ARTICLE

Climate Ecology

Complex multivariate model predictions for coral diversity with climatic change

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Abstract

Models of the future of coral reefs are potentially sensitive to theoretical assumptions, variable selectivity, interactions, and scales. A number of these aspects were evaluated using boosted regression tree models of numbers of coral taxa trained on ~1000 field surveys and 35 spatially complete influential environmental proxies at moderate scales (~6.25 km^2). Models explored influences of climate change, water quality, direct human-resource extraction, and variable selection processes. We examined the predictions for numbers of coral taxa using all variables and compared them to models based on variables commonly used to predict climate change and human influences (eight and nine variables). Results indicated individual temperature variables alone had lower predictive ability ($R^2 < 2\%$–7%) compared to human influence variables (6%–18%) but overall climate had a higher training–testing fit (70%) than the human influence (63%) model. The full variable model had the highest fit to the full data (27 variables; $R^2 = 85\%$) and indicated the strongly interactive and complex role of environmental and human influence variables when making moderate-scale biodiversity predictions. Projecting changes using Coupled Model Intercomparison Project (CMIP) 2050 Representative Concentration Pathways (RCP2.6 and 8.5) water temperature predictions indicated high local variability and fewer negative effects than predictions made by coarse scale threshold and niche models. The persistence of coral reefs over periods of rapid climate change is likely to be caused by smaller scale variability that is poorly simulated with coarse scale modeled predictions.

KEYWORDS
Africa, biodiversity, Coupled Model Intercomparison Project (CMIP), environmental drivers, Intergovernmental Panel on Climate Change (IPCC), machine learning, predictive spatial modeling, Scleractinia

INTRODUCTION

Understanding large-scale patterns of species distribution and richness is challenged by our limited modeling methods (Pilowsky et al., 2022). Most recent models are largely based on limited, coarse scale sampling (i.e., >100 km^2), existing environmental conditions, and widespread interpolations and extrapolations. Therefore, the inferred patterns and distributional maps may often reflect the incompleteness of habitat information and sparse sampling (Kusumoto et al., 2020). Consequently, predicted distributions may be poorly connected to the local underlying environmental and habitat elements that produce and maintain local diversity. For example, many large-scale distributional maps are based on presence/absence data, rarefaction, niche modeling, and interpolative mapping (Ateweberhan & McClanahan, 2016; Couce et al., 2023; Jenkins & Van Houtan, 2016; Molinos et al., 2016; Selig et al., 2014). Critical evaluations suggest that these methods can fail to estimate local and fine-scale diversity, particularly in poorly sampled regions (Kusumoto et al., 2020; Lee-Yaw et al., 2022; McClanahan, Friedlander, Wickel, et al., 2024). The consequence is often reliance on other indirect or proxy metrics of biodiversity and impacts, such as spatial patterns of connectivity or satellite-derived thermal stress (Beyer et al., 2018; Crochelet et al., 2016; Maina et al., 2011, 2020). Consequently, conservation prioritization has a history of using anecdotal information that often fails to correspond between studies and modelled predictions (McClanahan, Friedlander, Wickel, et al., 2024). Given recent advances in predictive algorithms and fine-scale data and mapping, how can climate and predictive sciences better evaluate finer scale distributions of current and future biodiversity?

Predicting and mapping diversity metrics using fine-scale and globally complete environmental proxies is an emerging approach (Pilowsky et al., 2022). Models that use satellite and shipboard data with broad coverage can make predictions at the scale of the collected, binned, or mapped environmental data (i.e., <10 km^2). For example, coral cover and taxonomic diversity have been predicted on large scales based on coral metrics and satellite-derived environmental data relationships (Couce et al., 2023; Kim et al., 2023; McClanahan & Azali, 2021; Shlesinger & van Woesik, 2023). Specifically, algorithms such as random forest and boosted regression tree (BRT) use machine learning methods to predict biodiversity at scales finer than past rarefaction and correlational methods (McClanahan, Friedlander, Wickel, et al., 2024). Comparing and competing multiple options is expected to improveunderstanding and model predictions used to establish biodiversity priority locations (McClanahan & Sola, 2024).

The coral reef diversity and climate change context

Contemporary studies of coral reefs have focused on how increasing heat, coral bleaching, and benthic cover are responding to climate change (Chan et al., 2023; McClanahan & Azali, 2021; Santana et al., 2023; Shlesinger & van Woesik, 2023; Sully et al., 2019, 2022; Vercammen et al., 2019). Numbers of coral taxa remain less evaluated, but coarse spatial scale models suggest they are potentially threatened by species' rarity and susceptibility to climate stress (Carpenter et al., 2008; Couce et al., 2023; Kim et al., 2023; Sheppard et al., 2020). Consequently, historical and contemporary environmental change may be among the strongest predictors of coral diversity to climate threats (McClanahan et al., 2019, McClanahan, Maina, et al., 2020; van Woesik et al., 2012). Therefore, increasing the knowledge of coral taxa-environmental relationships should improve climate change predictions.

This study presents an effort to evaluate the application of predictive spatial models in order to improve biodiversity predictions and climate forecasts for coral reefs in the Western Indian Ocean (WIO). Current predictions have largely relied on the rates of temperature rise and the frequency of annual excess heat thresholds (i.e., International Panel on Climate Change (IPCC) projections; Cornwall et al., 2021; Hoegh-Guldberg et al., 2018). Past and projected excess heat metrics greatly influence public communications, policies, and conservation actions (Klein et al., 2024; Lee et al., 2023). Annual excess heat was, however, largely developed to predict the summer loss of coral symbionts ("bleaching"). Excess heat is just one of many environmental factors that influence coral community variables, which range from gene expression to species composition changes. Moreover, aggregated coral bleaching and cover studies are simple proxies for a more complex evaluation of coral reef health and diversity.

Five advancements in environmental science have created the potential to better understand current and future coral reef biodiversity. These include (1) moderate-resolution mapping of coral reefs, (2) global-scale satellite coverage of environmental variables and proxies of impact, (3) increased scale of field data collection and data sharing, (4) climate model predictions at moderate scales, and (5) statistical machine learning algorithms. We combined these tools as described below to create a 6.25-km^2 resolution predictive map of numbers of coral taxa for the currently mapped reefs in the WIO biogeographic province. The Coupled Model Intercomparison Project (CMIP) models' variables were then used to predict numbers of taxa in 2020 and 2050 under a high Representative Concentration Pathways RCP8.5 and

modest RCP2.6 emission scenario. The carbon emissions have tracked RCP8.5 between 2005 and 2020 and suggest a 4–5°C temperature increase by 2100 (Schwalm et al., 2020). At the time of this writing (2024), global temperatures had reached the 2050 thresholds 26 years prior to predictions. These are likely due to reduced atmospheric particles and increased irradiance that appear to be hastening climate warming (Hansen et al., 2023; Yuan et al., 2024). However, there are also ongoing changes that suggest declining nonrenewable energy usage and carbon emissions (Hausfather & Peters, 2020). The consequence of this uncertainty and changes in aerosols and nonrenewable energy consumption since the original formulation of scenarios makes it difficult to predict the year when future heat stress will be consistently at or above RCP predictions. For simplicity of the text, the RCP8.5 predictions are referred to here as an extreme and RCP2.6 as a modest emission scenario. Relationships between changes in coral cover and numbers of taxa were used to estimate community change for all reef cells across the 2020–2050 RCP prediction periods.

METHODS

Study region

A coral reef satellite-based map was used to establish the distribution of coral reefs (https://data.unep-wcmc.org/datasets/1) (Burke et al., 2011). Specifically, we used the map of the WIO and 9 ecoregions, namely, the Northern Monsoon Current Coast, East African Coral Coast, Seychelles, Cargados Carajos/Tromelin Island, Mascarene Islands, Southeast Madagascar, Western and Northern Madagascar, Bight of Sofala/Swamp Coast, and Delagoa (Spalding et al., 2007). Empirical coral surveys of taxonomic diversity were available using comparable methods for six of these ecoregions. The WIO province comprises 11 national jurisdictions that were also included in the model (Appendix S1: Figure S1). The WIO was chosen as a pilot location due to widespread collection of a shared rapid-assessment method to estimate coral taxonomic composition and diversity (McClanahan et al., 2007). Therefore, our focus was on predicting and mapping numbers of coral taxa at a faunal provincial level while contextualizing the finding within IPCC-CMIP climate change scenarios.

Modeling framework

To diversify and compare models, we selected commonly published variables often chosen when investigating impacts of climate change, water quality, and human resource on coral biodiversity. We were interested in knowing how an investigator's selection of variables might influence the understanding of causative relationships and subsequent predictions. Comparisons of different variable and model choices and statistical procedures allowed us to evaluate their importance on potential associations, causation, and predictions of numbers of taxa. Specifically, we used a multivariate machine learning predictive modeling algorithms (BRT) to predict and evaluate changes in coral cover and taxonomic diversity over the 2020 and 2050 prediction period using the CMIP sea-surface temperature projections. This approach was provoked by a review of climate impacts on corals, which found that common excess heat models used to make predictions have infrequently implemented variable choice and selection procedures (McClanahan, 2022). Many variables known to influence the condition of coral communities have therefore not been used for making predictions. Our study examines the consequences.

Environmental data sources

Spatially complete environmental data are now available for coral reefs at moderate scales of resolution. For example, we were able to compile 70 environmental databases of variables with spatially resolved layers potentially associated with coral condition. Variables were subjected to standard selection and ensemble model processes to evaluate local scale diversity of hard corals (Scleractinia and Milleporidae) in the WIO province. We considered many variables and followed a standard procedure of variable selection and fits to data, while addressing concerns about "unfairly" eliminating causative variables. We then compared this approach to two models with the climate or direct human impact selected variables.

Environmental data compilations using several online sources resulted in a compilation of 70 variables derived from satellite and shipboard measurements (Tyberghein et al., 2012; Yeager et al., 2017) (Appendix S1: Table S1). The compilations were a mixture of oceanographic information, such as surface photosynthetically active radiation (PAR), pH, calcite and dissolved oxygen concentrations, diffusion attenuation, salinity, net primary productivity, chlorophyll *a* variables, phytoplankton carbon, and wave height. The units and data sources are described in more detail in Appendix S1: Table S1. Several seawater temperature (SST) or thermal stress metrics were calculated over the 1985–2020 satellite data period including SST mean, median, range, standard deviation, skewness, kurtosis, rate of rise, and cumulative degree-heating weeks (cumDHW)

(https://coralreefwatch.noaa.gov/product/5km/index_5km_sst.php). Several composite variables were used. These included an integration of nine thermal variables (i.e., temperature and light variables) combined into a global stress model variable developed by Maina et al. (2011). Similarly, a water quality stress metric was used based on the composite nutrient and sediment concentration estimates developed by Andrello et al. (2022). Reef connectivity calculations were used to assess larval dynamics including measures of net flow, indegree, outdegree, and retention for each cell in this region (Fontoura et al., 2022). Geographic variables comprised latitude, ecoregion, nation, and wilderness (>4 h travel time from human populations). Human impacts were determined from variations of a human gravity metric, where human populations onshore or in cities were divided by the square of the distance or travel time to the sampled cell (Maire et al., 2016). Cells were assigned four fishery management categories including unrestricted fishing (42% of all cells), restricted fishing (42%), low compliance closures (14%), and high compliance closures (2%). These classifications were based on information in published literature, the experience of the observers, and discussions with knowledgeable observers (McClanahan, Graham, et al., 2015).

Field data collection

Coral cover and numbers of taxa were sampled haphazardly while snorkeling or scuba diving in either visually estimated or measured quadrats of ~2 m^2 between 1998 and 2022. All corals >5 cm were identified and counted in ~15–20 replicates (McClanahan et al., 2007). We also recorded the depth and habitats of the sites as reef edge, reef crest, reef flat, or reef lagoon. Thus, the values used here were the total numbers of taxa in ~40 m^2. Taxa identification was to the genus level, but *Porites* colonies were distinguished further as massive, branching, or *Porites rus*, and *Galaxea* as either *Galaxea astreata* or *Galaxea fascicularis*. A total of 67 taxa in 1001 sites were sampled in six of the ecoregions (Appendix S1: Figure S1). Observers were included in the statistical analysis to determine and account for expected variations between observers, their specific methods, and taxonomic identification experience. Sixteen observers contributed to the database, but most contributed few sites. There were significant differences between observers but not among the three observers who sampled 939 of the 1001 sites. Data collected in the same reef cell grid within a 5-year window of time were pooled into 575 6.25 km^2 cells prior to analyses. We included observers/methods in the statistical analysis to evaluate its effect on numbers of taxa, but differences were accounted for in the final predictive model by partial effects methods described below.

Data analyses

Variable selection

We began our investigation using variable choice procedures for 70 environmental spatially complete variables to evaluate their potential (Appendix S1: Figure S2). For example, first we investigated collinearity between predictor variables. Variables with a Spearman rank correlation coefficient ≥0.7 were either removed from the analysis or used to build an alternative model if the variables were suspected of causative relationships (Dormann et al., 2013). Second, we further investigated associations using variance inflation factors (VIF) with a cutoff VIF <5. Employing these redundancy procedures, the final number of variables evaluated for fits to field data was reduced from 70 to 37.

We further investigated two likely models based on variables commonly used by coral-environmental modelers (McClanahan, 2022). First, a model based on eight climate and oceanographic variables identified by many investigators as important metrics for climate impacts. Second, nine commonly used human resource extraction and water pollution variables assessed human impacts (Table 1; Appendix S1: Table S1). These two models were compared to the full model of 37 variables that passed the variable selection process. The comparisons allowed us to test investigators, and disciplinary choices might influence conclusions. Nevertheless, the final ecoregional and national model, mapping, and forecasts used the final selected variables that passed the above redundancy and data-fit procedures.

BRT models

We implemented BRT models with a Poisson distribution against numbers of taxa. We used the *gbm* package version (2.1.8) in the *R* statistical programming language (Greenwell et al., 2020; R Core Team, 2021). BRT has a number of advantages for addressing complexity including the ability of the users to fit inputs of number of trees, a shrinkage parameter to handle an expanding model, tree complexity that allows for variable interactions, minimum number of observations, and stochasticity of the training data to propose the next tree (Breiman, 1996; Elith et al., 2008). BRT has also been shown to make better predictions of numbers of taxa than common rarefaction methods when evaluated by fits to environmental

TABLE 1 Statistical results of (a) the boosted regression tree (BRT) relative contributions (in percent) to numbers of coral taxa for the two full variables and two models selected based on climate and human influences foci; (b) R^2 fits of best model to all data, and a 70% training and 30% testing of the data (see *Methods*).

Variable	Full variable models		Climate variable model	Human variable model
	Model 1	Model 2		
(a) Variable importance				
1. Observers	15.6	15.2	NI	NI
2. Depth (m)	9.2	9.4	15.4	NI
3. Cumulative DHW (°C-weeks)	6.9	NI	14.4	NI
4. SST kurtosis	5.6	NI	11.1	NI
5. Mean wave energy (kW m^{-2})	5.0	4.1	NI	NI
6. Dissolved oxygen (ml l^{-1})	4.3	2.4	NI	NI
7. Country	4.0	3.6	NI	18.5
8. Salinity (PSS)	4.0	2.3	NI	
9. Reef visitation value, number of tourist visits	3.8	3.2	NI	13.5
10. Median chlorophyll a (mg m^{-3})	3.8	NI	NI	NI
11. Calcite concentration (mol m^{-3})	3.7	3.9	NI	NI
12. Travel time to market (h)	3.4	NI	NI	11.1
13. SST rate of rise (°C)	3.3	4.0	16.3	NI
14. Maximum photosynthetically active radiation (einsteins m^{-2} day^{-1})	3.1	3.7	NI	NI
15. Retention connectivity	2.7	2.8	NI	NI
16. Indegree connectivity	2.4	1.8	NI	NI
17. Net primary productivity (mg C m^{-2} day^{-1})	2.2	NI	NI	NI
18. Habitat	2.2	2.2	NI	NI
19. SST median (°C)	2.1	NI	8.2	NI
20. Travel time nearest population (h)	2.0	NI	NI	7.5
21. Hard coral cover (%)	1.9	1.8	5.7	NI
22. Ecoregion	1.9	0.3	NI	NI
23. Netflow connectivity	1.9	1.6	NI	NI
24. Outdegree connectivity	1.9	1.5	NI	NI
25. Fisheries management	1.6	1.6	NI	5.7
26. Nutrients (nitrogen, tons km^{-2})	1.6	NI	NI	9.0
27. SST skewness	NI	7.3	19.2	NI
28. Climate stress model	NI	6.0	NI	NI
29. Current velocity (m s^{-1})	NI	4.6	NI	NI
30. pH	NI	3.6	NI	NI
31. Gravity to nearest population, population/travel time (h)^2	NI	3.1	NI	13.4
32. Gravity to nearest city, population/travel time (h)^2	NI	3.0	NI	10.9
33. Diffuse attenuation coefficient (m^{-1})	NI	2.8	NI	NI
34. SST bimodality	NI	2.0	9.7	NI
35. Sediments (tons km^{-2})	NI	2.0	NI	10.4

(Continues)

T A B L E 1 (Continued)

Variable	Full variable models		Climate variable model	Human variable model
	Model 1	**Model 2**		
(b) Model performance (R^2)				
Full data	0.83	0.81	0.70	0.63
70% training and 30% testing	0.46	0.45	0.42	0.41

Note: See Appendix S1: Table S1 for all variables, additional details, and sources of access. Cumulative degree-heating weeks (cumDHW) is the annual sum from 1985 to the mid-point of the cells sampling date.

Abbreviations: NI, not included in the model when the model was fit to field data; PSS, practical salinity scale; SST, sea surface temperature.

data (McClanahan, Friedlander, Chabanet, et al., 2024). Finally, variables can be held constant via partial effect methods to make predictions when nuisance variables (i.e., variable sampling methods or observers) mask the comparisons of key predictions.

We initially calibrated the model by considering up to 400 model parameter combinations and comparing the other models by their error rates. The parameter combination that produced the smallest error rate, with >1000 trees, was used to specify the coral taxa BRTs (i.e., nt = 5000, lr = 0.01, tc = 3, minobs = 8). We set bag fraction to 0.5 and performed a 10-fold cross validation to determine the optimal number of trees needed to minimize deviance and maximize predictive performance.

Model performance was evaluated by testing the best-fit model to the original data (full data) and by splitting the data into a 70% training and 30% testing set (Kuhn & Johnson, 2013). The calculated performance metrics included Theil's U statistic, percent deviance explained (analogous to R^2), and Pearson correlation coefficients. Further, we assessed the relative influence of each predictor variable, calculated by averaging the number of times a variable was selected to split a tree, and weighted by the squared improvements from the splits (Friedman, 2001). Partial dependence plots were generated to characterize relationships between the responses and each predictor variable using the pdp package (version 0.8.1) in R (Greenwell, 2017). To reduce the possibility of removing potentially causative variables, we developed an ensemble model based on two sets of variables and models. Both models included all potentially strong variables, but the second model included those eliminated in the first model suspected of a potential causative association (i.e., SST mean, SD, skewness, and kurtosis) (Table 1). This ensemble model process reduces the chances of eliminating variables that could be important but eliminated based on small differences in predictive strength. Thereafter, we used the average of the two models weighted by each model's explained deviance when creating the final predictive map, holding depth constant at 10 m.

Forecasting climate scenarios

The CMIP5.0 model scenarios make predictions of seawater temperature changes. Predictions include calculations of median, kurtosis, cumDHW, rate of rise, and skewness for each reef cell in 2020 and 2050. As described in the results, these variables were among the top predictive variables by our empirical field-based BRT analysis. The cumDHW variable used for 2020 predictions was the CMIP5.0 annual DHW sum from 1985 to 2019, whereas for 2050, it was the DHW sum from 2020 to 2050. The multiyear predictions should be better for predicting coral community attributes, such as taxa, rather than annual DHW values used to predict coral bleaching. Moreover, the empirical predictive model is based on the summed DHW from 1985 to the midpoint sampling of corals for each grid cell.

Coral predictions in 2020 and 2050 included the other BRT empirically selected variables but they were held constant. Specifically, using environmental variable values taken from the time that the corals were sampled. In other words, the variables of waves, dissolved oxygen, calcite, salinity, and others in 2020 and 2050 were the values extracted for the cell grid when sampled. Therefore, predictions should be seen as influenced mostly by temperature. We present model predictions for 2020 and 2050 for both the RCP8.5 and the RCP2.6 scenarios.

Coral cover predictions for 2020 and 2050 used similar BRT methods described by McClanahan and Azali (2021). Specifically, these modeled cover predictions were used for producing scatterplots of changes in coral cover and numbers of taxa for the two CMIP scenarios at the scale of the evaluated cells. Calculations of differences between years (2050–2020) were normalized relative to the 2020 values. In one calculation, we compared the 30-year change in coral cover and numbers of taxa to itself or the same cell, whereas in a second evaluation, we compared each cell to the WIO provincial averages in 2020. These normalized averages of numbers of taxa and cover were referred to as local and provincial resilience. Normalized resilience metrics (−1 to 1 scale) were

mapped for the 7039 cells. No human influenced variables were included in the climate-change scenarios. The data and code used in the analyses are located at 10.5061/dryad.3xsj3txn1 and 10.5281/zenodo.13463413, respectively.

RESULTS

Model fits to numbers of coral taxa

By the BRT procedures, the local numbers of taxa predicted per ~40 m^2 was sensitive to the observer and depth (Table 1). Numbers of taxa peaked and leveled at >10 m depth. Using partial effects to account for observer and depth influences, the strongest variables were shown to depend on the specific model. When fitted to the empirical field data, the full Model 1 selected 26 variables while the alternative Model 2 selected 27 variables. These best-fit predictions had similarly high fits to the full data (Model 1 $R^2 = 0.83$ and Model 2 $R^2 = 0.81$) and similarly weaker fits to the 70/30 training and testing procedure ($R^2 = 0.46$ and 0.45). For the climate and human influence variable models, the climate model fit to the full data was higher ($R^2 = 0.70$) than the human variable model ($R^2 = 0.63$), but both were similar for the 70/30 training and testing procedure ($R^2 = 0.42$ and 0.41).

The full variable Model 1 was the methodological default and indicated that only five variables contributed >5% in explaining the variance, underlining the importance of SST excess heat (6.9%) and kurtosis (5.6%) after accounting for observer, depth, and wave energy. In Model 2, replacing kurtosis with skewness resulted in moderate predictive values for SST skewness (7.3%) and climate stress (6.0%) while no other environmental variables contributed >5% of the explained variance. This arises because important SST variables of excces heat, median, kurtosis, skewness, and bimodality are highly correlated. Therefore differentiating their influences on number of coral taxa is challenging.

While all models selected several similar variables, their ranks differed based on the inclusion or exclusion of variables. For example, the climate selected variables frequently ranked highly were SST skewness (7.3%), cumulative excess heat (6.9%), rate of SST rise (3.3%–4.0%), kurtosis (5.6%), wave energy (4.1%–5.0%), dissolved oxygen (2.4%–4.3%), salinity (2.3%–4.0%), chlorophyll (3.8%), calcite (3.7%–3.9%), sunlight (PAR) (3.1%–3.7%), net primary productivity (2.2%), and median SST (2.1%). Some of the selected human influence variables, such as country (18.5%), gravity to population and city (13.4% and 10.8%), reef visitation value (13.5%), travel times to markets and population (11.1% and 7.5%), fisheries management (5.7%), and sediments and nutrients (10.4%

and 9.0%), had higher fits than individual temperature metrics. Given the overall climate model had a somewhat higher fit to the full data than the human influence model, the inclusion of many physio-chemical environmental variables increased the predictive ability. Connectivity metrics in all models had <3% relative influences. Larval retention and indegree were stronger than the larval net flow and outdegree variables.
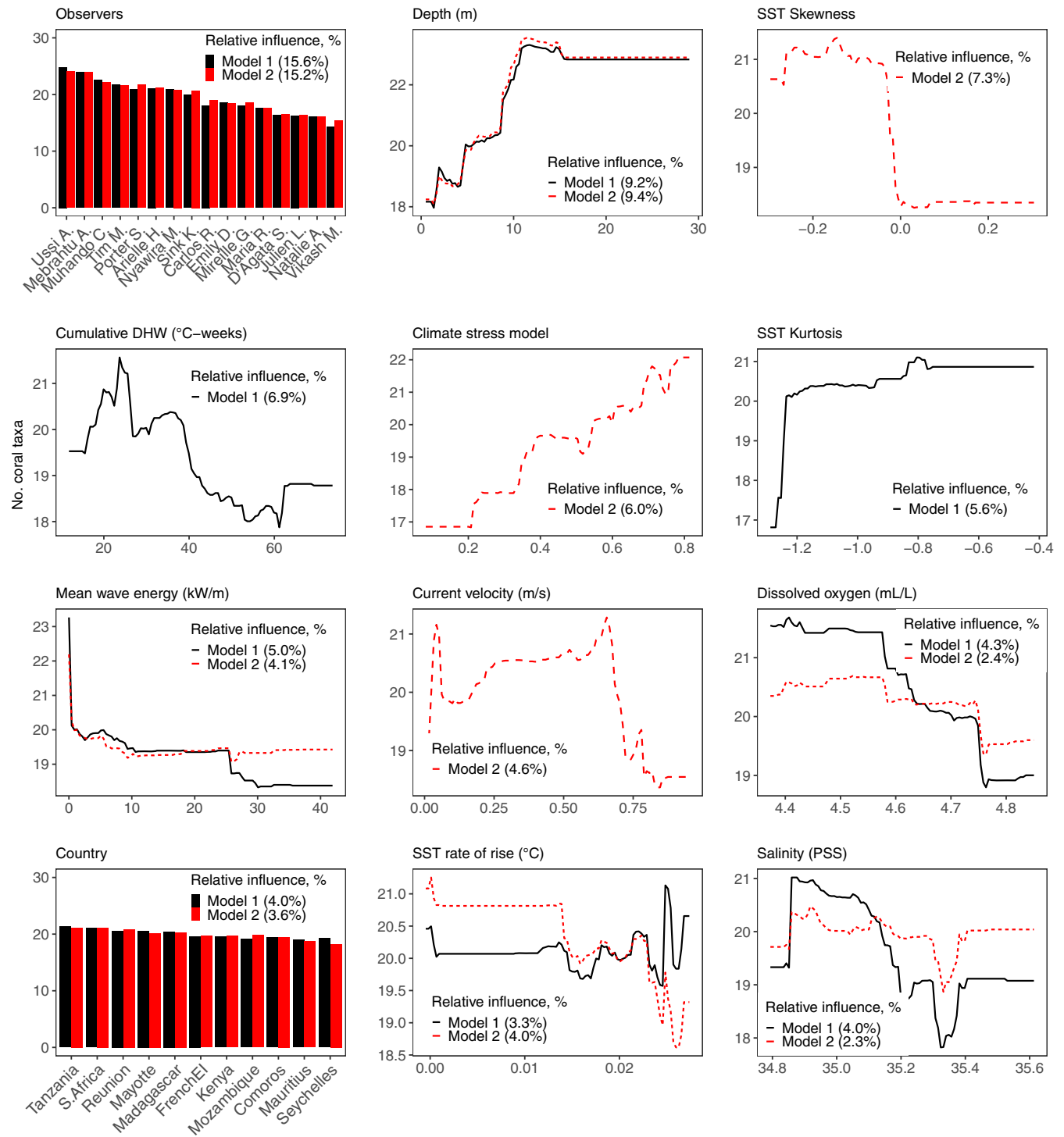
Response relationships

The response relationships among the full model's top variables with numbers of coral taxa indicated several different relationships (Figure 1). There were saturating relationships for depth, SST kurtosis, and the climate stress model; more hump-shaped relationships for SST skewness, cumDHW, and current velocity; and declining relationships for mean wave energy, dissolved oxygen, rate of SST rise and mean salinity. The two models' responses largely tracked each other when variables were shared but Model 2 had lower numbers of taxa for dissolved oxygen and higher numbers for SST rate of rise.

The response relationships among the selected climate change variables indicated high numbers of taxa were associated with cool-water skewness, a centralized to mildly flat SST distribution, moderate excess heat of 15–25 cumDHW, moderate SST bimodality, and median SSTs of ~27–28°C (Figure 2a,b). The relationship with SST rate of rise was more u-shaped with the lowest numbers of taxa predicted at ~0.015°C/year. The numbers of taxa and coral cover relationship were more sinusoidal, but high numbers of taxa were generally predicted when coral cover exceeded 40%.

Selected human influenced variables identified country as the strongest variable with the highest local taxa predicted for Tanzania and offshore to Mayotte and the Comoros Islands (Figure 2c,d). The adjacent continental countries of South Africa, Kenya, and Mozambique had moderate numbers. Madagascar and Seychelles were the two islands with the highest numbers followed by the more remote France's Eparses Islands, Reunion, and Mauritius. Distances from people and cities were weaker and had various relationships that generally suggested that number of taxa increased away from humans but local fishery management had minor influences. Numbers of taxa were maximized at moderate to low numbers of tourist visits and were highest with low levels of nutrients or nitrogen loading.

Forecasting coral changes

The CMIP model's predicted change in mean SST for all WIO ecoregions across the 30 years was 0.47 ± 0.54°C

FIGURE 1 Boosted regression tree (BRT) response relationships for top selected variables for two versions of the model predicting numbers of coral taxa in the Western Indian Ocean (WIO) province. Model fits based on 37 evaluated variables of which 26 were selected in Model 1 and 27 in Model 2. See Table 1 for relative importance for all selected variables. Cumulative DHW, cumulative excess heat above summer temperature threshold as degree-heating weeks; PSS, practical salinity scale; SST, sea surface temperature.

(mean ± SD) for the extreme RCP8.5 and 0.19 ± 0.55°C for the modest RCP2.6 scenarios (Table 2). Consequently, CMIP models predict high spatial variability in temperature rises with emissions forcing, with the greatest increases in mean temperatures in the northern regions of the Northern Monsoon Coast (RCP8.5 = 0.80 ± 0.09°C), the Seychelles (0.88 ± 0.23°C), the southern Bight of Sofala/Swamp coast (1.02 ± 0.11°C), and the most at Delagoa (1.33 ± 0.19°C) or spanning the Mozambican and South African coastlines. The central ecoregions of

the Western and Northern Madagascar (0.33 ± 0.73°C), East African Coral Coast (0.49 ± 0.19°C), and Southeast Madagascar (0.36 ± 0.51°C) had more moderate temperature increases. The lowest temperature changes for RCP8.5 were predicted for both the off-continent Mascarene Islands (−0.03 ± 0.10°C) and Cargados Carajos/
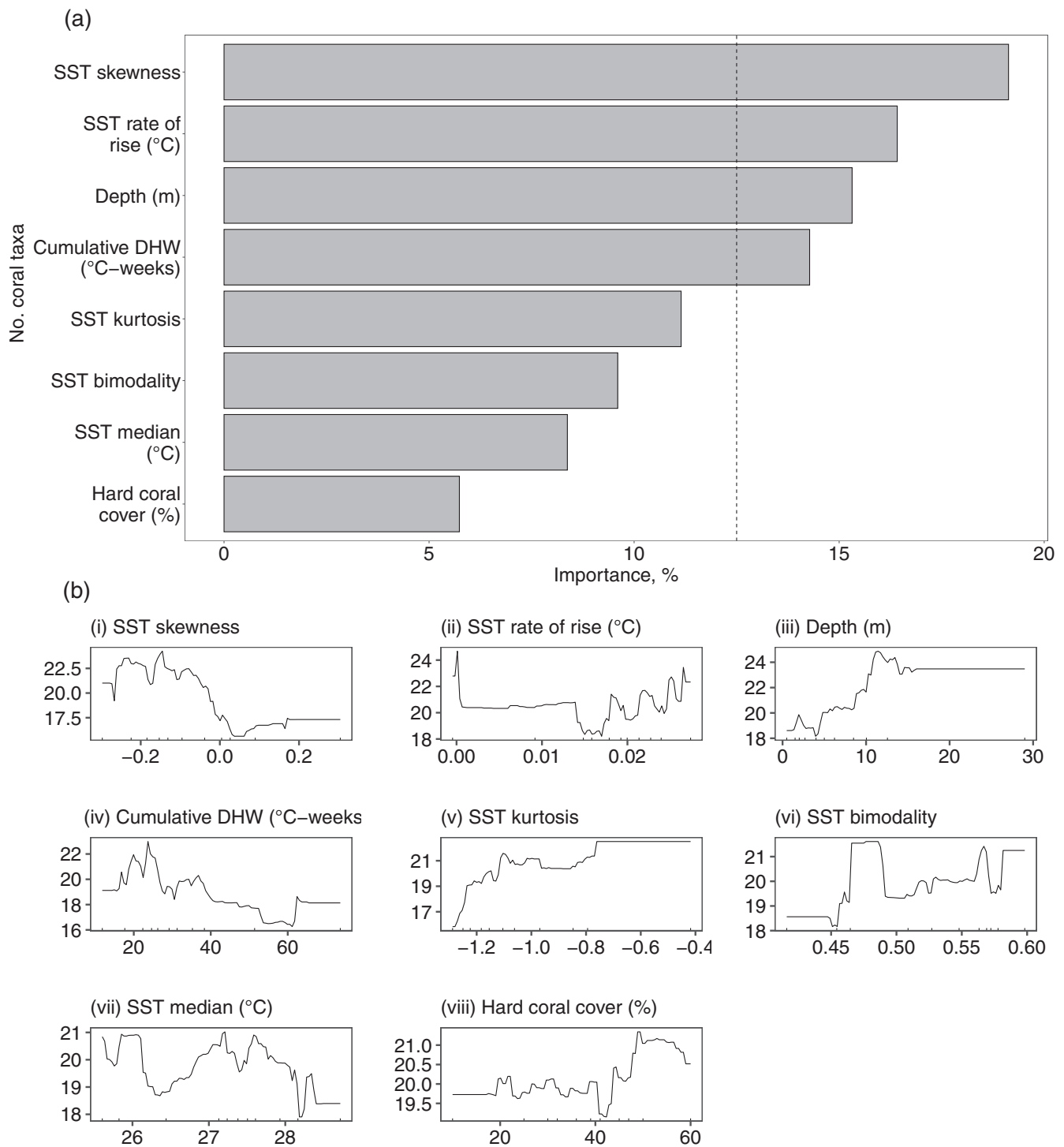
FIGURE 2 (a, c) Relative importance and (b, d) responses of top variables selected for predicting the number of coral taxa and human influences variables by the boosted regression tree (BRT) analysis. See Table 1 for relative importance of selected variables. Sediments and nutrients derived from satellite information are a multivariate value taken from Andrello et al. (2022) that is a measure of nitrogen delivery from a plume model. Cumulative DHW, cumulative excess heat above summer temperature threshold as degree-heating weeks; SST, sea surface temperature.
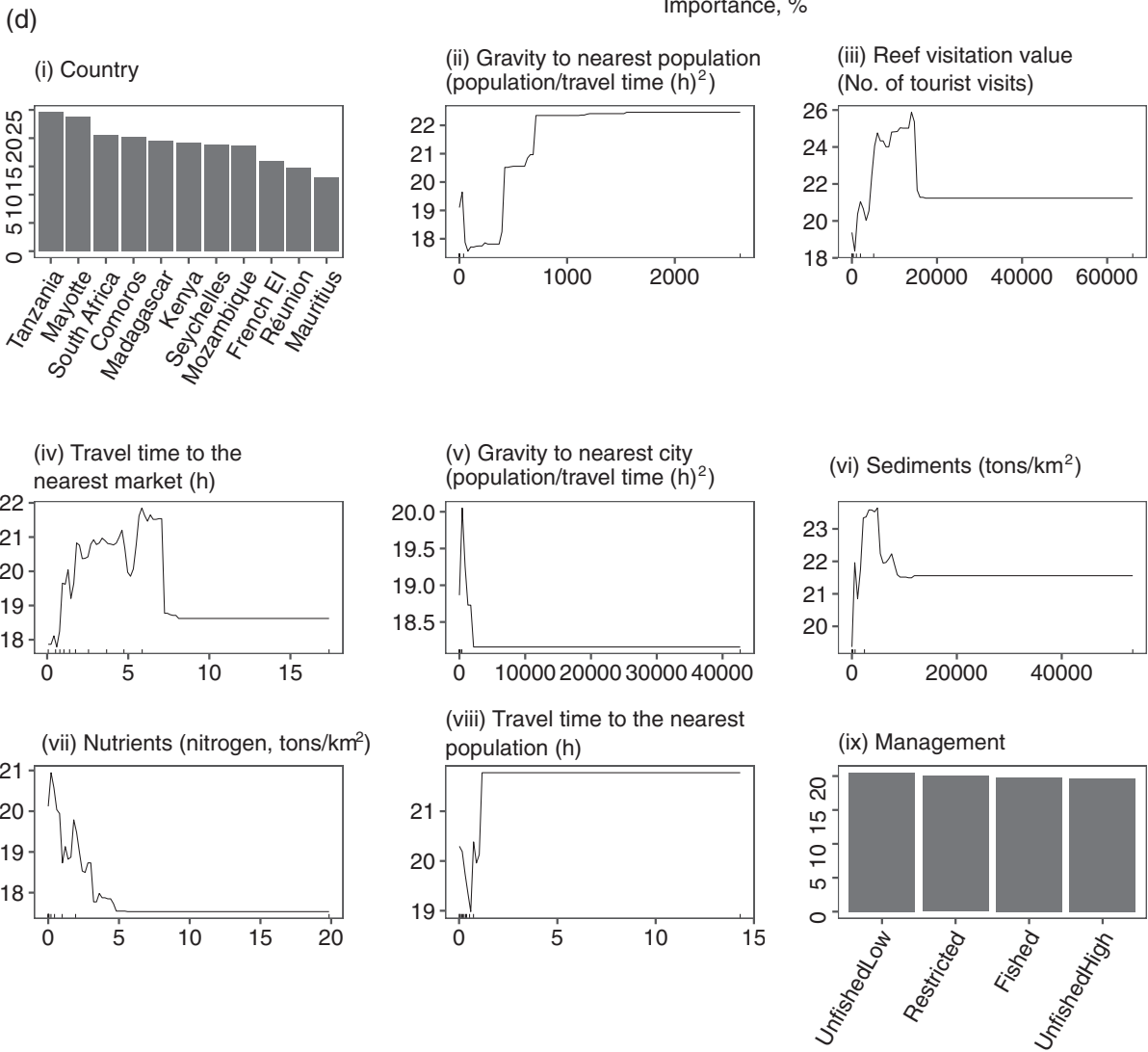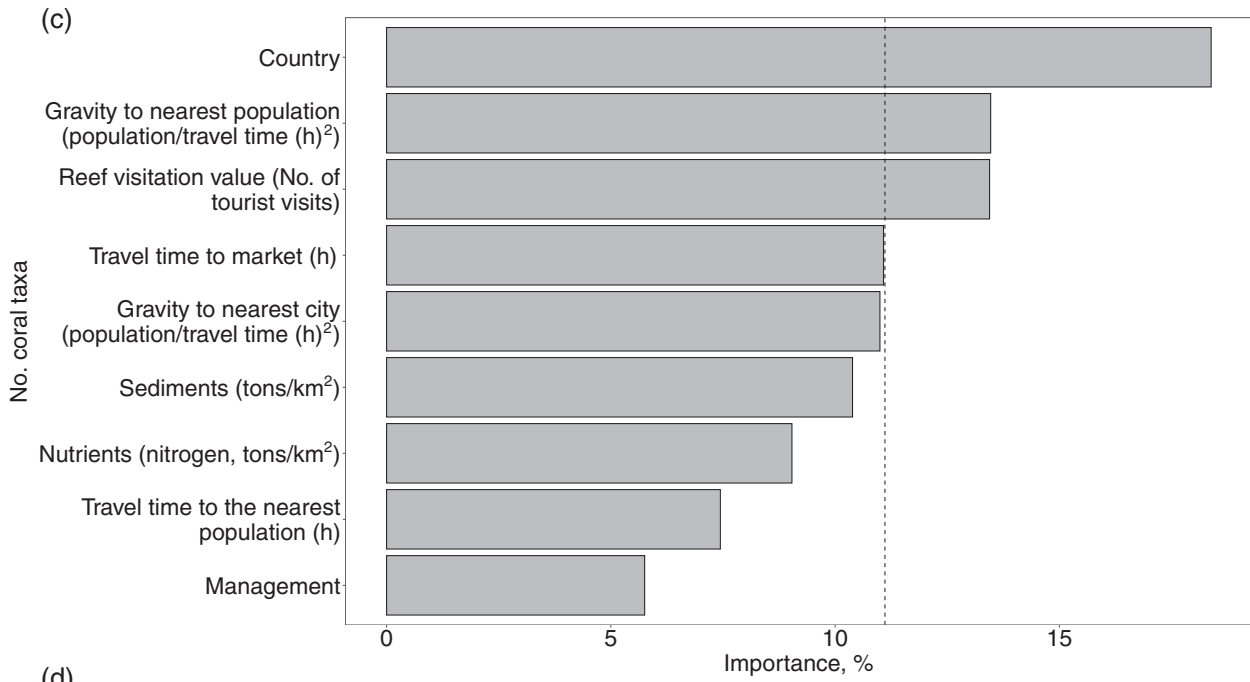
(c)

(d)

FIGURE 2 (Continued)

TABLE 2 Results of impacts on coral cover and numbers of taxa for two climate change scenarios using Coupled Model Intercomparison Project 5.0 (CMIP5.0) variables for Relative Concentration Pathways (a) RCP8.5 and (b) RCP2.6: predicted coral cover (in percent) and numbers of taxa (per ~40 m^2) in 2020 and 2050; the number of coral reef cells predicted to have the four combinations of gains and losses (2050–2020) of coral cover and numbers of taxa; measures of local and provincial resilience or the normalized average of the change in coral cover and numbers of taxa.

Country or ecoregion	Coral cover (%)		No. taxa		No. cells (%)				Local resilience	Provincial resilience	Delta SST
					Cover loss/ taxa loss	Cover loss/ taxa gain	Cover gain/ taxa loss	Cover gain/ taxa gain			
	2020	2050	2020	2050							
(a) CMIP5.0 RCP8.5 extreme scenario											
Madagascar	34.6	24.6	16.5	15.6	1643	183	289	167	−0.14	−0.28	0.29
	(11.1)	(9.9)	(1.9)	(1.5)	(72)	(8)	(12.7)	(7.3)	(0.2)	(0.15)	(0.79)
Tanzania	36.4	21.8	25.8	22.6	1524	0	0	0	−0.26	−0.16	0.45
	(5.4)	(5.9)	(2.9)	(2.2)	(100)				(0.07)	(0.1)	(0.15)
Mozambique	37.6	21.5	24.4	22.0	1091	80	0	9	−0.26	−0.17	0.60
	(5.2)	(6.9)	(3.3)	(2.4)	(92.5)	(6.8)		(0.8)	(0.09)	(0.14)	(0.14)
Seychelles	41	13.7	20.4	18.6	574	127	0	0	−0.38	−0.37	0.88
	(3.9)	(6.2)	(1.2)	(1.4)	(81.9)	(18.1)			(0.1)	(0.11)	(0.23)
Kenya	18.8	17.3	21.3	20.0	145	13	197	17	−0.01	−0.28	0.78
	(6.5)	(3.1)	(2.4)	(1.6)	(39)	(3.5)	(53)	(4.6)	(0.22)	(0.06)	(0.08)
Mauritius	32.6	37.2	16.8	17.1	23	31	125	125	0.09	−0.07	0.02
	(7.8)	(9.6)	(2.2)	(2.2)	(7.6)	(10.2)	(41.1)	(41.1)	(0.13)	(0.13)	(0.14)
Mayotte	47.1	44.8	25.5	23.1	214	0	55	0	−0.07	0.18	0.75
	(3)	(4.2)	(2)	(1.4)	(79.6)		(20.4)		(0.04)	(0.07)	(0.20)
Comoros	31.5	29.5	23.4	22.6	236	2	0	0	−0.05	−0.05	0.27
	(5)	(5.5)	(1.7)	(1.6)	(99.2)	(0.8)			(0.02)	(0.08)	(0.07)
French Eparses Islands	35.9	28	14.8	14.3	80	50	8	0	−0.12	−0.27	0.32
	(6.3)	(9)	(1.8)	(1.2)	(58)	(36.2)	(5.8)		(0.1)	(0.14)	(0.67)
Reunion	33.1	43.2	16.4	16.8	0	0	6	19	0.17	0.01	−0.14
	(1)	(1.3)	(1.9)	(1.9)			(24)	(76)	(0.03)	(0.04)	(0.11)
South Africa	43.4	24.4	20.2	17.6	6	0	0	0	−0.29	−0.24	0.89
	(2.3)	(20.5)	(0.7)	(0.8)	(100)				(0.22)	(0.27)	(0.33)
(b) CMIP5.0 RCP2.6 scenario											
Madagascar	34.6	31.4	16.5	15.7	1259	48	656	319	−0.03	−0.18	0.01
	(11.1)	(16)	(1.9)	(1.6)	(55.2)	(2.1)	(28.7)	(14)	(0.28)	(0.24)	(0.80)
Tanzania	36.4	28.6	25.8	24.2	1345	179	0	0	−0.14	−0.02	0.18
	(5.4)	(5.6)	(2.9)	(2.7)	(88.3)	(11.7)			(0.05)	(0.1)	(0.15)
Mozambique	37.6	30.7	24.4	22.6	1086	34	3	57	−0.13	−0.03	0.32
	(5.2)	(6.3)	(3.3)	(2.6)	(92)	(2.9)	(0.3)	(4.8)	(0.09)	(0.12)	(0.35)
Seychelles	41	31.7	20.4	19.1	583	42	76	0	−0.15	−0.1	0.60
	(3.9)	(10.5)	(1.2)	(1.1)	(83.2)	(6)	(10.8)		(0.1)	(0.16)	(0.23)
Kenya	18.8	20.0	21.3	20.7	139	1	90	142	0.05	−0.23	0.53
	(6.5)	(5.5)	(2.4)	(1.6)	(37.4)	(0.3)	(24.2)	(38.2)	(0.16)	(0.1)	(0.08)
Mauritius	32.6	30.8	16.8	16.9	112	83	4	105	−0.03	−0.17	−0.28
	(7.8)	(10)	(2.2)	(2.4)	(36.8)	(27.3)	(1.3)	(34.5)	(0.1)	(0.16)	(0.15)

(Continues)

TABLE 2 (Continued)

Country or ecoregion	Coral cover (%)		No. taxa		No. cells (%)				Local resilience	Provincial resilience	Delta SST
	2020	2050	2020	2050	Cover loss/ taxa loss	Cover loss/ taxa gain	Cover gain/ taxa loss	Cover gain/ taxa gain			
Mayotte	47.1	56.7	25.5	24.7	17	0	212	40	0.08	0.38	0.44
	(3)	(9)	(2)	(1.8)	(6.3)		(78.8)	(14.9)	(0.09)	(0.15)	(0.20)
Comoros	31.5	20.7	23.4	22.3	226	12	0	0	−0.2	−0.18	−0.04
	(5)	(4.6)	(1.7)	(1.9)	(95)	(5)			(0.03)	(0.08)	(0.07)
French Eparses Islands	35.9	32.2	14.8	14.1	78	0	1	59	−0.06	−0.21	0.04
	(6.3)	(10.4)	(1.8)	(1.2)	(56.5)		(0.7)	(42.8)	(0.19)	(0.14)	(0.70)
Reunion	33.1	35.7	16.4	16.3	8	4	7	6	0.04	−0.11	−0.44
	(1)	(5.9)	(1.9)	(1.9)	(32)	(16)	(28)	(24)	(0.09)	(0.09)	(0.10)
South Africa	43.4	29.9	20.2	18.2	6	0	0	0	−0.21	−0.15	0.68
	(2.3)	(12.9)	(0.7)	(0.5)	(100)				(0.14)	(0.17)	(0.33)
(c) CMIP5.0 RCP8.5 extreme scenario											
Western and Northern Madagascar	35.7	27.2	17.9	16.9	2126	224	337	167	−0.13	−0.22	0.33
	(10.8)	(10.9)	(3.7)	(3.2)					(0.18)	(0.2)	(0.73)
East African Coral Coast	35.8	21.9	25.3	22.4	2645	14	68	16	−0.24	−0.16	0.49
	(6.9)	(5.6)	(2.9)	(2.1)					(0.1)	(0.1)	(0.19)
Seychelles	41	13.7	20.4	18.6	574	127	0	0	−0.38	−0.37	0.88
	(3.9)	(6.2)	(1.2)	(1.4)					(0.1)	(0.11)	(0.23)
Mascarene Islands	38	42.4	16.3	17.6	0	31	21	144	0.1	0.01	−0.03
	(3.9)	(5)	(2.2)	(2.2)					(0.05)	(0.08)	(0.1)
Cargados Carajos/ Tromelin Island	24.2	30.4	17.2	16.1	23	0	118	0	0.09	−0.19	0.05
	(3.4)	(9.8)	(2.1)	(1.8)					(0.18)	(0.11)	(0.17)
Northern Monsoon Current Coast	14.3	18.6	20.5	19.6	0	0	129	1	0.14	−0.27	0.80
	(2.1)	(1.6)	(1.4)	(1.4)					(0.1)	(0.04)	(0.09)
Bight of Sofala/ Swamp Coast	30.5	18.2	20.5	21.6	31	73	0	9	−0.17	−0.23	1.02
	(4.8)	(7.9)	(1.5)	(1.6)					(0.16)	(0.12)	(0.11)
Delagoa	39.2	7.2	17.2	16	90	6	0	0	−0.45	−0.52	1.33
	(8.4)	(8)	(1.4)	(1.1)					(0.08)	(0.12)	(0.19)
Southeast Madagascar	31.3	19.6	14.7	13.9	47	11	7	0	−0.21	−0.39	0.36
	(3.5)	(10.8)	(1.1)	(1.1)					(0.2)	(0.17)	(0.51)
WIO province	35.6	23.6	21.0	19.3	5536	486	680	337	−0.19	−0.21	0.47
	(9.2)	(10.1)	(4.7)	(3.6)					(0.18)	(0.17)	(0.54)
(d) CMIP5.0 RCP2.6 moderate scenario											
Western and Northern Madagascar	35.7	33.2	17.9	17.1	1523	51	862	418	−0.03	−0.13	0.05
	(10.8)	(16.8)	(3.7)	(3.5)					(0.26)	(0.27)	(0.74)
East African Coral Coast	35.8	29.2	25.3	23.6	2393	185	66	99	−0.12	−0.03	0.22
	(6.9)	(5.6)	(2.9)	(2.5)					(0.09)	(0.1)	(0.20)
Seychelles	41	31.7	20.4	19.1	583	42	76	0	−0.15	−0.1	0.60

TABLE 2 (Continued)

Country or ecoregion	Coral cover (%) 2020	Coral cover (%) 2050	No. taxa 2020	No. taxa 2050	Cover loss/ taxa loss	Cover loss/ taxa gain	Cover gain/ taxa loss	Cover gain/ taxa gain	Local resilience	Provincial resilience	Delta SST
	(3.9)	(10.5)	(1.2)	(1.1)					(0.1)	(0.16)	(0.23)
Mascarene Islands	38	37.7	16.3	17.1	10	87	11	88	0.02	−0.06	−0.34
	(3.9)	(7.3)	(2.2)	(2.2)					(0.08)	(0.11)	(0.10)
Cargados Carajos/ Tromelin Island	24.2	21.3	17.2	16.2	118	0	0	23	−0.09	−0.31	−0.23
	(3.4)	(2.6)	(2.1)	(2.6)					(0.07)	(0.08)	(0.18)
Northern Monsoon Current Coast	14.3	14.5	20.5	20.4	59	1	27	43	0.01	−0.31	0.56
	(2.1)	(3.4)	(1.4)	(1.5)					(0.14)	(0.07)	(0.09)
Bight of Sofala/ Swamp Coast	30.5	29.8	20.5	21.4	34	22	0	57	0.01	−0.07	0.75
	(4.8)	(9.1)	(1.5)	(1.8)					(0.16)	(0.13)	(0.12)
Delagoa	39.2	21.5	17.2	16.1	90	6	0	0	−0.26	−0.31	1.11
	(8.4)	(10.7)	(1.4)	(1.1)					(0.11)	(0.16)	(0.19)
Southeast Madagascar	31.3	20.8	14.7	13.6	49	9	7	0	−0.21	−0.38	0.04
	(3.5)	(8.1)	(1.1)	(1)					(0.09)	(0.12)	(0.5)
WIO province	35.6	30.7	21.0	19.9	4859	403	1049	728	−0.08	−0.10	0.19
	(9.2)	(12.5)	(4.7)	(4.3)					(0.19)	(0.21)	(0.55)

Note: Values in parentheses are SDs. Local resilience compared a cell to itself while provincial compared a cell to the provincial average of cover and numbers of taxa. Nation and ecoregions are ordered from most to least coral reef cells.

Abbreviations: SST, sea surface temperature; WIO, Western Indian Ocean.

Tromelin Island ($0.05 \pm 0.17°C$). The moderate RCP2.6 scenario reduced these changes, such that temperatures were predicted to decline in the Mascarene and Cargados Carajos/Tromelin islands.

Scatterplots of predicted changes in coral cover and numbers of taxa indicated larger losses for the RCP8.5 versus the RCP2.6 scenarios (Figure 3; Table 2). Responses differed considerably among countries and ecoregions (Figure 4). For example, there were cells in all four loss-gain categories in both scenarios. Overall, in the extreme RCP8.5 scenario, the WIO province was predicted to change from $35.6 \pm 9.2\%$ (SD) to $23.6 \pm 10.1\%$ cover and 21.0 ± 4.7 to 19.3 ± 3.6 taxa per 40 m² between 2020 and 2050. Coral cover in the moderate RCP2.6 scenario declined to $30.7 \pm 12.5\%$ (−4.9%) and taxa to 19.9 ± 4.3 (−1.1 taxa). The between cells variability of cover and numbers of taxa were predicted to increase over the 30 years.

In the RCP8.5 scenario, 5536 of 7039 or 79% of the reef cells were predicted to lose coral cover and taxa while only 337 or 5% were predicted to both gain cover and taxa. The remaining 1160 cells were split between cover and taxa gains and losses. Under the moderate RCP2.6, 4859 or 69% of the cells were predicted to lose both cover and taxa, 728 gain both, and 1452 split the gains and losses. Most of the cover and taxa-gain cells were in Madagascar and Mauritius. Under the extreme RCP8.5, most of the cover gains but taxa losses were similarly found in Madagascar and Mauritius but also in Kenya and Mayotte. Cover losses but taxa gains were broadly distributed with the exceptions of Tanzania, Mayotte, Reunion, and South Africa. Tanzania and South Africa were predicted to lose both cover and taxa in the RCP8.5, but Tanzania was predicted to gain taxa in 12 cells under the RCP2.6 scenario.

The resilience metric combined cover and numbers of taxa changes. Results are presented as local change relative to the specific cell or provincial change relative to the provincial average baseline in 2020 (Table 2; Figure 4). Most nations and ecoregions were predicted to lose cover and numbers of taxa or resilience. The peripheral and small Cargados Carajos/Tromelin Island Ecoregion was the only exception. Mayotte was the jurisdiction predicted to be most locally and provincially resilient across the two RCP scenarios. The relationship between local and provincial resilience
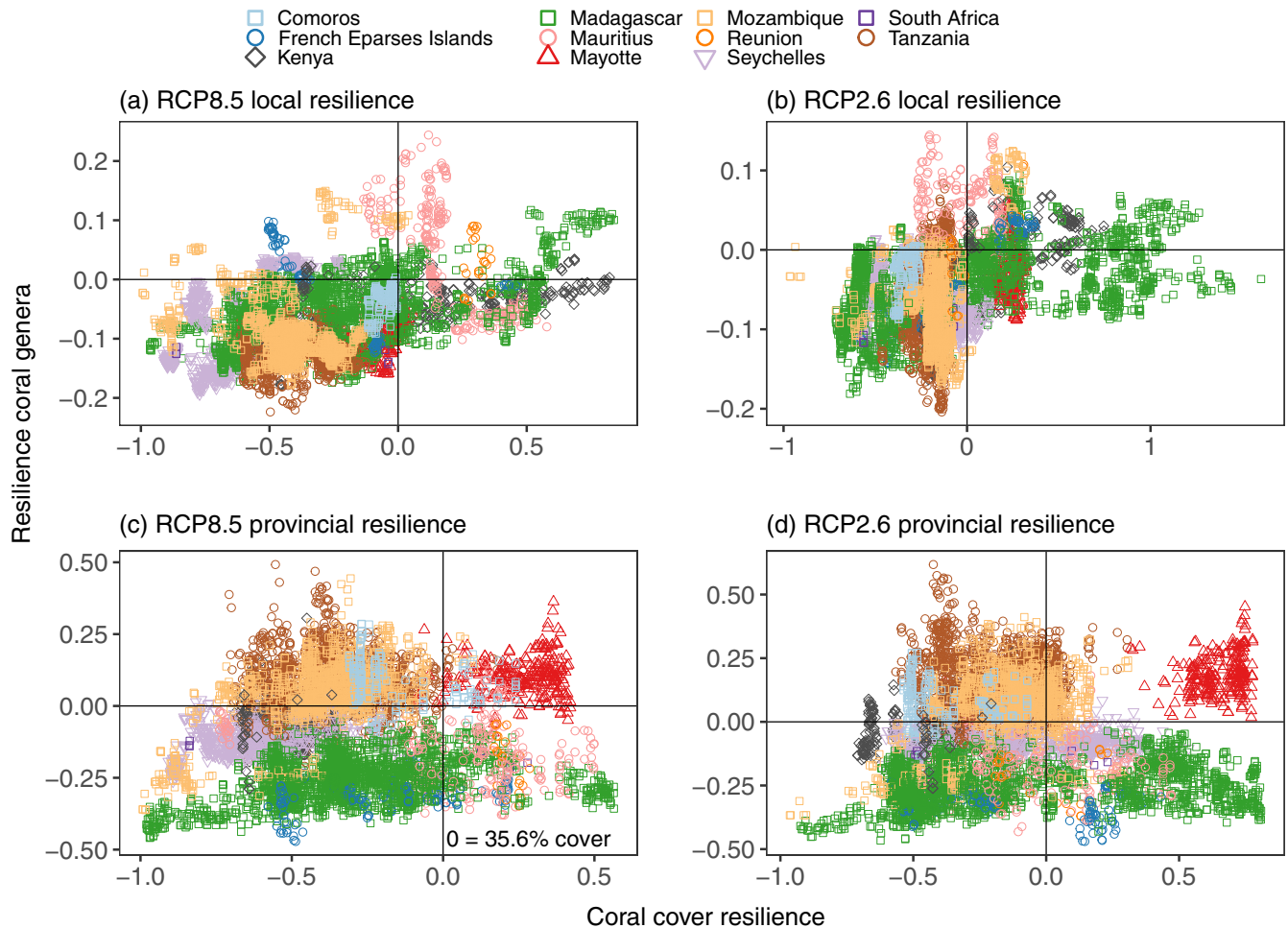
FIGURE 3 Scatterplots of the predicted changes (2050–2020 relative to zero change) in coral cover and numbers of taxa in 7039 reef cells of the western Indian Ocean province distinguishing cells by their national jurisdiction delineations. (a, b) The changes in each cell relative to itself and (c, d) changes in cells relative to the provincial average coral cover and numbers of taxa in each year. Thus, plots represent a local and provincial resilience metric mapped in Figure 4. The predictions are based on the Coupled Model Intercomparison Project 5.0 (CMIP5.0) temperature predictions under the extreme Relative Concentrations Pathways 8.5 (RCP8.5) on the left and the moderate RCP2.6 scenario on the right. The five variables shared by CMIP5.0, and our boosted regression tree model were the median sea surface temperature, skewness, kurtosis, bimodality, and cumulative excess heat (degree-heating weeks). No human influenced variables were included in the scenarios.

found that variability increased with increasing local resilience (Figure 5). In general, reefs with high coral cover and numbers of taxa were losing more local but less provincial resilience over the 30-year period. These plots demonstrated that many, but particularly some reefs in Mayotte, the Mascarene Islands, Northwest Madagascar, and Mozambique, should experience increases in resilience under the moderate emissions RCP2.6 scenario.

DISCUSSION

Our findings indicate the complexity of the relationship between environmental variables and numbers of coral taxa and the subsequent distribution of coral diversity.

Moreover, there are considerable consequences arising from investigators' foci, variable reduction methods, and selectivity decisions. These choices affect the relative or rank importance of variables. Comparing models improves understanding potential sources of causation, predictions, and subsequent policies. Despite the complexity, there was a common suite of interacting environmental variables associated with the numbers of coral taxa response. Among the temperature variables, skewness, excess heat (cumDHW), rate of rise, kurtosis, and median SSTs were frequently selected as influential. Several of these variables have been identified in the WIO and elsewhere as influential predictors of coral bleaching and cover (Ateweberhan & McClanahan, 2010; McClanahan & Azali, 2021; Safaie et al., 2018; Shlesinger &
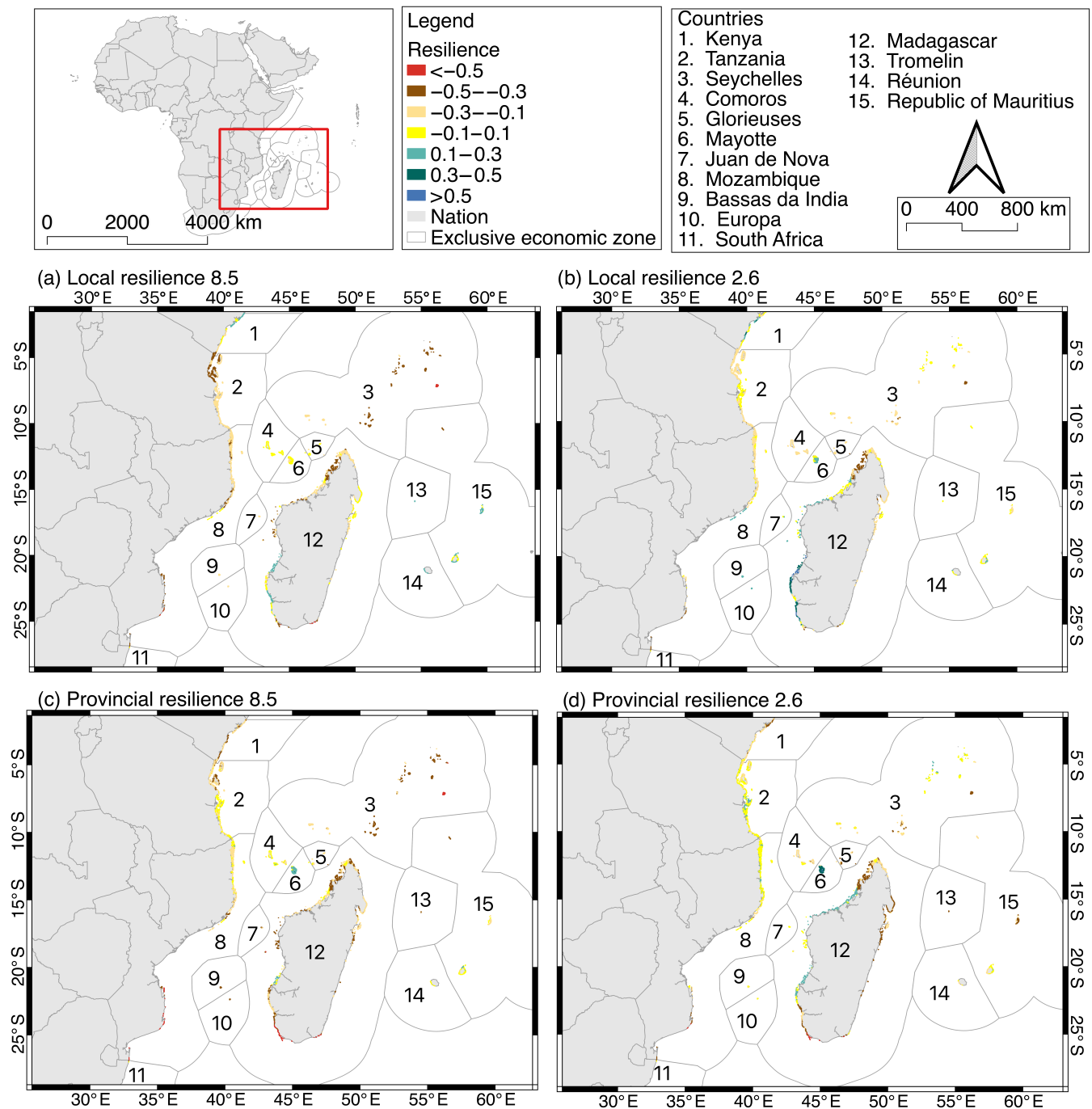
FIGURE 4 Maps of the distribution of changes in local and provincial resilience or coral cover and numbers of taxa over 30 years (2050–2020) predicted by the Coupled Model Intercomparison Project 5.0 model Relative Concentration Pathways 8.5 (RCP8.5) and RCP2.6 scenarios. The two resilience metrics are the percentage difference relative to the 2020 predicted values for each cell (local resilience) or relative to the average 2020 prediction for all Western Indian Ocean countries (provincial resilience).

van Woesik, 2023; Vercammen et al., 2019). Nevertheless, our results suggest temperature metrics are among other several important influential variables including human impacts.

Coral cover and numbers of coral taxa have been shown to be influenced by similar temperature variables (McClanahan & Azali, 2021). However, the patterns of response often differed between number of taxa and coral cover. For example, similar modeling procedures found coral cover peaked in the WIO at 30–35 cumDHW, while numbers of taxa peaked at lower values of 15–25 cumDHW or excess heat. Moreover, numbers of taxa were high but cover low at median temperatures of ~27–28°C. Coral cover declined with increasing warm-water temperature skewness
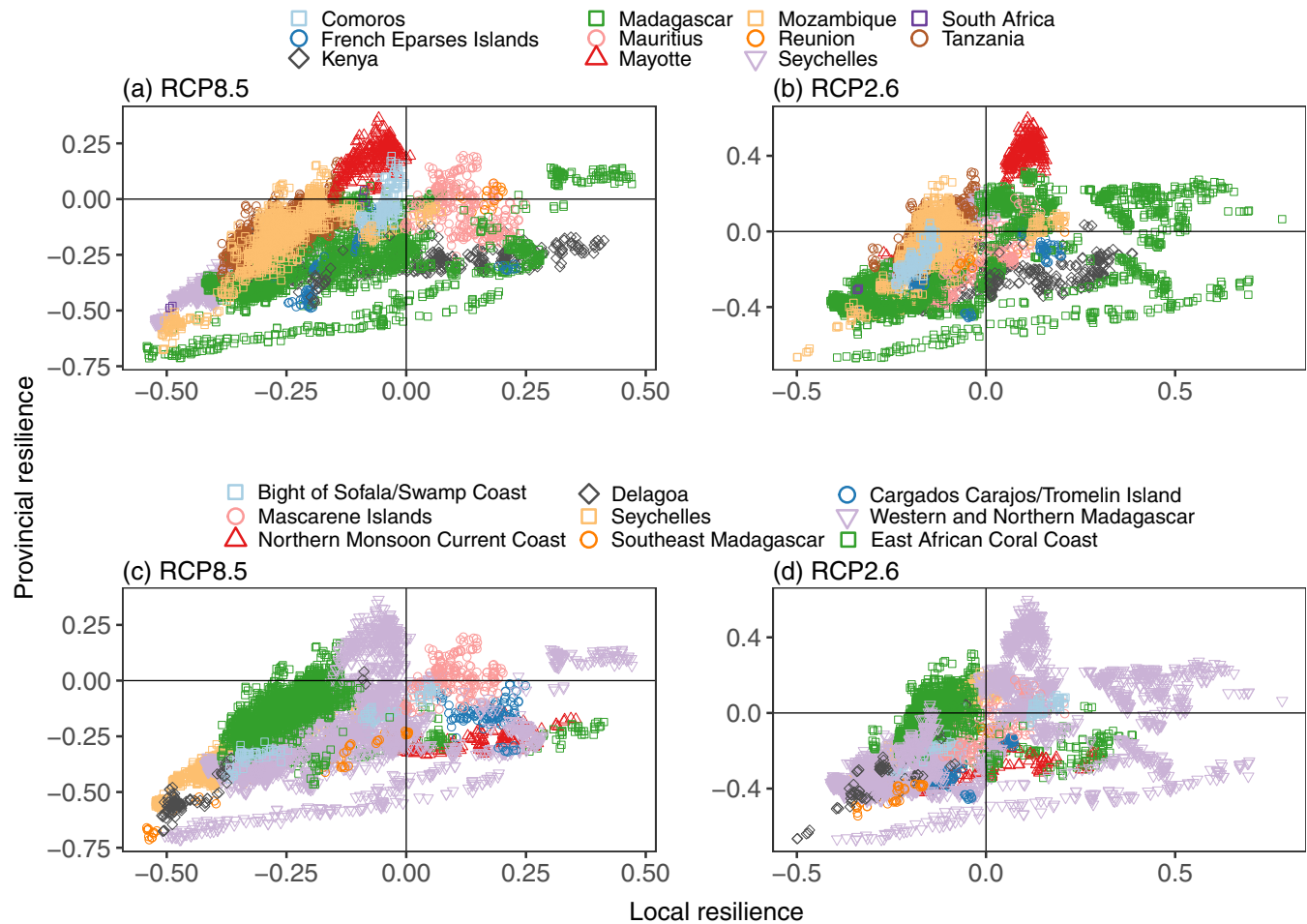
FIGURE 5 Scatterplots showing the relationship between local and provincial resilience for (a,b) national jurisdictions and (c,d) ecoregions for the two Coupled Model Intercomparison Project (CMIP) climate scenarios changes between 2020 and 2050. Resilience is the average of the change in coral cover and numbers of taxa presented as normalized z score. RCP, Relative Concentration Pathways.

and kurtosis, while numbers of taxa increased as temperature distributions were more centralized and tolerated some cool-water skewness. Consequently, numbers of coral taxa were not as tolerant of chronic heat stress as cover. We suggest these differences reflect niches, coexistence, and dominance relationships among coral taxa. Stable and optimal conditions promote higher numbers of taxa. In contrast, increases in chronic and acute climate disturbances impact cover and dominance by reducing the sensitive taxa that contribute to high cover (i.e., Acroporidae) (Darling et al., 2013). Numbers of taxa and cover may be high in historically stable environments, but these metrics are also most influenced by acute climate disturbances in recent times (McClanahan, 2020a, 2020b). Specifically, these studies show that high cover taxa, such as acroporids, generally lack tolerance to acute warm temperatures. Therefore, coral status is better evaluated by including changes in both cover and numbers of taxa as reflected in our resilience metric.

Consequences of modeling decisions

Selecting variables is likely to be dependent on the disciplinary focus and impact concerns of investigators. For example, temperature and ocean acidity are core concerns among climate change scientists (Steffen et al., 2015). However, our full analysis found that several non-temperature variables ranked higher than these variables for predictions of numbers of taxa. These included wave energy, dissolved oxygen and calcite concentrations, salinity, chlorophyll, sunlight, and net primary productivity. Several of these variables have been infrequently evaluated or chosen by coral-climate change investigators despite their potential to be influenced by climate change (McClanahan & Azali, 2021; Porter et al., 2017; Vercammen et al., 2019). When evaluating numbers of taxa on large scales, distance from centers of evolution, habitat extent, thermal energy, and stress have been more commonly selected (Ateweberhan et al., 2018; Bellwood et al., 2005; Bellwood & Hughes, 2001). Here,

we included fewer biogeographic variables and assumptions apart from including ecoregion, which was a weak predictor, and reef clustering in the full model. Rather, we utilized many available spatially complete data layers in the full model, which resulted in stronger predictions than for the investigator or discipline selected variable models. This full variable approach is recommended for making applied predictions where causative relationships are speculative (Kuhn & Johnson, 2013).

Studies of coral bleaching and cover, including those used in the IPCC report, have relied on similar excess heat metrics but seldom include the contextual temperature variations (i.e., kurtosis and skewness) and non-temperature variables (Asner et al., 2022; Donovan et al., 2021; Hoegh-Guldberg et al., 2018). Therefore, the stated influences of excess heat may be overestimated (De Carlo, 2020; McClanahan et al., 2019). For example, we found selecting fewer or eight variables raised the cumulative excess heat (cumDHW) influence from 6.9% to 14.4%, making it the highest ranked variable, after observer and depth, in the selected climate influenced model. Empirical studies have shown that depth is a strong unimodal predictor of numbers of taxa (Cornell & Karlson, 2000). Most coral climate change impact models rely heavily on similar and autocorrelated excess heat variables (Beyer et al., 2018; Dixon et al., 2022).

Comparing the four models uncovered some of the challenges faced by environmental modeling investigators that have specific views on causation, optimality, and impacts (Thompson & Smith, 2019). Investigator selection of a limited number of variables may overestimate the influence of chosen variables. For example, nutrients and management had 9.0% and 5.7% influence in the human influence model but only ~1.6% in the ensemble model. Country was also the strongest variable in the human influence model (18.5%) compared to <4% in the ensemble model. Furthermore, the rate of SST rise was the second strongest variable (16.3%) after skewness in the climate-only model but had <4% relative influence in the ensemble model. Rate of SST rise is correlated with other temperature variables, and therefore, interactive influences are difficult to disarticulate. These types of between-model choices and deviations suggest some caution when inferring forces of causation and predictive strengths, especially when investigators select just a few variables (Arif et al., 2022). Given the complexity and challenges of understanding causation in tropical ecosystems, some complexity, redundancy, and comparison of models should improve understanding and strengthen forecasts (McClanahan & Sola, 2024). The problem for coral reefs and the IPCC predictions is that they are largely based on a single or a few autocorrelated variables (McClanahan, 2022, 2024). Models based on simple proxy metrics may do reasonably well when data are sparse but are expected to underperform when diverse and ubiquitous data are available.

A second concern is the influences and efficacy of model structures and specific algorithms. Underlying assumptions and subsequent calculations can shape evaluation processes and predictions. Model capacity and complexity have increased over time through increased data quantity, time and spatial resolution, and machine learning algorithms. However, previous taxa-distribution models interpolated distributions over large and potentially uninhabitable areas. This procedure will inevitably reflect a poor connection between species' distributions and their environmental and habitat requirements.

Niche modeling is a popular development that has addressed several large-scale coral biodiversity distribution and climate impact problems (Molinos et al., 2016). Some recent coral distribution models have included several variables, such as SST, aragonite saturation, salinity, nutrients, PAR levels, and light penetration. Using these variables, Couce et al. (2023) predicted a net 80% losses of coral species in the WIO region by 2080–2090 in their 625 km^2 grid under the Paris Agreement high emission scenario (8.5 watts m^{-2}). This prediction is considerably more extreme than our more spatially resolved model (6.25 km^2) and suggests that the model assumptions and spatial scale of predictions affected results more then the variable choices. We suggest that coarse spatial cell predictions will poorly reflect local conditions important for determining species occupations. Coarse resolutions and realized rather than fundamental niche estimates should produce interpolation and extrapolation errors. These may be among several reasons that niche modeling is poor at predicting many population attributes (Lee-Yaw et al., 2022). The high spatial heterogeneity of numbers of coral reef taxa recorded at small latitudinal scales suggests that coarse geographic grid models (>0.1°) will fail to make accurate predictions (McClanahan, 2023a, 2023b). Coral species have been shown to persist in small refuges even in some of the most degraded reefs of the WIO (Andrefouet et al., 2013). We acknowledge significant spatial heterogeneity below our 6.25 km^2 cell size that will limit our own model's accuracy.

Comparing climate impact models

Common future coral reef prediction models (i.e., until 2022) have been based largely on excess heat and rate of temperature rise metrics. Specifically, bleaching uses a 1°C threshold above summer temperatures for 4–8 weeks and IPCC predictions are based on the accumulation of

excess heat over time (Lee et al., 2023). Yet, there are several poorly understood linkages between excess heat and the biological responses of coral bleaching, mortality, cover, dominance, and taxonomic changes (McClanahan, 2022). Excess heat alone has infrequently predicted both coral bleaching and cover well (DeCarlo, 2020; Gonzalez-Espinosa & Donner, 2021; McClanahan et al., 2019; van Hooidonk & Huber, 2009; Whitaker & DeCarlo, 2024). Rather, the combination of several heat and other interacting environmental measures produces stronger and less dire predictions (McClanahan, Maina, et al., 2015, 2019; Santana et al., 2023; Vercammen et al., 2019). When few interacting variables are considered, excess heat as a single proxy is likely to overestimate impacts. Moreover, predictions of community attributes are sensitive to variable selection, model complexity, and other model-building assumptions.

Our multivariate model found greater resilience of coral cover and numbers of taxa than past threshold models. For example, our multivariate models predicted a provincial 8.1% decline in coral taxa and a 34.0% decline in cover with the Paris target of ~1.5°C SST increase. Moreover, the spatial variability of our models' predictions is considerably higher than previous models (Cornwall et al., 2021; Couce et al., 2023; Dixon et al., 2022). Our model suggests that the predicted "disappearance of reefs" (Lee et al., 2023) is not supported by models with higher spatial resolution and complex environmental interactions. Future efforts need to reconsider the outcomes of scale and variable choices on the confidence of future reef assessments (Klein et al., 2024). Specifically, improved evaluations of the causative links connecting heat stress to coral community variables, particularly those that provide key reef functions and ecological services (Chan et al., 2023; Darling et al., 2019; Vercammen et al., 2019). Nevertheless, the state of data resolution and predictive modeling has improved to where a new models and associated coral reef predictions and policies are needed (McClanahan, 2024).

We acknowledge the weakness of our and other models built on historical relationships as future conditions are expected to exceed the current environmental data envelope. For example, the increase in ocean temperatures after 2022 to the time of this writing saw global temperature rising ~1.5°C above baseline, or many years ahead of the IPCC 2050 predictions (https://www.ncei.noaa.gov/). Spatial variability and extreme events of the ocean's El Niño Southern oscillations is another example where IPCC makes weak predictions (Cai et al., 2023; McManus et al., 2020). Extreme events are expected to be more common in the future (Jentsch et al., 2007). The metric of SST skewness reflects these extreme events and shown here to be among the most predictive and non-linear variables.

Conservation prioritization

Numbers of taxa and their persistence can assist prioritizing locations for reef conservation (McClanahan, Friedlander, Wickel, et al., 2024). Prioritization decisions are influenced by the spatial scale, boundaries of delineation, and persistence relative to benchmarks. For example, high numbers of taxa were predicted in the East Africa Coral Coast Ecoregion, but several reefs were predicted to lose more taxa than locations with fewer taxa. This outcome has already been observed in Kenyan reefs where the high diversity fully protected marine parks were shown, after severe climate disturbances, to be losing taxa faster than low diversity reefs (McClanahan, 2020a). Nevertheless, scatterplots at the provincial scale indicate that the persistence of taxa is likely to occur in scattered locations with high numbers of taxa. Finding and better managing resilient locations will help to maintain provincial diversity as climate change impacts increase and erode diversity on large scales.

Priority locations for conservation were visibly different among geographies and climate change scenarios. For a geographic example, northern Kenya was predicted to have high local resilience with rapid increases in SST, but this was associated with low numbers of taxa and cover relative to the WIO province. Therefore, the Northeast Monsoon Coast Ecoregion of northern Kenya is a local or national but not a provincial priority from a climate resilience perspective. Mascarene reefs are another example of high local but lower provincial resilience attributable to their geographic remoteness and reduced numbers of taxa. The two climate emission scenarios also influenced taxa richness-based prioritizations. For example, many East African Coral Coast Ecoregion reefs were predicted to have high provincial resilience for RCP2.6, but to lose local resilience under the extreme RCP8.5 scenario. Therefore, the scenarios and classification of sites as either local or provincial priorities will affect conservation choices. Mayotte (France) and some reefs in northern section of southeast Madagascar were among the few jurisdictions predicted to have both high local and provincial resilience for both scenarios.

Recommendations

Future predictions were based on only five variables common to both the CMIP5.0 projections and our full variable model. To further improve climate projection models, we recommend the inclusion of more and finer spatial resolution of environmental and human influenced variables. For example, models that forecast variables, such as dissolved oxygen and calcite concentration,

and chlorophyll are possible and, if spatially resolved and included in models, should improve estimates of climate impacts. Inclusion of some of these variables will change predictions to both reduce and increase the losses of coral resilience. Nevertheless, the net direction of change with introduced oceanographic variables is difficult to predict until the models are built and tested. For example, dissolved oxygen is expected to decline with climate change and potentially increase stress to coral (Hughes et al., 2020). However, greater coral cover and numbers of taxa models have been found at modest dissolved oxygen values (i.e., 4.4 mL/L) (Vercammen et al., 2019; McClanahan & Azali, 2021). Experimental findings have shown that lower oxygen values in tropical waters create cotolerance to heat stress (Alderdice et al., 2021). Thus, we should expect other complex responses to contribute to the high spatial variability observed in our model outputs.

Current excess heat models were developed prior to the advent of high-resolution environmental proxies and the common usage of applied predictive modeling (Hoegh-Guldberg, 1999). Subsequently, increased availability of the numerous environmental variables and their complex influence on coral community responses has been revealed (McClanahan, 2022; McClanahan & Azali, 2021). Therefore, we suggest updating future iterations of biodiversity mapping and climate predictions with more environmental proxies and field data (Kuhn & Johnson, 2013; Pilowsky et al., 2022). It is not simply the coarse resolution of model predictions but also the selection of variables, model assumptions, structure, and algorithmic capacity that needs reconsideration, modification, and updating. Future predictive models can improve if based on an increasingly rich investigative, variable, and modeling context. Given that corals are adapting and communities' reorganizing to climate stresses (DeCarlo & Harrison, 2019; McClanahan, Darling, et al., 2020; McClanahan, Maina, et al., 2020; Shlesinger & van Woesik, 2023), even current complex predictive models should eventually be outcompeted by more informed, resolved, and intelligent models. Additionally, prioritization policies and management responses will need to recognize the changing science and uncertainty of the predictions. Nevertheless, the findings here provide the context to build a portfolio of ecologically rich and resilient locations to secure reef biodiversity.

AUTHOR CONTRIBUTIONS

Conceptualization: Tim R. McClanahan and Maxwell K. Azali. *Data contribution*: Tim R. McClanahan, Nyawira A. Muthiga, Sean N. Porter, Michael H. Schleyer, and Mireille M. M. Guillaume. *Data analysis*: Maxwell K. Azali and Tim R. McClanahan. *Original draft*: Tim R. McClanahan. *Substantial contribution to text*: Nyawira A. Muthiga, Sean N. Porter, Michael H. Schleyer, and Mireille M. M. Guillaume.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data are available from the Knowledge Network for Biocomplexity (McClanahan, 2023a): 10.5063/F1K35S3H and Dryad (McClanahan, 2023b): 10.5061/dryad.3xsj3txn1. Code is available from Zenodo (Azali, 2024): 10.5281/zenodo.13463413.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.