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RESEARCH PAPER

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Large geographic variability in the resistance of corals to thermal stress

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Abstract

Aim: Predictions for the future of coral reefs are largely based on thermal exposure and poorly account for potential geographic variation in biological sensitivity to thermal stress. Without accounting for complex sensitivity responses, simple climate exposure models and associated predictions may lead to poor estimates of future coral survival and lead to policies that fail to identify and implement the most appropriate interventions. To begin filling this gap, we evaluated a number of attributes of coral taxa and communities that are predicted to influence coral resistance to thermal stress over a large geographic range.

Location: Western Indo-Pacific and Central Indo-Pacific Ocean Realms.

Major taxa studied: Zooxanthellate Scleractinia – hard corals.

Methods: We evaluated the geographic variability of coral resistance to thermal stress as the ratio of thermal exposure and sensitivity in 12 countries during the 2016 global-bleaching event. Thermal exposure was estimated by two metrics: (a) historical excess summer heat (cumulative thermal anomaly, CTA), and (b) a multivariate index of sea-surface temperature (SST), light, and water flow (climate exposure, CE). Sensitivity was estimated for 226 sites using coordinated bleaching observations and underwater surveys of coral communities. We then evaluated coral resistance to thermal stress using 48 generalized linear mixed models (GLMMs) to compare the potential influences of geography, historical SST variation, coral cover and coral richness.

Results: Geographic faunal provinces and ecoregions were the strongest predictors of coral resistance to thermal stress, with sites in the Australian, Indonesian and Fiji-Caroline Islands coral provinces having higher resistance to thermal stress than Africa-India and Japan-Vietnam provinces. Ecoregions also showed strong gradients in resistance with highest resistance to thermal stress in the western Pacific and Coral Triangle and lower resistance in the surrounding ecoregions. A more detailed evaluation of Coral Triangle and non-Coral Triangle sites found higher resistance to thermal

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stress within the Coral Triangle, associated with *c.* 2.5 times more recent historical thermal anomalies and more centralized, warmer, and cool-water skew SST distributions, than in non-Coral Triangle sites. Our findings identify the importance of environmental history and geographic context in future predictions of bleaching, and identify some potential drivers of coral resistance to thermal stress.

Main conclusions: Simple threshold models of heat stress and coral acclimation are commonly used to predict the future of coral reefs. Here and elsewhere we show that large-scale responses of coral communities to heat stress are geographically variable and associated with differential environmental stresses and histories.

KEYWORDS
adaptation, biodiversity, climate change, coral bleaching, diversity hotspots, oceanographic change, refugia

1 | INTRODUCTION

The capacity of corals to adapt to climate change is among the Earth's most pressing environmental challenges (Hughes et al., 2017). Localized studies have shown that corals acclimate or adapt by changing protein expressions (Palumbi et al., 2014), switching of symbionts (Boulette et al., 2016), acclimating to variable sea-surface temperature (SST) environments (Safaie et al., 2018; Sully et al., 2019), and after experiencing warm-SST anomalies (Guest et al., 2012; Hughes et al., 2019; McClanahan, 2017). However, the responses of scleractinian corals to thermal stress at large spatial scales are increasingly important for predicting the future of coral reefs and implementing appropriate conservation actions (Sully et al., 2019; Van Hooidonk et al., 2016).

Ecological responses to stress are often mediated by resilience, a concept that integrates the ability of ecosystems to resist and recover from disturbances. With recovery windows shrinking for coral reefs (Hughes et al., 2018), here we focus on the ability of coral communities to resist large-scale thermal stress events influenced by climate change. Resistance is a measure of system change when exposed to stress, and a key component of coral reef resilience that determines how coral communities survive major disturbances, such as climate change and increasing thermal stress (McClanahan et al., 2012). Under the increasing impacts of climate change, coral bleaching, or the rapid decline of coral's endosymbiotic microalgae, is an early and obvious indicator of thermal stress (Hughes et al., 2018). Nevertheless, bleaching can be patchy in space and time, whereby some corals bleach either more or less than expected given the exposure to thermal stress, and this patchiness can be mediated by historical and current environmental conditions (McClanahan et al., 2020; Sully et al., 2019). Ultimately, the resistance of corals to stress should be influenced by variation in geographic and evolutionary history and associated genotypic diversity, adaptation rates and taxonomic composition (Edmunds & Gates, 2008; Palumbi et al., 2014). However, these patterns remain untested across large biogeographic scales. These tests will, however, be critical for calibrating future climate impact models that are based on the spatial and temporal variability of the current and projected thermal exposures (Couce et al., 2013; Freeman et al., 2013; McManus et al., 2019).

Here, we combine satellite SST observations with a globally coordinated effort to survey corals exposed to a large-scale thermal stress event in 2016 in order to evaluate their resistance across a large geographic gradient (Figure 1a). We evaluated resistance as the exposure to thermal stress and the resulting sensitivity of ecological communities. We define exposure as the degree, duration and extent of perturbations beyond background levels. Corals are threatened by exposure to heat and light extremes and their variability exacerbated by climate change. However, the impacts may be attenuated by variability in the sensitivity of coral taxa and locations (Sully et al., 2019). To evaluate coral reef exposure, we considered two models derived from the United States National Oceanic and Atmospheric Administration (NOAA) Advanced Very High Resolution Radiometer multivariate satellite measurements as proxies for a number of essential ocean variables that are used to estimate stress to corals (Eakin et al., 2010; Maina et al., 2008, 2011; Muller-Kager et al., 2018).

To evaluate sensitivity, we used coordinated field surveys to estimate coral bleaching and therefore the sensitivity of different coral taxa and community assemblages, which can be influenced by previous thermal stress or other disturbances that can alter coral assemblages and their sensitivity to further disturbances (Darling et al., 2013, 2019). Sensitivity can take various forms, but here we define and document it as the percentage of bleached corals as a proxy for coral morbidity and mortality (Fitt et al., 2001; McClanahan et al., 2001). Our objectives were to: (a) assess coral resistance to the 2014–2016 mass bleaching event in the Indo-Pacific; and (b) evaluate the influences of geography, historical SST variation, coral cover and coral richness on bleaching resistance.

2 | MATERIALS AND METHODS

Resistance is a system-level metric used to estimate the balance between environmental exposure and biological sensitivity. There are

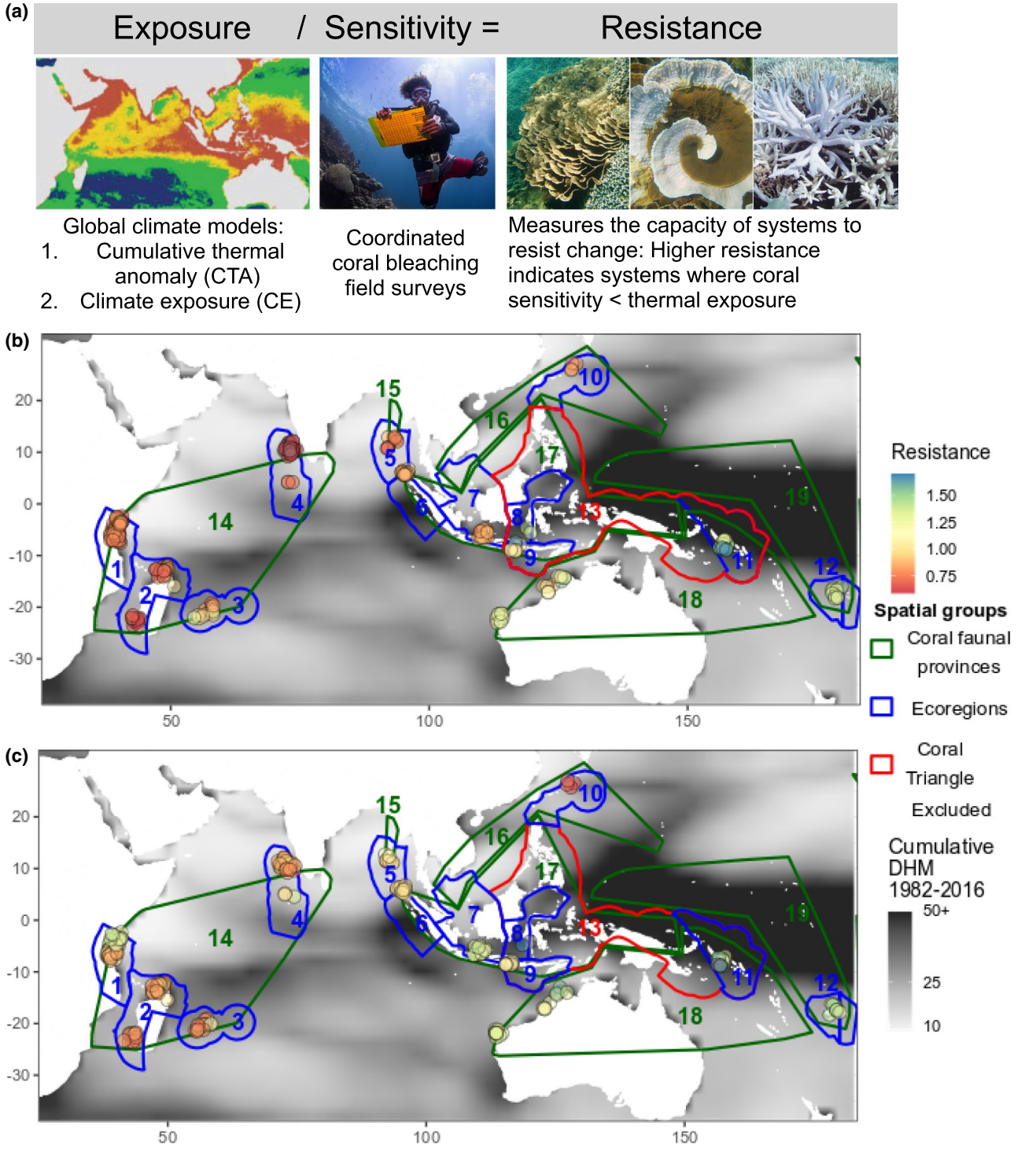

FIGURE 1 Distribution of geographic regions and coral reef resistance to the pan-tropical thermal stress event of 2014–2016. (a) Resistance is a metric for measuring the capacity of coral reefs to resist bleaching, estimated from exposure to environmental stress divided by ecological sensitivity. (b) Map of 226 Indo-Pacific coral reefs showing resistance calculated using a cumulative thermal anomaly (CTA) exposure model and (c) using a multivariate climate exposure (CE) model. Coloured dots show resistance; background shading represents chronic heat stress, evaluated as cumulative degree-heating months (DHM) between 1982 and 2016 estimated from satellite data. Spatial groups are overlain as polygons differentiated by colour, numbers represent spatial subgroups. Ecoregions (blue) – 1: East African Coral Coast, 2: Northern Madagascar, 3: Mascarene Islands, 4: Maldives, 5: Andaman and Nicobar Islands, 6: Western Sumatra, 7: Sunda shelf/Java sea, 8: Sulawesi sea/Makassar strait, 9: Lesser Sunda, 10: South Kuroshio, 11: Solomon archipelago and 12: Fiji islands. Coral Triangle (red) – 13. Coral faunal provinces (dark green) – 14: Africa-India, 15: Andaman Nicobar islands, 16: Japan-Vietnam, 17: Indonesian, 18: Australian and 19: Fiji-Caroline islands

a number of potential variables affecting resistance and, therefore, a number of ways to calculate resistance. Here, for example, higher resistance can indicate sites with high thermal exposure and low resulting sensitivity, while lower resistance can identify sites with low thermal exposure yet high sensitivity. Exposure and sensitivity can be measured by single or multiple variables, having different units, and often require being weighted, standardized or normalized for appropriate comparisons. Moreover, resistance can be calculated as either the difference or ratio between exposure and sensitivity. We evaluated a series of possibilities to assess resistance based on this framing, which we describe below for our study of 226 coral reef sites from East Africa to the South Pacific (detailed in McClanahan et al., 2019). Overall, we evaluate coral resistance across six coral faunal provinces (Keith et al., 2013) and 12 marine ecoregions (Spalding et al., 2007).

2.1 | Exposure

We considered two exposure models: (a) a single metric of temperature stress that measures the cumulative incremental sum of SSTs above local summer SSTs (cumulative thermal anomaly, CTA), and (b) a multivariate metric of climate exposure (climate exposure, CE) that combines heat, light, and water flow variables weighted by each variable's strength of association with field observations of coral bleaching (Maina et al., 2008, 2011).

The CTA model is based on the concept of cumulative degree-heating weeks or months, or the amount of excess temperatures above a summer baseline, and is the most commonly used metric to assess the probability of coral bleaching and the future state of coral reefs (Donner & Carilli, 2019; Eakin et al., 2010; Van Hooidonk et al., 2013). To estimate CTAs, we extracted daily SST time series for each site from the 5-km NOAA Coral Reef Watch version 3.1 products between 1985 and 2015, available from the NOAA website (https://coralreefwatch.noaa.gov/product/5km/). Daily temperature measurements were used to calculate monthly hotspots, defined as positive SST anomalies referenced to the maximum of the monthly mean (MMM) SST climatology (Strong et al., 2004). We then calculated the degree-heating months (DHM) as the sum of hotspots with monthly means ≥ 0 °C. To derive the cumulative DHM product for each site, we summed cells with DHM ≥ 0 °C for each year over the 1985–2015 time series. We did not include the 2016 SST satellite measurements in this metric of historical thermal stress to maintain statistical independence with the sensitivity metric, which was derived from surveys completed in 2016. CTAs between 1985–2015 ranged from 7.8 to 48.0 DHM across the 226 reef sites included in this study.

The CE values were extracted from an existing multivariate model published in Maina et al. (2008, 2011), which used variables of historical SST (mean, variability, maximum, minimum), ocean current velocity in zonal and meridional direction, wind velocity (number of doldrum days and wind speed magnitude), and average satellite derived UV and photosynthetic active radiation measurements. Based on Maina et al. (2008, 2011), climate exposure is weighted based on past bleaching observations to produce values ranging between 0 (least exposure) and 1 (highest exposure). Overall, this multivariate metric of coral exposure has a strong relationship to previous compilations of coral bleaching data (Maina et al., 2008; McClanahan et al., 2015).

The distributions of CTA and CE values for the 226 sites indicated that the CTA values were lower (< .50 normalized values) and had a right skew (i.e., less frequent high-stress values) compared to CE values that were higher (> .50 normalized values) and had a left skew (i.e., less frequent low values) (Supporting Information Figure S1). This suggests these models capture different characteristics of thermal stress and are useful in estimating different aspects of exposure.

2.2 | Sensitivity

Coral sensitivity to thermal stress was based on coordinated field surveys of coral bleaching during the 2016 El Niño-Southern Oscillation (ENSO). Surveys were conducted within 3 weeks of peak SSTs when bleaching was greatest (McClanahan et al., 2020). We surveyed 226 sites in 12 countries during summer months between March and September 2016. We used a roving observer methodology where an observer evaluated the frequency and severity of bleaching for every coral colony in a series of haphazardly replicated quadrats (*c*. 1.5 m^2 × *c*. 15 replicates, across an area of *c*. 1,000 m^2, and an 18-m depth range). Within each quadrat, we identified hard coral colonies > 5 cm to the genus using the taxonomy of Veron (2000), and scored each colony on a seven-point scale for bleaching severity (McClanahan et al., 2007). We recorded the site's depth, habitat type and management. Further, we estimated hard coral cover in each quadrat to the nearest 5% and summarized number of observed colonies, coral taxa richness and relative abundance for each site. The full details of the sites are presented in a companion paper where 26 environmental variables associated with bleaching in 2016 were evaluated (McClanahan et al., 2019; Supporting Information Table S1).

2.3 | Data analyses

2.3.1 | Sensitivity estimates

Sensitivity was estimated in two ways, using both an unweighted and a weighted seven-point ordinal bleaching intensity model that accounted for the intensity of the bleaching. Three sites were missing one or more of the variables leading to slightly reduced sample sizes in some analyses. The unweighted bleaching sensitivity method calculated the percentage of coral colonies that were pale to fully bleached as the percentage of all corals sampled.

$$\text{Percentage bleached} = \frac{(c1+c2+c3+c4+c5)}{(c0+c1+c2+c3+c4+c5)} \times 100\% \quad (1)$$

where $c0$ = number of unbleached coral colonies, $c1$ = number of pale, $c2$ = number of 0–20%, $c3$ = number of 21–50%, $c4$ = number of 51–80%, $c5$ = number of 81–100%. The weighted method scales each of these bleaching categories, as described in McClanahan et al. (2007). The two bleaching sensitivity estimates were highly correlated ($r = .92$, $p < .0001$). Nevertheless, comparison between the percent bleaching versus the weighted bleaching index against the independent predictor variables indicated lower corrected Akaike information criterion (AICc) values for the percentage [AICc = 125.7 ± 97.1 (± SD), $n = 28$ comparisons] than the weighted bleaching index (AICc = 141.1 ± 78.1, $n = 28$). Thus, only the percentage bleached corals (unweighted) were used in subsequent evaluations.

Bleaching susceptibility is a related metric used to estimate the sensitivity of the community to bleaching, where the relative abundance of each taxon was multiplied by the mean weighted bleaching intensity (BI) for that taxon based on historical observations and summed.

$$\text{Bleaching susceptibility} = \sum_{i=1}^{N} \frac{BI_i \times D_i}{N} \quad (2)$$

where i is one taxon, D is the relative abundance of this taxon and N is the total number of taxa. Here, we used the 2016 bleaching intensity observations for each taxon. Bleaching susceptibility provides a single number for each site, where higher values indicate a coral assemblage with a higher susceptibility to bleaching and lower values indicate a coral assemblage that is less susceptible to bleaching.

2.3.2 | Selecting the resistance estimate

Before calculating a resistance metric, the timing of the exposure, based on satellite temperature observations, and ecological sensitivity, based on the percentage of bleached corals, were evaluated for the strength of their relationships with predictor variables. First, we extracted daily 5-km SST time series for 90 days prior to field survey at each site and calculated the date of maximum observed DHMs. We found that all of the final 226 selected sites were sampled within 21 days after peak SSTs. Thereafter, we evaluated the unweighted percent bleaching metric for its distribution, outliers, and associations with seven predictor variables based on AICc values. We found that 10 sites in Ningaloo reefs were outliers as per the multivariate Mahalanobis distance method that calculates the distance from a point to the normalized distribution of a principal component axis. Exploration of these outliers suggests local oceanographic effects at Ningaloo were overriding the broader-scale satellite measurements (Woo et al., 2006; Xu et al., 2016). Some sampling error is expected in these analyses due to the mismatch in spatial coverage between the satellite and field surveys – field survey locations were contained within the spatial dimensions of the satellite measurements but covered less area. Nevertheless, all sites were retained in all analyses as they represented some natural and sampling variability that is expected for the locations and models we explored.

2.3.3 | Resistance estimates

To evaluate coral resistance to thermal stress, we first normalized the exposure of the two metrics and the metric of ecological sensitivity selection for all sites between 0 and + 1, added + 1 to all values and then divided exposure by sensitivity. These transformations eliminated zeros and negative numbers and produced resistance values between 0.5 and 1.75 (Supporting Information Figure S1). Prior to calculating resistance, we evaluated statistical attributes of the single variables, interacting variables, and the exposure-sensitivity ratio versus subtraction methods to calculate resistance. Comparing the subtraction and the ratio method for estimating resistance found the ratios produced considerably lower AICc values (AICc = 62.8 ± 56.6, $n = 28$) than subtraction (AICc = 204.1 ± 46.1, $n = 28$) and the ratio was therefore used in subsequent evaluations. Distributions of the chosen exposure, sensitivity, and the two metrics of resistance showed good spread and continuous distributions with weak centralization that should increase the probabilities of detecting patterns (Supporting Information Figure S1).

2.3.4 | Spatial structure and comparisons

We were interested in knowing if resistance varied by biogeographic locations based on environmental forces, the attributes of the coral taxa and communities, and the historical conditions that influenced the taxa in their locations. Therefore, we estimated resistance as exposure divided by sensitivity (% bleached corals) and tested the hypothesis that resistance differed locally and geographically. All sites were allocated to one of the six studied coral faunal provinces (Keith et al., 2013) and 12 ecoregions (Spalding et al., 2007) based on position within the geographic polygons. An ecoregion is defined as a modern association of similar taxa, and faunal provinces have similar geological and evolutionary histories (Spalding et al., 2007). These two groupings were used as random effects within the statistical modelling approach to help account for existing biogeographic and latitudinal patterns in coral reef productivity and diversity. We made one change to the existing classifications by including the Lakshadweep Islands of India in the Africa-India coral province due to their close proximity (205 ± 63 km) to other sites in this same region. Additionally, due to concerns about the threats of climate change to global marine biodiversity (McManus et al., 2019), we specifically evaluated whether the sampled sites in coral fauna provinces, Coral Triangle and non-Coral Triangle, and in ecoregions differed in resistance. To classify sites as Coral Triangle versus non-Coral Triangle, we used identified sites within the Eastern and Western Coral Triangle provinces identified by Spalding et al. (2007).

We tested for differences within these three spatial groupings (ecoregion, faunal province, and Coral Triangle versus non-Coral Triangle) using the Kruskal–Wallis test and Dunn's test for multiple comparisons where p-values were adjusted by both the Bonferroni and Benjamin-Hochberg's methods, as it was not possible to distinguish the efficacy of these two evaluation methods for our data and

hypotheses. More detailed comparisons of sites in the Coral Triangle (n = 27) and non-Coral Triangle (n = 199) included tests for differences in resistance, thermal environments, coral communities, and bleaching by major taxon. Most data failed to pass tests of normality [using Kolmogorov–Smirnov–Lilliefors (KSL) tests] and therefore nonparametric Wilcoxon tests were undertaken for comparisons of all variables. Temperature data were pooled to visualize their distributions in the two regions. To test for differences in coral communities that might confound spatial comparisons, we described them using multivariate community correspondence analysis (CCA) using the vegan package in R (Oksanen et al., 2020; R Core Team, 2019). Thereafter, the first and second axis CCA values for each site were extracted and tested for differences between the two geographies.

2.3.5 | Model building, variables and selection procedures

Previous studies have suggested that background SST distribution metrics, such as the standard deviation, skewness (a measure of the thickness of the tails of the SST data distributions), and kurtosis (a measure of shape and spread of data distributions) can influence bleaching and mortality by influencing coral acclimation and adaptation mechanisms (Ainsworth et al., 2016; Ateweberhan & McClanahan, 2010; Grottoli et al., 2014; Langlais et al., 2017; Safaie et al., 2018). Many of these temperature distribution metrics can covary to inflate covariance in multivariate models. However, visualization of the scatterplot matrix of the independent variables indicated that mean SST and kurtosis were the only strongly correlated variables (r = .83) while all other variables' correlations were weaker (r < .56.) Therefore, we specified the model below to not simultaneously include kurtosis and mean SST. Variance inflation factor (VIF) scores, another indicator of multicollinearity, were < 3, which indicates that collinearity was not a serious concern.

We fit generalized linear mixed models (GLMMs) with different random structures to account for the spatial structure of the sampling sites. After comparing diagnostic tests, we chose a random factor of a spatial exponential covariance structure that uses the latitude-longitude coordinates of each site. This models the correlation of observations using spatial coordinates to estimate distance between sites using an exponential function (Dormann et al., 2007; Nishida & Chen, 2004). We used the R package glmmTMB (R Core Team, 2019) and the function 'numFactor' to add coordinate information to the observational-level random effect (Equation 3; Lewy & Kristensen, 2009). Models were fit with a gamma family distribution and a log link error structure in the glmmTMB package in R (Brooks et al., 2017; R Core Team, 2019); we considered this error structure to account for the non-negative distribution of our calculated resistance metrics. The gamma-log link error structure (AICc = −264) improved model AICc by c. 20 points as compared to the Gaussian log link error structure (AICc = −245), thus it was retained in subsequent models. Thereafter, we used a multi-model inference framework and fit the GLMMs with the resistance ratio calculated from each of the two exposure models (CTA versus CE) against the six predictor variables for each spatial group with the following equation.

3. Generalized linear mixed model equation	Formula
$z = X\beta + u(x,y) + \varepsilon$; where: $Z = N \times 1$ column vector; $X\beta = X$ is a $N \times p$ matrix of the p predictor variables; β is a $p \times 1$ column vector of the fixed-effects regression coefficients; u = observational-level grouping; x = Longitude; y = Latitude; $\varepsilon = N \times 1$ column vector of the residuals	Resistance ~ Intercept + Ecoregion + Faunal Province + Coral Triangle versus non-Coral Triangle + Hard Coral Cover + Number of Genera + Skewness + Kurtosis or SST + Spatial exponential covariance structure (random factor)

Models were constructed and implemented using a custom function that generates all possible combinations of the fixed effects and then tests each combination for multicollinearity using VIFs using the usdm package in R (Naimi et al., 2014; R Core Team, 2019). Model combinations that passed a multicollinearity threshold (VIF < 1.5) were then passed on for model construction and fitting, and ultimately evaluation and AICc ranking using the model.sel function in the MuMIn package (Barton, 2020). This generated 48 model options for each resistance and spatial group combination. We evaluated all possible mechanistically sound models to minimize subjectivity that may arise when selecting significant variables but not the most parsimonious models (Burnham & Anderson, 1998). All R code is provided at the link in the Data accessibility section.

We present all the results of the top set of models where delta AICc values were < 2. To ensure the Akaike weights of the top models were not confounded by uninformative variables (Arnold, 2010), we excluded duplicate models and recalculated their weights. To compare among predictor variables using coefficients and associated confidence intervals, we performed conditional model averaging of the top models (Supporting Information Table S1).

3 | RESULTS

3.1 | Provincial and ecoregional patterns

We found that resistance varied considerably across our study sites (Figure 1b,c). Statistical comparisons indicated a number of differences between provinces and ecoregions, which depended on the metric of resistance and multiple-comparison corrections (Figure 2; Supporting Information Table S2). Resistance, based on the CE metric, indicated two to four significant groups of shared resistance depending on the method used to adjust p-values. Regardless of specific statistical differences, there was a gradient of most to least resistance in the order of the Australian, Fiji-Caroline Islands, Indonesian, Andaman Nicobar Islands, Africa-India, and Japan-Vietnam coral provinces (Figure 2a). Resistance, based on the CTA metric, was similar but showed fewer differences between the Andaman Nicobar Islands, Africa-India, and Japan-Vietnam provinces (Figure 2b). The 12 ecoregions showed similar

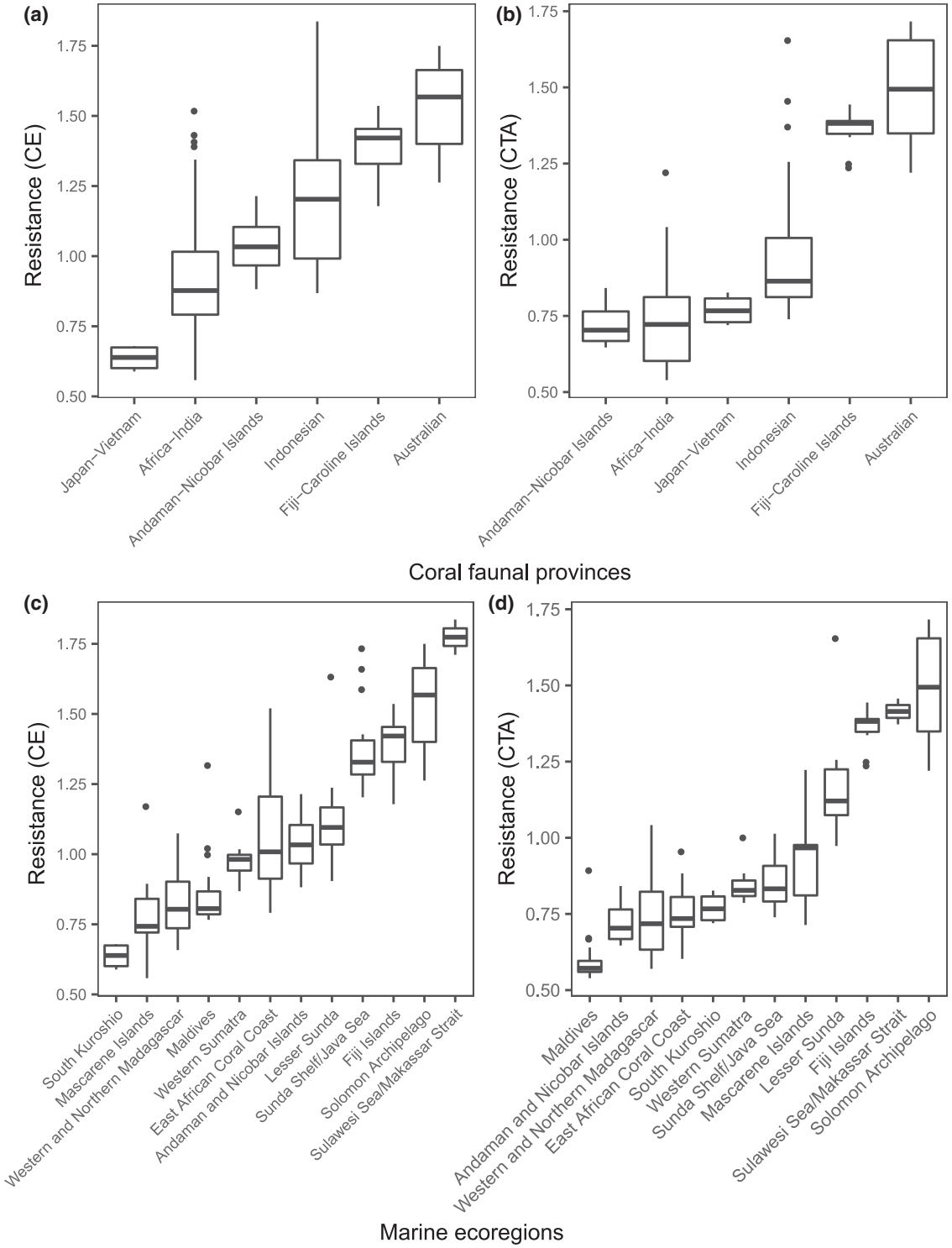

FIGURE 2 Box plots of the variation in the sites' coral resistance metrics based on (a, b) coral faunal provinces and (c, d) marine ecoregions for the two metrics of resistance. Box plot symbols – thick bars: medians; boxes: interquartile range; whiskers: minimum and maximum values < 1.5 the interquartile range. Statistical differences and multiple comparisons are presented in Supporting Information Table S2. CE = climate exposure; CTA = cumulative thermal anomaly.

gradients where CE distinguished ecoregions more than the CTA metric (Figure 2c,d). The order of resistance was also more variable between the two metrics but generally the Indian Ocean and Japanese ecoregions had lower resistance than the Pacific and Indo-Pacific ecoregions.

3.2 | Resistance models

Geography, as represented by the three regional classifications, played a significant role in affecting resistance in the top models (< 2 AICc), with ecoregion performing better than coral provinces and

TABLE 1 Results and ranks of multi-model inference statistics. Ranks and fit of model outputs of the best models of 48 options where 6 predictors were tested for associations with two resistance metrics at the study sites, using a generalized mixed model with a spatial covariance structure (exp(position + 0|ID)) where position refers to the Euclidean distance matrix calculated internally based on the coordinates and 0|ID, which is a dummy group factor used as a random term in the model. For comparison, results of the single factors and the direction of influence used in the best models are included. Ranks are based on corrected Akaike information criterion (AICc) criteria, AICc weights have been recalculated for the top model set while single model weights are based on all 48 options

Rank	Models	df	logLik	AICc	Delta	Weight	Marginal/ conditional R^2	Significance
a) Resistance (climate exposure, CE)								
	Set 1: Best models set (< 2 AICc); Coral Provinces spatial groups							
1	Resistance (CE) ~ Intercept + Skewness + SST + exp (position + 0|ID)	6	142.43	−272.44	0.00	0.24	.38/.88	.02*
2	Resistance (CE) ~ Intercept + Kurtosis + Skewness + exp (position + 0|ID)	6	142.25	−272.08	0.36	0.20	.42/.88	.03*
3	Resistance (CE) ~ Intercept + SST + exp (position + 0|ID)	5	141.07	−271.84	0.60	0.18	.22/.89	.03*
4	Resistance (CE) ~ Intercept + Coral Province + exp (position + 0|ID)	9	144.80	−270.68	1.76	0.10	.51/.88	.03*
5	Resistance (CE) ~ Intercept + Coral Province + Kurtosis + Skewness + exp (position + 0|ID)	11	146.97	−270.58	1.86	0.10	.58/.88	.02*
6	Resistance (CE) ~ Intercept + Hard corals + Skewness + SST + exp (position + 0|ID)	7	142.52	−270.47	1.97	0.09	.37/.88	.05.
7	Resistance (CE) ~ Intercept + Number of genera + Skewness + SST + exp (position + 0|ID)	7	142.52	−270.47	1.97	0.09	.38/.88	.05.
	Set 1b: Single variable models [note SST (+) and Coral Province appear in top model set]							
9	Kurtosis (+)	5	140.19	−270.09	2.35	0.03	.16/.89	.08.
27	Skewness (−)	5	139.04	−267.79	4.65	0.01	.07/.89	NS
30	Hard corals (+)	5	138.78	−267.25	5.19	0.008	.0003/.90	NS
31	Number of genera (+)	5	138.76	−267.22	5.21	0.008	.0003/.90	NS
	Set 2: Best models set (< 2 AICc); Ecoregion spatial groups							
1	Resistance (CE) ~ Intercept + Ecoregion + Kurtosis + exp (position + 0|ID)	16	162.24	−289.60	0.00	0.54	.77/.94	< .0001***

(Continues)

TABLE 1 (Continued)

Rank	Models	df	logLik	AICc	Delta	Weight	Marginal/ conditional R^2	Significance
2	Resistance (CE) ~ Intercept + Ecoregion + Kurtosis + Number of genera + exp (position + 0|ID)	17	162.64	−288.00	1.60	0.24	.78/.94	< .0001***
3	Resistance (CE) ~ Intercept + Ecoregion + Kurtosis + Skewness + exp (position + 0|ID)	17	162.55	−287.83	1.77	0.22	.78/.94	< .0001***
	Set 2b: Single variable models							
9	Ecoregion	15	156.85	−281.18	8.42	0.005	.74/.94	.0001***
27	SST (+)	5	141.07	−271.84	17.75	5.01E-5		
31	Kurtosis (+)	5	140.19	−270.09	19.51	2.08E-5		
41	Skewness (−)	5	139.04	−267.79	21.81	6.60E-6		
42	Hard corals (+)	5	138.78	−267.25	22.35	5.04E-6		
43	Number of genera (+)	5	138.76	−267.22	22.37	4.98E-6		
	Set 3: Best models set (< 2 AICc); Coral Triangle spatial groups							
1	Resistance (CE) ~ Intercept + Skewness + SST + exp (position + 0|ID)	6	142.43	−272.44	0.00	0.23	.38/.88	.02*
2	Resistance (CE) ~ Intercept + Kurtosis + Skewness + exp (position + 0|ID)	6	142.25	−272.08	0.36	0.19	.42/.88	.03*
3	Resistance (CE) ~ Intercept + SST + exp (position + 0|ID)	5	141.07	−271.84	0.60	0.17	.22/.89	.03*
4	Resistance (CE) ~ Intercept + Region + SST + exp (position + 0|ID)	6	141.95	−271.48	0.96	0.14	.31/.88	.04*
5	Resistance (CE) ~ Intercept + Region + Skewness + SST + exp (position + 0|ID)	7	142.66	−270.75	1.69	0.10	.39/.88	.04*
6	Resistance (CE) ~ Intercept + Hard corals + Skewness + SST + exp (position + 0|ID)	7	142.52	−270.47	1.97	0.09	.37/.88	.05
7	Resistance (CE) ~ Intercept + Number of genera + Skewness + SST + exp (position + 0|ID)	7	142.52	−270.47	1.97	0.09	.38/.88	.05.
	Set 3b: Single variable models [note SST (+) appears in top model set]							
9	Kurtosis (+)	5	140.19	−270.09	2.35	0.03		
18	Region (Coral Triangle)	5	139.56	−268.83	3.69	0.02	.12/.88	NS
28	Skewness (−)	5	139.04	−267.79	4.65	0.01		

(Continues)

TABLE 1 (Continued)

Rank	Models	df	logLik	AICc	Delta	Weight	Marginal/ conditional R^2	Significance
30	Hard corals (+)	5	138.78	−267.25	5.19	0.008		
31	Number of genera (+)	5	138.76	−267.22	5.21	0.008		
b) Resistance (cumulative thermal anomaly, CTA)								
	Set 1: Best models set (< 2 AICc); Coral Provinces spatial groups.							
1	Resistance (CTA) ~ Intercept + Coral Province + Skewness + SST + exp (position + 0|ID)	11	207.05	−390.73	0.00	0.55	.77/.93	.0001***
2	Resistance (CTA) ~ Intercept + Coral Province + Skewness + exp (position + 0|ID)	10	205.03	−388.92	1.80	0.23	.73/.93	.0002***
3	Resistance (CTA) ~ Intercept + Coral Province + Hard corals + Skewness + SST + exp (position + 0|ID)	12	207.23	−388.85	1.88	0.22	.77/.93	.0001***
	Set 1b: Single variable models							
17	Skewness (−)	5	196.29	−382.27	8.46	0.005	.41/.92	.003**
21	Coral province	9	199.88	−380.85	9.88	0.002	.64/.93	.008**
38	Kurtosis (+)	5	192.64	−374.98	15.75	0.0001	.05/.94	NS
39	Hard corals (+)	5	192.59	−374.87	15.86	0.0001	.001/.93	NS
40	Number of genera (+)	5	192.22	−374.14	16.59	0.0001	.0001/.93	NS
41	SST (+)	5	192.22	−374.14	16.59	0.0001	.007/.93	NS
	Set 2: Best models set (< 2 AICc); Ecoregion spatial groups							
1	Resistance (CTA) ~ Intercept + Ecoregion + Kurtosis + Skewness + exp (position + 0|ID)	17	218.06	−398.84	0.00	0.34	.84/.94	< .0001***
2	Resistance (CTA) ~ Intercept + Ecoregion + Skewness + exp (position + 0|ID)	16	216.63	−398.36	0.48	0.27	.84/.94	< .0001***
3	Resistance (CTA) ~ Intercept + Ecoregion + Number of genera + Skewness + exp (position + 0|ID)	17	217.47	−397.67	1.17	0.19	.84/.94	< .0001***
4	Resistance (CTA) ~ Intercept + Ecoregion + Kurtosis + Number of genera + Skewness + exp (position + 0|ID)	18	218.62	−397.56	1.27	0.18	.84/.94	< .0001***
	Set 2b: Single variable models							
12	Ecoregion	15	213.01	−393.49	5.35	0.01	.82/.93	< .0001***

(Continues)

TABLE 1 (Continued)

Rank	Models	df	logLik	AICc	Delta	Weight	Marginal/ conditional R^2	Significance
26	Skewness (–)	5	196.29	−382.27	16.57	5.41E-5		
38	Kurtosis (+)	5	192.64	−374.98	23.86	1.34E-6		
39	Hard corals (+)	5	192.59	−374.87	23.97	1.27E-6		
40	Number of genera (+)	5	192.22	−374.14	24.69	8.81E-7		
41	SST (+)	5	192.22	−374.14	24.70	8.80E-7		
	Set 3: Best models set (<\ 2 AICc); Coral Triangle spatial groups							
1	Resistance (CTA) ~ Intercept + Region + Skewness + exp (position + 0|ID)	6	198.55	−384.68	0.00	0.38	.50/.92	.001**
2	Resistance (CTA) ~ Intercept + Region + Hard corals + Skewness + exp (position + 0|ID)	7	198.83	−383.08	1.59	0.17	.50/.92	.003**
3	Resistance (CTA) ~ Intercept + Region + Number of genera + Skewness + exp (position + 0|ID)	7	198.70	−382.83	1.84	0.15	.51/.92	.004**
4	Resistance (CTA) ~ Intercept + Region + SST + Skewness + exp (position + 0|ID)	7	198.63	−382.69	1.98	0.14	.51/.92	.004**
5	Resistance (CTA) ~ Intercept + Region + exp (position + 0|ID)	7	196.49	−382.68	1.99	0.14	.35/.91	.003**
	Set 3b: Single variable models [note Region (Coral Triangle) appears in top model set]							
8	Skewness (–)	5	196.29	−382.27	2.40	0.04		
38	Kurtosis (+)	5	192.64	−374.98	9.70	0.001		
39	Hard corals (+)	5	192.59	−374.87	9.81	0.001		
40	Number of genera (+)	5	192.22	−374.14	10.54	0.001		
41	SST (+)	5	192.22	−374.14	10.54	0.001		

Note.: SST = sea surface temperature. Based on 204 sites because some sites lacked coral cover estimates. Grey shaded models have redundancy with other similarly ranked models.

NS = not significant.

[a]. = $p < .1$;

*$p < .05$;

**$p < .01$;

***$p < .0001$.

Coral Triangle/non-Coral Triangle, but it also interacted with SST variables depending on the resistance metric (Table 1).

3.2.1 | Coral exposure resistance

When evaluating coral provinces, the top CE resistance models included the site's mean, skewness, and kurtosis of SSTs along with the geographic position. Model averaged coefficients for resistance based on CE suggested that ecoregion spatial group explained CE based resistance better than coral provinces (Supporting Information Table S1). In this set of models, resistance to thermal stress increased with increasing temperature and kurtosis but decreased with increasing skewness. When evaluating ecoregions, CE resistance indicated the high strength of the ecoregion as a single variable and also when kurtosis and geographic location were included, which then had a high conditional R^2 of .94. When evaluating the Coral Triangle with non-Coral Triangle sites, CE resistance indicated the strength of the SST's mean, skewness, kurtosis, as well as the geographic position of the sites in the top three models. The Coral Triangle region was included in the fourth ranked model and all models were statistically significant and had a high conditional R^2 of .88.

3.2.2 | Cumulative thermal anomaly resistance

When evaluating coral provinces, the top CTA resistance models included the province, mean and skewness of SST distributions and geographic position, which were all strongly significant and had a high conditional R^2 of .93. SST-skewness and province were the two variables that were statistically significant as single variables and ranked 17th and 21st among all models. When evaluating ecoregions, resistance by the CTA methods found high model strength for the variables of ecoregion, SST-kurtosis, SST-skewness, and geographic position, with ecoregion being the strongest single variable and ranked 12th. Evaluation of the Coral Triangle versus non-Coral Triangle sites by the CTA resistance metric indicated a high conditional R^2 of .92 for the variables of region, SST-skewness, and geographic position.

3.3 | Comparison of Coral Triangle versus non-Coral Triangle sites

The more detailed comparisons of the Coral Triangle and non-Coral Triangle sites illuminated some associations in the distinct patterns of SST, coral communities, and resistance (Table 2). Pooling and evaluating the SST time series indicated considerable differences between regions in the distributions of temperature (Figure 3a). The higher CTA in the Coral Triangle was one of the most pronounced difference with 2.5 times more 1985–2015 CTAs than non-Coral Triangle sites. Moreover, Coral Triangle sites had warmer SSTs, more bell-shaped distributions (neutral kurtosis), and more frequent rare cold water (negative skewness) compared to non-Coral Triangle sites (Figure 4). In fact, distinct differences in the SST-skewness kurtosis associations were some of the main distinctions between these localities. Coral Triangle sites had only neutral to high SST-kurtosis and, as kurtosis increased, skewness declined and was negative. SST-kurtosis was highly variable in non-Coral Triangle sites but rare warm-water was more frequent when temperature distributions were centralized.

Differences in the resistance of corals to thermal stress between Coral Triangle and non-Coral Triangle sites cannot be attributable to differences in the coral communities but, rather, to taxon sensitivity. While there were more taxa in the Coral Triangle, we found that coral cover, the relative generic composition and the community's generic susceptibility to bleaching metrics did not differ between localities (Table 2 and Figure 5). What did consistently differ was the percentage of bleached corals and the percentage of the dominant genera that were bleached in 2016. All metrics showed higher bleaching outside the Coral Triangle despite the lower mean SSTs.

4 | DISCUSSION

Mean SSTs, rates of temperature rise, and CTAs are the key metrics used to model current and future impacts of thermal stress and refuge from climate change (Beyer et al., 2018; Hoegh-Guldberg, 1999; Van Hooidonk et al., 2013, 2016). Use of these and related thermal metrics produce dire predictions for corals, especially in warm equatorial regions (Couce et al., 2013; McManus et al., 2019). Yet, these models largely fail to account for taxa, regional, or other large-scale differences in coral resistance to thermal stress. We see here that there are large regional differences in responses of corals to thermal exposure. Spatial differences in the rates of acclimation/adaptation to thermal stress at the coral taxa and community levels are unknown but are also expected to change with the location and histories of stress and adaptation (2020). This spatial variability in resistance was found in both metrics of resistance and all evaluations of provincial or regional biogeographic structure. Community compositions were not different between Coral Triangle and non-Coral Triangle sites, therefore differences in the measured resistance were likely due to taxa having different sensitivity to exposure and not attributable to community structure (Figure 5). Thus, resistance appears to have a strong component of regionalism that is not clearly related to differences in coral community composition but more likely related to variable sensitivity responses to environmental conditions of SST distributions and possibly other stress variables.

Coral provinces, marine ecoregions, and the marine biodiversity centre or Coral Triangle were all metrics of regionalism that were statistically strong and frequently picked in the top CE and CTA models. Definitively distinguishing between regional classifications in terms of their AIC model strengths would be premature as our ad-hoc sampling design was not random or balanced, and the areas and habitats covered varied between regions. The models were strongest when SST distribution, coral metrics and regions were all

TABLE 2 Regional comparisons of temperature, coral community, and dominant taxa

Variable	Coral Triangle mean (*SD*)	Non-Coral Triangle mean (*SD*)	*Z*	Prob > |*Z*|
Resistance variables				
Resistance, CTA	1.38 (0.23)	0.83 (0.22)	7.5	< .0001
Resistance, CE	1.42 (0.27)	1.03 (0.26)	5.7	< .0001
Temperature variables				
Mean sea-surface temperature	28.93 (0.44)	27.57 (1.16)	6.3	< .0001
Kurtosis	0.05 (0.31)	−0.70 (0.49)	6.3	< .0001
Skewness	−0.48 (0.19)	0.03 (0.27)	−7.3	< .0001
Cumulative DHM	43.10 (4.30)	18.80 (7.40)	8.3	< .0001
Coral community variables				
Hard coral cover, %	43.65 (21.59)	43.75 (21.64)	0.2	NS
Number of coral taxa	21.26 (5.78)	18.18 (7.16)	2.5	.01
Community axis 1	−0.11 (0.78)	0.02 (0.76)	−1.0	NS
Community axis 2	−0.17 (0.39)	0.02 (0.74)	−0.4	NS
Community bleaching susceptibility, %	27.34 (2.69)	27.98 (2.43)	−1.4	NS
Coral bleaching				
Bleached colonies, %	39.78 (25.11)	59.71 (28.60)	−3.4	.0007
Acropora, %	43.33 (30.03)	60.86 (34.36)	−2.7	.008
Montipora, %	32.85 (24.31)	59.98 (40.17)	−2.8	.005
Pocillopora, %	59.32 (35.88)	71.62 (36.29)	−1.9	.05
Porites branching, %	19.38 (29.48)	54.12 (38.41)	−3.6	.0003
Porites massive, %	26.36 (27.65)	53.84 (34.44)	−3.8	.0002

Note.: DHM = degree-heating months from 1985 to 2015; CTA = cumulative thermal anomaly model based on sum of DHM; CE = climate exposure model based on multiple environmental variables. Long-term temperature metrics (mean, kurtosis and skewness) for sites within the Coral Triangle ($n = 27$) and sites outside the Coral Triangle ($n = 199$) compared by the Wilcoxon tests of significance. Metrics of the coral communities and two measures of their bleaching responses. Community axes 1 and 2 are the first and second community correspondence axes of a multivariate evaluation of coral taxa. Susceptibility weights taxa abundance by a mean bleaching response during the 2016 period.

included in the model, which indicates the importance of the interaction between the region's corals and the recent environmental conditions. Nevertheless, our findings show the importance of a site's location in geographic regions that are currently distinguished by biogeographers.

Provinces and ecoregions differed in their levels of resistance. The comparison of the Coral Triangle and non-Coral Triangle shows how unique temperature environments can harbour similar taxa of corals but with differential resistance to exposure. Historically, the Coral Triangle has been influenced by oceanographic processes, such as ENSO and the Pacific Decadal Oscillation (PDO). The strengths and interaction of ENSO with the PDO have long fluctuated to create geographic differences in thermal stress and ocean productivity across the Pacific (Cobb et al., 2003; Houk et al., 2020). Consequently, we hypothesize that tropical oceanographic variation and inter-annual warm thermal anomalies in the western Pacific may be primary drivers of coral resistance along the east–west equatorial gradient from East Africa to Fiji. Moreover, resistance of corals to thermal stress is higher but unequally distributed towards the equator (Sully et al., 2019). This indicates that exposure to thermal radiation alone is insufficient to explain the regional variability. Latitudinal variation in resistance may explain the overall higher bleaching reported in mid-tropical latitudes (15–20°) despite equal or higher CTA near the equator (Sully et al., 2019). Some variation in bleaching was attributable to average background SST variation but we found that the interactions and variation in the SST shape parameters of kurtosis and skewness was more likely to distinguish sites along this equatorial belt.

The evaluated Coral Triangle sites differed from non-Coral Triangle sites in having more cool and evenly-spread variance in temperature distributions, which were associated with increased resistance to thermal stress. The causes of these temperature distribution patterns require more investigation but the island nature of the Coral Triangle is expected to create localized variability in water clarity, ocean currents, and up- and downwelling (Gove et al., 2016; Peñaflor et al., 2009). Archipelagos may also create higher stability

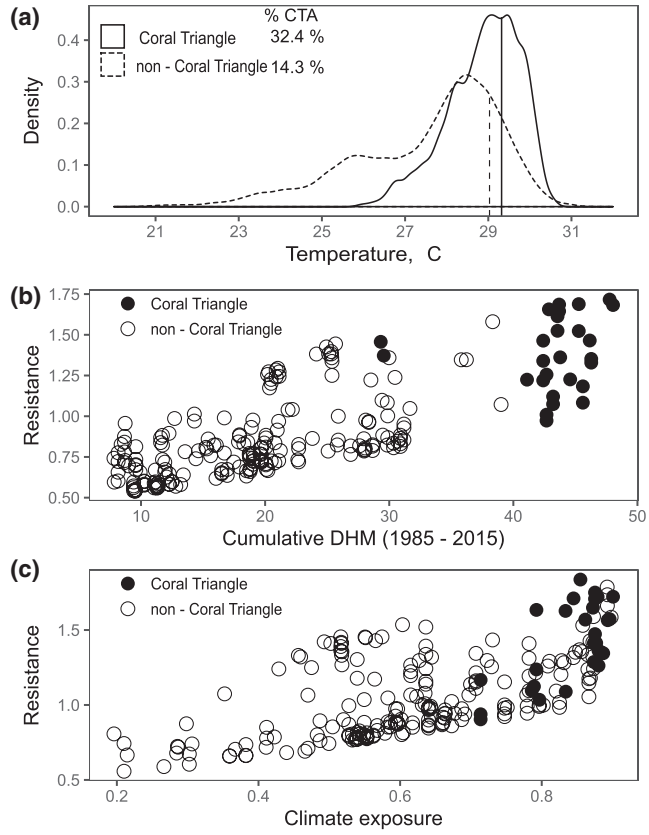

FIGURE 3 Temperature distributions, exposure, and the two coral resistance metrics in the Coral Triangle compared to non-Coral Triangle sites. The (a) density of temperature distributions of the 27 sites in and 199 sites outside the Coral Triangle based on monthly temperatures from 1985 to 2015. (b) Resistance as a function of the cumulative thermal anomaly (CTA) exposure model, and (c) resistance as a function of the multivariate climate exposure (CE) model in and outside the Coral Triangle. MMM = mean monthly summer maximum temperatures and CTA is based on the cumulative degree-heating months. DHM = degree-heating months.

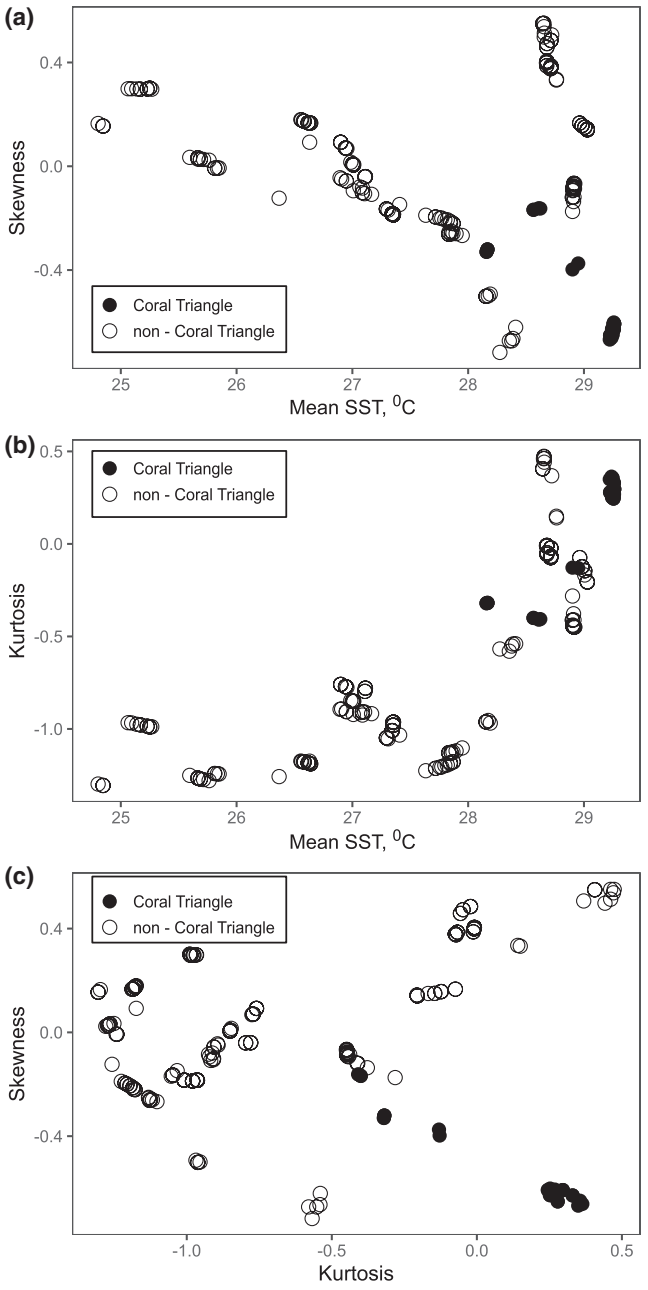

FIGURE 4 Scatterplots between the three sea-surface temperature (SST) metrics in the Coral Triangle and non-Coral Triangle sites. Relationships between mean SST, kurtosis, and skewness variables used to test the factors influencing resistance models based on 226 study sites

of temperatures if islands are separated by deep water channels that buffer or prevent the penetration of large-scale oceanographic fluctuations (McClanahan 2020). Thus, islands and archipelagos provide some combination of stability and localized variation in radiation, temperatures, planktonic productivity, and coral resistance (Gove et al., 2016; McClanahan et al., 2005).

The statistical outlier sites found at Ningaloo reef may provide some insights into coral resistance. These sites were an exception to the differences between Coral Triangle and non-Coral Triangle sites and mid-latitude patterns. We speculate that the higher than expected resistance found in Ningaloo arose from some combination of localized upwelling, onshore geostrophic transport, and stirring by offshore eddies that produced lower than expected bleaching (Xu et al., 2016). Satellite measurements, even at 5 km^2, may not capture these local processes well (Woo et al., 2006; S. Wilson, personal communication, March 2019). Similar reductions in thermal stress have been observed for internal sub-surface waves that can cool water at depths and prevent bleaching (Wyatt et al., 2020). Regardless, all these sites fall within the most resistant Australian coral province and may share similar environmental and evolutionary histories. It should be appreciated that bleaching observations are done at a smaller scale than the satellite-based exposure estimates, a problem that troubles most ground-truthing studies, which can result in errors and anomalous observations that can weaken predictions (McClanahan et al., 2019).

Variability in SST distributions have produced similar coral community patterns in other studies. For example, change in coral cover over the 1998 bleaching event was influenced by variation in the

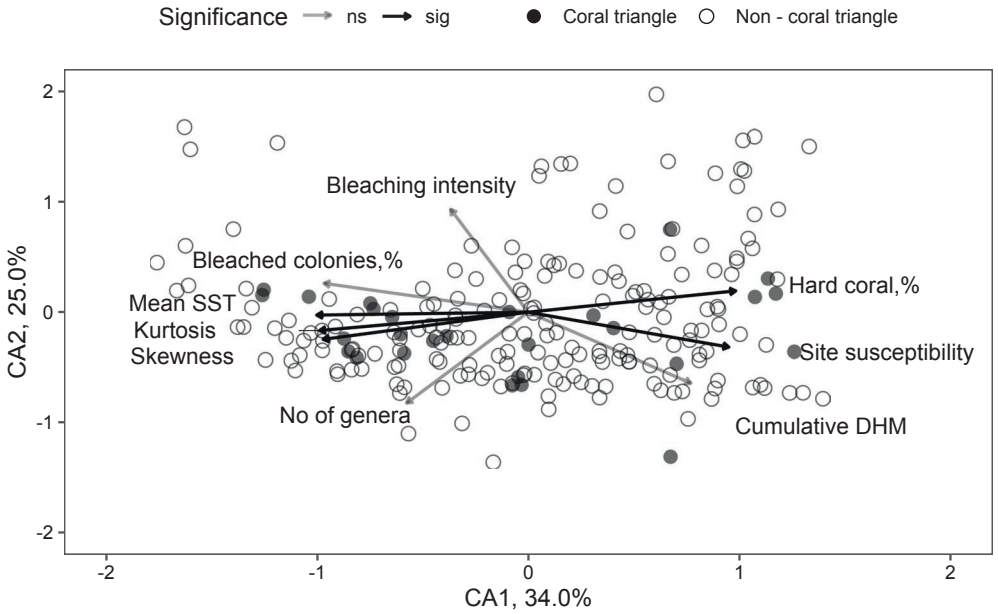

FIGURE 5 Community correspondence analysis (CCA) of the coral communities in and out of the Coral Triangle region indicate that communiteis were not statistically different. Summary of the statistical comparisons of the Coral and non-Coral Triangle are presented in Table 2

shapes of SST distributions – more frequent rare warm-water distributions associated with higher coral mortality (Ateweberhan & McClanahan, 2010). Further, in a large-scale study of coral cover and community composition in Western Australia, SST-kurtosis and skewness were frequently among the top variables for predicting coral abundance (Zinke et al., 2018). Right-skewed SST distributions were associated with lower cover of all corals and those classified as stress-resistant. Both of these SST shape variables would be expected to influence physiological processes that promote or limit the potential for coral acclimation.

On the basin scale of the Indian Ocean, coral taxonomic richness was found to be positively influenced by mean SST and negatively influenced by more frequent rare warm-water SST distributions (Ateweberhan et al., 2018). Consequently, background SSTs have repeatedly been shown to influence taxon sensitivity and resistance and differ most clearly in the complex relationships between SST-standard deviations, kurtosis and skewness (McClanahan et al., 2020). Thus, the mean SSTs–bleaching association (Claar et al., 2018; Sully et al., 2019) has the potential to be modified by other background SST distribution factors and not just the standard deviation (Langlais et al., 2017; Safaie et al., 2018). For example, we found that the potentially negative effects of centralized temperature distributions may not be detrimental when temperature profiles lack frequent rare warm temperatures. Thus, the interaction between these key temperature distribution variables in space and time may prove useful in exposing some of the complexities of chronic and acute stress and subsequent coral responses.

Coral community variables of hard coral cover and number of genera were frequently chosen indicators of resistance but seldom among the top models. Both metrics contributed to resistance measures but, given that they are often correlated with mean SST and geography, they could be proxies rather than ecological drivers of resistance. Nevertheless, there is the possibility that the diversity-portfolio provides some resilience to disturbances such as thermal stress with number of taxa being a proxy for this resilience mechanism (Cardinale et al., 2012; Schindler et al., 2015). Distinguishing cause and effect between these variables and associations with resistance is a priority area for future research that might be uncovered by stronger scientific experimental designs. Moreover, how taxon- and community-specific sensitivities have changed in the past few decades among these disparate localities should lend further insight into the differences in resistance observed here. Patterns seen here may actually underestimate the differences in resistance, given some of the recent large-scale losses of sensitive taxa in the East African ecoregion, for example (Darling et al., 2013, McClanahan et al., 2014, 2020).

Measuring future resistance of corals to thermal stress and the future state of reefs will depend on the effectiveness of exposure and sensitivity metrics to reveal tolerance and adaptation to stresses. Exposure will also vary over time in unique ways for each region (Houk et al., 2020). Climate change and increasing ocean variability in heating patterns mean that exposure and locally adapted sensitivity could change and potentially decouple in the future (Abram et al., 2020; McClanahan et al., 2019, 2020). Moreover, there is the question of how good bleaching or the loss of coral colour are at measuring sensitivity to thermal stress (Buddemeier et al., 2004). Bleaching is potentially one of a number of possible stress or adaptive responses to heat or climate warming stress. Mortality without bleaching, for example, is an infrequently examined response that could influence resistance estimates (McClanahan, 2004). Differential rates and clearly identified causes of mortality and recovery among taxa create challenges for large-scale evaluations of climate impacts

(Darling et al., 2019; McClanahan et al., 2001). Estimating mortality requires inter-annual monitoring to evaluate changes that could be poorly tied to heat stress alone (Darling et al., 2013; Donner & Carilli, 2019). While we acknowledge this weakness, bleaching is currently the most commonly used and quantifiable way to measure sensitivity to heat stress (Donner et al., 2017; Sully et al., 2019).

The difference between the two exposure models contributes to understanding the geography of environmental stress in the tropics. The propagation of east–west inter-annual SST variability driven by the ENSO and Indian Ocean Dipole (IOD) are critical exposure forces (Abram et al., 2020; DeCarlo, 2020). Longitudinal propagation of thermal exposure is likely to explain the uneven distribution of CTAs, differences between the two exposure models, the types of stresses that corals experience, and the separate responses of the various geographic regions. For example, CTA was better at distinguishing the Pacific from the Indian Ocean regions than the CE metric (Supporting Information Table S1). ENSO and PDO are likely to be the dominant oceanographic forces over historical time, controlling reef development in the eastern Pacific and recently increasing in strength in the western Pacific (Peñaflor et al., 2009; Toth et al., 2015). Thus, CTAs are likely to be a distinguishing feature and driver of Pacific coral population dynamics (Houk et al., 2020).

The increasing strengths of ENSO and IOD variability are emerging oceanographic phenomena (Abram et al., 2020; Cai et al., 2019). Increasing ENSO strength has been associated with increases in the penetration of warm waters into the eastern Indian Ocean (Abram et al., 2008; Zinke et al., 2015). More importantly, there are broad-scale teleconnections and occasionally strong coupling between these two ocean-basin oscillations (Abram et al., 2020). The IOD has been increasing in strength since the 1920s and, when coupled with ENSO, adds to heat stress (Abram et al., 2008; McClanahan, 2017; Nakamura et al., 2009). IOD changes since 1200 CE are complicated with, for example, periodicity changing from 25 to 8 years at the 1590 CE boundary. Moreover, between the 1800s and 1960, the IOD was not strong or regular compared to strong and reoccurring ENSO oscillations with 2- to 7-year periodicities (Cobb et al., 2003). At times, however, IOD is more tightly coupled with ENSO and promoted by ocean states with shallow thermoclines (Abram et al., 2020). Finally, warm IODs show clustering associated with shallow thermoclines, such that there may be short periods of intense thermal stress punctuating longer periods of stability. Ocean models indicate that greenhouse warming decreases the depth of the thermocline and, therefore, the Indian Ocean is expected to experience stronger and more clustered warm IOD events (DiNezeo et al., 2020). Consequently, the more recent origins, current, and expected increase of these inter-annual thermal forces in the Indian Ocean may explain the higher sensitivity and lower resistance of corals observed here. This history and associated resistance are likely to increase the risk of detrimental climate impacts of climate change on Indian Ocean more than Indo-Pacific corals.

The higher resistance of corals to thermal stress in the western Pacific and some Indo-Pacific ecoregions is associated with the global marine biodiversity centre. This suggests that coral resistance is positively associated with coral reef diversity but, as shown here, not with differences in community structure (Parravicini et al., 2013; Veron et al., 2011). The Coral Triangle has a geographically variable SST environment (McLeod et al., 2010; Peñaflor et al., 2009) but we found a similar combination of high anomalies, neutral to cold SSTs, and more bell-shaped SST distributions in our study sites. We suggest that these SST distribution patterns provided some resistance to episodic strong thermal disturbances. High biodiversity in the Coral Triangle has arisen from a number of interacting forces that are likely to include environmental as well as geological complexity, isolation, and changing sea level forces (Barber & Meyer, 2015). Nevertheless, the coverage of sampling in the Coral Triangle was not extensive enough to make conclusions about resistance beyond our study sites. Additionally, ecoregions including the Philippines, Borneo, Timor-Leste, Central and Northern Sulawesi, and reefs in Molucca, Halmahera, and Ceram Seas will need to be sampled for thermal sensitivity to determine coral resistance and evaluate the full spatial extent of the Coral Triangle resistance patterns.

Our findings support the contention that historical forces may be associated with a higher capacity to tolerate episodic large-scale global heat stress, as observed here during this pan-tropical thermal stress event of 2014–2016. Many models that predict the future of coral reefs treat CTAs, bleaching and mortality as interchangeable. Yet, we show here and elsewhere that sensitivity is highly variable and geographically contextual (McClanahan et al., 2019, 2020). Therefore, predictions for coral reefs should be improved by the use of taxa and regionally-specific coral resistance metrics rather than just simple exposure metrics, such as the initial and projected SSTs. Greater resistance to thermal stress in some provinces and regions may delay and attenuate the observed increases in warm-water stress responses (Hughes et al., 2018). Thus, our findings here indicate a limited window of opportunity to better manage the impacts and produce less severe outcomes arising from multiple human stresses. Stronger experimental sampling designs and broader spatial coverage of sensitivity of corals exposed to variable environmental conditions will be needed to better understand regional and global climate change outcomes. Nevertheless, reducing heat-retaining gas emissions, developing sustainable fisheries, and improving watershed and pollution management remain priorities for coral reef persistence.

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DATA AVAILABILITY STATEMENT

Data are available at Dryad (https://doi.org/10.5061/dryad.73n5tb2tc) and the Knowledge Network for Biocomplexity (https://knb.ecoinformatics.org) via https://doi.org/10.5063/F1WQ024C.

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BIOSKETCH

Tim R. McClanahan studies coral reefs in relationship to management, climate change, and fishing impacts.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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