Forecasting intensifying disturbance effects on coral reefs

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1 Running title

Modelling the structure of reef communities

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3 Abstract

Anticipating future changes of an ecosystem’s dynamics requires knowledge of how its key communities respond to current environmental regimes. The Great Barrier Reef (GBR) is under threat, with rapid changes of its reef-building hard coral community structure already evident across broad spatial scales. While many of the underlying relationships between hard corals and multiple disturbances have been documented, responses of other benthic communities to disturbances are not well understood. Here, we used statistical modelling to explore the effects of broad-scale climate-related disturbances on benthic communities to predict their structure under scenarios of increasing disturbance frequency. We parameterized a multivariate model using the composition of benthic communities estimated by 145,000 observations from the northern GBR between 2012 and 2017. During this time, surveyed reefs were variously impacted by two tropical cyclones and two heat stress events that resulted in extensive hard coral mortality. This unprecedented sequence of disturbances was used to estimate the effects of discrete versus interacting disturbances on the compositional structure of hard corals, soft corals, and algae. Discrete disturbances increased the prevalence of algae relative to hard corals while the interaction between cyclones and heat stress was the main driver of the increase in soft corals relative to algae and hard corals. Predictions from disturbance scenarios included relative increases in algae versus soft corals that varied by the frequency and types of disturbance interactions. However, high uncertainty of compositional changes in the presence of several disturbances shows that responses of algae and soft corals to the decline in hard corals needs further research. Better understanding the effects of multiple disturbances on benthic communities as a whole is essential for predicting the future status of coral reefs and managing them in the light of new environmental regimes. The approach we develop here opens new
opportunities for reaching this goal.

4 Introduction

Ecological forecasting is needed to anticipate ecosystem changes under future environmental regimes (Clark et al., 2001). Ecological forecasts are based on observations of community dynamics in response to environmental changes, and help define how future levels of disturbances may affect the distribution and abundance of living organisms at scales relevant to management (Clark, 2004). The iterative learning and probabilistic nature of statistical modelling provide a robust way to continually correct predictive models and methods in order to reduce uncertainty and refine current scientific knowledge in the light of new environmental regimes (Dietze et al., 2018).

Coral reefs, like most ecosystems, are being exposed to more and more intense disturbances (Hoegh-Guldberg, 2014; Hughes et al., 2017a; Bellwood et al., 2019b; Hoegh-Guldberg et al., 2019). These disturbances can affect the survival of key functional groups such as reef-building scleractinian hard corals and can lead to a phase shift from coral-dominated reefs to other organisms (Scheffer et al., 2001; Norström et al., 2009; Mumby and Steneck, 2008; Hughes et al., 2010; Graham et al., 2015). Mechanisms associated with shifts in reef community composition have been well documented and have helped inform management efforts in response to disturbance events (Mumby and Steneck, 2008; Hughes et al., 2010). These efforts have focused on developing adaptive management strategies to enhance ecological resilience (i.e. resistance and recovery) of key communities and maintain their ecological functions (Graham et al., 2013; Anthony et al., 2015; Lam et al., 2017; Bellwood et al., 2019b). However, the increasing frequency of disturbances is challenging reef management given the decreasing amount of time for recovery between events (Hughes et al., 2019a). As a consequence, the effects of future disturbance regimes on coral reefs are becoming more and more uncertain given that this new disturbance regime is producing different ecosystem responses (Ingeman et al., 2019). An example is a slowdown of hard coral recovery rates estimated in some locations along the Great Barrier Reef (GBR).
Vercelloni et al., 2017; Osborne et al., 2017; Ortiz et al., 2018; Hughes et al., 2019a; Mellin et al., 2019; MacNeil et al., 2019) including permanent changes to community structure (Johns et al., 2014).

The recent and singular sequence of disturbance events and associated changes in coral community composition have been relatively well documented (Hughes et al., 2017b, 2018a; Madin et al., 2018; Hughes et al., 2019a,b; Tebbett et al., 2019). During the period 2014-2017, the northern sections of the GBR were affected by a series of tropical cyclones (Ita in 2014 and Nathan in 2015) and heat stress periods that led to back-to-back mass coral bleaching in 2016 and 2017. The effects of these disturbances resulted in the lowest regional hard-coral cover on record; a trend also reported for other regions of the GBR (https://www.aims.gov.au/reef-monitoring/gbr-condition-summary-2018).

A shift in the cover of benthic groups other than hard corals has been reported after back-to-back mass coral bleaching (Tebbett et al., 2019), but previous broad-scale studies of the GBR during this time period focused on the effects of the heat stress events and quantification of the resulting extensive coral mortality (Hughes et al., 2017b). The most intense heat stress event affected this region in 2016 and resulted in a shift in coral community composition (Hughes et al., 2018b). It also triggered declines in coral recruitment (Hughes et al., 2019a) and reduced the damage of the 2017 heat stress event, despite a higher intensity, because most of the heat-susceptible corals died in 2016 (Hughes et al., 2019b). This unprecedented sequence of disturbances offers a unique opportunity to learn about changes in coral community composition following disturbances between which reefs have insufficient time to fully recover. It also provides the opportunity to gain valuable insights about future reef community composition under new disturbance regimes.

Here, we used data extracted from 145,000 observations of benthic community composition collected by the XL Catlin Seaview surveys on the northern sections of the GBR between 2012 and 2017 (González-Rivero et al., 2019, 2020). A total of 23 coral reefs were surveyed in 2012 and some of them were resurveyed in order to monitor fine-scale changes in community composition resulting from repeated exposure to cyclones and heat stress events. The relative abundance of hard coral, soft coral
and algae as well as predicted reef exposure to disturbances at kilometre scales were used to develop a multivariate compositional model designed to estimate the effect of discrete and interactive disturbances at a regional scale. Disturbance scenarios were consequently generated and used with the model outputs to predict reef compositional structure as the frequency of cyclones and heat stress events increased including their interactions within a fixed time window. The integration of high-resolution ecological and environmental datasets within a multivariate statistical framework allowed us to better understand the effects of multiple disturbances on benthic communities as a whole. This approach provides new insights into how intensifying disturbance effects might impact the future status of coral reefs and allows us to predict their composition.

5 Methods

5.1 Environmental factors

The spatial distribution of likely cyclone impacts was estimated using the 4MW model (Puotinen et al., 2016), which predicts the duration of damaging waves from cyclones using the duration and speed of modelled cyclonic winds, and estimates of fetch at 4 km resolution. The model defines damaging waves as the average of the highest one-third of wave heights over a sustained period of high winds, and which are four metres in amplitude or greater. Here, significant damage to benthic communities was assumed to be possible for each cyclone from 2012 to 2016 (Ita – 2014; Nathan – 2015) when the threshold was reached or exceeded for at least 10 hours of exposure to damaging waves.

Degree Heating Weeks (DHW) was used to estimate heat stress impacts leading to mass coral bleaching (hereafter referred to as bleaching). DHW is derived from the Coral Bleaching HotSpot product that provides an instantaneous estimate of heat stress at a spatial resolution of 5 km over a 12-week window (Liu et al., 2018). Mass coral bleaching and associated coral mortality have been observed for DHWs ≥ 4°C weeks (Eakin et al., 2010; Hughes et al., 2017b; Skirving et al., 2019). In this study, we used DHW of at least 4 °C weeks as an indicator of potential significant impacts.
on corals from heat stress. This was done for the northern sections of the GBR using DHW generated twice weekly by NOAA Coral Reef Watch (Heron et al., 2016) from 1 January 2012 to 31 December 2017 and then selecting the maximum values of DHW for a given year.

In accordance with the 4MW and DHW tools, we assumed significant impacts from cyclones or bleaching when values of damaging wave exposure of ≥10 hours and ≥4 °C heating weeks were exceeded, respectively. Impacts were transformed into a binary variable with 1 and 0 representing the presence and absence of significant disturbance impact, respectively. The cumulative impacts of specific disturbances were used as predictors in the statistical model by summing their presence across observation units. Cumulative disturbances were defined in a particular location as consecutive disturbances that occurred at different times. The cooling effect of cyclonic wave action and its potential to reduce bleaching occurrence and severity (Carrigan and Puotinen, 2011) were not considered here.

5.2 Composition of coral reef communities

In 2012, 23 reefs were surveyed in the northern GBR. We resurveyed many of these individual reefs (n=15) in October to November 2014, 2016 (n=21) and 2017 (n=14, González-Rivero et al. (2019)). Each year, we chose to resample reefs that had been disturbed in previous years using the spatial estimates of disturbance extent described above. This approach allowed us to capture coral reef community responses across a combination of different disturbance types and exposures between 2012 and 2017.

Relative abundances of coral reef communities were estimated from downward facing reef images at 10 m depth on the outer reef slopes. Underwater surveys were conducted using self-propelled diver operated vehicles fitted with cameras that acquired 1 x 1 m² high definition reef images every three seconds along 2 km geo-located transects (González-Rivero et al., 2014, 2016). A convolutional neural network was developed to automatically classify benthic communities based on 50 random points for each geo-referenced image (González-Rivero et al., 2020). The machine learning algorithm was trained and outputs validated using 2660 images that were manu-
ally annotated by experts in coral-reef species identification using the CoralNet online platform (Beijbom et al., 2015; Williams et al., 2019). Abundances of 19 benthic categories were automatically estimated by the best-performing neural network (González-Rivero et al., 2016) on a total of ∼ 145,000 images taken between 2012 and 2017 (González-Rivero et al., 2019).

Benthic categories were aggregated into hard corals, soft corals, and algae by summing different sub-categories to produce relative abundance of the three categories for each image (Table S1). Hard coral included scleractinian families (Acroporidae, Faviidae, Mussidae, Pocilloporidae and Poritidae); algae included all fleshy and encrusting macroalgae, cyanobacteria, crustose coralline species and turf algae, and soft corals of the common Alcyoniidae family, and other forms like sea fans, plumes and whips. The benthic categories that did not belong to the three groups were removed and relative abundances rescaled for each image. Sub-transects were defined within each 2 km transect as areas of 100 m² in size in each surveyed year. These sub-transects represent the typical size at which benthic communities form largely stable aggregates on the GBR (González-Rivero et al., 2016), and allowed us to assume quasi homogeneity between sampling units in order to compare their structures. Sub-transects were generated using hierarchical clustering based on Euclidean distance between geo-located images within transects. We retained sub-transects composed of a minimum of three images per surveyed year. A total of 6957 sub-transects (2,310 in 2012; 1,204 in 2014; 2,067 in 2016, and 1,376 in 2017) were generated based on an average of 18.46 ± 6.98 (SD) images per sub-transect. Standard Deviations (SD) are used throughout the paper to indicate variations around the mean of measured variables. The relative proportions of hard corals, soft corals and algae were then averaged per sub-transect, with only those sub-transects that were resurveyed at least three times retained. This process of data aggregation also improved the computational speed of the analyses.

5.3 Compositional data transformation

The abundances of hard coral, algae and soft coral that were extracted from the classified images, expressed as counts, were relative to each other and formed a composition.
Parts of a composition denoted as $j$ (with $j = 1,\ldots, J$), sum to either 1 or a constant if the research interests are to consider abundance data as proportion/coverage or counts, respectively (Bacon-Shone, 2011). Here, abundances of benthic categories were treated as relative counts that summed to 50 as per the sampling design (González-Rivero et al., 2016). A composition is also defined in terms of equivalence classes represented by a vector of proportional positive components (Egozcue and Pawlowsky-Glahn, 2011). Preserving the observed ratios of the composition improves the estimation of the covariance structure in which multivariate model-based approaches focus on (Gross and Edmunds, 2015; Allen et al., 2017; Chong and Spencer, 2018). The isometric log-ratio ($ilr$) transformation is a technique often used to model relative counts using the log-ratios of the compositional parts $j$ within a coordinate system of $J - 1$ dimensions (Egozcue et al., 2003). This transformation is defined by an orthonormal basis matrix that represents the sequence of splits between parts to compose the $ilr$ log-ratios. The construction of the matrix can be based on meaningful ecological or phylogenetic characteristics of reef communities (Chong and Spencer, 2018) or a sequential binary partition (SBP). The SBP aims to build the $ilr$ log-ratios such that the sum of the variances for each split is equal to the total variance across the entire data set. This approach satisfies several assumptions associated with the analysis of compositional data as described in Pawlowsky-Glahn et al. (2011).

Here, we adopted SBP to compute the composition of the $ilr$ log-ratios between the three groups using relative abundances at the sub-transect level. Our approach consisted to perform a hierarchical clustering of components using the Ward’s distance between two groups of parts as variance estimator (Pawlowsky-Glahn et al., 2011). The “balance” package (Quinn, 2018) in the R statistical software (R Core Team 2018) was used to compute the basis matrix, which was subsequently scaled and centred before being used in the statistical model.

The $ilr$ log-ratios were determined using the values and signs of the basis matrix given $J = 3$ groups (hard coral, algae and soft coral) and the following equation from Egozcue et al. (2003):
where \( j \) is the dimension of the coordinate system \( (j = 1 \text{ and } 2) \), \( \ln \) is the natural logarithm, \( r \) is the sum of \(+1\) in the basis matrix, \( s \) is the sum of \(-1\) in the matrix, \((y_{Algae} + 1, y_{Hard\text{Coral}} + 1, y_{Soft\text{Coral}} + 1)^{\frac{1}{2}}\) is the geometric mean of the benthic groups associated with \(+1\) and \((y_{Algae} - 1, y_{Hard\text{Coral}} - 1, y_{Soft\text{Coral}} - 1)^{\frac{1}{2}}\) is the geometric mean of the benthic groups associated with \(-1\).

The 6957 sub-transects and associated relative proportions of the three benthic groups were used to estimate the basis matrix \( V \) and determine the isometric log-ratios \( ilr_1 \) (1) and \( ilr_2 \) (2).

\[
V = \begin{pmatrix}
-1 & 1 \\
-1 & -1 \\
1 & 0
\end{pmatrix}
\]

\[
ilr_1 = \sqrt{\frac{r}{s}} \ln \left( \frac{\text{Soft corals}}{(Algae, Hard\text{Coral})^{\frac{1}{2}}} \right)
\]

\[
ilr_2 = \sqrt{\frac{r}{s}} \ln \left( \frac{\text{Algae}}{\text{Hard corals}} \right)
\]

The first log-ratio \( ilr_1 \) denotes changes in soft corals as a function of the geometric mean of hard corals and algae. The second log-ratio \( ilr_2 \) expresses changes in algae as a function of hard corals.

5.4 Modelling coral reef composition

We used the model developed by Chong and Spencer (2018) to quantify the effect sizes of cyclonic wave damage and bleaching, as well as their interactions, on hard corals, soft corals and algae from the northern sectors of the GBR. An advantage of this model is that it preserves the statistical properties of multivariate and compositional
response variables used to estimate relative proportions of reef communities, \( \rho_i \), at the
sub-transect level \( i \). For example, Chong and Spencer (2018) introduced an \( ilr \) back-
transformation (\( ilr^{-1} \)) directly into their multivariate model to retrieve the predicted
proportions in the same dimension as the observed data (\( J = 3 \)). The model formulation
implies that the effects of disturbance predictors (\( \beta_1, \beta_2 \) and \( \beta_3 \)) are estimated
on the \( ilr \) coordinate system of \( J - 1 \) dimensions, which make direct interpretations of
their effect sizes on the benthic groups challenging. However, biological characteristics of the log-ratios can be used to interpret these effects. For example, the effect size of a cyclone on a log-ratio between hard coral and algae is expected to be negative because the abundance of hard coral typically decreases after a cyclone. The multivariate random effects, \( \varepsilon_i \), were parameterized via a correlation matrix, \( \Sigma \), with a LKJ correlation distribution (Lewandowski et al., 2009) and weak independent Cauchy prior distributions were used for the other model parameters (Chong and Spencer, 2018).

\[
Y_i = (Y_{Algae,i}, Y_{HardCoral,i}, Y_{SoftCoral,i})^T \\
Y_i \sim Multinomial(n_i, \rho_i) \\
\rho_i^T = ilr^{-1}(x_i^T V_g^{-1}) \\
x_i = \beta_0 + \beta_1 \text{Cyclone}_i + \beta_2 \text{Bleaching}_i + \beta_3 \text{Cyclone} \times \text{Bleaching}_i + \varepsilon_i \\
\varepsilon_i \sim \mathcal{N}(0, \Sigma)
\]

where \( V_g^{-1} \) is the generalized inverse of the basis matrix and the regression coefficient vectors \( \beta_0, \beta_1, \beta_2 \) and \( \beta_3 \) are assumed to be independent and identically distributed with each element following a Cauchy distribution with 0 as location parameter and 2.5 for the scale parameter.
The transformation \( ilr^{-1} \) is defined as:

\[
\begin{align*}
  z_i &= (z_{Algae}, z_{HardCoral}, z_{SoftCoral})^T \\
  z_i^T &= \exp(x_i^T V^{-1}) \\
  \rho_i &= \frac{z_i}{\sum z_i} \\
  x_i &= (ilr_1, ilr_2)^T
\end{align*}
\]

where \( ilr_1 \) and \( ilr_2 \) are the values of the \( ilr \) log-ratios for the sub-transect \( i \), in \( J - 1 \) dimensions and \( \rho_i \) are the predictive proportions in the same dimension as the observations \( (J) \). Note that the exponential and the division operators should be interpreted as element-wise operations.

The best model formulation was selected based on the log likelihood for the Watanabe-Akaike information (WAIC) criterion (Vehtari et al., 2017), ecological significance and the trade-off in computing time. A hierarchical version of the model, which included longitudinal measurements and three hierarchical spatial scales (region, reef and sub-transect), was implemented without significant improvements to model performance.

The model was implemented using the R package rstan (Team et al., 2018) on a high performance computing system. Posterior distributions based on 900 iterations were derived from three Markov Chain Monte Carlo (MCMC) chains of length 10,000 each, with the first 5,000 discarded as the warmup period and a thinning rate of 50 iterations. Convergence diagnostics of MCMC chains were visually assessed using trace and density plots of parameters and autocorrelation plots between MCMC draws (Figure S1) and estimation of effective sample size and \( \hat{R} \) statistics to ensure robust estimations of model parameters (Table S1).

The model validation diagnostics included assessing the following: (1) distribution of the model residuals to ensure that they met the assumption of normality; (2) relationship between the model residuals and predictions to confirm absences of spatial and/or temporal residual correlations; and (3) posterior predictive fit to ensure that the posterior distributions included field observations. A last validation diagnostic involved computing the discrepancy distributions, estimated from the differences between pos-
terior predictive distributions and observations for each MCMC simulation. These distributions were used to compute posterior predictive p-values and root mean squared errors (RMSE). These diagnostics are equivalent to the typical cross-correlation approaches with the added benefit of being implemented directly from model outputs (Figure S2).

The new predictions of hard corals, soft corals and algae were calculated from the model outputs (i.e. posterior distributions of intercept and disturbance predictors) and used estimated values of \( \hat{x}_i \) which represent the predictive compositional structure in the \( J - 1 \) dimension. For each MCMC simulation, the values of \( \hat{x}_i \) were then multiplied by the basis matrix \( V_g \) and \( ilr \)-transform to retrieve predictions in the \( J \) dimensions of the data (Chong and Spencer, 2018). Predictive compositions were estimated based on simulated environmental regimes described by the disturbance scenarios and summarized across the MCMC simulations using two-dimensional kernel densities and, mean values and 2.5% and 97.5% quantiles. The R packages "compositions" (van den Boogaart and Tolosana-Delgado, 2008) was used to implement the \( ilr \)-transformation and "ggtern" (Hamilton and Ferry, 2018) to visualize the compositional data and kernel density estimations.

5.5 Disturbance scenarios

A total of 14 disturbance scenarios were generated in order to project compositional structure composed of hard corals, soft corals, and algae under different levels of disturbance (Table 1). These scenarios described increasing frequencies of cyclones and bleaching over a five-year window, which was chosen to match the temporal extent of data used to implement our multivariate model. These scenarios assumed significant disturbance impacts including damaging wave exposure >10 h (Puotinen et al., 2016) and DHWs ≥ 4°C weeks (Eakin et al., 2010), as well as their interactions at any time and order within the 5-year time frame. First, we generated a baseline scenario which represented the reef composition in the absence of significant disturbances over a five year window. Shifts in composition were then estimated with increasing number of disturbances and compared to the baseline scenario. Note that the baseline scenario as-
sumes that these reefs were not impacted by relatively recent disturbance(s) (less than 5 years prior 2012) which was confirmed using the online long-term records of the Australian Institute of Marine Sciences (https://www.aims.gov.au/docs/research/monitoring/reef) and the 4MV results for all cyclones across the GBR from 1985 (Puotinen et al., 2016).

6 Results

6.1 Environmental factors

The surveys enabled us to estimate changes in the relative cover of hard coral, soft coral and algae in response to two cyclones and two bleaching events across broad spatial scales based on observations at the sub-transect level. Cyclone Ita was a category 5 cyclone when it crossed the northern GBR and then tracked southeast across most of coastal Queensland in April 2014; while Nathan crossed the coast as a category 4 cyclone and subsequently travelled westward in March 2015. Impacts of cyclone Ita were detected on 10 surveyed coral reefs (Fig. 1a), where the average time of exposure to damaging waves was 13.17 hours ± 3.17 hours. More coral reefs (n=14) showed an impact on sub-transects from cyclone Nathan (Fig. 1a), in accordance with exposure to damaging waves estimated to be more than three times longer (43.74 hours ± 19.81 hours) than Ita. The two heat stress periods that led to back-to-back mass coral bleaching events occurred in March-November 2016 and January-April 2017. In 2016 and 2017, the average DWH index was 8.36 ± 2.02 and 10 ± 1.94, respectively (Fig. 1b). These disturbances co-occurred within a short time period and impacted the same coral reefs with different intensities and in different combinations. In 2016, two coral reefs were affected by 1 bleaching only, 15 reefs by 1 cyclone & 1 bleaching and six reefs by 2 cyclones & 1 bleaching. In 2017, we estimated that three reefs were impacted by the 2 bleaching, seven reefs by 1 cyclone & 2 bleaching and six reefs by 2 cyclones & 2 bleaching. We estimated intra-reef variability in the impacts of cyclone Ita on Ribbon Reef 10 with two transects over three being impacted and one transect over two in St. Crispin Reef. Note that all sub-transects were impacted by at least 1 bleaching (Fig. 1a,b).
6.2 Coral reef community compositional data

The relative proportions of hard coral dominated the compositions by more than 50% in all years and surveyed locations. In 2012, the relative proportion of soft corals and algae were equal to 20% (Fig. 2a). In 2014, soft corals declined and algae became more abundant (Fig. 2b). The 10 coral reefs impacted by cyclone Ita in 2014 were on average composed of 60.6% ± 13.48% hard corals, 32.7% ± 17.53% algae and 16.1% ± 12.63% soft corals. In 2016, the average percentages of hard corals were relatively similar for reefs impacted by 1 bleaching & 1 cyclone & 1 bleaching (Fig. 2c). These were estimated to be 60.9% ± 9.17% and 67.0% ± 14.50%, respectively. Percent hard corals was lower on reefs impacted by 2 cyclones & 1 bleaching which was estimated to be 44.0% ± 9.72% with compositions dominated by algae with an averaged cover of 46.0% ± 14.8%. In 2017, coral reef compositions were the most different as a function of disturbance combinations (Fig. 2d). Hard corals dominated the composition by 62.7% ± 11.2% and 66.3% ± 16.44% in the presence of the 2 bleaching & 1 cyclone and 1 cyclone & 2 bleaching, respectively. Algae was the most dominant group (46.30% ± 18.34%) in the presence of 2 cyclones & 2 bleaching.

6.3 Estimation of disturbance effects

In the first dimension (ilr1), the effects of intercept and discrete disturbances were significantly negative (95% credible intervals that did not include zero). Intervals associated with parameter estimates always indicate the 95% credible intervals. The estimates were to be -0.85 [-0.89, -0.82] for the intercept, -0.39 [-0.46, -0.32] for the effect of a cyclone and -0.06 [-0.12, -0.01] for the effect of a bleaching event (Fig. 3). The effect of the interaction between cyclone and bleaching was significantly positive and estimated to be 0.21 [0.16, 0.27]. These results show that the interaction between cyclone and bleaching increased the relative proportions of soft corals relative to the geometric mean of hard corals and algae whereas the discrete disturbances had the opposite effect.

In the second dimension (ilr2), the intercept was significantly negative and esti-
mated to be -1.17 [-1.2, -1.14] and the discrete effects of cyclone and bleaching were significantly positive (0.45 [0.39, 0.51] and 0.1 [0.06, 0.15], respectively). The effect of interactive disturbances was estimated to be negative with its 95% credible interval that included zero (Fig. 3).

Overall, the model tended to slightly under-predict the relative proportion of hard corals and slightly over-predict the relative proportion of soft corals and algae (Figure S2). The root mean square errors were similar across the benthic groups and estimated to be 0.06 for hard corals, 0.051 for algae and 0.045 for the soft corals (Figure S2). These validation diagnostics show that the model provides a satisfactory fit to the data.

6.4 Predictions under disturbance scenarios

The two-dimensional kernel densities show a gradual shift of the predicted composition toward the dominance of algae first and then soft corals with increasing disturbance frequency (Fig. 4). The scenario, “3 cyclones & 1 bleaching”, resulted in an estimate of 58.82% [54.75%-62.92%] for algae (Figure S3). The predictive compositions tended to shift toward increase in soft corals to 45.09% cover [25.68%, 67.68%] in the presence of 3 cyclones & 4 bleaching (Figure S3). Uncertainties associated with the predicted composition increased with the number of disturbances, with a larger spread of the kernel densities from the scenario “3 cyclones & 3 bleaching” (Fig. 4).

6.5 Relative change with disturbance scenarios

The relative proportions of benthic groups from the baseline scenario (i.e. no disturbance) show a gradual decline in hard corals of 1.58% [1.47%, 1.82%] associated with 1 bleaching and 8.53% [7.44%, 9.73%] with 1 cyclone (Fig. 5). The maximum predicted decline in hard corals was 71.06% [63.10%, 76.65%] for the scenario that included 4 cyclones & 3 bleaching in a five-year time window, at the regional scale. The present disturbance scenario (i.e. 2 cyclones & 2 bleaching) produced an estimated relative decline in hard corals of 33.19% [29.95%, 35.85%]. The decline in hard corals in the presence of 3 cyclones & 2 bleaching was associated with an increase in algae to a maximum of 48.56% [41.61%, 54.2%]. This was followed by a decline in algae to
27.24% [10.05%, 46.39%] for the scenario of 3 cyclones & 4 bleaching. Interestingly, the decline in algae in the presence of three-fold disturbances was associated with a steady increase in soft corals with estimated increases of 40.22% [21.15%, 62.47%] in the presence of 3 cyclones & 4 bleaching, and 22.81% [21.15%, 62.47%] in the presence of 4 cyclones & 3 bleaching.

7 Discussion

Conserving coral reefs in the Anthropocene will require better knowledge of how disturbance regimes will change and how coral reef communities are likely to respond to these changes (Bellwood et al., 2019a). Ecological forecasting uses insights from current environmental regimes to create dynamic ecological knowledge that can better and iteratively inform management (Clark et al., 2001; Clark, 2004; Dietze et al., 2018). By exploiting observation of responses in reef community structure at fine spatial and taxonomic scales to a singular sequence of broad spatial scale disturbances, we were able to estimate their effects in two different ways. It also allowed us to predict potential future reef compositional structure under simulated environmental regimes at a regional scale.

Partitioning the effects of the cyclones and bleaching events into discrete and interactive disturbance effects revealed distinct relationships to the compositional reef structure. Based on model estimates, the discrete effect of disturbances tended to result in a greater proportion of algae relative to hard corals and lower proportion of soft corals relative to the geometric mean of hard corals and algae. In contrast, the interactive effect of disturbances resulted in a relative increase of soft corals relative to the geometric mean of hard corals and algae. Soft corals are thought not to respond much to disturbances because of their low relative abundances typically recorded on the outer-reefs of the GBR (Fabricius, 1997; Woolsey et al., 2012; Halford et al., 2004; Emslie et al., 2011). Across our surveys, soft corals were the only benthic group that slightly decreased in relative abundance between 2012-2014 and then increased in subsequent years. This relative decrease was attributable to both encrusting and erect soft
corals from the Alcyoniidae family and non Alcyoniidae family, but only the Alcyoni-
idae recovered and reached greater coverage in 2017 compared to 2012. These soft
corals have a wide habitat range with high rates of asexual recruitment and mortality
(Fabricius, 1995) and can grow quickly but at small sizes only (Bastidas et al., 2004).
They also have some capability to fission and create two distinct colonies. However,
these traits were not found across all genera of the Alcyoniidae family (Fabricius,
1995). In the absence of major disturbances, coral reefs dominated by soft coral
community type were estimated to recover 30% slower than reefs dominated by tab-
lulate Acropora spp. (MacNeil et al., 2019). They also support butterflyfish diversity
(Emslie et al., 2010) and some other planktivores, corallivores, and microcarnivores
fishes (Epstein and Kingsford, 2019). Further studies, however, are required for under-
standing if soft corals are able to persist under high-disturbance environmental regimes.
A recent 91-year study on reef composition (Fine et al., 2019) estimated a relative in-
crease of Alcyoniidae soft corals by more than fivefold in response to multiple stressors
on an inshore reef of the northern GBR. Comparing these results with our predictions
has utility as a time-for-space substitution, demonstrating the plausibility of increased
prevalence of soft corals across broad spatial scales as potential responses to different
disturbance regimes.

The predicted compositions associated with disturbance scenarios estimated an ab-
solute regional loss in hard corals of 71.06% [63.10%, 76.65%] between the scenario
without disturbance to the most disturbed one (4 cyclones & 3 bleaching). In response
to increasing levels of disturbance, algae and soft corals were predicted to increase
in relative proportions at different rates along this trajectory. Algae were the first to
increase with the highest proportions in the composition predicted for scenarios 8 (3
cyclones & 1 bleaching) and 10 (3 cyclones & 2 bleaching), but remained more or less
similar to hard corals proportions at this level of disturbance. In our surveys, algae
increased the most, estimated to be 52.32% ± 2.02% in relative changes from 2012-
2017 and mostly driven by the crustose coralline algae. Responses of algae to hard
coral losses can happen quickly (Mumby and Steneck, 2008; Hughes et al., 2010) but
algal domination of the compositional reef structures remains relatively uncommon.
across broad spatial scales (Bruno et al., 2019). In our study, we estimated that algae could potentially dominate the composition but this dominance is unlikely to persist as soft corals were positively associated with interactive disturbances in which their effects doubled between scenario 10 (3 cyclones & 2 bleaching) and 14 (3 cyclones & 4 bleaching). However, the high uncertainty in the relative proportions associated with these scenarios demonstrated that more work is needed to understand how algae and soft coral will respond to the relative decline in hard corals under increasing disturbance. A first step must be an improved understanding of the mechanisms underlying interactions between hard corals, algae, and soft corals in response to broad-scale interacting disturbances. Our approach could be also used to investigate the temporal clustering of disturbances such as cyclones that affect coral responses (Mumby et al., 2011; Wolff et al., 2016) and coral recovery (Ortiz et al., 2018). Such an understanding will help to reduce this uncertainty and provide important information for the development and application of new management approaches to rapid environmental change.

The multivariate statistical model presented here has a twofold benefit of (1) preserving the compositional aspect of the benthic group measurements (i.e. the relative abundance) at a fine spatial scale while (2) estimating the effects of disturbances. This model-based approach has the flexibility to predict abundance in benthic groups across a combination of different disturbance exposures which traditional distance-based multivariate statistics cannot achieve (Brown and Hamilton, 2018). The use of compositional data is not often considered in the field of coral reef ecology possibly because of the complexity of the analysis and ecological interpretations of log-ratios (Gross and Edmunds, 2015; Chong and Spencer, 2018). One example here is the relative increases in soft corals and algae estimated by the model - these could also be driven by the loss of hard corals via their relationships in the constructions of the log-ratios ilr1 and ilr2. Despite these challenges, preserving the nature of the data is important in order to enhance the estimation of interactions between benthic groups (Bacon-Shone, 2011; Allen et al., 2017). Improving estimation of these inter-group interactions can help to increase the accuracy in the projections of future reef status in a way that has not yet been attempted. Studies of coral reef communities still ig-
nore interactions when using biodiversity metrics (Loiseau and Gaertner, 2015) or consider responses of individual communities to disturbances and consequently remain more often descriptive than informative from a community composition perspective (Warton et al., 2015; Brown and Hamilton, 2018). Yet modern quantitative ecology provides new approaches and statistical tools to reveal hidden patterns in community data and help to predict future responses at an ecosystem level (Warton et al., 2015; Hui, 2016; Ovaskainen et al., 2017; Chong and Spencer, 2018; Brown and Hamilton, 2018), such as we have done here.

The establishment of marine protected areas, fishery restrictions, water quality regulations and restoration actions are some of the management strategies that contribute to coral reef resilience (Lam et al., 2017). While these actions have resulted in positive outcomes at local spatial scales (Mellin et al., 2016), they are less effective in the presence of broad-scale disturbances (Bruno et al., 2019; Bellwood et al., 2019a). Understanding community responses to these disturbances and associated underlying relationships requires huge amounts of data in order to estimate all the potential responses to different disturbance exposures and their interactions. Emerging technologies for environmental conservation including artificial intelligence (González-Rivero et al., 2020), coupled with modern quantitative frameworks for collecting and analyzing ecological data, can help to learn from current environmental impacts, refine our knowledge and adapt our management practices as environmental regimes change into the future. Our results here demonstrate the necessity to consider both ecological and environmental interactions when studying coral reef responses to disturbances given that the decline in hard corals is expected to generate different reef dynamics. Parallel actions to stabilize the climate that could reduce the number of broad-scale disturbance events and protect corals that are least exposed to them (Beyer et al., 2018) should be part of management prioritization strategies if we want to improve our chances of successfully managing coral reef ecosystems.
8 Data and R codes availability

All data and associated images used in this study are freely accessible on https://espace.library.uq.edu.au/view/UQ:734799. The Stan model and R codes to compute and extract outputs of the Bayesian model are available in Supplementary Material.

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9.1 Data Sharing and Data Accessibility

All data and associated reef images used in this study are freely accessible on https://espace.library.uq.edu.au/view/UQ:734799. The reef composition model and R codes to implement the model in R are accessible in the Supporting Information.

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28

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### Table 1: Disturbance scenarios. Significant cyclonic impacts are defined by >10 h of exposure to damaging waves and significant heat stress events by ≥ 4°C heating weeks.

| Scenario number | Scenario name               | Scenario description                                      |
|-----------------|-----------------------------|----------------------------------------------------------|
| 1               | Baseline                    | No disturbances during a five-year period.                |
| 2               | 1 cyclone                   | Significant impact of one cyclone during a five-year period. |
| 3               | 1 bleaching                 | Significant impact of one heat stress event during a five-year period. |
| 4               | 1 cyclone & 1 bleaching     | Significant impacts of one cyclone and one heat stress during a five-year period. |
| 5               | 1 cyclone & 2 bleaching     | Significant impacts of one cyclone and two heat stress during a five-year period. |
| 6               | 2 cyclones & 1 bleaching    | Significant impacts of two cyclones and one heat stress during a five-year period. |
| 7               | 2 cyclones & 2 bleaching    | Significant impacts of two cyclones and two heat stress during a five-year period. |
| 8               | 3 cyclones & 1 bleaching    | Significant impacts of three cyclones and one heat stress during a five-year period. |
1 cyclone & 3 bleaching  
Significant impacts of one cyclone and three heat stress during a five-year period.

3 cyclones & 2 bleaching  
Significant impacts of three cyclones and two heat stress during a five-year period.

2 cyclones & 3 bleaching  
Significant impacts of two cyclones and three heat stress during a five-year period.

3 cyclones & 3 bleaching  
Significant impacts of three cyclones and three heat stress during a five-year period.

4 cyclones & 3 bleaching  
Significant impacts of four cyclones and three heat stress during a five-year period.

3 cyclones & 4 bleaching  
Significant impacts of three cyclones and four heat stress during a five-year period.

9.3 Figure legends

Figure 1: Distributions of environmental pressures for each surveyed reef based on 100² metres sub transects. (a) Significant cyclonic impacts based on a threshold of >10 h of exposure to damaging waves. (b) Significant heat stress impacts leading to mass coral bleaching based on a threshold of ≥ 4°C heating weeks. The ”No impact” category includes environmental pressure values below these thresholds for a given year.

Figure 2: Relative proportions in percentage of hard corals (HC), soft corals (SC) and algae by year with (a) 2012, (b) 2014, (c) 2016 and (d) 2017, and disturbance combinations. Each dot shows the benthic composition observed at one 100² metres

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sub transect. For each year, the associated distributions in coverage of hard corals, soft corals and algae are shown below the ternary plot.

Figure 3: Effect size of disturbances on the isometric log-ratio coordinates over the five-year period. \( ilr_1 \) denotes changes in soft corals relative to the geometric mean of hard corals and algae and \( ilr_2 \) expresses changes in algae relative to hard corals. Error bars indicate the 95% credible intervals estimated from the posterior distributions of model parameters.

Figure 4: Posterior density regions of predicted benthic compositions associated with the 14 disturbance scenarios (Table 1). For each scenario, the coloured lines represent the two-dimensional kernel density estimate with Gaussian kernels to delineate the confidence levels of the posterior distributions.

Figure 5: Predicted composition of hard corals, soft corals and algae for each of the 14 scenarios. The composition of benthic groups presented in order of changes from the baseline scenario, which is labelled as "No disturbance". The baseline scenario estimated 86.76% [86.17%, 87.36% 95% credible intervals] of hard corals, 8.37% [7.94%, 8.9%] of algae and 4.87% [4.53%, 5.21%]. The bars show absolute changes per benthic group and include error-bars representing the 95% credible intervals.
Figure 1
Figure 4
We present a novel approach to estimate the effects of disturbances on benthic communities and predict their structure under scenarios of increasing disturbance frequency. The model was parameterized using 145,000 observations of benthic communities from the Great Barrier Reef. During 2012-2017, surveyed coral reefs were variously impacted by two tropical cyclones and two heat stress allowing us to estimate changes in reef composition when there is not enough time for hard corals to recover. Better understanding the effects of multiple disturbances on benthic communities as a whole is essential for predicting the future status of coral reefs.

Figure 6: Graphical Abstract
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