision, funding acquisition. Zhixin Zhang: Conceptualization, methodology, supervision, writing – review and editing, funding acquisition.

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Conflicts of Interest

None declared.

Data Availability Statement

Distribution data and code for cold-water corals used in this study are available in the Figshare Repository (https://figshare.com/s/ce263019b1b9a58ad3af). Marine predictors underpinning the model development were obtained from Bio-ORACLE version3.0 (https://www.bio-oracle.org).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

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