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BIODIVERSITY RESEARCH

WILEY Diversity and Distributions

Gradients of disturbance and environmental conditions shape coral community structure for south-eastern Indian Ocean reefs

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Abstract

Aim: To describe, model and assess the relative importance of environmental and climatic factors likely influencing the regional distribution of coral cover and assemblages with contrasting life histories and susceptibilities to bleaching.

Location: We compiled the first comprehensive empirical dataset for coral communities in the south-eastern Indian Ocean (SEIO), incorporating information from 392 sites along the western coast of Australia and offshore atolls/islands across ~19° of latitude.

Methods: We assessed hard coral cover and community composition to genus using point-intercept transects or point-count analysis of digital images taken along transects. We explored spatial variation in environmental conditions and in composition of corals with contrasting life histories. After de-trending the temporal patterns, we assessed the relative importance of environmental metrics to coral cover, life histories and bleaching susceptibility using a full subsets model-selection approach with generalized additive mixed models, accounting for both temporal and among site variation.

Results: The distribution of temperature, light, the frequency of temperature anomalies and tropical cyclones appear to be drivers of coral community structure. Functional diversity of low- to mid-latitude coral communities may convey some resilience to thermal stress, while higher latitude communities dominated by Competitive and Bleaching-Susceptible taxa may lack this functional resilience. These patterns likely reflect varying historical exposure to cyclones and temperature anomalies.

Main conclusions: As evident in recent years, changing background conditions and regimes of disturbance in coming decades will shift the distribution, functional diversity and resilience of coral reefs throughout the SEIO. The rate and magnitude of environmental change will ultimately determine the future of the tropical reefs and whether the higher latitude reefs provide some refuge from climate change. Our study highlights the need to quantify the distributional properties of key environmental metrics to better understand and predict reef condition through coming decades.

KEYWORDS

biodiversity, coral bleaching, coral life-history traits, Indian Ocean, sea surface temperature, tropical cyclones

1 | INTRODUCTION

Cycles of disturbance and recovery are a key feature of coral reef ecosystems (Connell, 1978; Rogers, 1993), where multiple diversity–disturbance relationships exist depending on the interaction between the frequency and intensity of disturbances (Hall et al., 2012). Management actions aimed at maintaining the diversity, functional integrity and resilience of coral reef ecosystems are ideally based on understanding how inherent environmental conditions interact with disturbance regimes to shape coral community structure (Iwamura, Wilson, Venter, & Possingham, 2010; Klein et al., 2013; Maynard, Beeden, et al., 2015). This type of information is increasingly important, because many reefs face cumulative threats from a combination of natural and anthropogenic stressors operating at multiple scales (Hughes, Graham, Jackson, Mumby, & Steneck, 2010; Hughes et al., 2003, 2017).

Spatial variation in environmental forces produces different ambient conditions, which influence the distribution of corals and create heterogeneity in the resilience of coral reefs (Graham, Jennings, MacNeil, Mouillot, & Wilson, 2015; Richards & Hobbs, 2014). Coral communities are routinely structured by temperature regimes (McClanahan, Ateweberhan, Muhando, Maina, & Mohammed, 2007), light penetration (Anthony & Connolly, 2004; Muir, Wallace, Done, & Aguirre, 2015; Sommer, Beger, Harrison, Babcock, & Pandolfi, 2017), wave energy (Lowe & Falter, 2014; Madin & Connolly, 2006), tidal amplitude (Richards, Garcia, Wallace, Rosser, & Muir, 2015), sediment delivery and re-suspension (Fabricius, Logan, Weeks, & Brodie, 2014; Fisher, Stark, Ridd, & Jones, 2015; Maina et al., 2013), nutrient dynamics (Kroon et al., 2012) and ocean currents (Brinkman, Wolanski, Deleersnijder, McAllister, & Skirving, 2002; Lowe, Ivey, Brinkman, & Jones, 2012). For example, areas dominated by relatively benign conditions associated with shallow, clear waters as well as low wave action and nutrient loads are often characterized by the proliferation of corals with "Competitive" life-history traits (e.g., branching *Acropora*), following the definition of Darling, Alvarez-Filip, Oliver, McClanahan, and Côté (2012), Darling, McClanahan, and Côté (2013).

Acute disturbances, such as extreme temperature anomalies (Selig, Casey, & Bruno, 2010) and physical damage from waves associated with tropical cyclones, can, however, disrupt normal environmental conditions and coral assemblages (Beeden et al., 2015; Fabricius et al., 2008; Harmelin-Vivien, 1994). Similarly, longer term ecological stressors, such as outbreaks of coral-feeding crown-of-thorn starfish (De'ath & Fabricius, 2010; Hock, Wolff, Condie, Anthony, & Mumby, 2014) and coral disease (Bruno et al., 2007; Maynard, van Hooidonk, et al., 2015; Ruiz-Moreno et al., 2012), can affect the distribution and composition of corals. If both the supply of propagules and time before the next disturbance are sufficient, recovery from these disturbances is possible (Beeden et al., 2015; Gilmour, Smith, Heyward, Baird, & Pratchett, 2013; Graham, Nash, & Kool, 2011; Graham et al., 2015; Lukoschek, Cross, Torda, Zimmerman, & Willis, 2013; Sheppard, Harris, & Sheppard, 2008). Major factors that mediate recovery rates and the impacts of disturbances are local environmental conditions. These conditions can, in some cases, alter communities by promoting some life-history traits over others (Carreiro-Silva & McClanahan, 2012; Darling et al., 2013; McClanahan, 2014). For example, cooler water at greater depth (Tyler et al., 2014), or periodic upwelling of cool water (Riegl & Piller, 2003), can mediate the effects of acute warm-temperature anomalies and may produce different coral responses (McClanahan

& Maina, 2003). Additionally, the effects of disturbances can be patchy, possibly due to fine-scale variation in exposure, bathymetry and reef structure interacting with each taxon's susceptibility to this stressor variation (Harmelin-Vivien, 1994; Hoey et al., 2016). Finally, multiple stressors may combine to either enhance or reduce coral response to disturbance—such as reduced thermal stress from sea surface cooling induced by cyclone wind (Carrigan & Puotinen, 2011, 2014; Hughes et al., 2017; Manzello et al., 2007).

Making reasonable predictions about the impacts of climate change on corals is thus expected to benefit from a better understanding of the interactions between local environmental conditions and large-scale disturbances. A first essential step towards this is to investigate these interactions where other human impacts, such as fishing and eutrophication, have not significantly altered reefs. Commercial, recreational and subsistence fishing occur on many reefs within south-east Indian Ocean (SEIO) and dredging threatens reefs in some areas (Fletcher, Mumme, & Webster, 2017; Hanley, 2011). However, impacts from these activities are localized, and anthropogenic stress at regional scales is low compared to many other reefs in the world (Burke, Reytar, Spalding, & Perry, 2011). Moreover, the region is exposed to a wide range of background environmental conditions and large-scale natural disturbances, making it an ideal area for assessing how these processes influence coral assemblages.

Trait-based approaches to classifying organisms can reveal how coral communities, and the ecosystem services they provide, respond to disturbances (Darling et al., 2012, 2013). For example, large branching corals provide the structural complexity that supports reef-fish communities (Graham & Nash, 2013; Rogers, Blanchard, & Mumby, 2014). These Competitive corals grow rapidly and often dominate reefs, but decline rapidly following disturbances like heat stress, cyclones or outbreaks of predators (Hughes et al., 2017; Shedrawi et al., 2017). Moreover, susceptibility of coral to disturbances varies considerably among taxa, with a meta-analysis of 68 studies revealing that *Acropora* and *Pocilopora* corals readily bleach following heat stress, while many of the faviid genera are less likely to bleach (Hoey et al., 2016). Thus, some corals have life-history traits that make them more resilient to disturbances, allowing them to persist over longer timeframes (Darling et al., 2013; McClanahan, 2014; McClanahan, Ateweberhan, Darling, Graham, & Muthiga, 2014; McClanahan & Muthiga, 2014). Consequently, understanding the spatial distribution of coral life-history traits may facilitate the prediction of future changes in community structure (Darling et al., 2013; Done, Gilmour, & Fisher, 2015; Graham, Chong-Seng, Huchery, Januchowski-Hartley, & Nash, 2014; Sommer, Harrison, Beger, & Pandolfi, 2014).

Here, we used coral life-history traits (LHTs) to examine regional responses of coral cover, community structure and bleaching susceptibility (BS) along a continuum of environmental conditions and disturbance regimes of various types. We compiled in situ coral reef survey data collected between 1998 and 2014 across 392 sites, spanning 19° of latitude, to build the first comprehensive empirical dataset for coral communities in the SEIO. Specifically, we asked (1) how coral cover, coral life histories and BS are distributed over time and space; and (2) how key environmental factors likely shape the coral communities across space. Addressing these questions provides a basis for identifying resilient reefs and potential refugia from environmental change, which may be used to inform management of coral reefs.

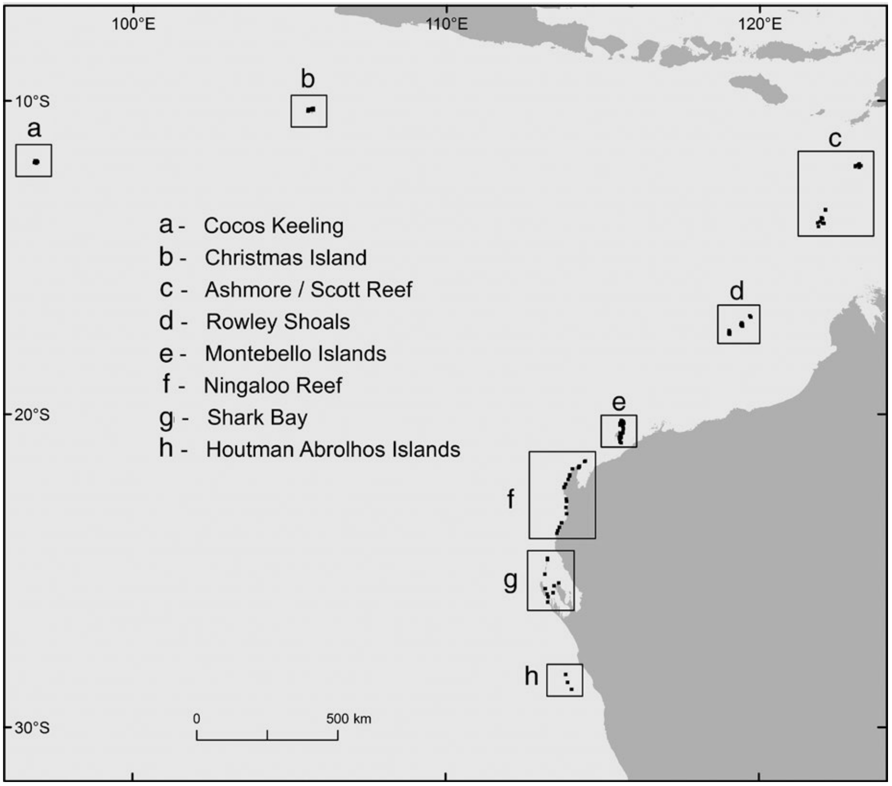


FIGURE 1 Study sites and regions in the south-east Indian Ocean Reefs (SEIO): (a) Cocos Keeling, (b) Christmas Island, (c) Ashmore and Scott Reefs, (d) Rowley Shoals, (e) Montebello Islands, (f) Ningaloo Reef, (g) Shark Bay and (h) Houtman Abrolhos Islands

TABLE 1 Regional mean of environmental metrics used in this study grouped into nine overarching categories. All environmental metrics included in this study and their mean values are summarized in Table S1. The environmental factors analysed in this study include changes in background conditions (e.g., sediment, chlorophyll, temperature, tidal amplitude, light and depth) and periodic disturbances (e.g., extreme temperature anomalies, cyclones)

Latitude		Low				Mid			High	
Environmental metric	Units	Cocos Keeling	Christmas	Ashmore	Scott Reef	Rowley Shoals	Montebello	Ningaloo	Shark Bay	Houtman Abrolhos
Location										
Depth	m	5.17	8.71	7.00	6.73	7.26	4.87	1.34	1.75	10.33
Latitude (South)	°	12.11	10.45	12.24	14.02	17.32	20.67	22.57	25.50	28.70
Thermal stress										
SSTA (mean)	Number per year (30 years)	16.87	15.88	15.89	16.91	18.21	20.98	19.99	20.88	17.78
SSTA (frequency)	Number per year (30 years)	4.99	4.83	4.64	5.55	6.15	7.67	6.93	7.60	5.83
TSA (frequency)	Number per year (30 years)	1.35	1.42	2.18	2.51	1.72	1.26	1.57	2.18	1.82
Temperature variability										
SST (kurtosis)	°C	0.19	−0.42	−0.66	−0.82	−1.05	−1.13	−0.81	−0.71	−0.67
SST (skewness)	°C	0.03	−0.23	−0.14	−0.13	−0.07	0.10	0.32	0.25	0.19
SST (*SD*)	°C	1.05	1.36	1.44	1.52	1.89	2.58	2.09	2.02	1.57
Cyclones										
Cyclone days (mean)	Counts/year	1.63	0.55	1.30	2.75	3.68	2.39	1.34	0.72	0.03
Cyclone days (*SD*)	Counts/year	2.67	1.31	2.31	3.71	3.14	3.28	2.66	1.91	0.18
Cyclone days (max)	Counts/year	11.00	5.00	8.00	14.00	10.52	12.00	10.41	7.90	1.00
Sediment										
TSM (kurtosis)	g/cm^3	1.99	0.64	15.00	16.22	3.03	5.43	7.54	7.62	2.65
TSM (median)	g/cm^3	0.35	0.35	0.45	0.50	0.30	0.74	0.62	0.49	0.42
TSM (skewness)	g/cm^3	−1.01	0.06	0.67	2.61	0.45	1.52	0.96	−0.74	0.20
TSM (*SD*)	g/cm^3	0.08	0.10	0.09	0.53	0.10	0.36	0.58	0.09	0.12
Light										
PAR skewness	$E\ m^{-2}\ day^{-1}$	−0.24	−0.25	0.05	−0.10	−0.31	−0.21	−0.21	−0.15	−0.09
PAR kurtosis	$E\ m^{-2}\ day^{-1}$	−0.94	−0.72	−1.06	−1.11	−1.08	−1.34	−1.36	−1.41	−1.43
Tide										
Average tidal range	m/day	0.68	0.77	1.57	1.59	1.68	1.37	0.78	0.56	0.51
Tide mean maximum	m/day	0.28	0.34	0.92	0.95	1.02	0.79	0.34	0.18	0.14

(Continues)

TABLE 1 (Continued)

Latitude		Low				Mid			High	
Environmental metric	Units	Cocos Keeling	Christmas	Ashmore	Scott Reef	Rowley Shoals	Montebello	Ningaloo	Shark Bay	Houtman Abrolhos
Nutrients										
Chl (kurtosis)	mg/cm^3	2.36	1.53	1.01	3.91	2.14	4.69	10.95	0.91	−0.14
Chl (median)	mg/cm^3	0.11	0.12	0.38	0.36	0.13	0.73	0.62	0.48	0.38
Chl (skewness)	mg/cm^3	1.48	1.34	0.63	1.09	1.26	1.67	2.59	1.05	0.49
Chl (*SD*)	mg/cm^3	0.04	0.07	0.12	0.28	0.05	0.38	0.46	0.18	0.12
Isolation										
Normalized centrally		0.01	0.36	0.43	0.56	0.78	0.98	0.86	0.53	0.28
Distance (median)	km	2,379	1,688	1,273	1,035	621	355	394	660	1,012
Distance (skewed)	km	−2.10	−0.83	0.21	0.64	1.71	0.85	0.75	0.69	0.46
Distance (kurtosis)	km	11.05	6.37	2.78	3.57	6.81	2.82	2.22	2.09	2.34

PAR, photosynthetically active radiation; TSM, total suspended matter; SST, sea surface temperature; TSA, thermal stress anomalies; SSTA, sea surface temperature anomalies.

2 | METHODS

2.1 | Study locations

The western coastline of Australia forms the south-eastern margin of the Indian Ocean, covering nearly 19° of latitude in the Southern Hemisphere (Figure 1). Southward-flowing currents (Halloway and Leeuwin) push warm tropical water along the length of the coast (Condie & Andrewartha, 2008; Feng, Biastoch, Boening, Caputi, & Meyers, 2008; Lowe et al., 2012), providing conditions favourable for extensive coral reef growth and development from the north Kimberley region as far south as the Abrolhos Islands (Veron & Marsh, 1988). Extensive coral reefs are also found on oceanic atolls and island territories adjacent to the north-west coast of Australia in the SEIO (Speed et al., 2013).

Data on percentage coral cover and abundance at the level of individual genera were obtained from nine coastal and oceanic SEIO regions from the west coast of Australia (Figure 1). In each region, information was collated from 3 to 26 sites at 1–15 m depth that were typically sheltered from prevailing wind and wave exposure (Table S1). Surveys took place between 1998 and 2014 and include data about impacts from warm-water anomalies and cyclonic activity (Ceccarelli, Richards, Pratchett, & Cvitanovic, 2011; Moore et al., 2012; Pearce & Feng, 2013). We define sites geographically as low- (north of 17°S), mid- (~17–22°S) or high-latitude (~22–29°S; Table S1). Hard coral cover and community composition (identified to genus) were assessed using point-intercept transects, or point-count analysis of digital images taken along transects (Table S1). Comparative studies indicate that differences between these methods arise mainly for corals from the genera *Stylophora* and *Goniastrea*, and estimates of cover from other genera with contrasting growth forms are similar (Leujak & Ormond, 2007).

2.2 | Environmental data

We examined nine environmental metrics representing potential drivers from 27 variables (Table 1). Seven metrics were derived from ocean satellite observations and/or modelled databases, including (1) sea surface temperature (SST); (2) thermal stress metrics; (3) total suspended matter (TSM), (4) photosynthetically active radiation (PAR); (5) tidal range; (6) nutrient concentrations (chlorophyll-*a*); and (7) frequency of exposure to extreme winds generated by tropical cyclones. The final two metrics, (8) depth and (9) physical location (latitude, longitude, isolation), were derived from in situ data. The nine metrics were specifically chosen for their relevance to physiological processes, productivity and stress responses in Scleractinian reef corals (Maina, McClanahan, Venus, Ateweberhan, & Madin, 2011; Maina, Venus, McClanahan, & Ateweberhan, 2008). All environmental data, where appropriate, were aggregated to capture long-term (~30 years; mean, median) averages, distribution (skewness and kurtosis), extremes (maximum) and variability (standard deviation [*SD*]; Table 1). We accounted for potential bias in ocean-colour constituents by extracting estimates for our sites from a reanalysis database (Maina et al., 2011;

Morel & Bélanger, 2006) that adjusts values for reflectance bias (Gove et al., 2015).

For each site, we obtained weekly SST data for the period 1982–2012 for our SEIO sites at a resolution of ~4 × 4 km from coral reefs thermal stress database (CoRTAD), which archives data from NOAA's Advanced Very High Resolution Radiometer (AVHRR; http://www.nodc.noaa.gov/sog/Cortad/; Selig et al., 2010). Site-level SST time series were used to characterize the distribution (skewness and kurtosis) and variability (standard deviation) of SST at each site. From the same database, we extracted thermal stress anomalies (TSA) and weekly SST anomalies (SSTA) that define the spatial and temporal patterns of temperature anomalies associated with coral bleaching and disease (1982–2012; Selig et al., 2010).

The bleaching-related anomalies (TSA) occur in the warmest weeks of the year, whereas disease-related anomalies (SSTA) can occur at any time of year (Bruno et al., 2007; Liu, Skirving, & Strong, 2003; Podesta & Glynn, 2001; Selig et al., 2006). Following Selig et al. (2010), TSA is defined as observed weekly averaged temperature >1°C warmer than the warmest climatological week (52 climatological weeks averaged over 30 years). Following Selig et al. (2010), SSTA are defined as observed weekly averaged temperature >1°C warmer than the weekly climatological value for each week of the year (over 30 years). Mean SST anomalies (mean SSTA) define the average number of anomalies in any given year. We calculated both the frequency of TSAs (TSA frequency; Table 1) and SSTAs (SSTA frequency; Table 1) based on the number of anomalies in each calendar year and cumulatively over the 30-year study (as per Selig et al., 2010).

Time series data for total suspended matter (hereafter TSM, g/m^3) and chlorophyll-*a* concentration monthly (2002–2010) were summarized to median values, distribution (skewness and kurtosis) and variability (standard deviation). Time series data (monthly; 2002–2010) of PAR were obtained from the Globcolour database (http://hermes.acri.fr/GlobColour) and summarized to median values, distribution (skewness and kurtosis) and variability (standard deviation) from the 8-year time series (Table 1).

Extreme winds generated during tropical cyclones can build large seas capable of damaging reefs. A particular coral colony's exposure and vulnerability to damage from such seas depends on a myriad of local-scale factors (Fabricius et al., 2008), most notably fine-scale bathymetry around the colony relative to the incoming wave direction during peak conditions. Such data are presently unavailable for most of our study area. Thus, we derived exposure to tropical cyclone winds as a proxy for the potential to cause damaging waves, accepting that damage within this zone will be patchy. We did this from 1985 to 2013 based on the International Best Track Archive for Climate Stewardship (IBTRACS—Knapp, Kruk, Levinson, Diamond, & Neumann, 2010). Cyclone winds were defined as those of gale force (17 m/s) or higher. These were mapped each day based on the reported or estimated radius of gale winds using methods detailed in Carrigan and Puotinen (2011). We extracted maximum cyclone days and their standard deviation per year from the 28-year database across the study area (Table 1).

We developed an Isolation Index to quantify each reef's relative potential for larval connectivity, given its location with respect to neighbouring reefs, assuming that more isolated coral communities may differ in structure and composition due to limited accessibility to coral larvae for recovery (Gilmour, Smith, & Brinkman, 2009; Underwood, Smith, van Oppen, & Gilmour, 2009). To measure isolation, we grouped reef habitat into 122 spatially distinct large-scale reef complexes, using remotely sensed reef data from the WCMC 2010 database (UNEP-WCMC, WorldFish Centre, WRI, TNC, 2010) and West Australia habitat maps from the WA Department of Parks and Wildlife (Bancroft, 2003). We calculated the distance in km between all pairs of reef complexes and calculated the Isolation Index as the normalized graph-theoretic closeness centrality (0—isolated, 1—maximum connected; Beger et al., 2010; Table 1).

As the data collected here quantified for the first time both the coral community and the broad-scale environmental features in this region, the spatial variation in environmental conditions was first illustrated with principal components analysis (PCA) of normalized environmental data (Clarke & Warwick, 2001). Within the groups of environmental conditions (e.g., different measures of light, sediment, thermal stress; Table 1), a single combined metric was derived for cases when several metrics were highly correlated (>0.7) with each other, resulting in 16 metrics of the initial 27. The final metrics used for PCA corresponded to those identified as being the most important correlates to variation in coral community composition in the generalized additive mixed model (GAMM) analyses (Table 2).

2.3 | Coral community data

To evaluate the distribution of coral assemblages across the SEIO, we standardized data to derive site-level estimates of total coral cover (%), coral LHT groups (%), and BS. Total coral cover was the average of live hard corals observed at each site for each sampling period. We classified corals into four coral LHT groups—Competitive, Stress-Tolerant, Weedy and Generalist—according to Darling et al. (2012), but adapted the categories for genera based on our expertize with Western Australia corals (co-authors ZR, JG, GS) (Table S2). For genera with species that grouped into different life histories, we assigned coral cover to each of the represented life histories in proportion to the number of species within each life history that occur in the Western Australian coral fauna (Veron & Marsh, 1988 sensu Darling et al., 2013).

Bleaching susceptibility of coral communities at each site was based on the relative abundance (RA) of genus *i* in the coral community weighted by a corresponding estimate of its bleaching response (BR_i) and summed across all genera in the community (Equation 1; McClanahan et al., 2007).

$$\text{Site bleaching susceptibility} = \sum_{i}^{n} (RA_i \times BR_i) \quad (1)$$

Bleaching responses were estimated by the observed bleaching intensity and mortality of genera during thermal stress events in the

TABLE 2 Generalized additive mixed model (GAMM) fits for best models (the simplest model within 2 Akaike information criterion [AICc] of the lowest AICc) for environmental predictor metrics influencing changes in cover of all corals, and those with contrasting life-history traits (LHT; following Darling et al., 2012, 2013) and bleaching susceptibility. Shown are the predictor metrics included in the best models, AICc, delta AICc, AICc weight (ω_i) values, R^2 and the number of other competing models within 2 AICc. Best models illustrated in Figure 5 are shown in bold

LHT	All best models (<2 AICc of min AICc)	AICc	ΔAICc	ω_i	R^2
Coral cover	SSTA (mean) + SST (kurtosis) + cyclone days (max)	1,139.3	0.0	0.492	.41
Competitive	SSTA (frequency) + cyclone days (max)	960.7	0.0	0.117	.39
	PAR (skewness) + SSTA (frequency)	961.1	0.4	0.094	.35
	SSTA (mean) + SST (kurtosis) + cyclone days (max)	961.3	0.6	0.086	.41
	SSTA (mean) + cyclone days (max)	961.7	1.1	0.069	.38
	SSTA (frequency) + cyclone days (max) + log (TSM [median])	961.9	1.2	0.065	.42
	PAR (skewness) + SSTA (frequency) + log (TSM [*SD*])	962.5	1.8	0.048	.36
Stress-tolerant	SST (kurtosis) + SST (skewness) + log (TSM [*SD*])	593.1	0.0	0.319	.42
	SST (kurtosis) + SST (skewness)	593.9	0.8	0.214	.38
	PAR (skewness) + SST (kurtosis) + SST (skewness)	594.1	1.0	0.193	.39
Weedy	PAR (skewness) + PAR (kurtosis)	374.7	0.0	0.14	.37
	Isolation + tide (mean maximum)	374.9	0.2	0.125	.35
	Isolation + average tidal range	375.6	0.9	0.09	.35
	PAR (skewness) + PAR (kurtosis) + TSM (skewness)	375.9	1.3	0.074	.38
	PAR (kurtosis) + TSM (skewness)	376.4	1.7	0.058	.36
Generalist	Depth + cyclone days (max)	701.2	0.0	0.692	.31
Bleaching susceptibility	SST (*SD*)	−195.2	0.0	0.463	.30

TSM, total suspended matter; PAR, photosynthetically active radiation; SST, sea surface temperature; SSTA, sea surface temperature anomalies; TSA, total stress anomaly; dist, isolation metric (distance).

western Indian Ocean (McClanahan, 2014; McClanahan et al., 2007, 2014), which are comparable to bleaching events observed on the Great Barrier Reef (McClanahan, Baird, Marshall, & Toscano, 2004).

2.4 | Environmental metrics and implications for coral communities

To assess the relative contribution of spatial variation in environmental metrics in explaining the spatial variability of total coral cover, life histories and BS while controlling for temporal trends, we adopted a full subsets model-selection approach, where models were compared using Akaike information criterion for small sample sizes (AICc) and AICc weight (ω_i) values (Burnham & Anderson, 2002). Prior to analyses, all environmental metrics were tested for collinearity, following Graham (2003). To avoid issues with multicollinearity among metrics (predictors), we excluded any models where the absolute correlation between the metrics was greater than 0.28. To limit the maximum complexity of resulting models, we fitted only models that included up to three metrics (in addition to "null" model terms, see below). Individual metrics were carefully screened to ensure a relatively even distribution across sites. Three metrics (Chl-*a* [*SD*], TSM [*SD*] and TSM [median]) were transformed to a log scale because they were highly skewed. TSM (kurtosis) was excluded because it exhibited highly uneven spread across the study domain. These restrictions reduced the total model set to 360 unique models.

All models were fit using GAMMs, via the GAMM function from the mgcv package (Wood, 2006) in R (version 3.1.0, R Core Team, 2014). GAMM was adopted rather than linear or nonlinear parametric multiple regression to allow for possible nonlinear effects of metrics on the response variable, without needing to define the functional form of each model. Smooth terms were fit using cubic splines (Wood, 2006) and limiting the basis dimension "*k*," which controls the degree of flexibility in curve fitting, to a maximum value of 5 to avoid over-fitting and to ensure monotonic relationships. Percentage cover, rather than raw count data, was available for analyses, precluding a model using a binomial distribution. Accordingly, the mean proportional cover values were logit-transformed and modelled using a Gaussian distribution. Site was included in all models as a random effect nested within region. In addition, the year of sampling was included in all models as a continuous cubic regression spline to capture broad-scale temporal trends, with optimal basis dimension (*k*) identified via cross validation following Wood (2006). A null model consisting of a random site effect and year was also included in the model set. The random site effect was not nested within region, as region was collinear with many of the environmental metrics of interest. Analyses at the genus level were also carried out for genera occurring at more than 25% of locations (see Table S3).

The simplest model within 2 AICc values of the model with the lowest AICc value was assumed to be the optimal model. To determine the relative contribution of each predictor metric to the spatial variation in response metrics across the whole model set, we summed the ω_i values for all models containing each predictor metric. The higher the combined weights for an explanatory predictor metric, the more important it was for the analysis (Burnham & Anderson, 2002).

3 | RESULTS

3.1 | Environmental gradients

The background environmental conditions at the SEIO reefs and their exposure to disturbances reflected their geographic setting, with variation being high among regions and comparably low among reefs within regions (Figure 2; Table 1). Temperature distributions along the inshore reefs of north-west Australia had negative kurtosis, indicating flat distributions with frequent but modest deviations from the mean (Table 1). The distributions are less flat offshore and were even slightly peaked or centralized in the further offshore reefs at Cocos Keeling Island, suggesting infrequent extreme temperatures. Skewness of temperature data varied among regions. Positive skewness at mid- and high-latitude reefs indicates that unusually high temperatures occasionally occur, while positive skewness on high-latitude reefs suggests there are occasions when unusually low temperatures occur. Variation (*SD*) in SST was highest at Ningaloo Reef, Shark Bay and the Rowley Shoals, indicating that these sites are exposed to a wide range of temperatures (Table 1). Sediment (TSM) concentrations were high at the Montebellos and Ningaloo Reef, and comparatively low at the offshore reefs, particularly the Rowley Shoals, Christmas and Cocos Keeling islands (Table 1). The kurtosis and skewness of available light (PAR) were negative at all sites, with the exception of Ashmore Reef, suggesting most reefs are regularly exposed to the same levels of light, with few extremes. Chlorophyll concentrations were highest at the Montebello Islands, Ningaloo and Shark Bay, while chlorophyll skewness and kurtosis were positive at all reefs, indicating extremely high chlorophyll concentrations were sometimes experienced at these locations, except at the Abrolhos where kurtosis was negative (Table 1). Tidal range and mean maximum tides were highest at Ashmore Reef, Scott Reef, the Rowley Shoals and the Montebello Islands (Table 1).

There was a clear latitudinal pattern to cyclone activity, which was highest from Ningaloo Reef in the south to Scott Reef in the north, infrequent at the lowest latitude reefs (Ashmore Reef, Christmas Island), and rare at the high-latitude reefs (Shark Bay, Abrolhos Islands—Table 1). In contrast, thermal stress varied according to both regional and local oceanography, with the highest frequency of temperature anomalies during the warmest months (TSA) at Scott Reef, Ashmore and Shark Bay, followed by Abrolhos and Rowley Shoals (Table 1).

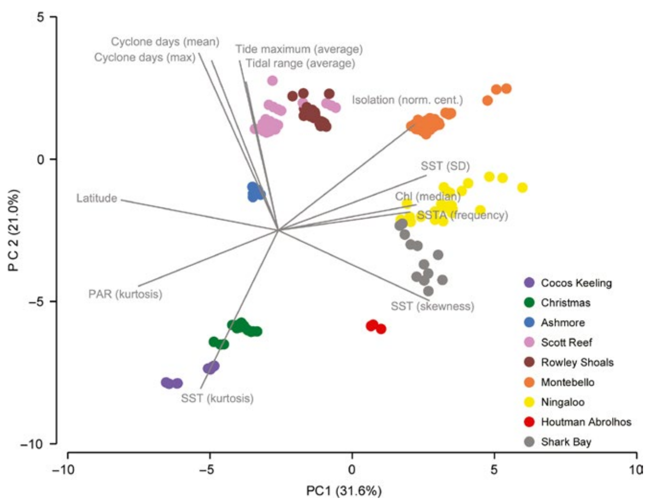


FIGURE 2 Spatial variation in physical conditions across the south-east Indian Ocean Reefs (SEIO). Principal components analysis of environmental predictor metrics at replicate reefs at each of the nine coral reef regions. The vectors and environmental predictor metrics (Table 1) responsible for the spatial separation among reefs are in grey; predictor metric abbreviations are PAR (photosynthetically active radiation), TSM (total suspended materials), Chl (chlorophyll-*a*), SST (sea surface temperatures), SSTA (sea surface temperature anomalies), TSA (thermal stress anomalies) and skew (skewness), kurt (kurtosis), med (median), max (maximum), freq (frequency) and av (average). [Colour figure can be viewed at wileyonlinelibrary.com]

3.2 | Coral community patterns

Coral cover and community composition varied through time at all reefs (Figure 3), influenced by their regional exposure to cyclones and particularly the impacts of temperature anomalies and coral bleaching across regions in 1998 and 2011 (Figure 4). However, this temporal variation differed among coral life-history groups, with large changes observed for the Bleaching-Susceptible and Competitive groups, and small changes for the Stress-Tolerant group (Figure 3b–d). The coral groups varied predictably according to their LHTs (e.g., growth form) and susceptibility to disturbances, and the genera within groups generally displayed comparable temporal variation, although there were exceptions (Figures S1–S3). For example, among the Stress-Tolerant genera, *Lobophyllia* changed little, but massive *Porites* displayed relatively large temporal change (Figure S2). Furthermore, within the Generalist life-history group, the many contributing genera displayed a range of variation through time (Table S3).

After accounting for temporal trends, coral cover and the BS of communities were similar among the broad regions, with few notable trends (Figures 3a,b and S4–S8). Of the life-history groups, only the cover of Weedy corals showed a slight trend, with highest cover at low to mid-latitudes, and higher latitude reefs showing very low cover (Figures 3e and S7).

3.3 | Environmental metrics and coral communities

After temporal trends were accounted for, spatial variation in total coral cover was best explained by temperature variation (SST kurtosis) and anomalies (mean SSTA), and exposure to cyclones (maximum days) (Table 1, Figures 4 and 5). Total coral cover declined at most sites with increasing temperature anomalies (mean SSTA) and with increasing exposure to cyclones, and was highest when SST kurtosis was negative (even spread of temperatures lacking extremes)

(Figure 5). Temperature variation (SST *SD*) alone explained the small spatial variation in the BS of the coral communities (Table 2; Figures 4 and 5), with cover remaining constant before declining when SST *SD* was greater than 2.0 (Figures 4 and 5).

Among the life-history groups, the variation in cover after the temporal trends were removed was often explained by measures of temperature distribution, in addition to the environmental metrics that reflected the group's susceptibility to disturbances and their LHTs (Figures 4 and 5). For the Competitive corals, there were six models of similar explanatory power (Table 2), but most included exposure to temperature anomalies (SSTA) and cyclones, and the distribution of available light (PAR skewness) (Figures 4 and 5). Competitive corals declined in cover with increasing PAR skewness (more extreme outliers) and SSTA, but there were some sites with high cover and SSTA (Figure 5). Within the assemblage of Competitive corals, *Acropora* was the dominant and most typical genus, and a similar pattern of change

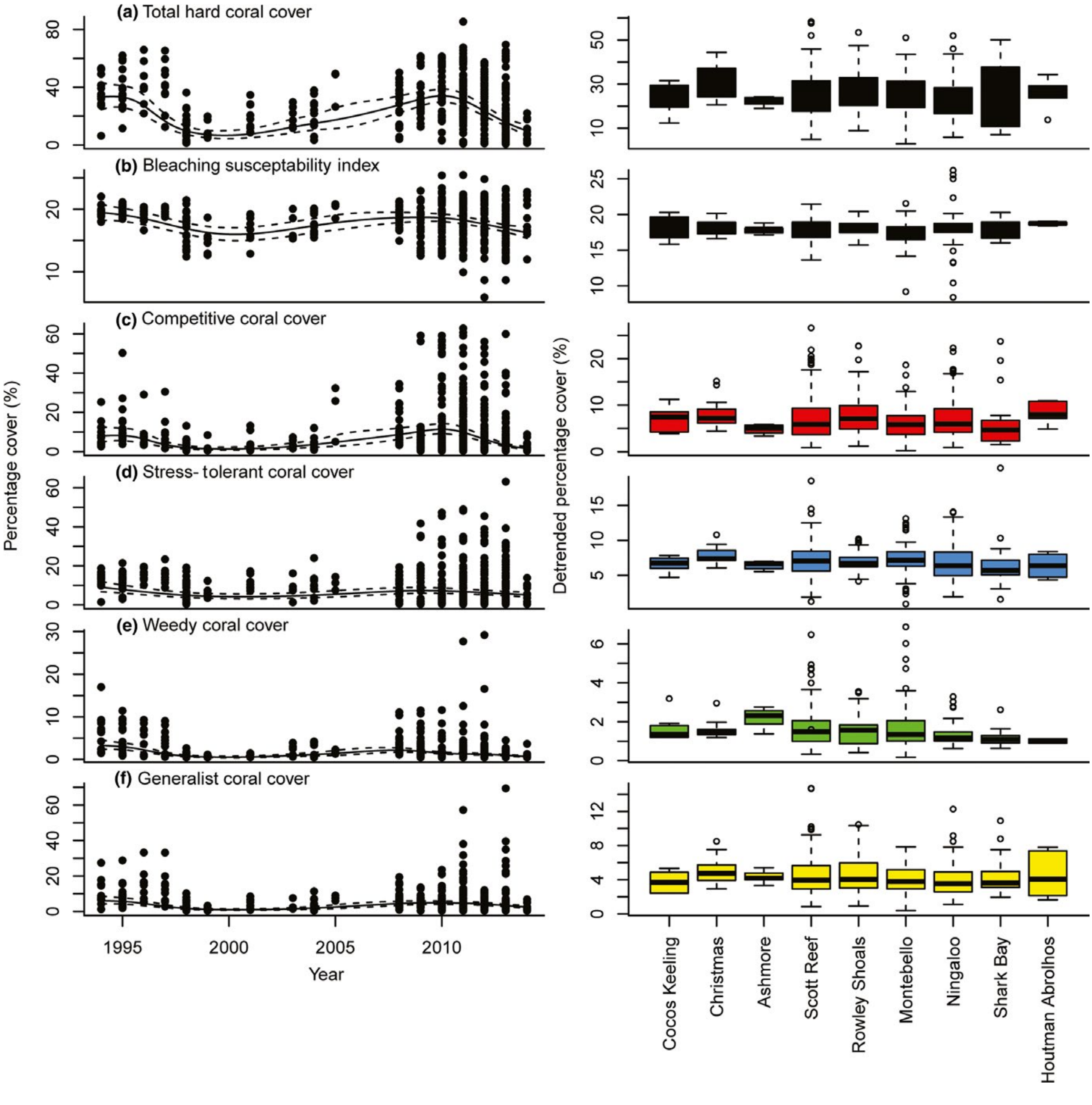


FIGURE 3 Temporal and spatial trends in community patterns of total hard coral cover (a), bleaching susceptibility index (b) and the four coral life-history groups (c–f) following Darling et al. (2012, 2013) across the south-east Indian Ocean Reefs (SEIO). Left hand panels show temporal trends fitted via GAMM smoothers (see Methods) and right hand panels show boxplots of residuals for each region, once this temporal trend is accounted for (these are effectively de-trended regional patterns). The box highlights the interquartile range with the mean for each indicated by a solid line. The whiskers show the maximum range and the open circles are outliers. [Colour figure can be viewed at wileyonlinelibrary.com]

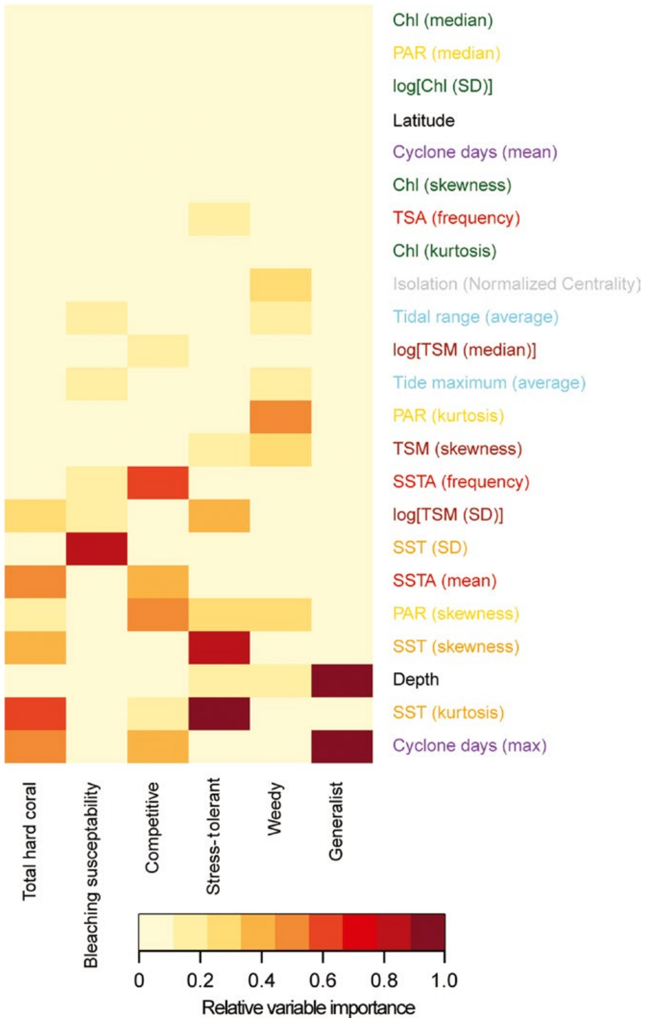


FIGURE 4 Variable importance (summed AICc weights) of environmental spatial predictor metrics in driving summed coral cover, coral groups with contrasting life-history traits (LHT) following Darling et al. (2012, 2013) and the estimate of bleaching susceptibility for the south-east Indian Ocean (SEIO) Reefs. Environmental metrics are defined in Table 1. [Colour figure can be viewed at wileyonlinelibrary.com]

was explained by their exposure to temperature anomalies (SSTA) and cyclones (Table S3, Figures S1–S3).

For the Stress-Tolerant corals, three competing models explained their spatial variation in cover, but all models included measures of their temperature distribution (Figures 4 and 5; Table 2). The cover of Stress-Tolerant corals decreased as both SST skewness and kurtosis became more positive, but there was little change when kurtosis was above −1.0. Within the assemblage of Stress-Tolerant corals, massive *Porites* was the most abundant genus, and its variation was best explained by water depth and exposure to cyclones (Figures S1–S3). The cover of massive *Porites* increased to a depth of approximately 8 m and was low in both the absence of cyclones and at intermediate levels of exposure. In response to cyclone exposure, the variation in cover of massive *Porites*, the dominant Stress-Tolerant genus, was inverse to that displayed by *Acropra*, the dominant Competitive genus (Figures S1–S8; Table S3).

Of all the life-history groups, the Weedy corals showed the only latitudinal variation in cover once the temporal trends were removed. Five competing models in which measures of water quality were consistently represented best explained this variation, especially the distribution of available light (PAR) (Table 2; Figures 4 and 5). Weedy coral cover was lowest at high-latitude reefs, when PAR distribution was flat or had negative kurtosis (< −1.2), or when the distribution of suspended solids (TSM) was positively skewed (Table 1). The most widespread and typical of the Weedy corals was *Seriatopora*, whose variation in cover was also best explained by the distribution of available light (PAR kurtosis, skewness) (Figures S1–S3; Table S3).

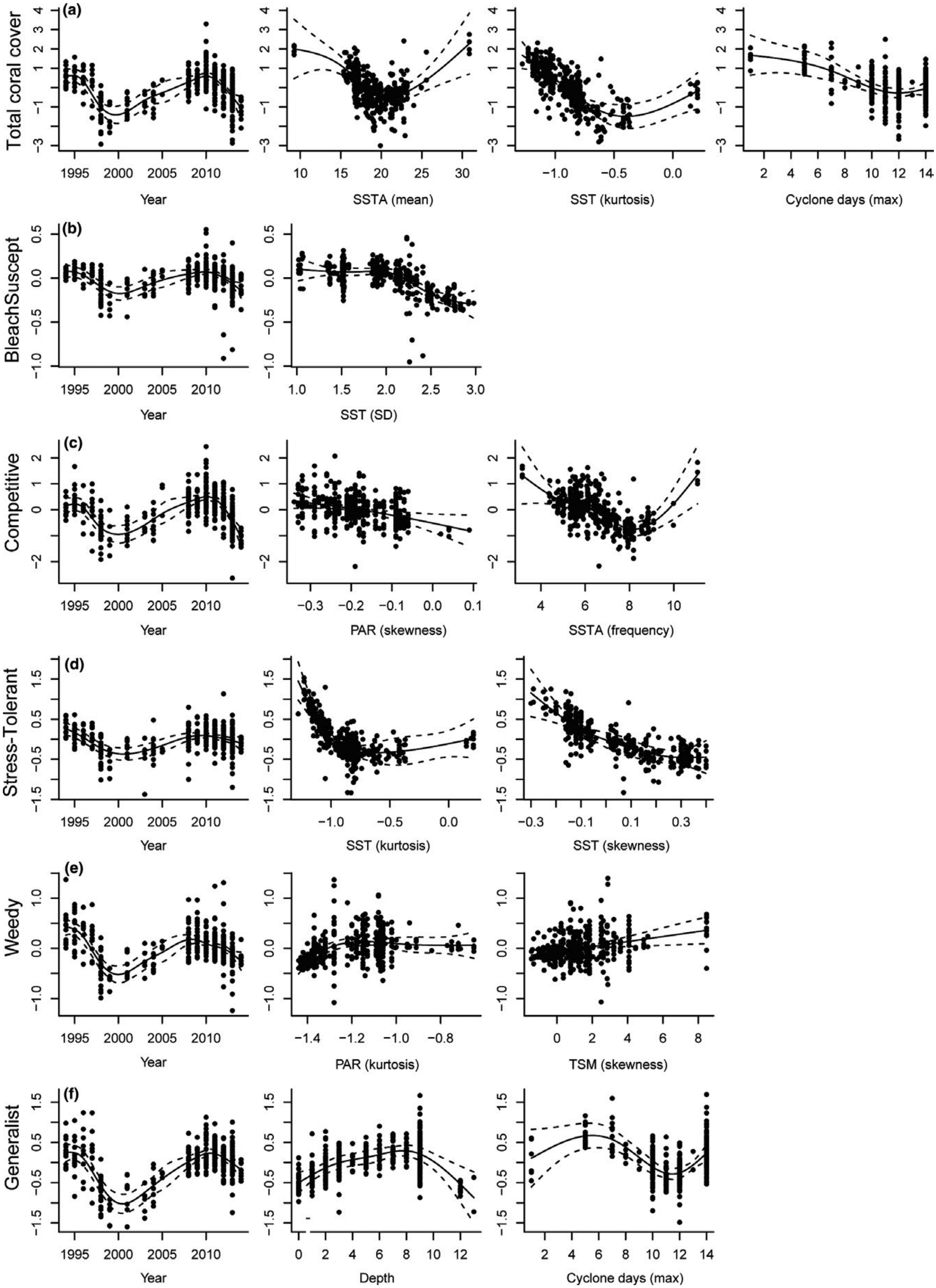
The maximum number of cyclone days and depth best explained the variation in cover of Generalist corals (Tables 2 and S3; Figures 4 and 5). Cover of Generalist corals was highest at intermediate depths (4–10 m), but varied unpredictably with exposure to cyclones, other than being highest when maximum cyclones days were low to moderate (4–8 days) (Figures 5). For the many (12) diverse genera (Table S2) within the Generalist life-history group, there was a corresponding range in the number of competing models and physical metrics explaining their variation once the temporal trends were removed (Table S3; Figures S1–S3). For example, the cover of *Turbinaria*, *Pocillopora* and *Isopora* predominantly varied in response with their background physical conditions (Figures S1–S3). Tides (mean maximum, range) were the dominant metric affecting the *Turbinaria* cover. *Pocillopora* cover varied with available light (PAR skewness) and water quality (chlorophyll kurtosis). *Isopora* cover varied with latitude and depths (Figure S1–S3; Table S3).

4 | DISCUSSION

Coral communities of the SEIO have varied considerably through time due to episodic disturbances. Pervasive changes in coral cover were likely a consequence of extreme temperature anomalies in 1998 and 2011 (Gilmour et al., 2013; Hughes et al., 2017; Moore et al., 2012), while localized impacts within some regions are attributable to cyclones (Speed et al., 2013). Declines were evident across all coral life-history groups following broad-scale temperature anomalies, although the magnitude of this impact varied. Declines were most noticeable among Bleaching-Susceptible taxa with competitive life histories.

Once these broad-scale disturbances were accounted for, our models indicated that coral community composition across the SEIO was associated with gradients in background environmental conditions. Importantly, the variance and frequency distribution of environmental

FIGURE 5 Generalized additive mixed model (GAMM) fits for the best models for coral cover (a), bleaching susceptibility (b) and the four coral life-history groups following Darling et al. (2012, 2013) (c–f; Table 2). Partial residuals for each smooth term are the residuals that would be obtained by dropping the predictor metric concerned from the model, while leaving all other estimates fixed (Wood, 2006). Note that all models were fit with year included to ensure temporal trends were accounted for. Where multiple models scored within 2 AICc of one another, the most “parsimonious” model (least summed estimated degrees of freedom) was plotted. All model plots are available in the supplementary material


(a)
Total coral cover
Year
SSTA (mean)
SST (kurtosis)
Cyclone days (max)
(b)
BleachSuscept
Year
SST (SD)
(c)
Competitive
Year
PAR (skewness)
SSTA (frequency)
(d)
Stress-Tolerant
Year
SST (kurtosis)
SST (skewness)
(e)
Weedy
Year
PAR (kurtosis)
TSM (skewness)
(f)
Generalist
Year
Depth
Cyclone days (max)

metrics were generally better predictors of coral cover and community composition than the mean values. Indeed, kurtosis, skewness and standard deviation of temperature (SST) or water quality (PAR, TSM) commonly explained observed variation in cover and some LHTs. This indicates that models based on mean values that do not consider a full set of environmental predictors and the distribution of these predictors may not accurately predict coral niches or their responses to disturbances (Cacciapaglia & van Woesik, 2015; McClanahan & Maina, 2003; McClanahan, Maina, & Ateweberhan, 2015; van Hooidonk, Maynard, & Planes, 2013).

Our results also indicate that exposure to cyclones may exert a strong effect on coral distribution in the SEIO, as was found for coral cover across the Great Barrier Reef over the period 1985–2012 (De'ath, Fabricius, Sweatman, & Puotinen, 2012). Tropical cyclones typically damage large branching or plating colonies, which can lead to a predominance of smaller encrusting or massive Generalist and Stress-Tolerant corals, as demonstrated for the Great Barrier Reef (Cheal, MacNeil, Emslie, & Sweatman, 2017; Madin, Baird, Dornelas, & Connolly, 2014; Madin, Hughes, & Connolly, 2012; Massel & Done, 1993). Intermittent cyclones maintain community diversity by preventing fast-growing, competitively dominant, species from monopolizing space (Connell, Hughes, & Wallace, 1997). Recovery from cyclones may, however, be rapid as asexual fragmentation can facilitate proliferation of Weedy corals. Such corals were common at mid-latitude reefs. Levels of cyclone exposure at mid to low-latitude SEIO reefs may rise in future, with an increase in total wind energy from cyclones predicted for Australia's NW shelf (Emanuel, 2006) as the most intense cyclones become more frequent worldwide (Kossin, Emanuel, & Camargo, 2016). If, as predicted, cyclones track further poleward when at their most intense (67 ± 55 km per decade for the South Indian basin—Kossin, Emanuel, & Vecchi, 2014), this may also increase exposure of high-latitude SEIO reefs to cyclones. How this increased exposure will effect SEIO reefs depends on interactions with other stressors. For example, repeated cyclone exposure combined with overfishing led to severe degradation in the Caribbean (Gardner, Cote, Gill, Grant, & Watkinson, 2005).

Despite the recent bleaching events along the SEIO, the Competitive corals and their dominant taxa (*Acropora*) were common at many sites, suggesting the historic disturbance regime has not been so severe as to cause their total replacement by Stress-Tolerant and Generalist corals. Additionally, consistent exposure to a range of water temperatures may confer some resistance to coral bleaching (Ateweberhan & McClanahan, 2010; McClanahan & Maina, 2003; McClanahan et al., 2007). This may change, however, if the frequency and intensity of warm-water anomalies increases (Hughes et al., 2017).

Across all study regions, the coral community was composed of taxa susceptible to bleaching, but the dominance of susceptible taxa declined when temperature variation exceeded 2.5 *SD*. A study of coral mortality after the 1998 El Niño found that mortality declined as sea surface temperature variation increased up to ~2.5 *SD* but increased for variations >2.5 *SD*, thus producing a U-shaped mortality curve (Ateweberhan & McClanahan, 2010). Consequently, while background temperature variation and distributions may infer some ability to acclimate to acute temperatures, there are limits. Extreme temperature anomalies are increasingly likely to reduce Bleaching-Susceptible taxa and change the structure of SEIO reefs possibly at both the low and the high ends of background SST *SD* (Ainsworth et al., 2016; Halpern et al., 2015). Indeed, in the last two decades, abnormally intense warm-water events have affected both high and low-latitude reefs in the SEIO, of which the 2011 heatwave was the most severe (Abdo, Bellchambers, & Evans, 2012; Depczynski et al., 2013; Feng, McPhaden, Xie, & Hafner, 2013; Hobbs & McDonald, 2010; Moore et al., 2012; Wernberg et al., 2012; Zhang, Feng, Hendon, Hobday, & Zinke, 2017; Zinke et al., 2015). Moreover, since 2011, anomalously warm SSTs have caused persistent summer heat stress and severe coral bleaching at many SEIO reefs (Caputi, Jackson, & Pearce, 2014; Feng et al., 2015; Lafratta, Fromont, Speare, & Schönberg, 2016). These stresses are likely to interact with aspects of background temperature variation to produce changes in coral communities that may not be linearly related to historical temperature variation.

Coral life histories provided a useful approach to understanding how gradients of environmental conditions and disturbances across the SEIO reefs likely shape reef communities. Reefs with a relatively higher frequency of environmental disturbances (e.g., cyclones, bleaching) were characterized by communities with more diverse life histories, while at less-frequently disturbed reefs, Competitive corals were more common. This is in accord with studies showing Stress-Tolerant, Generalist and fast-growing Weedy corals as more common in disturbed communities in Kenya (Darling et al., 2013), the Maldives (McClanahan & Muthiga, 2014), the Red Sea (Riegl & Piller, 2003), the Great Barrier Reef (Graham et al., 2014), and subtropical Australian reefs (Sommer et al., 2014). Here, we provide the first analysis of how different life-history coral groups respond to putative environmental drivers on reefs with limited exposure to local human impacts. The patterns of change in the different life-history groups and their key environmental correlates are also often similar for dominant and most-representative taxa, such as *Acropora* within the Competitive corals, and the massive *Porites* within the Stress-Tolerant corals. Nonetheless, taxa within the life-history groups can show substantial variation in their responses to environmental drivers, suggesting that approaches encompassing LHTs may benefit from further refinement. This was especially evident among corals in the Generalist life-history category, where environmental variables best predicting coral distribution varied among genera.

5 | CONCLUSION

In summary, we find that a diverse, and possibly more resilient, community prevails at reefs exposed to regular disturbances. However, extreme, extensive warming events have had a major impact on the current distribution, cover and community composition of corals in the SEIO, raising questions about the long-term stability of these patterns. Where and how frequently intense warming occurs will have a major impact on corals across the region. Reefs at high latitudes that have historically had little exposure to disturbances could be among the most susceptible to future climate change because climate impacts, including more intense cyclones (Kossin et al., 2014), penetrate further into subtropical reefs (Cacciapaglia & van Woesik, 2015; Hobday & Lough, 2011; van Hooidonk et al., 2013; van Woesik, Sakai, Ganase, & Loya, 2011). Conversely, functionally diverse corals at lower latitudes that are regularly exposed to some level of disturbance may be more resilient to ocean warming and environmental disturbances even as exposure to cyclones increases (Emanuel, 2006). Overall, regional compilations of community patterns are important to disentangle the effects of natural environmental variability. Our results provide a unique perspective on how natural environmental drivers likely shape coral community structure in the SEIO, providing a reference point to evaluate ongoing impacts of global change on coral reef ecosystems (Hughes et al., 2017).

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BIOSKETCH

Between 13 May and 15 May 2014, a group of international scientists (Wildlife Conservation Society; The University of North Carolina) and experts from federal and state government agencies in Western Australia (AIMS, CSIRO, DPaW, DoF, WA Museum) with colleagues from Australian Universities (The University of Western Australia, Curtin University, University of Queensland, James Cook University) met to discuss and develop a new framework that maps the susceptibility of Western Australian coral communities to chronic and acute thermal and cyclone stress events. The multidisciplinary team includes experts in coral reef ecology, management, oceanography and spatial modelling.

Author contributions: J.Z., S.K.W., J.P.G., M.S., M.P., E.D., T.R.M., Z.T.R. and R.F. conceived the ideas; all authors helped in collection of the data; R.F., M.P., E.D., J.M., M.B., J.P.G., Z.T.R. and S.K.W. analysed the data; and J.Z., R.F., J.P.G., M.P. and S.K.W led the writing.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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