



REPORT

# Suppressed recovery of functionally important branching *Acropora* drives coral community composition changes following mass bleaching in Indonesia

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**Abstract** Mass coral bleaching events may have disproportionate effects on branching corals, leading to coral community restructuring, reduced biodiversity, and decreased structural complexity. This affects overall reef health and resilience. Functionally important, fast-growing branching *Acropora* corals were a historically dominant and vital component of Indonesian reefs throughout the twentieth century, yet the genus is also one of the most vulnerable to external stressors. This study used long-term annual reef monitoring data from Indonesia's Wakatobi Marine National Park (WMNP) to investigate the effects of a mass bleaching event in 2010 on *Acropora* and other branching corals, evaluate their post-disturbance recovery trajectories, and analyse shifts in coral community composition. Post-bleaching scleractinian coral cover decreased across study sites, with losses in branching corals especially evident. Long-term branching *Acropora* cover decreased significantly and failed

to demonstrate the significant post-disturbance recovery of other branching corals (especially *Porites*). In areas characterised by relatively high branching *Acropora* cover (> 15% mean cover) prior to bleaching, long-term coral community composition changes have trended predominately towards branching and massive *Porites* and branching *Montipora*. The novelty and key contribution of this study is that results suggest suppressed recovery of *Acropora* in the WMNP. Contributing factors may include the Allee effect (inhibition of reproduction at low population densities), other forms of inhibited larval recruitment, direct and indirect spatial competition, and changes in the physical reef habitat. These findings have critical implications for this functionally important taxon, future reef conservation efforts, and overall reef health and resilience in the park.

**Keywords** Branching coral · *Acropora* · Indonesia · Bleaching · Coral community composition · Suppressed recovery

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## Introduction

Differences in the susceptibility to disturbance of different scleractinian coral genera and their contrasting recovery trajectories can cause successional shifts in community composition following disturbance (van Woesik et al. 2011). This may lead to associated losses in biodiversity and important ecosystem functions (Hughes et al. 2018) and can be affected by a number of interconnected environmental and biological factors (Marshall and Baird 2000; Baker et al. 2008).

Bleaching-susceptible genera include *Acropora*, *Pocillopora*, *Montipora*, and *Acanthastrea*, while *Porites* in particular is usually more bleaching-resilient (McClanahan et al. 2007). Scleractinian genera display dramatic differences in

post-bleaching responses. Morais et al. (2021) highlight a pronounced boom and bust pattern for *Acropora* (*Acropora* refers specifically to branching *Acropora* throughout, unless otherwise stated) on the northern Great Barrier Reef (GBR) spanning three bleaching events. *Acropora* colonies completely disappeared post-bleaching but then exhibited massive recruitment and fast growth, translating to “a marked capacity for apparent recovery”. At the other end of the spectrum, massive *Porites* showed “a precarious degree of resilience”, with almost all colonies surviving and the majority increasing their surface area, but no new colonies being found over five post-bleaching years (Morais et al. 2021).

In the Seychelles, coral decline and recovery spanning two mass bleaching events (1998 and 2016) over 23 years have been driven mainly by changes in branching coral cover – particularly *Acroporidae* and *Pocilloporidae* – while recovery on carbonate and patch reefs was characterised by *Acropora* (all growth forms), *Echinopora*, massive *Lobophyllia* and *Goniopora*, and encrusting *Galaxea* (Wilson et al. 2019).

The frequency and severity of bleaching events also influences post-bleaching recovery: frequent moderate disturbances favour *Porites*, while infrequent but severe disturbances favour *Acropora*, which can regrow rapidly (Pratchett et al. 2020). Often the most susceptible corals (e.g. *Acropora*) dominate after bleaching events due to boom and bust patterns. Pratchett et al. (2020) highlight a number of studies that demonstrate this, alongside *Acropora*'s reliance on recovery as opposed to resilience / resistance to bleaching.

Links between *Acropora* losses and decreases in the high levels of biodiversity associated with reef structural complexity are well-established in both the Caribbean (Alvarez-Filip et al. 2009) and the Indo-Pacific (Wilson et al. 2008), while shifts in coral community composition driven by bleaching events also decrease coral species diversity (Darling et al. 2013). This is especially significant considering the hypothesis that *Acropora* losses reduced the resilience of Caribbean reefs, shifting them into a position of vulnerability, and that patterns of post-disturbance recovery in the Indo-Pacific have historically been driven by fast-growing *Acropora* (Osborne et al. 2011; Roff and Mumby 2012). Suppressed recovery of *Acropora* post-disturbance may therefore represent a warning sign for Indo-Pacific reefs.

*Acropora* and other acroporids like *Montipora* are amongst the most sensitive scleractinian coral taxa to environmental stressors, including bleaching (Marshall and Baird 2000; Loya et al. 2001; van Woesik et al. 2011; Wilson et al. 2012; Clark et al. 2017). Along with other corals displaying ‘competitive’ life trait strategies (Darling et al. 2012), *Acropora* are often among the first corals to disappear in unfavourable and disturbed environments (Loya et al. 2001; McClanahan et al. 2007). However, they frequently exhibit steady recovery due to fast growth rates and high

fecundity; studies have shown the complete recovery of *Acropora* populations following acute thermal stress, for example, after seven years in Palau (Golbuu et al. 2007) and in 15 year cycles in the Arabian Gulf (Riegl and Purkis 2009). At the same time, even post-bleaching recovery may not be enough to halt a shifting baseline for *Acropora* and other bleaching-susceptible corals. Rapid recovery following disturbance “may represent a short-term boom in a new Anthropocene configuration, where fast-growing corals persist but are unlikely to attain their former abundance due to successive disturbances and suppression of recovery dynamics” (Morais et al. 2021).

On reefs affected by changing disturbance regimes related to climate change, the recovery of these competitive corals may be suppressed due to a loss of brood stock (Hughes et al. 2019). This inhibition of reproduction at low population densities (the Allee effect) has been shown to affect broadcast spawning corals (Teo and Todd 2018), and the high mortality of sensitive corals following mass bleaching is increasingly causing radical shifts in coral community composition and functional traits (Hughes et al. 2018). Following bleaching, a number of factors may affect the recovery of different scleractinian genera. Physiologically stressed corals may be more susceptible to disease (Bruno et al. 2007; Lesser et al. 2007), while various mechanisms inhibit the recruitment, settlement, and survival of planula larvae. These mechanisms include the direct effects of increased sedimentation on planula settlement (Tomascik 1991; Babcock and Davies 1991), reductions in grazing pressure and habitat complexity (Roth et al. 2018), and unconsolidated rubble fields (Fox et al. 2003).

In Indonesia, in addition to global climate change, local anthropogenic stressors pose both acute and chronic threats to coral reefs. Acute stresses include blast and cyanide fishing (Fox et al. 2000, 2003; Fox and Caldwell 2006; Gouraguine et al. 2019; Williams et al. 2019); mine waste disposal (Haywood et al. 2016); and coastal development, including coral mining (Caras and Pasternak 2009), while chronic stresses include the overexploitation of marine resources (Ainsworth et al. 2008; Burke et al. 2011); the destruction of seagrass beds (Unsworth et al. 2018; Exton et al. 2019); and sedimentation (Burke et al. 2011). This is the case throughout Indonesia (Burke et al. 2011) and in the Wakatobi Marine National Park (WMNP) in particular (Clifton et al. 2010; von Heland and Clifton 2015).

Following a mass bleaching event in the WMNP during the 2010 marine heat wave, the extent of bleaching was documented through park-wide surveys recording the loss of overall live scleractinian coral cover (LCC) (Wilson et al. 2012). The severity of the marine heat wave is illustrated by Degree Heating Week (DHW) maps published by the US National Oceanic and Atmospheric Administration (NOAA) (Supplementary Fig. 1).

Prior to this study conducted in the WMNP, *Acroporidae* and *Poritidae* had historically been of primary importance across Western Indo-Pacific reef communities (Highsmith 1982), while 48% of Indonesia's reefs were dominated by *Acropora* in the late 20<sup>th</sup> Century (Wallace et al. 2001). The genus's diverse and complex morphologies have also historically played a critical role in the health of the country's reef systems (Boekschoten et al. 1989; Wallace et al. 2001).

Bleaching surveys conducted throughout the WMNP in 2010 reported minimal bleaching (1–3%) for *Acropora*, although a high percentage of these colonies (25–57%) were recorded as 'pale' (Wilson et al. 2012). While this report stated that reefs in the WMNP were not badly affected by the bleaching in 2010, there has been no specific examination of rates of ecosystem-level recovery and reassembly of the coral community following this high-impact disturbance event. This is pertinent because changes in coral community composition may lead to reduced biodiversity and resilience even with no decline in LCC, while habitat complexity may vary greatly between different reefs with comparable levels of LCC (Alvarez-Filip et al. 2011; McWilliam et al. 2020). Reassembly meanwhile, ensures that processes and traits contributing to ecosystem function of a particular coral community are restored (Johns et al. 2014).

The present study fills an important knowledge gap by looking at the long-term recovery of fast-growing, structurally complex 'competitive' *Acropora* corals and other sensitive branching corals in the WMNP following this mass bleaching event. The key contribution and novelty of the study comes from the apparent limited recovery of *Acropora* compared to other branching corals, despite bleaching surveys suggesting minimal bleaching and immediate mortality (Wilson et al. 2012). The majority of previous research on post-disturbance recovery compares very different growth

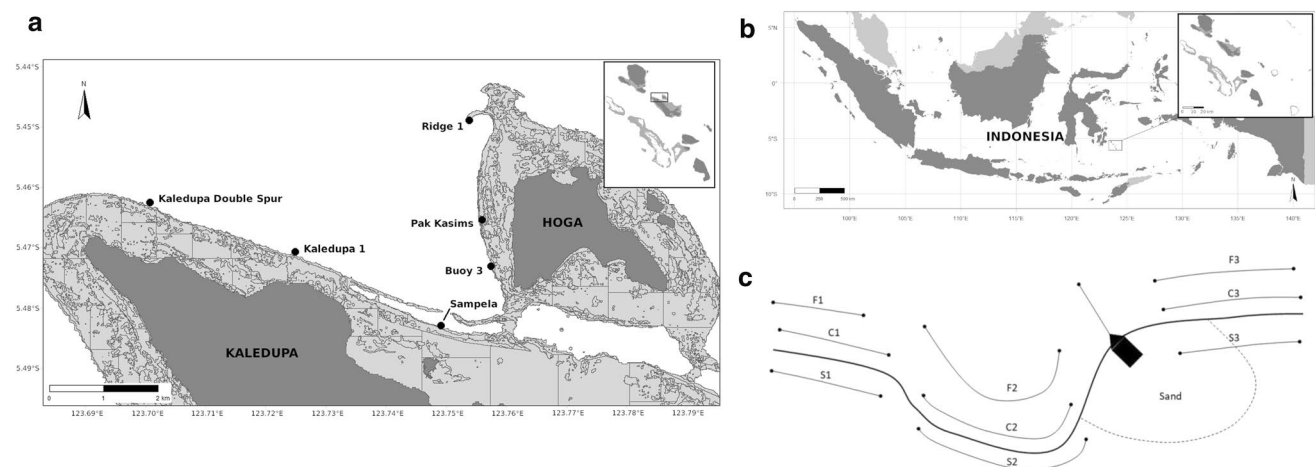
forms (e.g. Loya et al. 2001; McClanahan et al. 2007; Wilson et al. 2019; Pratchett et al. 2020; Morais et al. 2021). Here, however, we aim to provide more detail by comparing recovery within branching corals which, while exhibiting similar growth forms, provide distinct ecological services (see Munday 2004; Gardiner and Jones 2005; Pratchett et al. 2008). The study additionally examines short- and long-term shifts in coral community composition in reef areas previously characterised by high *Acropora* cover.

The study hypothesises that the cover of *Acropora* in the WMNP did not remain constant over the study period and furthermore that sites characterised by high *Acropora* cover prior to the bleaching event have undergone shifts in coral community composition. Possible reasons for the suppressed recovery of historically dominant *Acropora* relative to other branching corals are presented. Reasons for differential recovery trajectories following the 2010 mass bleaching event fall into four broad categories: recruitment limitation, direct and indirect competition from other organisms, environmental conditions, and changes in the physical reef environment.

## Materials and methods

### Study site

The Wakatobi Marine National Park (WMNP) is Indonesia's second largest MPA, covering 1.4 million hectares encompassing the Tukang Besi archipelago (Clifton et al. 2010) in the heart of the Coral Triangle region, to the south-east of Sulawesi (Fig. 1a). This is an extremely important area for global biodiversity, evolutionary biology, and biogeography (Tomascik et al. 1997). The Wakatobi comprises four main



**Fig. 1** The six survey sites in the central Wakatobi Marine National Park (a), south-east of Sulawesi between the Banda Sea to the north-east and the Flores Sea to the south-west (b). Permanent reef tran-

sects (c) were set up in a nested design, with replicates on the reef flat [F1-3], crest [C1-3], and slope [S1-3], as in this example from KDS (map not to scale)

islands: **W**Angi-Wangi, **K**Aledupa, **T**Omia and **B**Inongko, and 35 smaller islands, with a resident population of 95,892 according to the most recent available government information (BPS Statistics Indonesia 2021).

Regional studies have found that historically, species and genus richness of scleractinian corals in the park have been comparable to other high diversity sites in the region, with roughly 50,000 ha of various coral reef habitats boasting 396 species from 68 genera (Cesar et al. 2003). Diverse seagrass meadows and mangrove forests augment these rich coral communities (McMellor and Smith 2010).

### Data collection

Using standardised methodology in collaboration with the Indonesian Institute of Sciences (LIPI) and Makassar's Hasanuddin University, a team of researchers from several universities associated with Operation Wallacea (Opwall) have conducted a long-term reef monitoring programme at six sites along the north-eastern coast of Kaledupa and western coast of Hoga (Fig. 1b). Surveys recording benthic community composition were conducted annually from June to August, between 2006 and 2019. Fifty-one permanent 50-m transects were established in replicates of three on the reef flat (5 m landward from the reef crest), reef crest, and upper reef slope (defined by habitat type and 10-m approximate depth) using a nested design, with replicates placed a horizontal distance of at least 20 m apart. The study site at Ridge 1 has no reef flat. The start and end of transects were marked by steel pickets and transect locations at each site have been mapped (e.g. Figure 1c).

All surveys were conducted between 0700 and 1600 h depending on logistical considerations. A Line Point Intercept (LPI) technique was used, with observers recording the identity of the benthic material at 25-cm intervals along the transect, from a set of biotic and abiotic categories (Supplementary Table 1a). The number of times each category value appeared was converted to an overall percentage cover for each category in each transect. Before 2007, benthic identification was carried out by in-water observers, whereas after 2007 surveyors took downward-facing video recordings along each transect and observers recorded benthic material from video analysis. This slight change in observation method did not fundamentally alter data collection due to the low level of taxonomic detail recorded for benthic organisms; the main aim was to reduce time spent in-water by allowing post-dive identification and data entry.

As with most long-term datasets, logistical constraints including inclement weather prevented some transects from being surveyed in certain years. Of particular note was 2007, when data were collected for 20 of 51 transects, representing five of six survey sites, and neither reef flat transect nor coral growth form data were collected. In total, 674 transects

were sampled across the study period (247 crest, 236 slope, and 191 flat) from a potential 714, with 40 missing transects representing 5.6% of the total. Of a possible total 135,474 points on completed transects, 128 individual data points (0.095%) were missing.

### Statistical methods

Coral cover data from the study period were non-normal for both LCC and different taxa of branching corals. To test for significant changes in different types of coral cover between 2006 and 2019, the 2010 mass bleaching event was specified as a significant disturbance event, splitting the study period into two distinct time periods: pre-disturbance (2006–2009) and post-disturbance (2011–2019).

Data from 2010 were excluded from explicit comparisons between pre- and post-disturbance periods, because the peak of DHW stress (mid-April to mid-June) overlapped with the survey period (early June to early August). As such, it was unclear to what extent the bleaching event affected 2010 data, as benthic surveys did not include a category for bleaching. It is likely that the full effects of the bleaching event would not yet have become apparent when 2010 surveys were concluded (e.g. Hughes et al. 2018; Stuart-Smith et al. 2018), but this does not exclude the possibility that some bleaching effects were already evident, so data could not comfortably be categorised.

Definitions of coral growth form vary widely; surveys conducted for this study characterised arborescent, bushy, and corymbose (fused branching) colonies of *Acropora* as branching morphologies. Other branching genera surveyed are listed in Supplementary Table 1b. When looking at coral community composition changes, sub-massive and massive growth forms were collapsed into a single category.

### Model specification and selection

All data analyses were performed using R software v. 4.0.3 and RStudio v. 1.4.1106. Generalised Linear Mixed Models (GLMMs) were fitted using the R package 'glmmTMB'. When testing model specifications, ecologically relevant variables were fitted in combinations of fixed and random effects. Data exploration was carried out graphically and model fitness was assessed by running residual diagnostics with the R package 'DHARMA'. Any transects that did not contain data pertinent to a specific model were excluded prior to analysis.

Corrected Akaike Information Criterion (AICc) model selection was applied to different configurations of variables using the R package 'AICcmodavg' to select final models (Burnham and Anderson 2004) and compare the performance of different model families for the best-fit models, supporting final model selection (Table 1). The fixed effects



**Table 1** Formulas for the Generalised Linear Mixed Models fitted to test for significant relationships between Time Period (TP) and (a) branching *Acropora* (BA) and (b) other branching corals (OBC)

Model	Model type	Testing	Model formula
BAGp2	Generalised-Poisson	Effect of TP on BA	BApts ~ offset(log(TRpts)) + TP * Site + ReefZone + (1   Year), family = genpois, data = modelsdf
OBCgp2	Generalised-Poisson	Effect of TP on OBC	OBCpts ~ offset(log(TRpts)) + TP * Site + ReefZone + (1   Year), family = genpois, data = modelsdf

**Table 2** Analysis of Deviance Table for type II Wald chi-square tests applied to the generalised-Poisson generalised linear mixed models (GPR-GLMMs) fitted to test for a significant relationship between time period and *Acropora* (BA), as well as other branching coral (OBC) cover

	Chisq	Df	Pr (> Chisq)
<i>Acropora (Model A)</i>			
Period	12.2986	1	0.0004533***
Site	97.0552	5	< 2.2e-16***
ReefZone	2.6433	2	0.2666930
Period:Site	45.3056	5	1.257e-08***
<i>Other branching corals (Model B)</i>			
Period	4.2486	1	0.03928*
Site	105.2112	5	< 2.2e-16***
ReefZone	68.8042	2	1.146e-15***
Period:Site	13.8479	5	0.01660*

Significance codes: 0 ‘\*\*\*’ 0.001 ‘\*\*’ 0.01 ‘\*’ 0.05 ‘.’ 0.1 ‘.’ 1

The tests found a significant relationship between both BA and OBC and time period, study site, and the interaction between period and study site, while reef zone had a significant relationship with the level of OBC cover

of final models were evaluated for significance by type II Wald chi-square tests using the ‘Anova’ function from the R package ‘car’ and are detailed in Table 2.

Multivariate analyses of shifts in coral community structure used nonmetric-multidimensional-scaling (NMS) in the R package “vegan” to look at short- and long-term differences in coral community composition.

**Relationship between time period and types of branching coral cover**

The results for *Acropora* and other branching coral cover were analysed in two separate models. In each model, point counts, offset by the log() function of the total transect points, were used as the continuous response variable. Time period, survey site, and reef zone were set as categorical fixed variables. Year was set as a categorical random variable to represent annual fluctuations in

environmental conditions, different survey teams, and alterations in the exact positioning of the transect tape along the reef.

Overdispersion tests and residual diagnostics confirmed that a generalised Poisson regression (GPR) provided the best fit to test the relationship between time period and types of branching coral cover. GPR-GLMMs were fitted (Table 1) to account for overdispersed and/or zero-inflated residuals for a standard Poisson regression (Famoye 2005). This was supported by the non-significant results of ZI tests run on the GPR-GLMMs fitted for both models. Outlier tests were not significant.

The best-fit GPR-GLMM for testing the effect of time period on both response variables specified time period and survey site as interacting fixed variables (Table 1). Model A carried 100% AICc weight (AICcWt) and Model B carried 94% AICcWt. Full AICc results are returned in Supplementary Table 2.1.1a and 2.1.2a. When testing goodness of fit for model families, AICc supported the selection of a GPR-GLMM with a 99% AICcWt for Model A (Supplementary Table 2.1.1b). For Model B, the difference in goodness of fit between a GPR (49% AICcWt) and a quasi-Poisson regression (51% AICcWt) was negligible (Supplementary Table 2.1.2b). To be able to directly compare the models, GPR-GLMM was also chosen for Model B. Model validation indicated no problems for the GPR-GLMMs specified.

**Rates of change for *Acropora* compared to other branching corals**

Linear regression models for percentage cover ~ year were fitted for both groups of branching corals within the pre-disturbance (2006–2009) and post-disturbance (2011–2019) periods using the lm() function from the R package ‘stats’. To check for significant variations in mean cover in each distinct period, type II Wald chi-square tests were run on these regression models using the Anova() function, to test for significant year-on-year decreases and increases in mean cover for *Acropora* and other branching corals pre- and post-disturbance and compare recovery trajectories following the 2010 bleaching event.

### Changes in coral community composition in reef areas with high pre-disturbance *Acropora* cover

Because the community dynamics in areas where *Acropora* cover failed to recover post-bleaching were of particular interest, reef areas that exhibited relatively high cover for *Acropora* (at least 15% actual cover, representing at least 30% of total LCC) prior to 2010 were chosen. Four reef areas from three sites met these criteria: Buoy 3 reef flats and crest, Kaledupa Double Spur crest, and Ridge 1 slopes. Benthic cover was aggregated into 15 groups of different scleractinian coral taxa, other biotic organisms, and abiotic substrate to facilitate data visualisation (Supplementary Table 1c).

The NMS was run in four dimensions, with a maximum of 250 iterations and 150 runs of real data with random starting configurations to compare coral community composition in three distinct time periods, returning a stress result of 0.074. Data from 2009 were selected to represent pre-disturbance community composition, 2011 represented the community composition immediately after bleaching (short-term shifts), and the final year, 2019, represented long-term changes.

## Results

The 2010 bleaching event severely impacted the WMNP coral community. While many coral taxa recovered well post-bleaching, *Acropora* recovery was suppressed and coral community reassembly did not occur; areas of high *Acropora* cover failed to return over the course of nine years

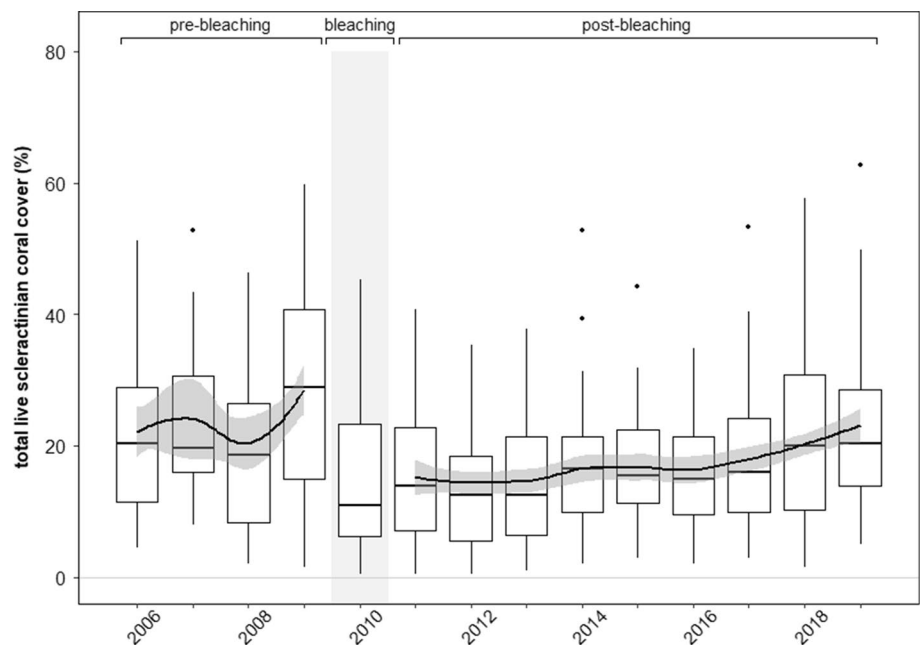
post-bleaching. Survey data demonstrated both short- and long-term shifts in the coral community at sites previously characterised by relatively high *Acropora* cover.

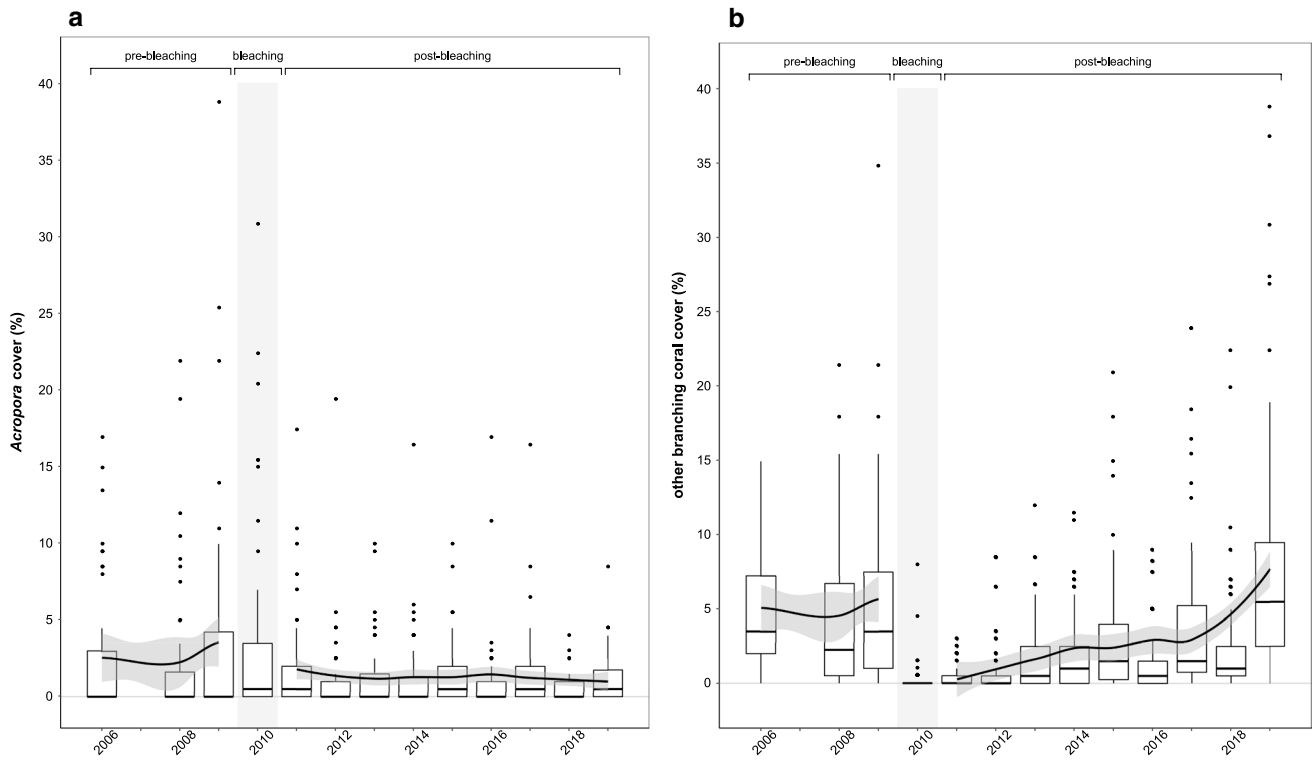
### Relationship between time period and types of branching coral cover

Total LCC decreased post-disturbance before recovering to pre-disturbance levels by 2019 (Fig. 2), while non-branching coral cover remained relatively consistent, trending gradually upwards post-disturbance (Supplementary Fig. 2). The cover of other branching corals initially decreased post-disturbance, then exhibited slow and steady recovery that surpassed pre-disturbance levels by 2019 (Fig. 3b). *Acropora* did not follow this recovery pattern, with cover decreasing noticeably post-disturbance, while median cover at no stage exceeded 0.5% (Fig. 3a).

The cover of both *Acropora* ( $p < 0.0005$ ) and other branching corals ( $p < 0.05$ ) was found to have a significant relationship with time period. The cover of *Acropora* and other branching corals also exhibited significant relationships with study site ( $p < 0.0001$  for both), as well as the interaction between time period and study site ( $p < 0.0001$  and  $p < 0.05$  respectively). The cover of other branching corals varied significantly ( $p < 0.0001$ ) across reef zones, with cover generally highest on the reef crest and lowest on the slopes (Fig. 5), while *Acropora* cover did not vary significantly between reef zone habitats. These findings were supported by type II Wald chi-square tests run on GPR-GLMM results (Table 2). Full results of the GPR-GLMMs fitted to test the relationship between time period and *Acropora*

**Fig. 2** Total live scleractinian coral cover recovered to pre-disturbance levels in the years following the 2010 mass bleaching event in the Wakatobi Marine National Park





**Fig. 3** *Acropora* median cover remained low post-disturbance, while median cover of other branching corals recovered to roughly pre-disturbance levels. High cover areas (> 15% cover) of *Acropora* disap-

peared by the end of the study period, but increased in number for other branching corals

and other branching corals are given in Supplementary Sect. 2.2.1 and 2.2.2, respectively.

**Rates of change for *Acropora* compared to other branching corals**

While the percentage cover of branching corals in general did not decrease over the course of the study period, this was due to the post-disturbance recovery of other branching corals. ANOVAs run on linear regression models for branching coral percentage cover ~ year across the entire study period (Table 3) supported this, finding a significant decrease ( $F_1 = 18.643, p < 0.0001$ ) in mean *Acropora* cover between years, but no significant change in other branching coral cover.

Prior to the bleaching event, *Acropora* cover was relatively stable, with mean cover ranging from a low of 2.17% ( $n = 48, sd 4.85$ ) in 2008 to a high of 3.41% ( $n = 51, sd 7.44$ ) in 2009. ANOVAs run on linear regression models for branching coral percentage cover ~ year within the pre-disturbance and post-disturbance periods respectively (Table 4) supported this. No significant differences in mean *Acropora* cover were found either between years in the pre-disturbance period, when there was a slight upward trend over time (Fig. 4a), or in the post-disturbance years, when

**Table 3** Type II Analyses of Variance (ANOVAs) run on linear regressions for the cover of branching *Acropora* (BA) and other branching corals (OBC) over the duration of the entire study period found a significant relationship between year and BA but not between year and OBC

	Sum Sq	Df	F value	Pr(> F)
<i>Branching Acropora</i>				
Year	290.5	1	18.643	1.821e-05 ***
Residuals	10,158.3	652		
<i>Other branching corals</i>				
Year	60.7	1	2.2675	0.1326
Residuals	17,466.2	652		

Significance codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

mean cover remained consistently low, ranging from 0.39% ( $n = 51, sd 0.80$ ) in 2018 to 1.53% ( $n = 51, sd 2.72$ ) in 2017 (Fig. 4b).

Mean cover for other branching corals was also relatively stable prior to 2010, ranging from a low of 4.33% ( $n = 48, sd 5.55$ ) in 2008 to a high of 5.39% ( $n = 51, sd 6.64$ ) in 2009, but recovered substantially post-disturbance from 0.25% ( $n = 51, sd 0.66$ ) in 2011 to 8.24% ( $n = 51, sd 9.37$ ) in 2019. This was again supported by statistical tests, with ANOVAs run on the linear regression models exhibiting no significant

**Table 4** Type II Analyses of Variance (ANOVAs) run on linear regressions for branching *Acropora* (BA) and other branching corals (OBC) within each time period found no significant relationship between BA and year in either time period, or between OBC and year in the pre-disturbance time period. A significant relationship between year and OBC was found in the post-disturbance period

	Sum Sq	Df	F value	Pr(> F)
<b>Pre-disturbance</b>				
<i>Branching Acropora</i>				
lm(formula = Year ~ BAperc, data = modelsdf, subset = (Period == "PreDist"))				
Year	0.814	1	0.5088	0.4768
Residuals	236.846	148		
<i>Other branching corals</i>				
lm(formula = Year ~ OBCperc, data = modelsdf, subset = (Period == "PreDist"))				
Year	0.207	1	0.1291	0.7198
Residuals	237.453	148		
<b>Post-disturbance</b>				
<i>Branching Acropora</i>				
lm(formula = Year ~ BAperc, data = modelsdf, subset = (Period == "PostDist"))				
Year	17.28	1	2.5662	0.1099
Residuals	3036.64	451		
<i>Other branching corals</i>				
lm(formula = Year ~ OBCperc, data = modelsdf, subset = (Period == "PostDist"))				
Year	395.09	1	67.016	2.785e-15 ***
Residuals	2658.83	451		

Significance codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

differences in mean cover during the pre-disturbance period (Fig. 4c) but presenting significant year-on-year post-disturbance differences ( $F_1 = 67.016$ ,  $p < 0.0001$ ). Taken in conjunction with the substantial upward trajectory of the linear regression (Fig. 4d), this illustrates the much higher rate of post-disturbance recovery of other branching corals in comparison to *Acropora*. The positive recovery trajectory for other branching corals and suppression of *Acropora* recovery was evident across all reef zones (Fig. 5).

#### Changes in coral community composition in reef areas with high pre-disturbance *Acropora* cover

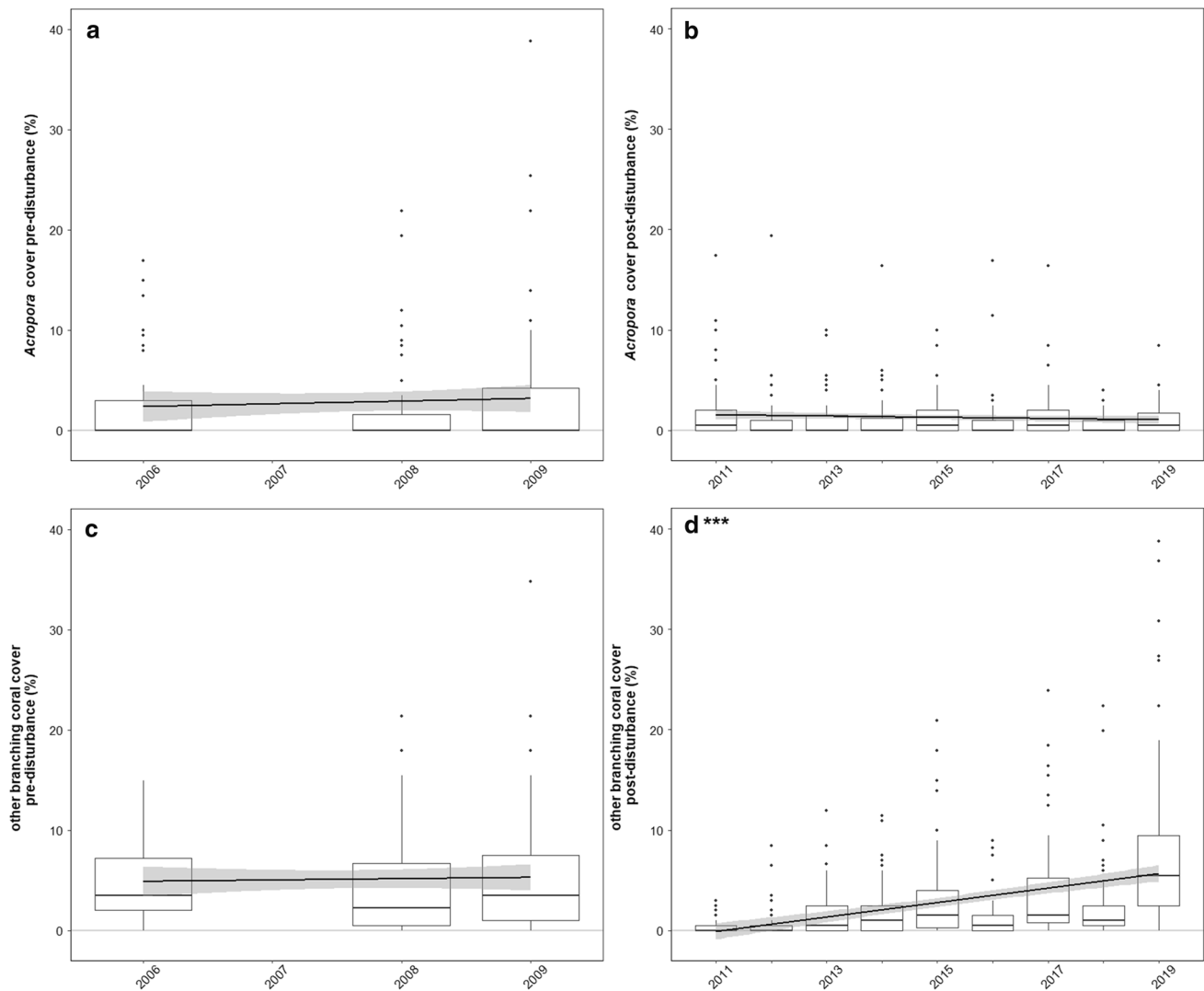
In the four reef areas characterised by high *Acropora* cover prior to the bleaching event, coral community shifts have taken place, with the biggest changes seen in growth forms of the three dominant genera: *Acropora*, *Porites*, and *Montipora* (Fig. 6a). Over the 12 transects (six reef crests, three flats, and three slopes), long-term changes have been dominated by increased *Porites* cover and the loss of *Acropora*. The NMS analysis (Fig. 6b) supports the theory that coral community composition in these areas has shifted post-bleaching, with some crossover but clear dissimilarities between the aggregated coral taxa groupings in the year

prior to the bleaching event (2009), the year after bleaching (2011), and the final year of the study (2019).

Massive *Porites* increased in the short-term, before decreasing slightly in the long-term. Branching *Porites* cover dropped sharply post-disturbance, but exhibited strong long-term recovery. Mean cover of other *Porites* growth forms was low both before and immediately after the bleaching event, but did show a small increase by 2019. In contrast, branching *Acropora* cover decreased post-bleaching, and then decreased further in the long-term. The cover of other growth forms of *Acropora* also failed to recover post-disturbance (Fig. 6a). Pre-disturbance branching *Montipora* cover was minimal and completely disappeared after the bleaching event but did show some recovery in the long-term. Other *Montipora* growth forms decreased post-disturbance and remained low in the long-term. Short-term changes also saw an increase in mean *Pocillopora* cover, which decreased back to pre-disturbance levels in the long-term.

Another noticeable trend in these areas is the change in abiotic cover post-bleaching (Fig. 6b). Abiotic cover increased from just over 25% of mean benthic cover in 2009 to almost 60% mean coverage post-disturbance, and elevated abiotic cover persisted to an extent in the long-term, with roughly 42% mean coverage recorded in 2019.





**Fig. 4** ANOVAs run on linear regressions of branching coral cover within each time period found no significant change in *Acropora* during either (a) pre-disturbance or (b) post-disturbance periods, while median levels of *Acropora* were extremely low throughout the study

period. The cover of other branching corals did not exhibit significant change pre-disturbance (c) but increased significantly ( $p < 0.0001$ ) post-disturbance (d)

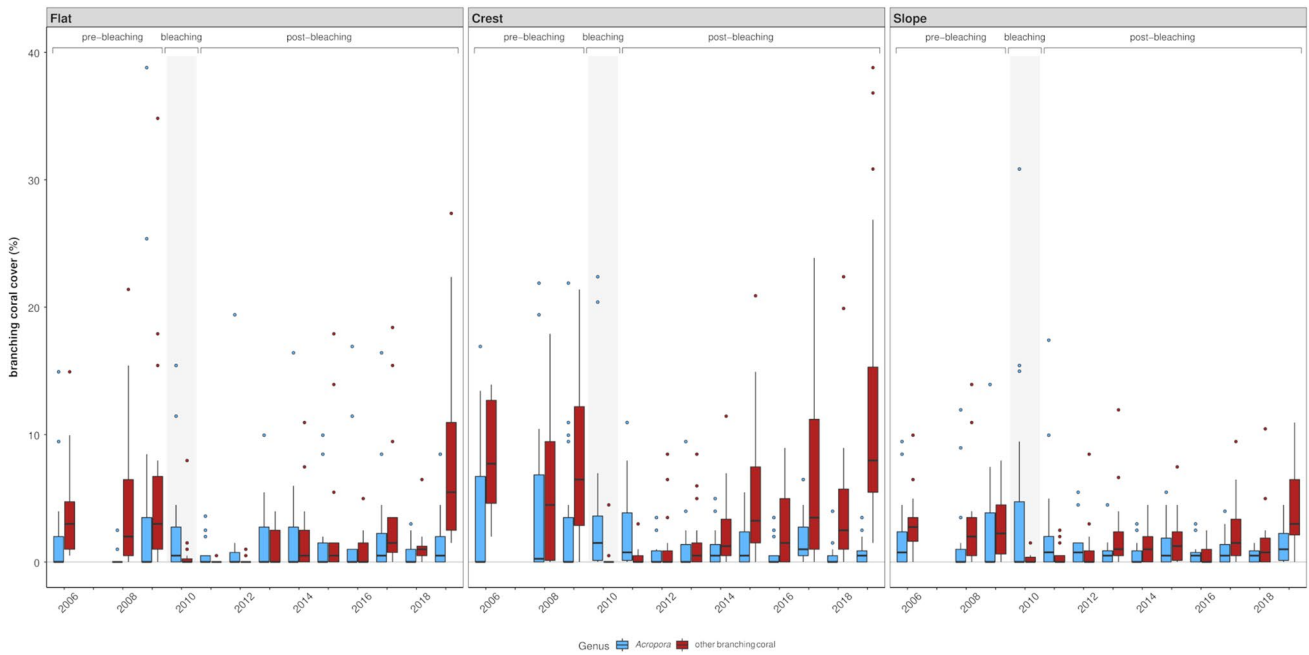
## Discussion

The results of this study show that long-term changes in coral community composition following the mass bleaching event in the WMNP in 2010 are predominantly due to the suppressed recovery of *Acropora* and the return of other types of branching coral, most notably *Porites* (Supplementary Fig. 3).

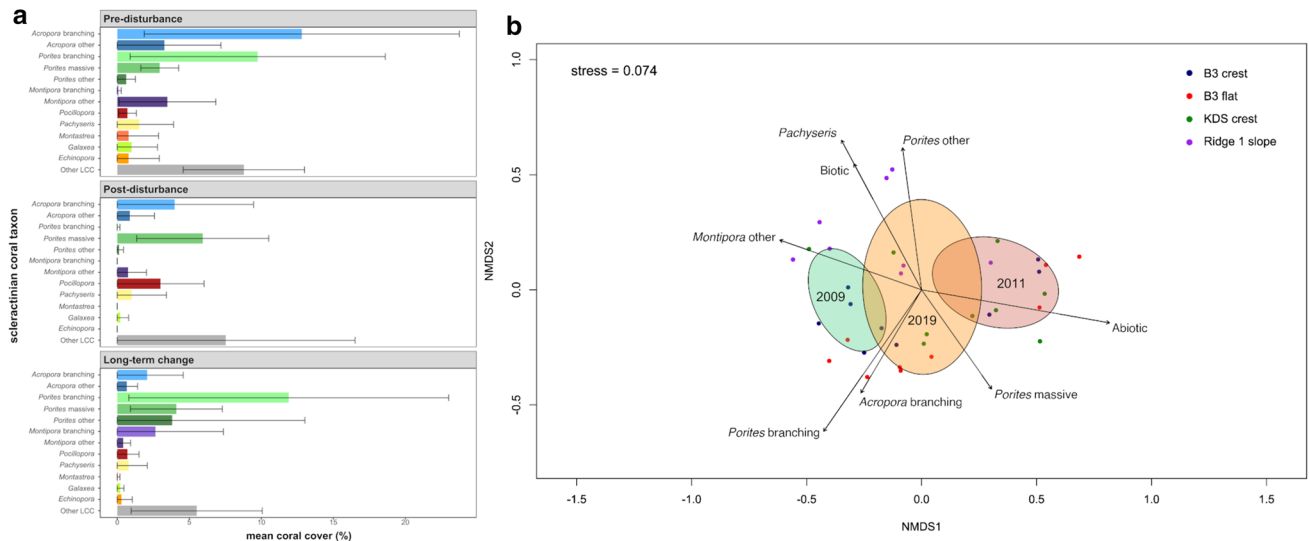
Despite previous studies documenting minimal mortality of *Acropora* across the wider WMNP following the 2010 mass bleaching event (Wilson et al. 2012), this study found significant decreases in *Acropora* cover post-disturbance. This appears to have been driven by the loss of localised high-cover areas: relatively high *Acropora* cover ( $> 15\%$ )

was recorded on 5% of transects between 2006 and 2010, but only on 1% of transects in the post-disturbance period (Fig. 3a). Average levels of *Acropora* cover were low across the whole study period (median percentage cover never exceeded 0.5%). However, outlying high percentage cover data points in the pre-disturbance period indicate a patchy distribution with spatial clusters dominated by thickets of *Acropora*. By contrast, the post-disturbance period had far fewer of these outliers, suggesting that thickets were destroyed by the bleaching and never recovered.

The suppression of *Acropora* recovery compared to the recovery demonstrated by other branching corals (e.g. *Porites*) may be due to some or all of a number of factors linked to a) limitation of reproduction and recruitment, b)



**Fig. 5** Other branching corals exhibited higher recovery across all reef zones compared to *Acropora*, with the contrast particularly evident on reef crests and reef flats



**Fig. 6 a** Mean cover of different coral taxa across four reef areas characterised by relatively high *Acropora* cover pre-disturbance (Buoy 3 flats and crest, KDS crest, and Ridge 1 slope). **b** Nonmetric-multidimensional-scaling (NMS) analysis of the dissimilarities

between the coral communities in these reef areas in 2009 (pre-bleaching), 2011 (post-bleaching), and 2019 (long-term change). The data represent Bray Curtis similarities of percentage cover of the different coral taxa ( $p=0.01$ )

direct and indirect competition from other organisms, c) environmental conditions, and d) changes to the physical reef environment.

*Acropora* recovery may have been limited by larval supply and recruitment in several ways. The Allee effect describing the inhibition of reproduction at low population densities (Courchamp et al. 1999) is thought to play a

role in the suppression of larval recruitment in low-cover areas. Riegl et al (2018) attributed the dramatic and rapid decline of a functionally important *Acropora* species in the Arabian Gulf at least partially to Allee effects and the failure of recruitment to adequately compensate for mortality. Similarly, Perry and Morgan (2017) found that favourable post-disturbance recovery trajectories for *Acropora* in

low-cover areas depends on adequate coral recruitment and survivorship. Teo and Todd (2018) found evidence for the Allee effect in broadcast-spawning corals (which includes most *Acropora* species) which are particularly vulnerable to reproduction failure when populations get low. The low level of mean *Acropora* cover across the study sites, even in 2009 prior to the mass bleaching event (< 4%), supports the theory that inhibited recruitment of *Acropora* has occurred in the WMNP.

In addition, fragmentation of existing colonies is either predominant or an important mode of reproduction in several species of *Acropora* in the Indo-West Pacific (Highsmith 1982). This could be a factor in the suppression of recovery in areas where a high percentage of cover has been lost.

Van Woesik et al. (2011) posited that genetic connectivity between reef systems is vital to supply recruits for *Acropora* recovery following mass bleaching events, so widespread loss of *Acropora* colonies throughout the WMNP is another potential factor in the suppression of recovery. Work in the Arabian Gulf supports this theory: *Acropora* populations and community structure were maintained despite repeated cyclical mass mortality caused by thermal stress, so long as the remaining population remained fecund or a larval supply from connected populations persisted (Riegl and Purkis 2009). Lukoschek et al. (2013) established links between the recovery of *Acropora* post-disturbance and the external input of coral larvae on the central GBR, while Gouezo et al. (2019) found that larval connectivity and juvenile coral density were prominent drivers of post-bleaching *Acropora* recovery in Palau.

Recovery trajectories are also known to be affected by species density and competition for both food and space (Hurlbut 1991). Turbid water corals such as *Pavona cactus*, for example, may have outcompeted *Acropora* in the central GBR following disturbance (Clark et al. 2017). The suppression of *Acropora* recovery may therefore also be partly attributable to increased spatial competition, including for larval recruitment.

Closely-spaced disturbance events have severely disadvantaged *Acropora* populations in the Arabian Gulf (Riegl and Purkis 2009) and the GBR (Pratchett et al. 2020). A continuation of this trend could see a permanent shift away from *Acropora* dominance on reefs across the Indo-Pacific. Pratchett et al. (2020) have noted, however, that more frequent major disturbances will not necessarily lead to selective loss of the most sensitive species, as long as they can recolonise vacant space and regrow quickly post-disturbance.

Given the relatively low levels of *Acropora* cover in the WMNP even prior to the 2010 mass bleaching event, this disturbance possibly represents a culmination of a series of historical stressors, at least partly explaining the lack of *Acropora* recovery over the last decade. These may include long-term damage from coral mining (Caras and Pasternak

2009) and increased sedimentation linked to this and to the destruction of seagrass beds on inner reef flats (Exton et al. 2019); blast fishing (von Heland and Clifton 2015); and previous localised coral disease outbreaks potentially afflicting *Acropora* populations (Haapkylä et al. 2009).

The persistence of higher levels of coral rubble in areas with previously higher cover of *Acropora* (Supplementary Fig. 4) may also have suppressed recovery, especially at more exposed sites (e.g. KDS and Ridge 1), because unconsolidated rubble fields can kill newly settled recruits where currents shift coral rubble (Fox et al. 2003).

More frequent and intense bleaching events and the perpetuation of other acute and chronic stressors have the potential to exacerbate these various impacts in coming years. In contrast to the post-disturbance loss of areas with relatively high *Acropora* cover, areas with relatively high cover of other branching corals increased substantially in the latter years of the study: despite no transects recording over 15% cover in the initial years following disturbance (2011 to 2014), 7% of transects had recovered to > 15% cover by the end of the study (Fig. 3b).

Another global mass bleaching event was extensively documented in 2016, although DHW maps suggest that the WMNP suffered minimal heat stress compared to 2010 (Supplementary Fig. 1). The results from the current study support this: no major decreases in overall LCC were recorded in 2017, unlike in 2011 (Fig. 2), despite the Wakatobi being cited as an affected area during both events (Wouthuyzen et al. 2018).

Previous exposure to high thermal variation may assist certain reef areas in the Wakatobi to acclimate to future elevated temperature events (Jin et al. 2020). Overall coral mortality across the WMNP following the 2010 mass bleaching event was estimated at no more than 10 to 15% (Wilson et al. 2012). Indonesia's westernmost province, Aceh, experienced far higher coral bleaching and mortality in 2010 despite experiencing less thermal stress; annual temperature variability and higher thermal variation during summer months in the WMNP may help reefs to acclimate to elevated temperature events (Wilson et al. 2012).

Survivors of bleaching events have more thermally resilient genotypes, making them better able to resist the impacts of future marine heatwaves. This may enable the integration of better-acclimated sensitive corals into reef rehabilitation efforts (e.g. Bowden-Kerby and Carne 2012) via the selection of surviving colonies. Rehabilitation techniques can be informed by continued research on thermally resilient corals (e.g. Barshis et al. 2013; Van Oppen et al. 2015; Epstein et al. 2019; Drury 2020) and corals surviving in extreme conditions (e.g. Osman et al. 2018; Greenwood 2021). Considering the high variability in scleractinian coral cover across sites geographically near to one another in the WMNP (Marlow et al. 2020), high priority areas can potentially be

pinpointed. These could be focal points for rehabilitated reef areas environmentally buffered against future environmental stress, and healthy repositories of structurally complex, fast-growing corals sensitive to heat stress.

This study has demonstrated the suppressed recovery of vulnerable and ecologically important *Acropora* corals in the WMNP and major long-term shifts in coral community structure in the park, fuelled at least in part by the 2010 mass bleaching event. This supports the findings of research conducted on the GBR which found region-wide loss of resilience in *Acropora* over the last century (Clark et al. 2017). *Acropora*'s high resilience and narrow recovery range post-bleaching has been observed on clear-water, mid- and off-shore reefs following acute natural disturbances (see also Arthur et al. 2006; Done et al. 2007), but recovery rates for reefs exposed to continued acute or chronic events remain poorly understood.

Further exploration of mechanisms driving the suppression of *Acropora* recovery following bleaching events can help to inform reef management and restoration efforts and identify priority areas for direct interventions. Promoting the return of *Acropora* and other fast-growing, bleaching-susceptible colonies in the WMNP, alongside a focus on benthic community reassembly, may have a significant role to play in safeguarding the future of a traditionally keystone ecosystem engineer on Indonesian reefs. Without these interventions, *Acropora* may face the risk of local extinctions.

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#### Declarations

**Conflict of interest** The authors have no relevant financial or non-financial interests to disclose. On behalf of all authors, the corresponding author states that there is no conflict of interest.

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