1. Title

Gradients of disturbance, environmental conditions and coral community structure for southeastern Indian Ocean reefs

Running head:

Environmental drivers of coral life histories

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2. Abstract

Predicting patterns of coral reef communities relies on understanding the processes that drive spatio-temporal change in these ecosystems. Here we compile coral community data across ~19 degrees of latitude from 392 sites in Western Australia and the southeastern Indian Ocean (SEIO). Exposed to relatively few local human impacts, the SEIO provides an ideal system for testing the effects of environmental drivers and climatic disturbances on coral reefs. We describe and model the regional distribution of coral cover, and assemblages with contrasting life histories and susceptibilities to bleaching, to investigate how they are structured by environmental variability and climatic disturbances. Our results demonstrate that water depth, sea surface temperature (SST) kurtosis and the frequency of tropical cyclones were key drivers of coral community structure. Notably, reefs in equatorial latitudes were characterized by functionally diverse and potentially resilient communities with competitive, generalist, stress-tolerant and weedy life histories, while reefs in higher latitudes were characterized by competitive and generalist corals. These patterns likely reflect historic disturbance regimes of frequent exposure to cyclones and regular exposure to a wide range of higher temperatures in lower latitudes, and escape from cyclones at higher latitudes. Interestingly, measures of environmental dispersion and frequency distribution were typically better predictors of coral cover, emphasizing the value of considering these metrics when assessing the effects of climate change on coral reefs.

3. Introduction

Cycles of disturbance and recovery are a key feature of coral reef ecosystems (Connell, 1978; Rogers, 1993). As with other diverse ecosystems, multiple diversity-disturbance relationships exist for corals reefs depending on the interaction between the frequency and intensity of disturbances (Hall *et al.*, 2012). Most reefs face increasing threats from a combination of natural and anthropogenic stressors operating at multiple scales (Hughes *et al.*, 2003, 2010). Ideally, management actions aimed at maintaining the diversity, functional integrity and resilience of coral reef ecosystems are based on an understanding of how the environment interacts with disturbance regimes to shape coral community structure. This information allows conservation actions to be strategically targeted towards areas of higher inherent resilience and can inform conservation and management planning across regional scales (Maynard *et al.*, 2015a).

Environmental variability creates spatial heterogeneity in the levels of resilience on coral reefs (Richards & Hobbs, 2014; Graham *et al*., 2015). Environmental conditions that routinely structure coral communities include; temperature regimes (McClanahan *et al.*, 2007), light penetration (Anthony & Connolly, 2004; Muir et al., 2015), wave energy (Madin & Connolly, 2006; Lowe & Falter, 2014), tidal amplitude (Richards *et al.*, 2015), sediment delivery and re-suspension (Maina *et al.*, 2013; Fabricius *et al.*, 2014), nutrient dynamics (Kroon *et al.*, 2012), and ocean currents (Brinkmann *et al.*, 2002; Lowe *et al.*, 2012). Acute disturbances disrupt normal environmental conditions via extreme temperature anomalies (Selig *et al.*, 2010), and physical wave damage from tropical cyclones (Woodley *et al.*, 1981; Harmelin-Vivien, 1994; Fabricius *et al.*; 2008, Beeden *et al.*, 2015). Similarly, longer term ecological stressors, such as predator outbreaks of crown-of-thorn starfish (COTS; Death & Fabricius 2010; Hock *et al.*, 2014) and coral disease (Bruno *et al.*, 2007; Ruiz-Moreno *et al.*, 2012; Maynard *et al.*, 2015b), can also affect the distribution of corals. If both the supply of propagules and time before the next disturbance are sufficient, recovery from disturbance is possible (for example, Chagos Archipelago – Sheppard *et al.*, 2008; central GBR – Lukoschek *et al.*, 2013, Beeden *et al.*, 2015; Scott Reef – Gilmour *et al.*, 2013; Seychelles – Graham *et al.*, 2015). Recovery rates and the impacts of disturbances are however mediated by local environmental conditions. For example, cooler water at greater depth (Tyler *et al.*, 2014), periodic upwelling of cool water (Riegl & Piller 2003), or sea surface cooling induced by intermittent cyclone wind (Manzello *et al.*, 2007, Carrigan & Puotinen 2011, 2014) can mediate the effects of temperature anomalies on corals. Additionally, the effects of disturbances are typically patchy due to fine-scale variation in exposure, bathymetry and reef structure (Harmelin-Vivien 1994), and due to differences in taxa susceptibility to specific stressors (Hoey et al. 2016).

There is an urgent need to understand coral responses to a combination of local environmental conditions and disturbances in order to make more accurate predictions about the realistic impacts of climate change. Notably, coral reefs in the southeast Indian Ocean (SEIO) experience relatively low levels of anthropogenic stress, such as fishing, pollution or coastal development, at both local and regional scales (Burke *et al.*, 2011). This creates an ideal study system to independently assess the relative contribution of environmental conditions, natural disturbances and climate change for coral reefs.

Trait-based approaches can reveal how coral communities – and the ecosystem services they provide – respond to disturbances (Darling *et al.*, 2012). For example, large branching corals provide the structural complexity and underwater architecture that supports reef fish communities (Graham & Nash, 2013, Rogers *et al.*, 2014), providing food and shelter for specialist species (Cole *et al.*, 2008; Coker *et al.*, 2014). Certain corals are also more susceptible, or resilient, to disturbances than others based on life history variation (Darling et al. 2013; McClanahan *et al.*, 2014a). Consequently, understanding the spatial distribution of coral life history traits may facilitate the prediction of future changes in community structure (Darling *et al.*, 2013, Graham et al. 2014, Sommer et al. 2014, Done *et al.*, 2015).

Here, we applied coral life history traits (LHTs) to examine regional responses of coral cover, community structure and bleaching susceptibility to environmental conditions and disturbances regimes. We compiled *in situ* coral reef survey data across 19 degrees of latitude and

392 sites, between 1998 and 2014, to build the first comprehensive empirical dataset for coral communities in the SEIO. Specifically, we asked: 1) how are the key environmental factors that may influence coral communities distributed, 2) what are the distributions of coral cover, coral life histories, and bleaching susceptibility, and 3) how might these environmental factors shape the coral communities. Addressing these questions will provide insight into potential refugia or vulnerability to environmental change, which can inform conservation planning.

4. Methods

4.1 Study locations

The western coastline of Australia forms the south-eastern margin of the eastern Indian Ocean, covering nearly 22 degrees of latitude in the southern hemisphere (Fig. 1). Southward flowing currents (Halloway and Leeuwin) push warm tropical water along the length of the coast (Condi & Andrewartha, 2008; Feng *et al.*, 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 in the SEIO are also found on oceanic atolls and island territories adjacent to the north-west coast of Australia (Speed *et al.*, 2013).

Data on percent coral cover and genera abundance were obtained from nine coastal and oceanic SEIO locations from the west coast of Australia (Fig. 1). At each location, information was collated from 3-26 sites that were typically sheltered from prevailing wind and wave exposure in between 1 and 15 m in depth (Table S1). Surveys took place between 1998 and 2014, and incorporate information on impacts from warm water anomalies and cyclonic activity (Ceccarelli *et al.*, 2011; Moore *et al.*, 2012, Pearce & Feng, 2013). Sites include low latitude (North of 20°S) and high latitude reefs (~20-28°S). 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 indicating that the two methods provide similar estimates of coral cover and composition (Carlton & Done 1995; Leujak & Ormond, 2007).

4.2. Environmental data

We examined nine environmental parameters representing potential drivers from 27 variables (Table S2). Seven parameters were derived from ocean satellite observations and databases, including: 1) sea surface temperature [SST] variability, 2) thermal stress metrics, 3) total suspended matter [TSM], 4) photosynthetically active radiation [PAR], 5) magnitude of tides, 6) nutrients (chlorophyll-a) and 7) frequency of exposure to tropical cyclone generated winds. The final two parameters, 8) depth and 9) physical location (latitude, longitude, isolation), were derived from *in situ* surveys. The nine parameters were specifically chosen for their relevance to physiological processes, productivity, and stress responses in scleractinian reef corals (Maina *et al.*, 2008; Maina *et al.*, 2011). All environmental data, where appropriate, were aggregated to capture long-term (~30 years; mean, median) averages, distribution (skewness and kurtosis), extrema (maximum) and variability (standard deviation; Table S2). As application of satellite observation data in coastal environments, particularly in coral reef areas, is biased by high bottom reflectance that can be wrongly interpreted as ocean colour constituents (Morel & Belanger, 2006), we derived estimates of ocean colour constituents for our sites from a reanalysis database (Maina *et al.*, 2011) that adjusts values for reflectance bias (Gove *et al.*, 2015).

We obtained weekly data of SST for the period 1982-2012 for our SEIO sites at a resolution of ~4x4 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). These data were aggregated to capture SST distribution (skewness and kurtosis) and variability (standard deviation). 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 to 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 (Podesta & Glynn, 2001; Liu *et al.*, 2003; Selig *et al.*, 2006; Bruno *et al.*, 2007). TSA is defined as observed weekly averaged temperature >1 °C warmer than the warmest climatological week (52 climatological weeks averaged over 30 years). 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 S2) and SSTAs (SSTA frequency; Table S2) based on the number of anomalies in each calendar year and cumulatively over the 30-year study (as per Selig *et al.*, 2010).

Total suspended matter (hereafter TSM, g m^{-3}) and chlorophyll-a concentration monthly time series (2002-2010) data were pooled to median values, distribution (skewness and kurtosis) and variability (standard deviation). Photosynthetically active radiation (PAR) monthly time series data (2002-2010) were obtained from the Globcolour database (http://hermes.acri.fr/GlobColour) and pooled to median values, distribution (skewness and kurtosis) and variability (standard deviation) from the 8-year time series (Tab. S2).

We derived exposure to tropical cyclone winds across the study area from 1985 to 2013 from the International Best Track Archive for Climate Stewardship (IBTRACS – Knapp *et al.*, 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 & Puotinen (2011). We extracted maximum cyclone days and their standard deviation per year from the 28-year database (Tab. S2).

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 *et al.*, 2009; Underwood *et al.*, 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 *et al.*, 2010), and Department of Parks and Wildlife, West Australia habitat maps (Bancroft 2003). We calculated the distance in kilometers between all pairs of reef complexes and calculated the Isolation Index as the normalised graph-theoretic closeness centrality (0 – isolated, 1 – maximum connected; Beger *et al.*, 2010; Tab S2).

The spatial variation in environmental conditions was explored with Principal Components Analysis (PCA) of normalised environmental data, and the spatial variation in composition of corals with contrasting life history traits was explored using Multi-Dimensional Scaling (MDS) of Log + 1 percentage cover data, in the software PRIMER (Clarke and Warwick 2001). Within the groups of environmental conditions (e.g. light, sediment, thermal stress; Table S2), a single parameter was used when highly correlated (>0.7) with others. Of 27 initial parameters, 16 remained, and the chosen parameters used for PCA corresponded to those identified as being the most important drivers of coral community composition in the Generalised Additive Mixed Model (GAMM) analyses (Table 2).

4.3. Coral community data

To evaluate the distribution of coral assemblages across the SEIO, we standardised data to derive site-level estimates of total coral cover (%), coral life history trait (LHT) groups (%), and bleaching susceptibility. Total coral cover was the average total cover of live hard corals observed at each site. We classified corals into four coral LHT groups – competitive, stress-tolerant, weedy and generalist - according to Darling *et al.* (2012), but adapted categories with expertise on Western Australia corals (co-authors ZR, JG, GS) to assign life-history classifications for genera (Table S2). For genera that included species in different life histories, we distributed 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 (*BS)* of coral communities at each site was based on the relative abundance (RA) of genera *i* in the coral community weighted by an estimate of bleaching response (BR) of genera *i* and summed across all genera in the community (Equation 1; McClanahan *et al.*, 2007, 2014b).

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

Bleaching responses were estimated by the observed bleaching intensity and mortality of genera during thermal stress events in the Western Indian Ocean (McClanahan *et al.*, 2007, 2014a; McClanahan 2014c) which are comparable to bleaching events observed on the Great Barrier Reef (McClanahan *et al.*, 2004) and Melanesia (Jupiter and Weeks, unpublished data).

4.4. Data Analysis

To assess the relative importance of environmental parameters on coral cover, life histories and bleaching susceptibility, we adopted a full subsets model selection approach, where models were compared using Akaike Information Criterion (AIC), Bayesian Information Criterion (BIC) and AIC weight (ωi) values (Burnham & Anderson, 2002). Prior to analyses, all environmental variables were tested for collinearity. To reduce multicollinearity among parameters (predictors), we only included models in the full set of candidate models if the absolute correlation between the predictor variables of a model was less than 0.4. To ensure that the resulting models remained ecologically interpretable, we only fitted models that included up to three predictor variables. These restrictions reduced the total model set to 3,644.

All models were fit using generalised additive mixed models, 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 non-linear parametric multiple regression to allow for possible non-linear effects of predictors on the response variable, without needing to define the functional form.

Smooth terms were fit using a cubic spline basis (Wood, 2006) and limiting the argument k to a maximum value of 5 to avoid over-fitting and to ensure monotonic relationships. Site was included as a random effect nested within Region. Assumptions of the analysis were evaluated using residual plots, and found to adequately meet the assumption of normality following a square root transformation. Analyses at the genus level were also carried out for genera occurring at more than 25% of locations (see Appendix S1). Genera data were modelled using a Gaussian distribution following a logit transformation,

The simplest model within 2 AIC values of the model with the lowest AIC value was assumed to be the optimal model. To determine the relative importance of each parameter across the whole model set, we summed the ωi values for all models containing each variable. The higher the combined weights for an explanatory parameter, the more important it was for the analysis (Burnham & Anderson, 2002). For these parameter importance metrics to be meaningful, it is necessary to have the same number of models containing each parameter (Burnham & Anderson, 2002). As this was not the case due to the removal of collinear models, we calculated per model-averaged parameter weights (average ωi) by dividing each weight (ωi) by the total number of models containing each parameter or class of parameters respectively.

5. Results

5.1. Environmental gradients

The background environmental conditions of the reefs reflected their geographic setting, variation being high among locations, but relatively small within locations (Fig. 2; Table S2). Temperature distributions along the inshore coast of northwest Australia had high negative kurtosis, reflecting a flat distribution pattern and regular exposure to a range of temperatures (Tab. S2). However, offshore towards Christmas and Cocos Keeling Islands, and at higher latitudes, temperature distributions were more peaked, suggesting temperatures at the extremes of the distribution were experienced less frequently. SST (stdev) were highest at Ningaloo, Shark Bay and the Rowley Shoals, while for the remaining sites they were much lower (Tab. S2). The highest frequency of TSA was observed at Scott Reef, Ashmore and Shark Bay, followed by Abrolhos and Rowley Shoals, suggesting more frequent thermal stress at these sites (Tab. S2).

Sediment (TSM) concentrations were high at the Montebellos (0.74 gm^{-3}) and Ningaloo Reef (0.62 gm^{-3}) and comparatively low (<0.30 gm^{-3}) at the offshore reefs, particularly the Rowley Shoals, Christmas and Cocos islands (Fig 2; Table S2). Exposure to cyclonic activity was highest at the mid-latitude reefs, from Ningaloo reef in the south to Scott Reef in the north (Tab. S2; Fig 2). There was less cyclone activity at the lowest latitude reefs (Ashmore Reef, Christmas Island), and cyclones were rare at the high latitude reefs (Shark Bay, Abrolhos Islands). PAR kurtosis and skewness were negative at all locations, with the exception of Ashmore Reef. Chlorophyll concentrations were highest at the Montebello Islands, Ningaloo and Shark Bay, while skewness and kurtosis were positive everywhere with the exception of negative kurtosis at Abrolhos (Tab. S2). Tidal range and mean maximum were highest at Ashmore Reef, Scott Reef, the Rowleys Shoals and the Montebello Islands (Tab. S2).

5.2. Coral community patterns

Mean coral cover across all reefs and survey years was 28.9 ±17.6% (SD), with some regional variation that did show strong latitudinal trends (Fig. 2b, 3a). Total cover was high (30-40%) at the Abrolhos Islands, Rowley Shoals, and the Montebello Islands, and low (<11%) at Cocos Island and Shark Bay (Fig. 3a).

Bleaching susceptibility was high at the Abrolhos and Ningaloo and low at the Montebellos, with the remaining regions showing intermediate bleaching susceptibility scores (Fig. 2b, 3b; Fig. S1). In some regions, such as Cocos Island and Shark Bay, there was substantial variation among sites, with communities ranging from a moderate to high susceptibility to bleaching (Fig. 3b; Fig. S1)

The relative abundance of coral LHT groups varied among regions (Fig. 2b, 3c-f; Figs. S2-S5), with lower latitude reefs generally having a greater relative abundance of weedy and stress-tolerant corals, whereas the higher latitude reefs had more competitive corals (Fig. 3c, d; Figs. S2-S5).

5.3. Environmental drivers of coral community patterns

Variation in total hard coral cover was best explained by water depth, SST kurtosis, and maximum cyclone days (Figs. 4 and 5; Tab. 1; Tab. S2). Coral cover was highest at intermediate depths (~ 6m), when SST kurtosis was most negative (more consistent across temperature range), and with less frequent exposure to cyclones (Figs. 4 and 5).

Among the different life history groups, variation in cover was often explained by variation in depth and SST kurtosis, but the combination of these variables with other environmental parameters reflected their contrasting life histories and responses to disturbances. Competitive corals declined in cover with increasing cyclone days on all reefs, as SST kurtosis became more peaked (less negative), and with increasing SST anomalies (but for one Ningaloo site) (Fig. 5). Within the assemblage of competitive corals, the *Acropora* were by far the most dominant and typical genera, and a similar pattern of change was explained by the same environmental parameters (see Appendix S1; Figs. S6-S8; Tab. S3).

For the stress-tolerant corals, there were six competing models that explained 36-38% of the change in cover (Tab. 1), but most models included water depth and SST kurtosis (Figs. 4 and 5; Tab. 1). The cover of stress-tolerant corals increased gradually with depth before declining rapidly at the deepest sites (> 8m, Fig. 5), and was highest when SST kurtosis was most negative, but changed little with more positive kurtosis (Fig. 5). The range of competing models for the stress tolerant assemblages reflects both the influence of multiple physical parameters and the many coral genera within the life history group (Tab. S2). Among these, the massive *Porites* were the most abundant and typical of the group, and their change in cover was best explained by water depth alone, with a similar pattern to the stress tolerant corals (see Appendix S1; Figs. S6-S8; Tab S3).

There were ten models of similar explanatory power for the weedy corals, but PAR kurtosis occurred in most models and alone accounted for 13% of the variability in cover (Figs. 4 and 5; Tab. 1). Weedy corals were lower in cover at the mid-latitude reefs (Ningaloo, Montebello Islands, Shark Bay), where PAR kurtosis was most negative and TSM concentrations highest (Tab. S2), reflecting their exposure to a consistent range of light levels (Fig. 5). The most widespread and typical of the weedy corals (see Table S3) was the *Seriatopora*, whose variation in cover was also best explained by PAR kurtosis, in addition to other measures of light and water quality (PAR, TSM; see Appendix S1; Fig. S6-S8; Tab. S3).

Two competing models explained 22-23% of the variation in cover of generalist corals and included both cyclone days (max. or s.d.) and depth, in addition to either isolation or SST (s.d.) (Table 1). The cover of generalist corals increased on reefs at intermediate depths (4-10m) and declined with increased frequency and variability of cyclones (Figs. 4 and 5; Tab. 1). The most widespread and representative of the generalist corals were the *Pectinia* and *Turbinaria*, whose variation in cover was also explained by SST (s. d.), in addition to Chlorophyll (skewness) or tidal range (see Appendix S1; Figs. S6-S8; Tab. S3).

Variation in relative abundance of bleaching susceptible corals among the reefs was best explained by five competing models, and all contained depth and SST (s.d.) (Tab. 1). The only single variable model among the five explained 18% of the variation in bleaching susceptibility, which decreased on reefs with greater temperature variability (Fig. 5; Tab. 1).

6. Discussion

Across the south-east Indian Ocean (SEIO) reefs, variation in the cover of all corals, and of assemblages with different life histories and susceptibility to bleaching, were related to background environmental variability and episodic disturbances. Mid-latitude reefs (13-23°S) were consistently exposed to a range of temperatures (negative SST kurtosis) and frequent cyclones, and their communities had a high proportion of corals with contrasting life history traits, potentially increasing their resilience to global environmental change (Cardinale *et al.*, 2012). In contrast, reefs at lower (<13°S) and particularly higher (25-29°S) latitudes experienced temperature extremes less frequently and had lower exposure to cyclones, with communities dominated by competitive and generalist corals due to the historic absence of key disturbances.

Reefs in the SEIO have not experienced the array and intensity of local anthropogenic pressures impacting many reefs around the world (Halpern et al 2015). Poor water quality, for example, is typically implicated in reef degradation (McCook 1999, Death & Fabricius 2010), and can exacerbate impacts from coral bleaching and outbreaks of coral diseases and predators (Baker et al. 2008; Wooldridge and Done 2009; Graham et al. 2011; Maina et al. 2013; Pollock et al. 2014). We found parameters associated with poor water quality (e.g. high turbidity and nutrients) rarely explained variation in cover of coral life history groups (Tab. S2) or their dominant genera, reflecting previous evidence of SEIO reefs having relatively good water quality (Maina et al. 2013). However, our data did not include many of the nearshore reefs along the Pilbara and Kimberley regions of Western Australia, which have naturally high sediment regimes (Ridgway et al., 2016) that can be further elevated in the Pilbara by industrial dredging (Fisher et al., 2015).

Gradients of environmental stress

Gradients in background environmental conditions and acute disturbances spanning the SEIO reefs drove the variation in community composition. In general, at mid- to low-latitude reefs, coral communities contained a mix of stress-tolerant, weedy, generalist and competitive corals, despite also experiencing the highest temperatures and exposure to cyclones. Tropical cyclones play a major role in structuring coral communities by damaging large branching or plating colonies, which can lead to a predominance of smaller encrusting or massive generalist and stress-tolerant corals (Massel & Done 1993, Madin *et al.*, 2012, 2014, Cheal *et al.* 2017). Cyclones maintain community diversity by preventing fast-growing, competitively dominant, species from monopolising space (Connell *et al.*, 1997), and can facilitate asexual fragmentation and the proliferation of weedy corals, such as *Seriatopora,* which were common at the lower latitude reefs. Despite the frequency of disturbances and bleaching events at lower latitude reefs, the competitive corals and their dominant taxa (*Acropora*) were still common, suggesting the historic disturbance regime has not been so severe as to cause their replacement by stress-tolerant and generalist corals. Additionally, consistent exposure to higher water temperatures may have conferred some resistance to bleaching among the most susceptible groups at these higher latitude reefs (McClanahan & Maina, 2003; McClanahan *et al.*, 2007; Ateweberhan *et al.*, 2010). We propose that the combination of frequent cyclones and exposure to a greater range in temperatures?? has created the diverse taxonomic assemblages typical at the lower latitude reefs.

In contrast, communities at the high latitude reefs had a low abundance of stress-tolerant and weedy corals, and were dominated by generalist and competitive corals. In particular, communities at Ningaloo Reef and the Abrolhos Islands had a very high cover of competitive corals, which are typically susceptible to temperature anomalies and cyclones (Marshall and Baird 2000; Hoey et al. 2016). Indeed, at Ningaloo Reef and the Abrolhos Islands over 75% of the community were competitive corals, particularly plating and branching *Acropora* (Speed *et al.*, 2013). The cover of competitive corals at the high latitude reefs reflects their less frequent exposure to cyclones and temperature anomalies, coupled with their relatively high reproductive output and connectivity (Thomas *et al.*, 2014a). The region identifies as a potential refuge for competitive corals most sensitive to increased cyclone severity and temperature anomalies. However, bleaching of these reefs has occurred recently (Moore et al 2012; Depczynski et al 2013), challenging their value as future climate refuges. Moreover, the apparent lack of clade D symbionts at high latitude reefs at the Abrolhos Islands suggests these competitive corals are highly susceptible to future thermal stress (Thomas *et al.*, 2014b).

Environmental variability and coral communities

An important finding of our study was that the variance and frequency distribution of environmental parameters were better predictors of change in coral communities than the mean values (Tab. 2; Fig. S8). Kurtosis, skewness, and standard deviation of temperature (SST) or water quality (PAR, TSM) metrics commonly explained variation in cover of all corals, and of assemblages with different life history traits. Models that do not consider a full set of environmental parameters and the distribution of these parameters may therefore not accurately predict coral niches or responses to disturbances (McClanahan *et al.*, 2015 van Hooidonk et al. 2013; Cacciapaglia & van Woesik 2015).

Across all study regions, bleaching susceptibility of the community was high at SST standard deviations between 1 and 2 and declined beyond 2.5 SD, largely due to cover losses of the more thermal sensitive taxa when temperature variability exceeded 2.5 SD. This is consistent with findings in the western Indian Ocean after the 1998 ENSO where coral mortality declined when SST seasonal variability varied by up to ~2.5 SD and then increased again producing a U-shaped mortality response (Ateweberhan & McClanahan 2010). Consequently, while temperature variation and flat distributions may infer some ability to acclimate to acute temperatures, there are limits, and extreme temperature anomalies are increasingly likely to structure SEIO reefs (Halpern *et al.*, 2015; Ainsworth et al., 2016). In the last two decades there have been coral bleaching events at both high and low latitude reefs in the SEIO, of which the 2011 heatwave was the most severe (Fromont & Garson, 1999; Hobbs & McDonald, 2010; Abdo *et al.*, 2012; Moore *et al.*, 2012; Wernberg *et al.*, 2012; Depczynski *et al.*, 2013; Feng *et al.*, 2013; Gilmour *et al.*, 2013; Zinke *et al.*, 2015). Since 2011, anomalously warm SST have caused persistent summer heat stress and severe coral bleaching at many SEIO reefs (Caputi *et al.*, 2014; Feng *et al.*, 2015; Lafratta et al., 2016). Our findings highlight the need to better incorporate the variability of temperature and other environmental parameters into predictions of extreme coral bleaching events associated with global climate change.

Coral life histories provided a useful approach to understanding complex latitudinal gradients of environmental conditions and disturbances across southeastern Indian Ocean reefs. More disturbed reefs at lower latitudes were composed of more diverse life history assemblages. At higher latitudes with fewer disturbances, generalist and competitive corals were more common. These are similar to findings in Kenya (Darling et al. 2013), the Maldives (McClanahan & Muthiga 2014d), the Red Sea (Riegl *et al.*, 2003) the Great Barrier Reef (Graham et al. 2014) and at subtropical Australian reefs (Sommer *et al.*, 2014), where stress-tolerant, generalist and fast-growing weedy corals were more common in disturbed communities. Here, we provide the first application of life history groups to coral communities on reefs with limited exposure to local human impacts. The patterns of change in the different life history groups and their key environmental drivers were similar for dominant and most representative taxa, such as the *Acropora* within the competitive corals, and the massive *Porites* within the stress-tolerant corals. It appears that life histories can indeed provide a useful lens to community responses to natural disturbances, especially when regional coral experts refine a global framework.

In summary, our findings reveal a prominence of bleaching-sensitive and competitive taxa at higher latitudes, and a diverse and resilient community at lower latitudes. These patterns mirror findings from the southern region of the Western Indian Ocean (McClanahan *et al.* 2014a,b), suggesting similar responses to disturbances across the Indian Ocean. However, even these higher latitude refuges continue to experience anthropogenic ocean warming (Feng *et al.*, 2015; Zinke *et al.*, 2015) and may suffer severe losses because they lack the proportional mix of coral life history traits that confer resilience. Instead of climate refuges, high latitude reefs could be among the most susceptible to future climate change (Van Woesik *et al.*, 2011; van Hooidonk *et al.*, 2012, 2013, 2015; Cacciapaglia & van Woesik, 2015). Increasing ocean warming and environmental disturbances under climate change may reveal the increasing importance of the functionally diverse and resilient corals of the lower latitudes. 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 shape coral community structure in the SEIO, providing a reference point to evaluate ongoing impacts of global change on coral reef ecosystems.

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Figure captions

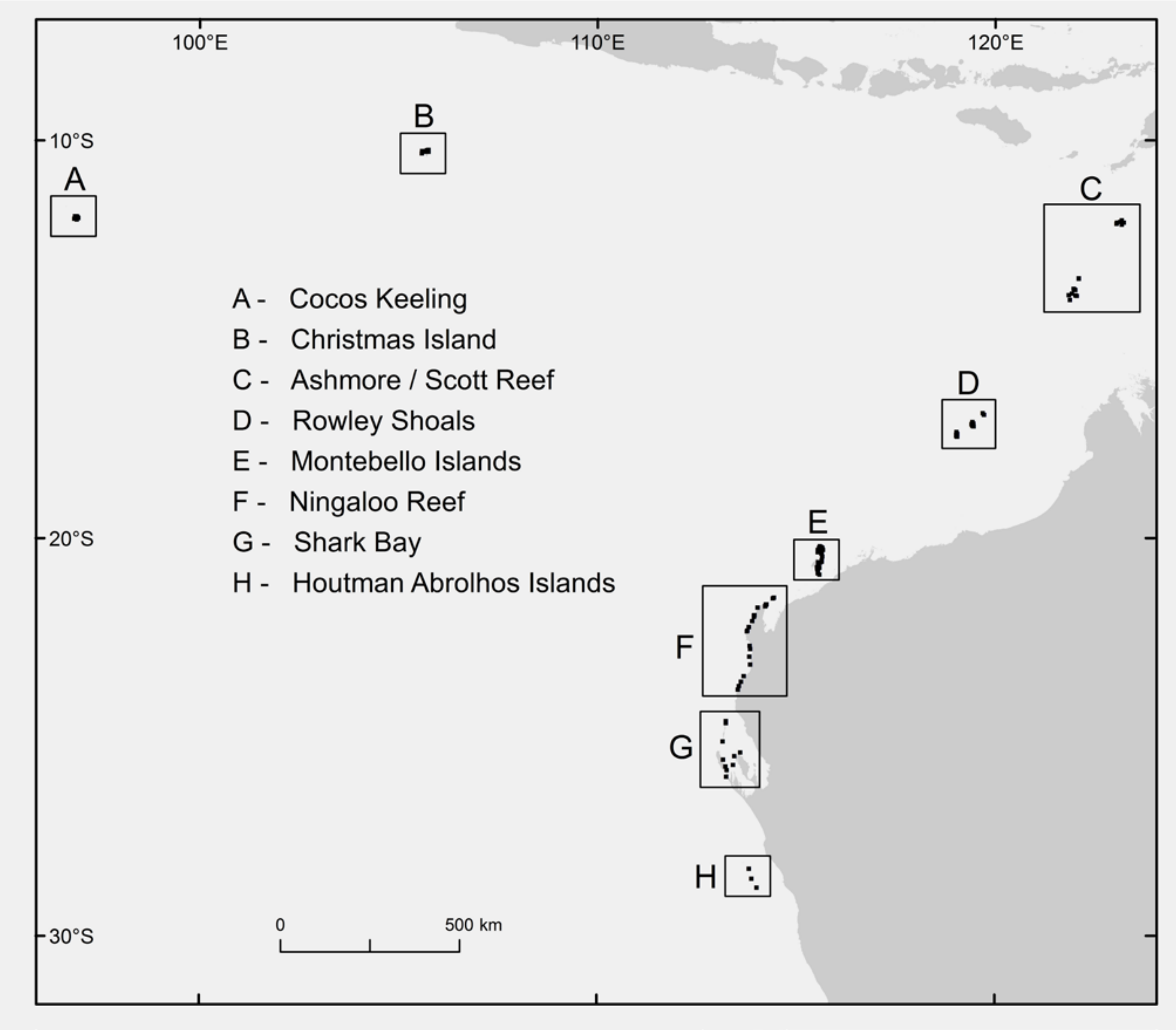

Figure 1 – Study locations marked A to H in panel A: A) Cocos Keeling, B) Christmas Island, C) Ashmore and Scott Reef, D) Rowley Shoals, E) Montebello Islands, F) Ningaloo Reef, G) Shark Bay and H) Houtman Abrolhos Islands.

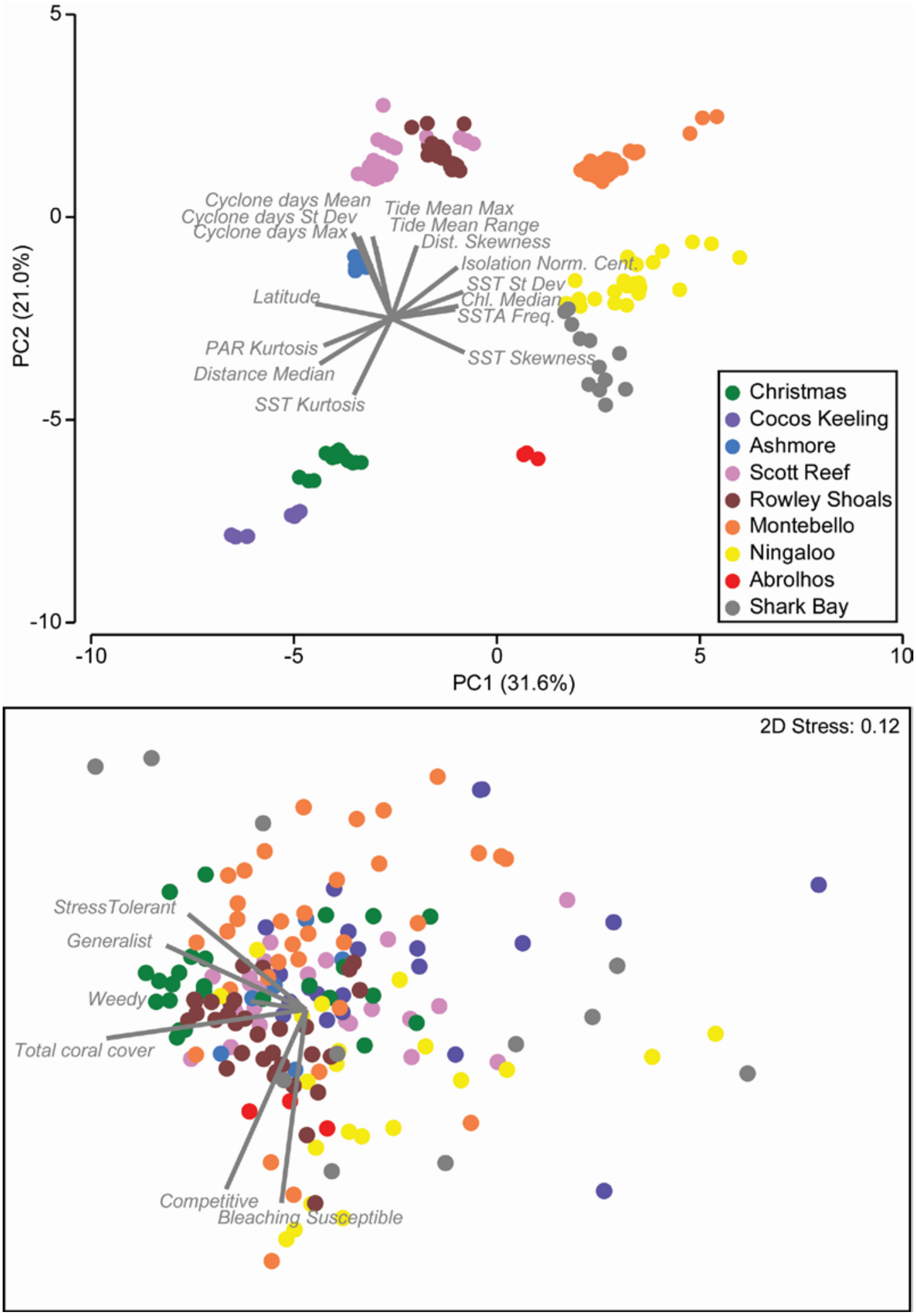

Figure 2 – Spatial variation in physical conditions and community composition across the southeast Indian Ocean Reefs. A) Principal Components Analysis of environmental variables at replicate reefs at each of the 9 coral reef regions. The vectors and environmental parameters (Table S1) responsible for the spatial separation among reefs are in grey; parameter abbreviations are PAR (Photosythetically Active Radiation), TSM (Total Suspended Materials), Chl (Chlorophyll), 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). B) Multi-Dimensional Scaling illustrating spatial variation in community composition of replicate reefs at each of the 9 coral reef regions, according to the total coral cover, the abundances of corals with contrasting life history traits (stress tolerant, generalist, weedy, competitive) and their susceptibility to bleaching. Vectors and coral groups responsible for the spatial separation among reefs are in grey.

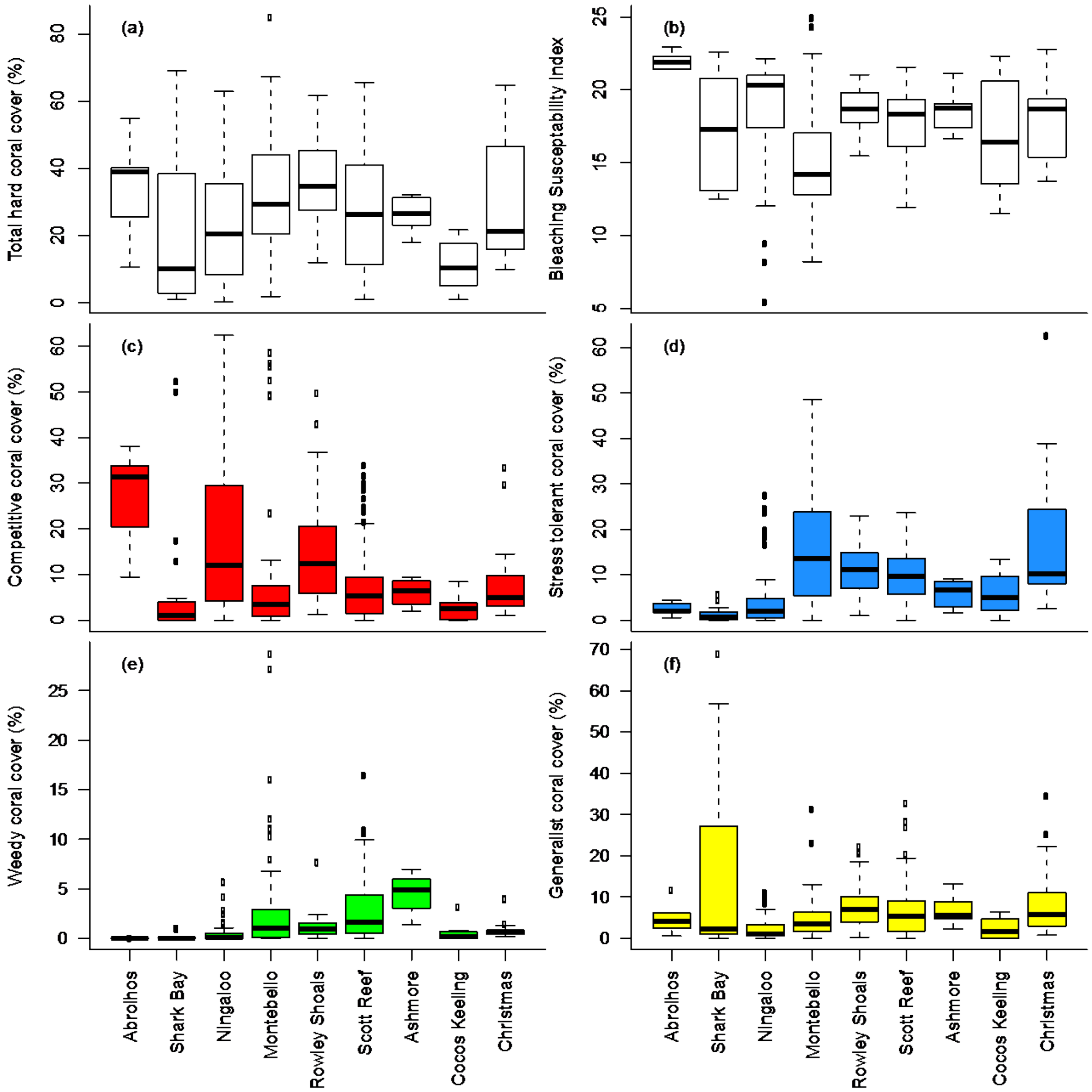

Figure 3 – Community patterns of total hard coral cover and coral life history groups across the SEIO. a) Boxplots of total hard coral cover, b) bleaching susceptibility, c) Competitive coral life history trait (LHT) group, d) Stress tolerant LHT, e) , Weedy LHT and f), Generalists LHT. The box highlights the area with 60% of the data with the mean for each indicated by a solid line. The whiskers show the maximum range and the open circles are outliers.

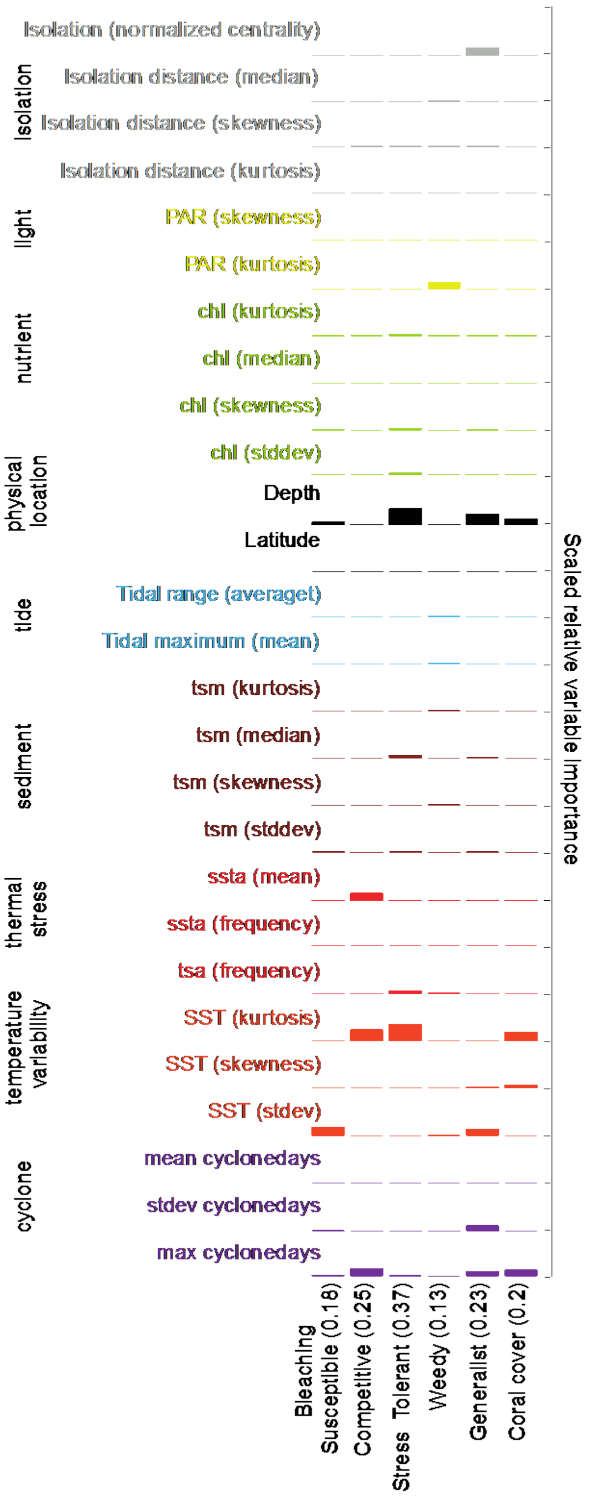

Figure 4 - Pooled environmental parameter importance driving summed coral cover, coral groups with contrasting life history traits (LHT) and the estimate of bleaching susceptibility for SEIO reefs. Environmental parameters are defined in Table S1. The R^2 values of the best model are shown in brackets. Variable importance values (see methods) have been multiplied by the best R^2, so column height indicates the relative importance of variables accounting for the overall strength of model fit.

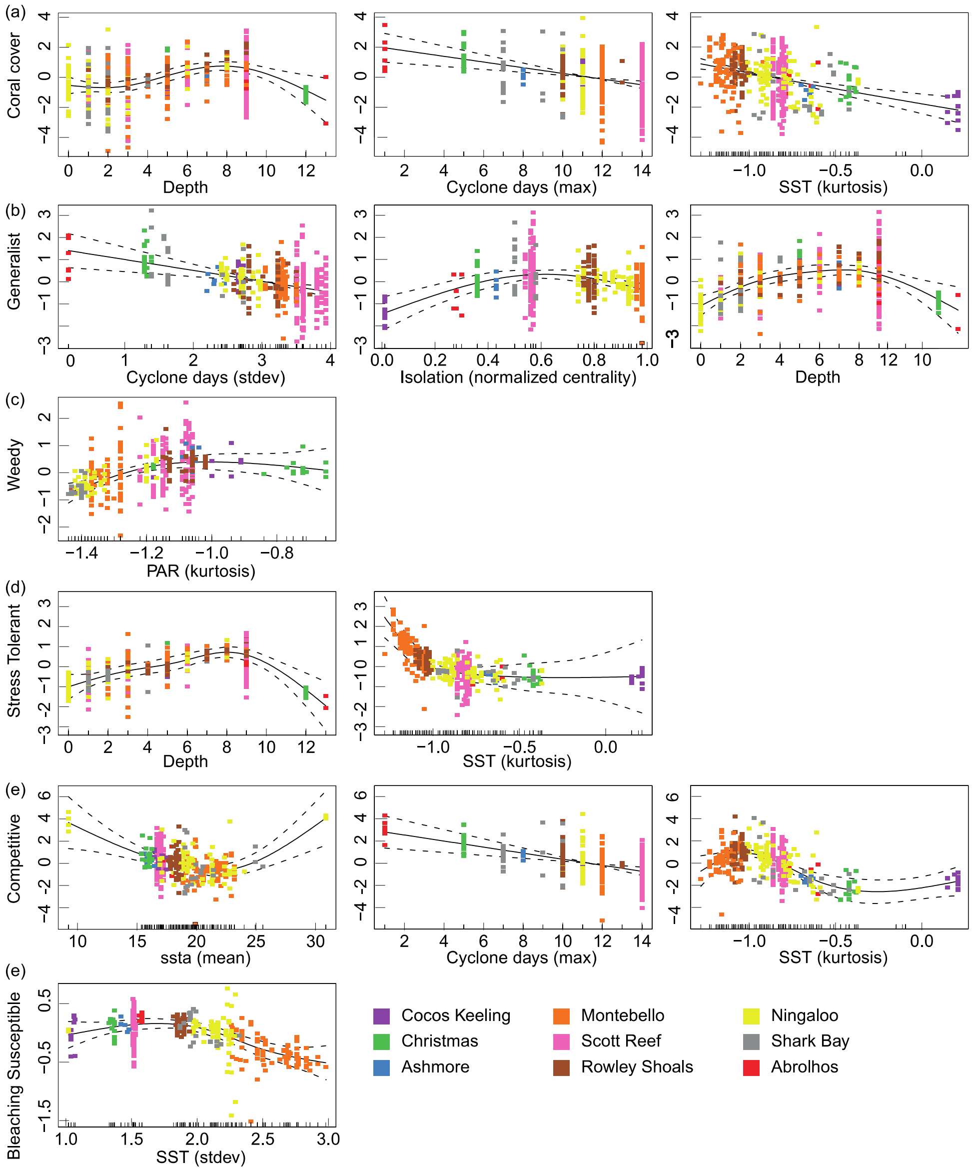

Figure 5 - Generalised Additive Mixed Model (GAMM) fits for the best model (see Table 2). Partial residuals for each smooth term are the residuals that would be obtained by dropping the term concerned from the model, while leaving all other estimates fixed (Wood, 2006). Variables are

shown in order of their relative importance (see Figs. S2). Data from the different regions included in the data set are shown in different colours.

Table captions

LHT	All best models (<2AIC of min AIC)	AIC	BIC	r.sq	wi
Coral cover	**Depth + SST (kurtosis) + Cyclone days (max)**	**1644.7**	**1685.2**	**0.20**	**0.734**
Generalist	**Isolation+ Depth + Cyclone days (s.d.)**	**1301.4**	**1342.0**	**0.23**	**0.257**
	Depth + SST (s.d.) + Cyclone days (max)	1301.6	1342.2	0.22	0.238
Weedy	PAR (kurtosis) + TSM (kurtosis)	989.3	1021.8	0.18	0.073
	PAR (kurtosis) + TSM (skewness)	989.5	1021.9	0.18	0.068
	PAR (kurtosis) + TSM (skewness) + tsafrequency	989.8	1030.3	0.18	0.059
	Dist (skewness) + PAR (kurtosis) + TSM (kurtosis)	990.1	1030.7	0.21	0.050
	Dist (skewness) + PAR (kurtosis) + TSM (skewness)	990.4	1031.0	0.21	0.043
	Dist (skewness) + PAR (kurtosis)	990.4	1022.9	0.20	0.042
	PAR (kurtosis) + TSM (kurtosis) + TSA frequency	990.5	1031.1	0.17	0.041
	Dist (median) + average tidal range + TSM (kurtosis)	991.0	1031.5	0.22	0.032
	Dist (median) + Tide (mean maximum) + TSM (kurtosis)	991.1	1031.7	0.22	0.031
	PAR (kurtosis)	**991.3**	**1015.7**	**0.13**	**0.027**
Stress Tolerant	Depth + TSM (median) + SST (kurtosis)	1111.0	1151.6	0.38	0.163
	Chl (skewness) + Depth + SST (kurtosis)	1111.2	1151.8	0.37	0.149
	Chl (s.d.) +Depth + SST (kurtosis)	1111.5	1152.1	0.38	0.129
	Chl (kurtosis) + Depth + SST (kurtosis)	1111.8	1152.4	0.37	0.110
	Depth + SST (kurtosis)	**1111.9**	**1144.4**	**0.37**	**0.104**
	Depth + TSA frequency + SST (kurtosis)	1112.4	1153.0	0.36	0.082
Competitive	**Mean SSTa +SST (kurtosis)+ Cyclone days (max)**	**1590.5**	**1631.1**	**0.25**	**0.896**
Bleaching Susceptibility	Depth + SST (s.d.)	238.3	270.8	0.24	0.160
	SST (s.d.)	**239.9**	**264.3**	**0.18**	**0.071**
	Depth + SST (s.d) + Cyclone days (max)	240.0	280.5	0.26	0.071
	Depth + TSM (skewness) + SST (s.d.)	240.3	280.9	0.22	0.059
	Depth + TSM (s.d.) + SST (s.d.)	240.3	280.9	0.24	0.059

Table 1. Generalised Additive Mixed Model (GAMM) fits for best models (the simplest model within 2 AIC of the lowest AIC) for environmental parameters influencing changes in cover of all corals, and those with contrasting life history traits (LHT) and bleaching susceptibility. Shown are

the variables included in the best models, Akaike Information Criterion (AICc), Bayesian Information Criterion (BIC), the best model R^2, AICc weight (ωi) values, and the number of other competing models within 2 AIC. Best models illustrated in Figure 6 are shown in bold.