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

Rowan Watt-Pringle<sup>1\*</sup>, David J Smith<sup>2,3</sup>, Rohani Ambo-Rappe<sup>1</sup>, Timothy AC Lamont<sup>4</sup> and Jamaluddin Jompa<sup>1,5</sup>

<sup>1</sup> Faculty of Marine Science and Fisheries, Hasanuddin University, Makassar, Indonesia

<sup>2</sup> Coral Reef Research Unit, School of Biological Sciences, University of Essex, Colchester, UK

<sup>3</sup> Mars Incorporated, 4 Kingdom Street, Paddington, London, W2 6BD, UK

<sup>4</sup> Lancaster Environment Centre, Lancaster University, Lancaster LA1 4YQ

<sup>5</sup> Graduate School, Hasanuddin University, Makassar, Indonesia

\* Corresponding Author: Rowan Watt-Pringle ([rwp.unhas@gmail.com](mailto:rwp.unhas@gmail.com))

## Author ORCID IDs

Rowan Watt-Pringle [0000-0002-9022-5830](https://orcid.org/0000-0002-9022-5830)

David J Smith [0000-0003-1886-8193](https://orcid.org/0000-0003-1886-8193)

Rohani Ambo-Rappe [0000-0001-9276-7492](https://orcid.org/0000-0001-9276-7492)

Timothy AC Lamont [0000-0002-0305-6603](https://orcid.org/0000-0002-0305-6603)

Jamaluddin Jompa [0000-0001-9740-333X](https://orcid.org/0000-0001-9740-333X)

## Keyword List

Branching coral, *Acropora*, Indonesia, bleaching, coral community composition, suppressed recovery

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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 20<sup>th</sup> 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.

## 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).

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

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

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

46 *Acropora* and other acroporids like *Montipora* are amongst the most sensitive scleractinian coral taxa to  
 47 environmental stressors, including bleaching (Marshall and Baird 2000; Loya et al. 2001; van Woesik et al. 2011; Wilson  
 48 et al. 2012; Clark et al. 2017). Along with other corals displaying 'competitive' life trait strategies (Darling et al. 2012),  
 49 *Acropora* are often among the first corals to disappear in unfavourable and disturbed environments (Loya et al. 2001;  
 50 McClanahan et al. 2007). However, they frequently exhibit steady recovery due to fast growth rates and high fecundity;  
 51 studies have shown the complete recovery of *Acropora* populations following acute thermal stress, for example, after  
 52 seven years in Palau (Golbuu et al. 2007) and in 15 year cycles in the Arabian Gulf (Riegl and Purkis 2009). At the same  
 53 time, even post-bleaching recovery may not be enough to halt a shifting baseline for *Acropora* and other bleaching-  
 54 susceptible corals. Rapid recovery following disturbance “may represent a short-term boom in a new Anthropocene  
 55 configuration, where fast-growing corals persist but are unlikely to attain their former abundance due to successive  
 56 disturbances and suppression of recovery dynamics” (Morais et al. 2021).

57 On reefs affected by changing disturbance regimes related to climate change, the recovery of these competitive corals  
 58 may be suppressed due to a loss of brood stock (Hughes et al. 2019). This inhibition of reproduction at low population  
 59 densities (the Allee effect) has been shown to affect broadcast spawning corals (Teo and Todd 2018), and the high  
 60 mortality of sensitive corals following mass bleaching is increasingly causing radical shifts in coral community  
 61 composition and functional traits (Hughes et al. 2018). Following bleaching, a number of factors may affect the recovery

62 of different scleractinian genera. Physiologically-stressed corals may be more susceptible to disease (Bruno et al. 2007;  
63 Lesser et al. 2007), while various mechanisms inhibit the recruitment, settlement, and survival of planula larvae. These  
64 mechanisms include the direct effects of increased sedimentation on planula settlement (Tomascik 1991; Babcock and  
65 Davies 1991), reductions in grazing pressure and habitat complexity (Roth et al. 2018), and unconsolidated rubble fields  
66 (Fox et al. 2003).

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

74 Following a mass bleaching event in the WMNP during the 2010 marine heat wave, the extent of bleaching was  
75 documented through park-wide surveys recording the loss of overall live scleractinian coral cover (LCC) (Wilson et al.  
76 2012). The severity of the marine heat wave is illustrated by Degree Heating Week (DHW) maps published by the US  
77 National Oceanic and Atmospheric Administration (NOAA) (Supplementary Fig. 1).

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

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

90 The present study fills an important knowledge gap by looking at the long-term recovery of fast-growing, structurally  
91 complex 'competitive' *Acropora* corals and other sensitive branching corals in the WMNP following this mass bleaching  
92 event. The key contribution and novelty of the study comes from the apparent limited recovery of *Acropora* compared to  
93 other branching corals, despite bleaching surveys suggesting minimal bleaching and immediate mortality (Wilson et al.

94 2012). The majority of previous research on post-disturbance recovery compares very different growth forms (e.g., Loya  
95 et al. 2001; McClanahan et al. 2007; Wilson et al. 2019; Pratchett et al. 2020; Morais et al. 2021). Here, however, we aim  
96 to provide more detail by comparing recovery within branching corals which, while exhibiting similar growth forms,  
97 provide distinct ecological services (see Munday 2004; Gardiner and Jones 2005; Pratchett et al. 2008). The study  
98 additionally examines short- and long-term shifts in coral community composition in reef areas previously characterised  
99 by high *Acropora* cover.

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

## 106 **Materials and Methods**

### 107 **Study site**

108 The Wakatobi Marine National Park (WMNP) is Indonesia's second largest MPA, covering 1.4 million hectares  
109 encompassing the Tukang Besi archipelago (Clifton et al. 2010) in the heart of the Coral Triangle region, to the south-  
110 east of Sulawesi (Fig. 1a). This is an extremely important area for global biodiversity, evolutionary biology, and  
111 biogeography (Tomascik et al. 1997). The Wakatobi comprises four main islands: **W**angi-Wangi, **K**aledupa, **T**omia and  
112 **B**Inongko, and 35 smaller islands, with a resident population of 95,892 according to the most recent available government  
113 information (BPS Statistics Indonesia 2021).

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

### 118 **Data collection**

119 Using standardised methodology in collaboration with the Indonesian Institute of Sciences (LIPI) and Makassar's  
120 Hasanuddin University, a team of researchers from several universities associated with Operation Wallacea (Opwall) have  
121 conducted a long-term reef monitoring programme at six sites along the north-eastern coast of Kaledupa and western  
122 coast of Hoga (Fig. 1b). Surveys recording benthic community composition were conducted annually from June to August,  
123 between 2006 and 2019. Fifty-one permanent 50-m transects were established in replicates of three on the reef flat (5m  
124 landward from the reef crest), reef crest, and upper reef slope (defined by habitat type and 10-m approximate depth) using

125 a nested design, with replicates placed a horizontal distance of at least 20m apart. The study site at Ridge 1 has no reef  
 126 flat. The start and end of transects were marked by steel pickets and transect locations at each site have been mapped (e.g.,  
 127 Fig. 1c).

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

136 As with most long-term datasets, logistical constraints including inclement weather prevented some transects from  
 137 being surveyed in certain years. Of particular note was 2007, when data were collected for 20 of 51 transects, representing  
 138 five of six survey sites, and neither reef flat transect nor coral growth form data were collected. In total, 674 transects  
 139 were sampled across the study period (247 crest, 236 slope, and 191 flat) from a potential 714, with 40 missing transects  
 140 representing 5.6% of the total. Of a possible total 135,474 points on completed transects, 128 individual data points  
 141 (0.095%) were missing.

### 142 **Statistical methods**

143 Coral cover data from the study period was non-normal for both LCC and different taxa of branching corals. To test  
 144 for significant changes in different types of coral cover between 2006 and 2019, the 2010 mass bleaching event was  
 145 specified as a significant disturbance event, splitting the study period into two distinct time periods: pre-disturbance  
 146 (2006–2009) and post-disturbance (2011–2019).

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

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

## 157 **Model specification and selection**

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

163 Corrected Akaike Information Criterion (AICc) model selection was applied to different configurations of variables  
 164 using the R package ‘AICcmodavg’ to select final models (Burnham and Anderson 2004) and compare the performance  
 165 of different model families for the best-fit models, supporting final model selection (Table 1). The fixed effects of final  
 166 models were evaluated for significance by type II Wald chi-square tests using the ‘Anova’ function from the R package  
 167 ‘car’ and are detailed in Table 2.

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

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

171 Results for *Acropora* and other branching coral cover were analysed in two separate models. In each model, point  
 172 counts, offset by the log() function of the total transect points, was used as the continuous response variable. Time period,  
 173 survey site, and reef zone were set as categorical fixed variables. Year was set as a categorical random variable to represent  
 174 annual fluctuations in environmental conditions, different survey teams, and alterations in the exact positioning of the  
 175 transect tape along the reef.

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

181 The best-fit GPR-GLMM for testing the effect of time period on both response variables specified time period and  
 182 survey site as interacting fixed variables (Table 1). Model A carried 100% AICc weight (AICcWt) and Model B carried  
 183 94% AICcWt. Full AICc results are returned in Supplementary Table 2.1.1a and 2.1.2a. When testing goodness of fit for  
 184 model families, AICc supported the selection of a GPR-GLMM with a 99% AICcWt for Model A (Supplementary Table  
 185 2.1.1b). For Model B, the difference in goodness of fit between a GPR (49% AICcWt) and a quasi-poisson regression  
 186 (51% AICcWt) was negligible (Supplementary Table 2.1.2b). To be able to directly compare the models, GPR-GLMM  
 187 was also chosen for Model B. Model validation indicated no problems for the GPR-GLMMs specified.

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

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

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

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

201 The NMS was run in 4 dimensions, with a maximum of 250 iterations and 150 runs of real data with random starting  
 202 configurations to compare coral community composition in three distinct time periods, returning a stress result of 0.074.  
 203 Data from 2009 was selected to represent pre-disturbance community composition, 2011 represented the community  
 204 composition immediately after bleaching (short-term shifts), and the final year, 2019, represented long-term changes.

## 205 **Results**

206 The 2010 bleaching event severely impacted the WMNP coral community. While many coral taxa recovered well  
 207 post-bleaching, *Acropora* recovery was suppressed and coral community reassembly did not occur; areas of high *Acropora*  
 208 cover failed to return over the course of nine years post-bleaching. Survey data demonstrated both short- and long-term  
 209 shifts in the coral community at sites previously characterised by relatively high *Acropora* cover.

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

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

216 The cover of both *Acropora* ( $p < 0.0005$ ) and other branching corals ( $p < 0.05$ ) were found to have a significant  
 217 relationship with time period. The cover of *Acropora* and other branching corals also exhibited significant relationships  
 218 with study site ( $p < 0.0001$  for both), as well as the interaction between time period and study site ( $p < 0.0001$  and  $p <$   
 219  $0.05$  respectively). The cover of other branching corals varied significantly ( $p < 0.0001$ ) across reef zones, with cover

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220 generally highest on the reef crest and lowest on the slopes (Fig. 5), while *Acropora* cover did not vary significantly  
 221 between reef zone habitats. These findings were supported by type II Wald chi-square tests run on GPR-GLMM results  
 222 (Table 2). Full results of the GPR-GLMMs fitted to test the relationship between time period and *Acropora* and other  
 223 branching corals are given in Supplementary Section 2.2.1 and 2.2.2 respectively.

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

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

230 Prior to the bleaching event, *Acropora* cover was relatively stable, with mean cover ranging from a low of 2.17% (n  
 231 = 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  
 232 coral percentage cover ~ year within the pre-disturbance and post-disturbance periods respectively (Table 4) supported  
 233 this. No significant differences in mean *Acropora* cover were found either between years in the pre-disturbance period,  
 234 when there was a slight upward trend over time (Fig. 4a), or in the post-disturbance years, when mean cover remained  
 235 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).

236 Mean cover for other branching corals was also relatively stable prior to 2010, ranging from a low of 4.33% (n = 48,  
 237 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  
 238 = 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  
 239 on the linear regression models exhibiting no significant differences in mean cover during the pre-disturbance period (Fig.  
 240 4c) but presenting significant year-on-year post-disturbance differences ( $F_1 = 67.016, p < 0.0001$ ). Taken in conjunction  
 241 with the substantial upward trajectory of the linear regression (Fig. 4d), this illustrates the much higher rate of post-  
 242 disturbance recovery of other branching corals in comparison to *Acropora*. The positive recovery trajectory for other  
 243 branching corals and suppression of *Acropora* recovery was evident across all reef zones (Fig. 5).

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

245 In the four reef areas characterised by high *Acropora* cover prior to the bleaching event, coral community shifts have  
 246 taken place, with the biggest changes seen in growth forms of the three dominant genera: *Acropora*, *Porites*, and  
 247 *Montipora* (Fig. 6a). Over the 12 transects (six reef crests, three flats, and three slopes), long-term changes have been  
 248 dominated by increased *Porites* cover and the loss of *Acropora*. The NMS analysis (Fig. 6b) supports the theory that coral  
 249 community composition in these areas has shifted post-bleaching, with some crossover but clear dissimilarities between  
 250 the aggregated coral taxa groupings in the year prior to the bleaching event (2009), the year after bleaching (2011), and  
 251 the final year of the study (2019).

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

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

## 263 Discussion

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

267 Despite previous studies documenting minimal mortality of *Acropora* across the wider WMNP following the 2010  
 268 mass bleaching event (Wilson et al. 2012), this study found significant decreases in *Acropora* cover post-disturbance. This  
 269 appears to have been driven by the loss of localised high-cover areas: relatively high *Acropora* cover (>15%) was recorded  
 270 on 5% of transects between 2006 and 2010, but only on 1% of transects in the post-disturbance period (Fig. 3a). Average  
 271 levels of *Acropora* cover were low across the whole study period (median percentage cover never exceeded 0.5%).  
 272 However, outlying high percentage cover data points in the pre-disturbance period indicate a patchy distribution with  
 273 spatial clusters dominated by thickets of *Acropora*. By contrast, the post-disturbance period had far fewer of these outliers,  
 274 suggesting that thickets were destroyed by the bleaching and never recovered.

275 The suppression of *Acropora* recovery compared to the recovery demonstrated by other branching corals (e.g.,  
 276 *Porites*) may be due to some or all of a number of factors linked to a) limitation of reproduction and recruitment, b) direct  
 277 and indirect competition from other organisms, c) environmental conditions, and d) changes to the physical reef  
 278 environment.

279 *Acropora* recovery may have been limited by larval supply and recruitment in several ways. The Allee effect,  
 280 describing the inhibition of reproduction at low population densities (Courchamp et al. 1999) is thought to play a role in  
 281 the suppression of larval recruitment in low-cover areas. Riegl et al (2018) attributed the dramatic and rapid decline of a  
 282 functionally important *Acropora* species in the Arabian Gulf at least partially to Allee effects and the failure of recruitment

283 to adequately compensate for mortality. Similarly, Perry and Morgan (2017) found that favourable post-disturbance  
284 recovery trajectories for *Acropora* in low-cover areas depends on adequate coral recruitment and survivorship. Teo and  
285 Todd (2018) found evidence for the Allee effect in broadcast-spawning corals (which includes most *Acropora* species)  
286 which are particularly vulnerable to reproduction failure when populations get low. The low level of mean *Acropora* cover  
287 across the study sites, even in 2009 prior to the mass bleaching event (< 4%), supports the theory that inhibited recruitment  
288 of *Acropora* has occurred in the WMNP.

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

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

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

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

309 Given the relatively low levels of *Acropora* cover in the WMNP even prior to the 2010 mass bleaching event, this  
310 disturbance possibly represents a culmination of a series of historical stressors, at least partly explaining the lack of  
311 *Acropora* recovery over the last decade. These may include long-term damage from coral mining (Caras and Pasternak  
312 2009) and increased sedimentation linked to this and to the destruction of seagrass beds on inner reef flats (Exton et al.  
313 2019); blast fishing (von Heland and Clifton 2015); and previous localised coral disease outbreaks potentially afflicting  
314 *Acropora* populations (Haapkylä et al. 2009).

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

318 More frequent and intense bleaching events and the perpetuation of other acute and chronic stressors have the  
319 potential to exacerbate these various impacts in coming years. In contrast to the post-disturbance loss of areas with  
320 relatively high *Acropora* cover, areas with relatively high cover of other branching corals increased substantially in the  
321 latter years of the study: despite no transects recording over 15% cover in the initial years following disturbance (2011 to  
322 2014), 7% of transects had recovered to >15% cover by the end of the study (Fig. 3b).

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

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

333 Survivors of bleaching events have more thermally-resilient genotypes, making them better able to resist the impacts  
334 of future marine heatwaves. This may enable the integration of better-acclimated sensitive corals into reef rehabilitation  
335 efforts (e.g., Bowden-Kerby and Carne 2012) via the selection of surviving colonies. Rehabilitation techniques can be  
336 informed by continued research on thermally resilient corals (e.g., Barshis et al. 2013; Van Oppen et al. 2015; Epstein et  
337 al. 2019; Drury 2020) and corals surviving in extreme conditions (e.g., Osman et al. 2018; Greenwood 2021). Considering  
338 the high variability in scleractinian coral cover across sites geographically near to one another in the WMNP (Marlow et  
339 al. 2019), high priority areas can potentially be pinpointed. These could be focal points for rehabilitated reef areas  
340 environmentally buffered against future environmental stress, and healthy repositories of structurally complex, fast-  
341 growing corals sensitive to heat stress.

342 This study has demonstrated the suppressed recovery of vulnerable and ecologically important *Acropora* corals in  
343 the WMNP and major long-term shifts in coral community structure in the park, fuelled at least in part by the 2010 mass  
344 bleaching event. This supports the findings of research conducted on the GBR which found region-wide loss of resilience  
345 in *Acropora* over the last century (Clark et al. 2017). *Acropora*'s high resilience and narrow recovery range post-bleaching  
346 has been observed on clear-water, mid- and off-shore reefs following acute natural disturbances (see also Arthur et al.

347 2006; Done et al. 2007), but recovery rates for reefs exposed to continued acute or chronic events remain poorly  
 348 understood.

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

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## Declarations

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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## 521 **Figure Legends**

522  
 523 **Fig.1** The six survey sites in the central Wakatobi Marine National Park (a), south-east of Sulawesi between the Banda  
 524 Sea to the north-east and the Flores Sea to the south-west (b). Permanent reef transects (c) were set up in a nested  
 525 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  
 526 scale).

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

529 **Fig.3** *Acropora* median cover remained low post-disturbance, while median cover of other branching corals recovered  
 530 to roughly pre-disturbance levels. High cover areas (>15% cover) of *Acropora* disappeared by the end of the study  
 531 period, but increased in number for other branching corals.

532 **Fig.4** ANOVAs run on linear regressions of branching coral cover within each time period found no significant change  
 533 in *Acropora* during either (a) pre-disturbance or (b) post-disturbance periods, while median levels of *Acropora* were  
 534 extremely low throughout the study period. The cover of other branching corals did not exhibit significant change pre-  
 535 disturbance (c) but increased significantly ( $p < 0.0001$ ) post-disturbance (d).

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

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



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

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545 **Online Resource 1** contains two sections. Section 1 consists of supplementary figures and tables, while Section 2 contains  
546 the full results of both model selection and final generalised poisson regression GLMMs described in Materials and  
547 Methods.

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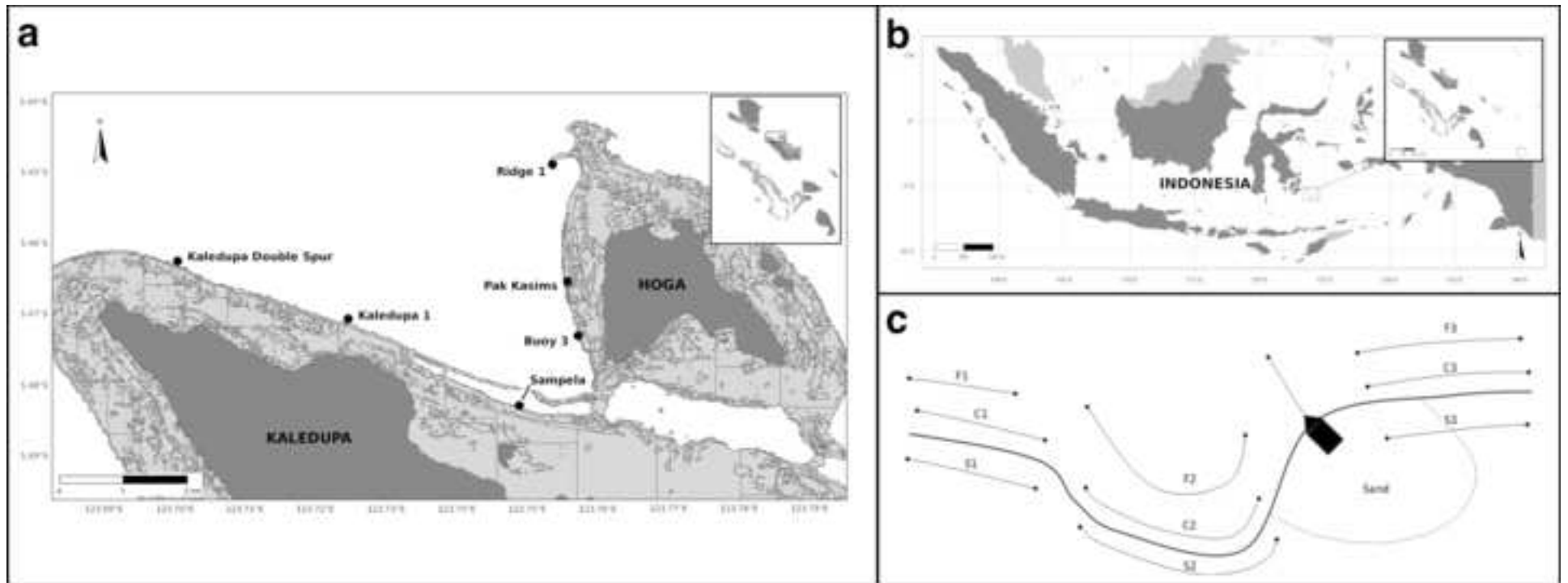
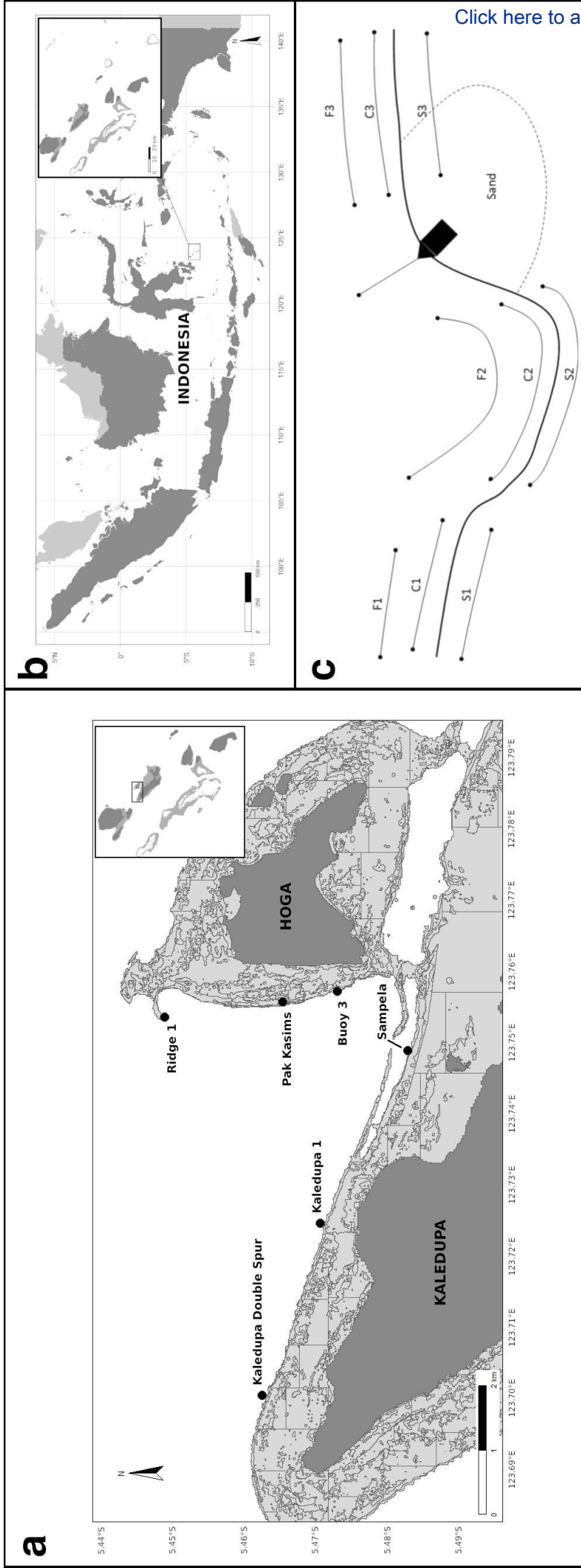
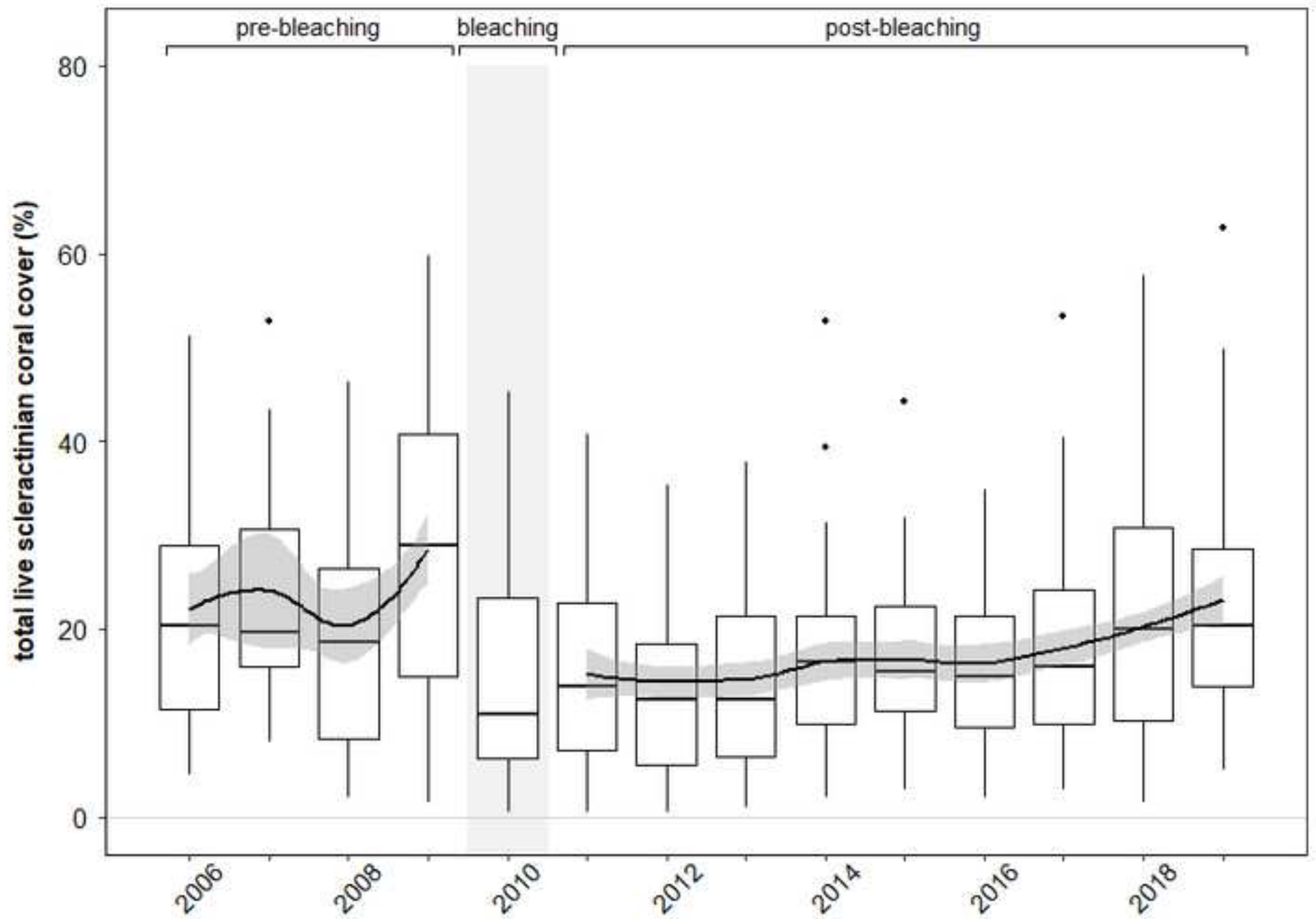
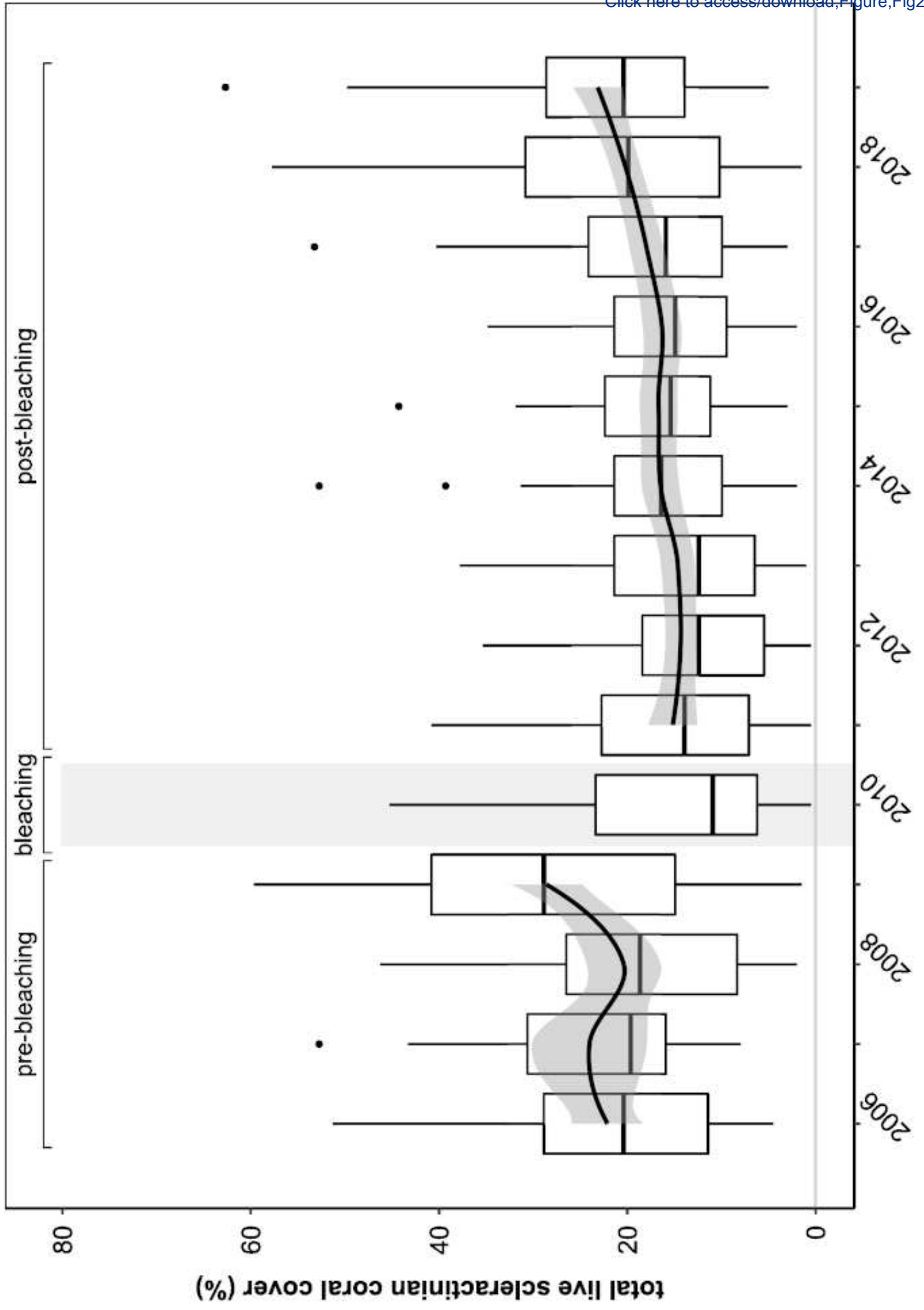
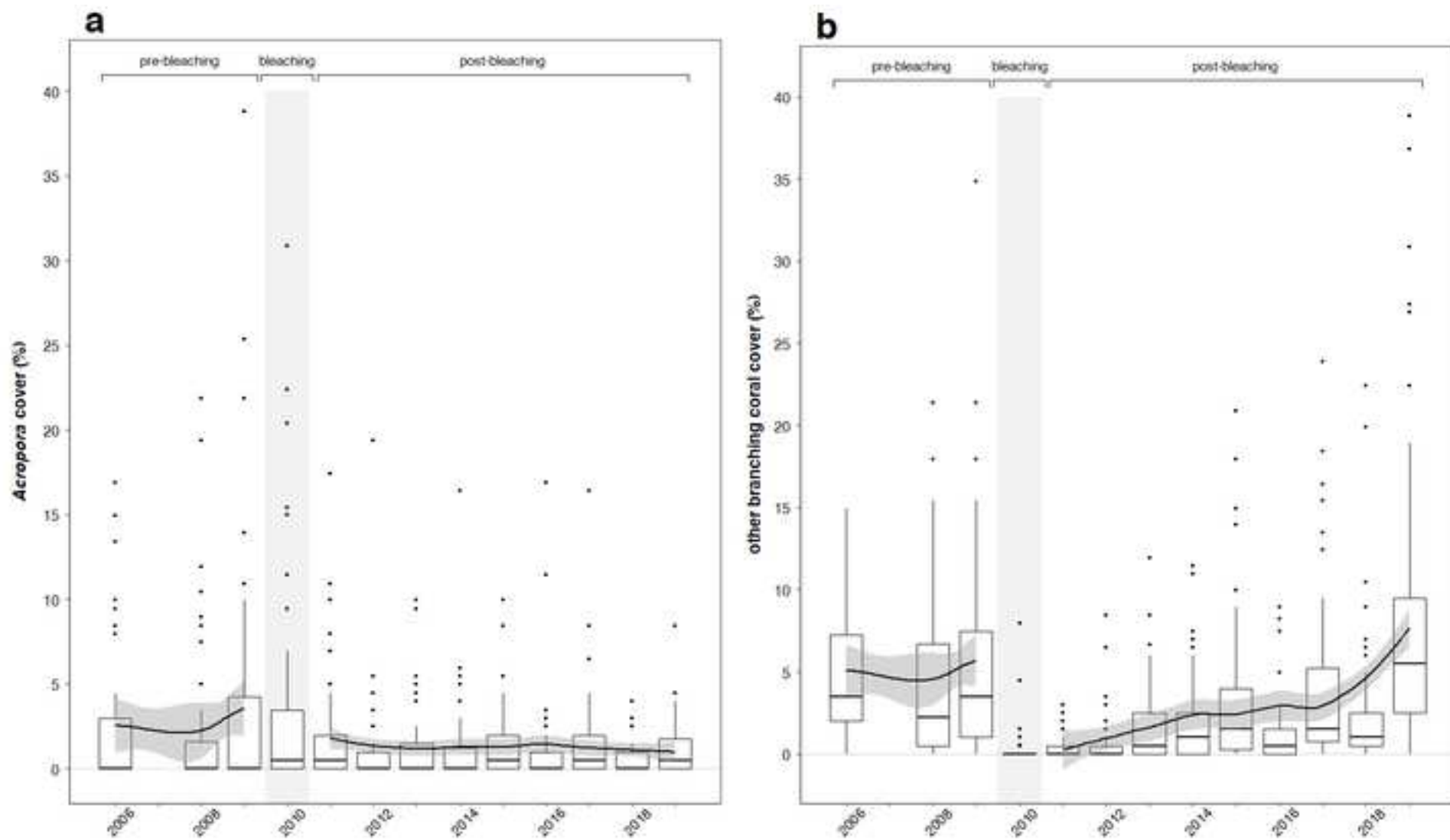


Fig1

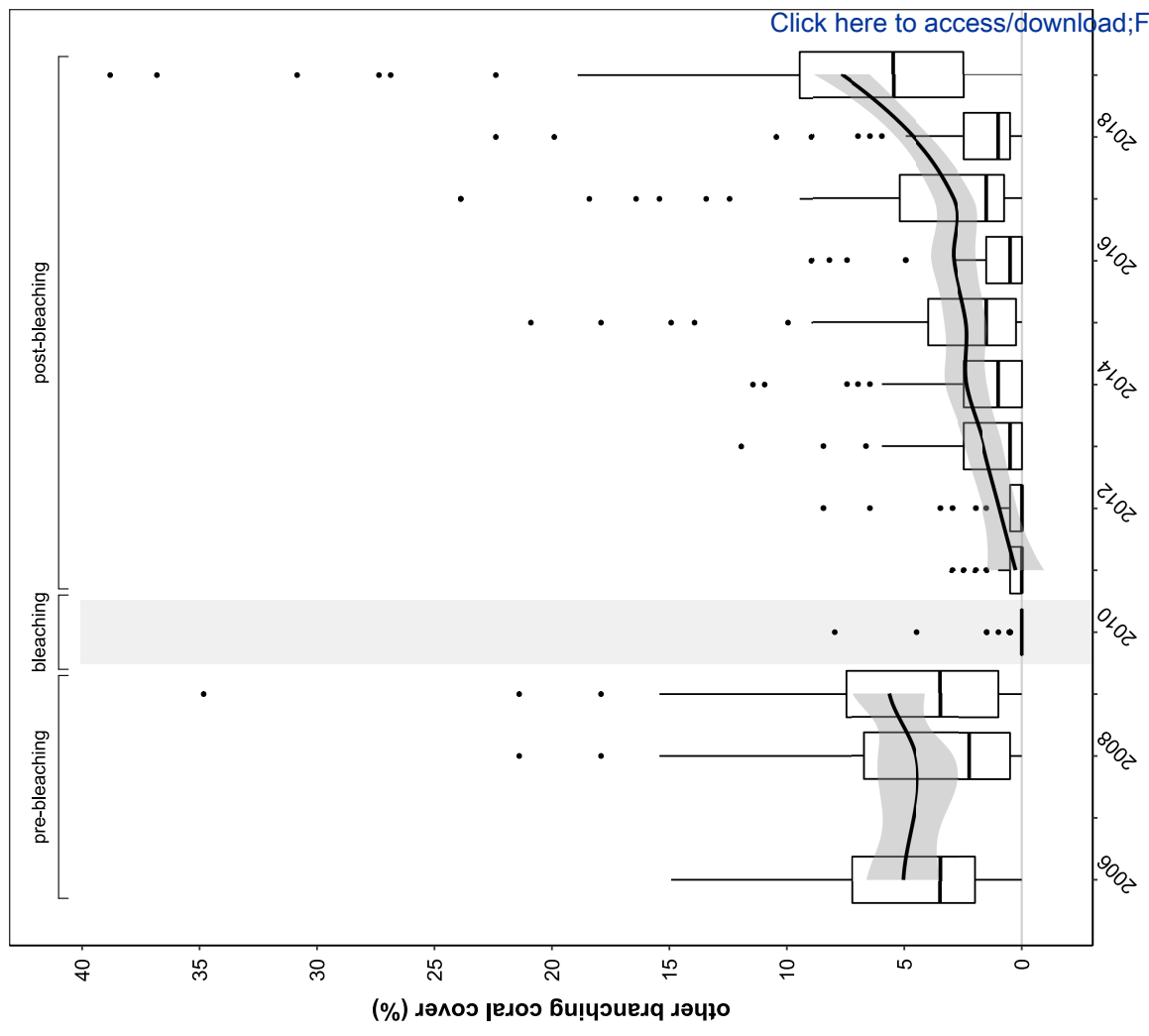




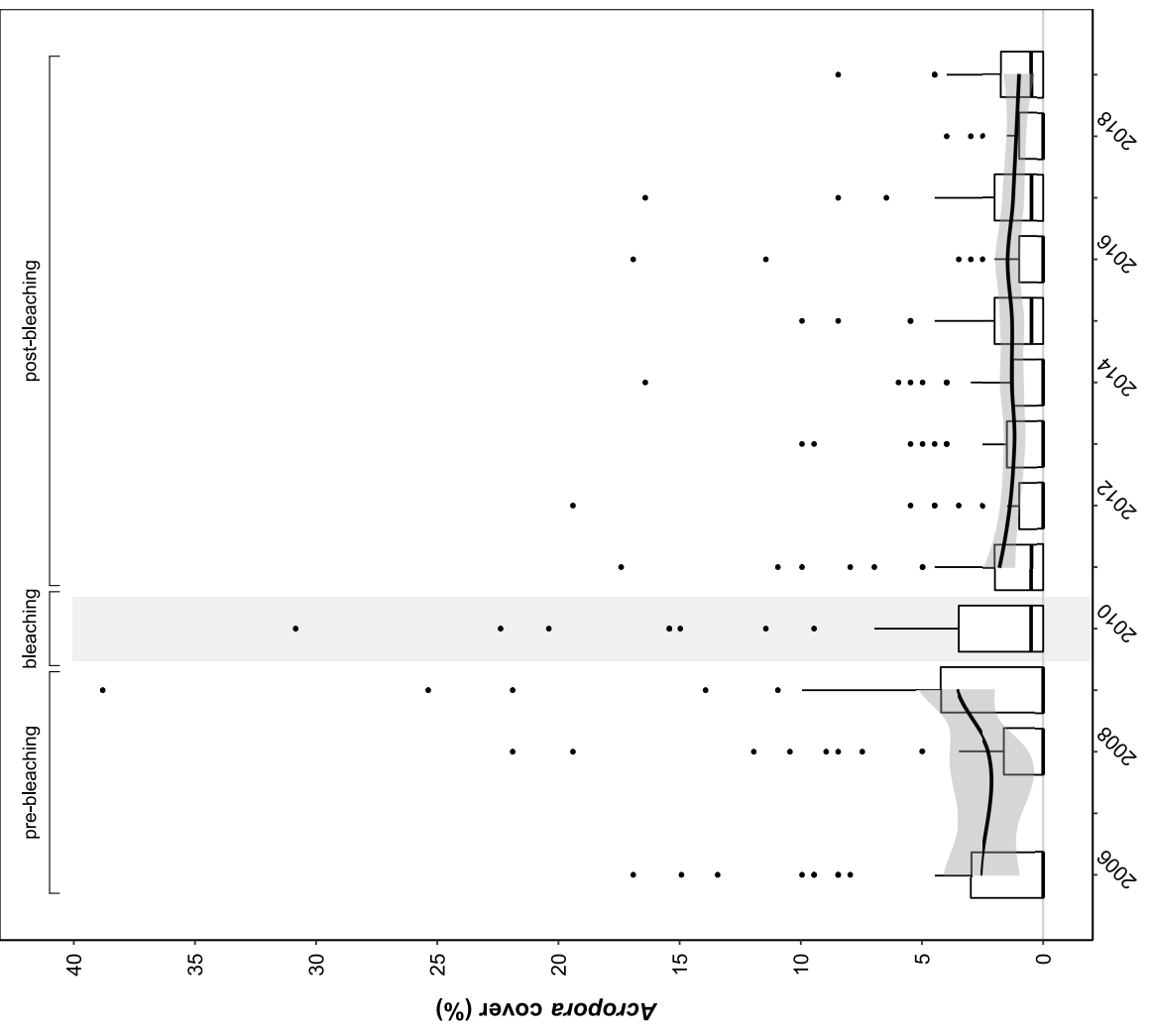


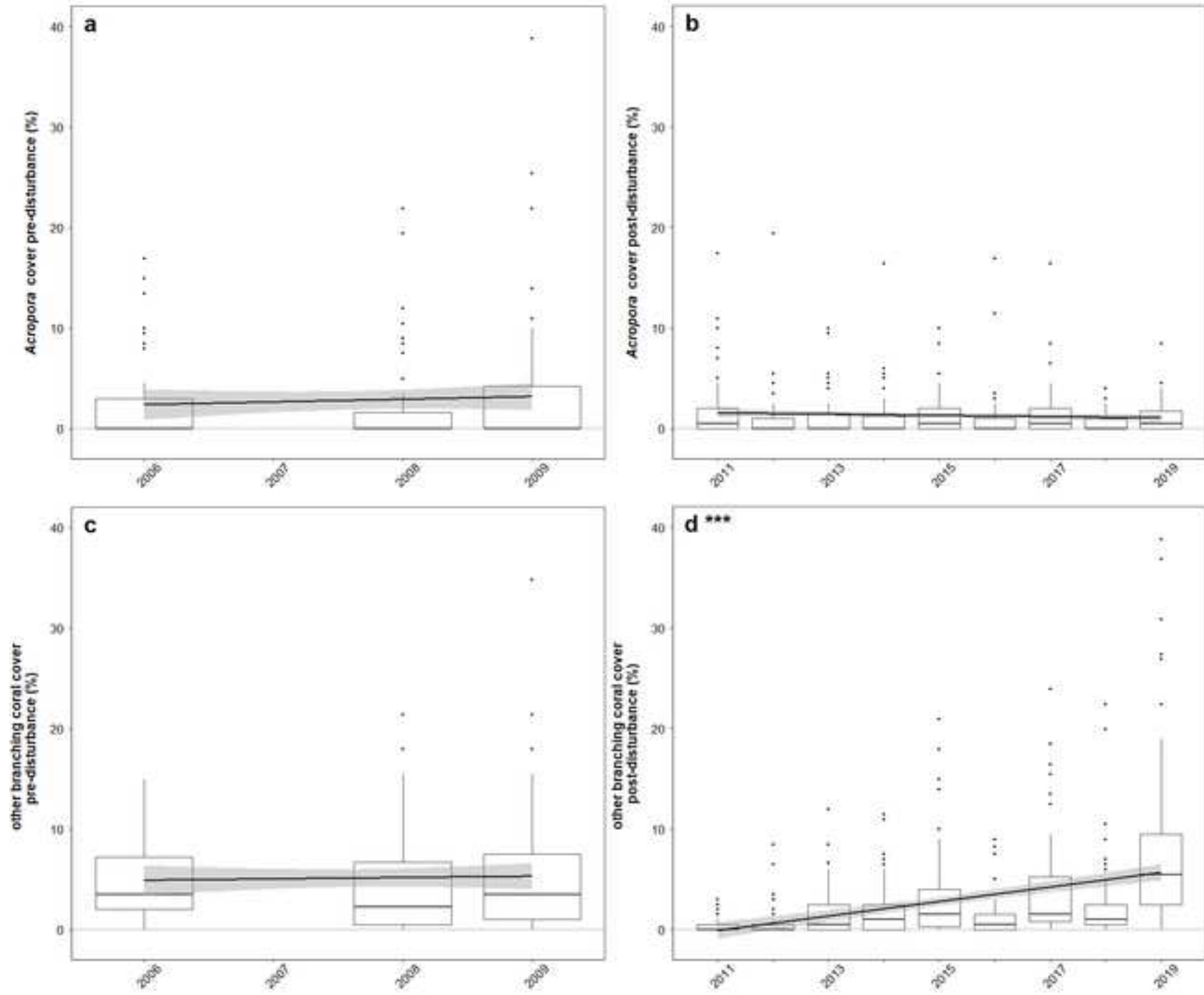


**b**

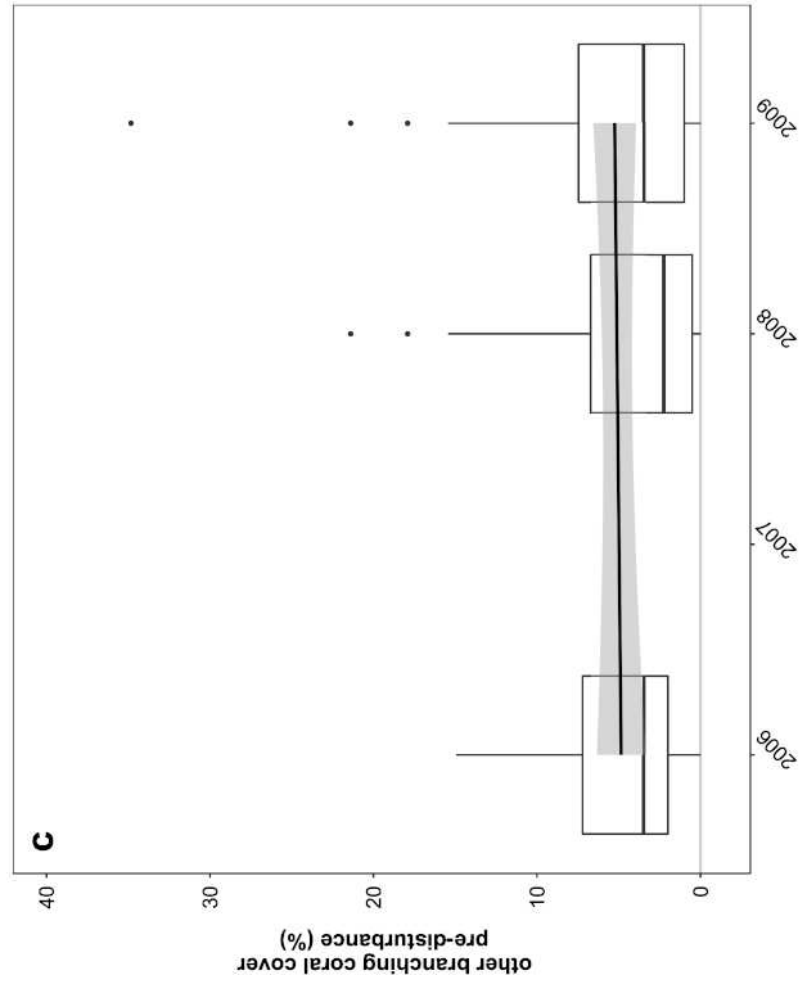
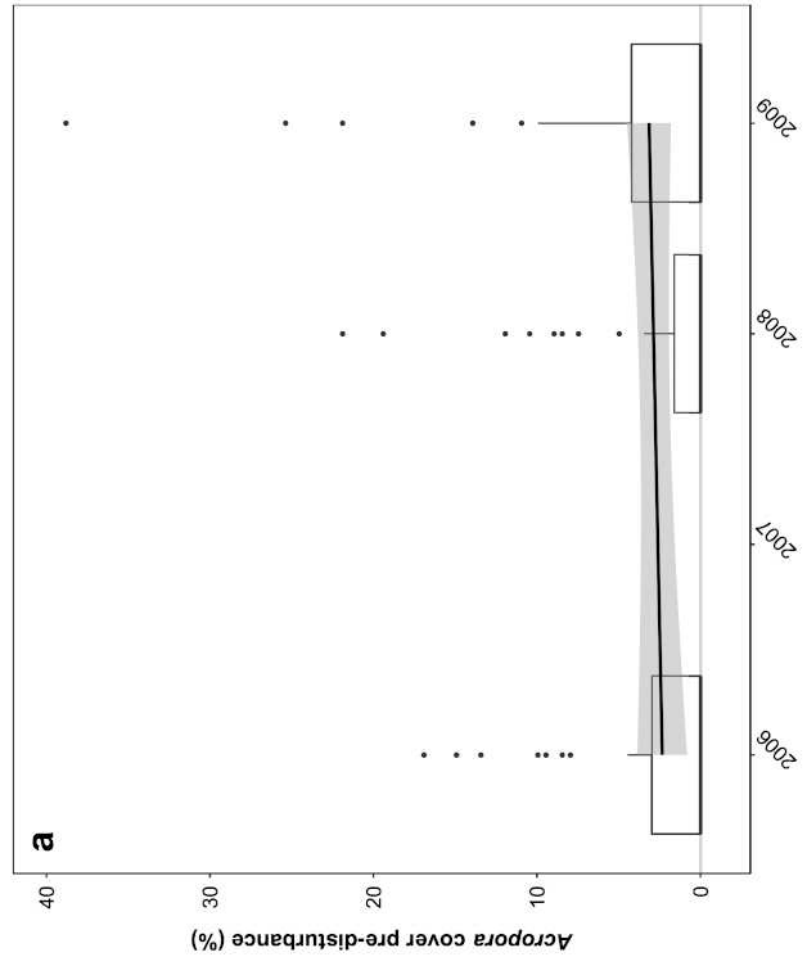
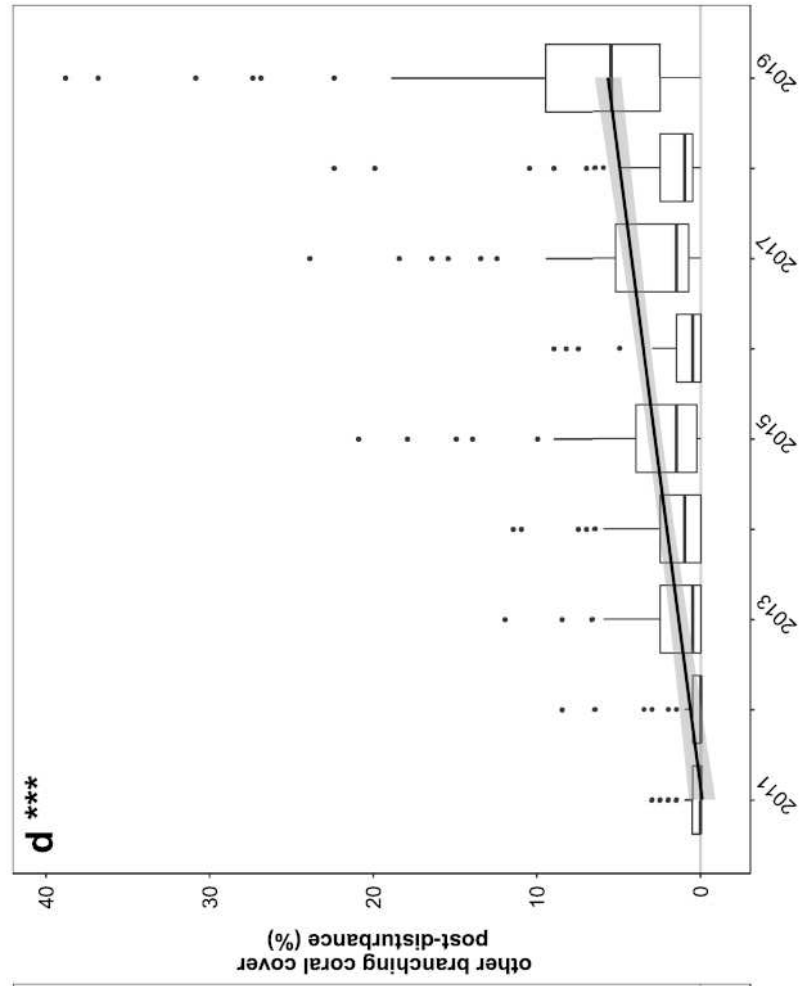
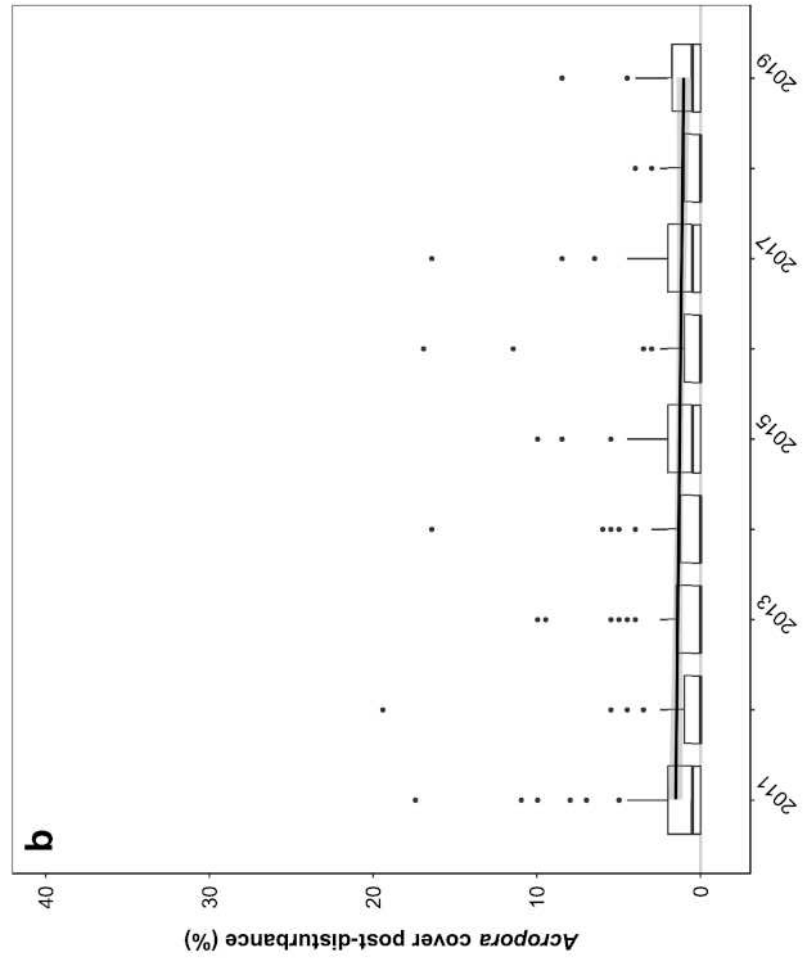


**a**









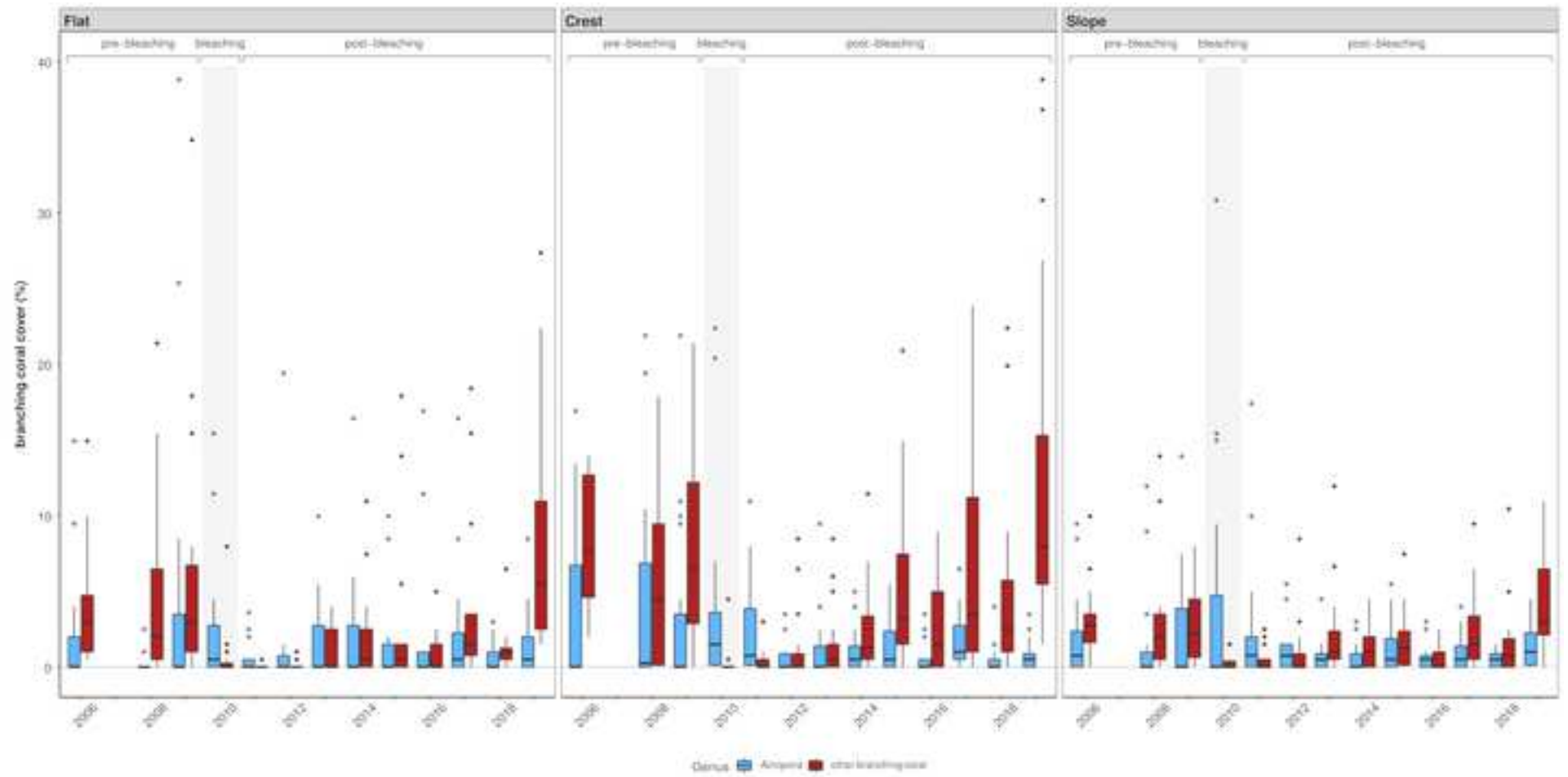
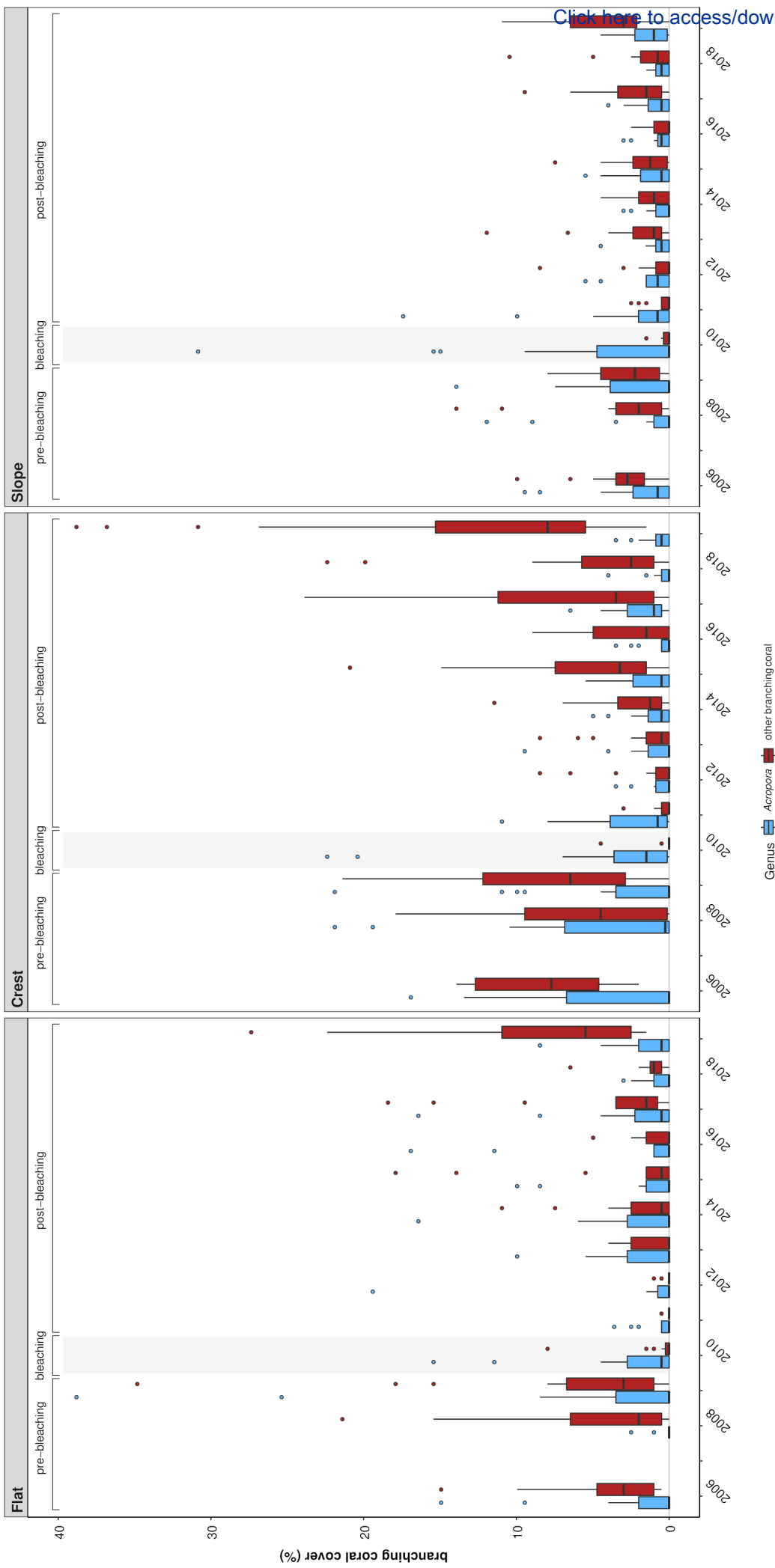
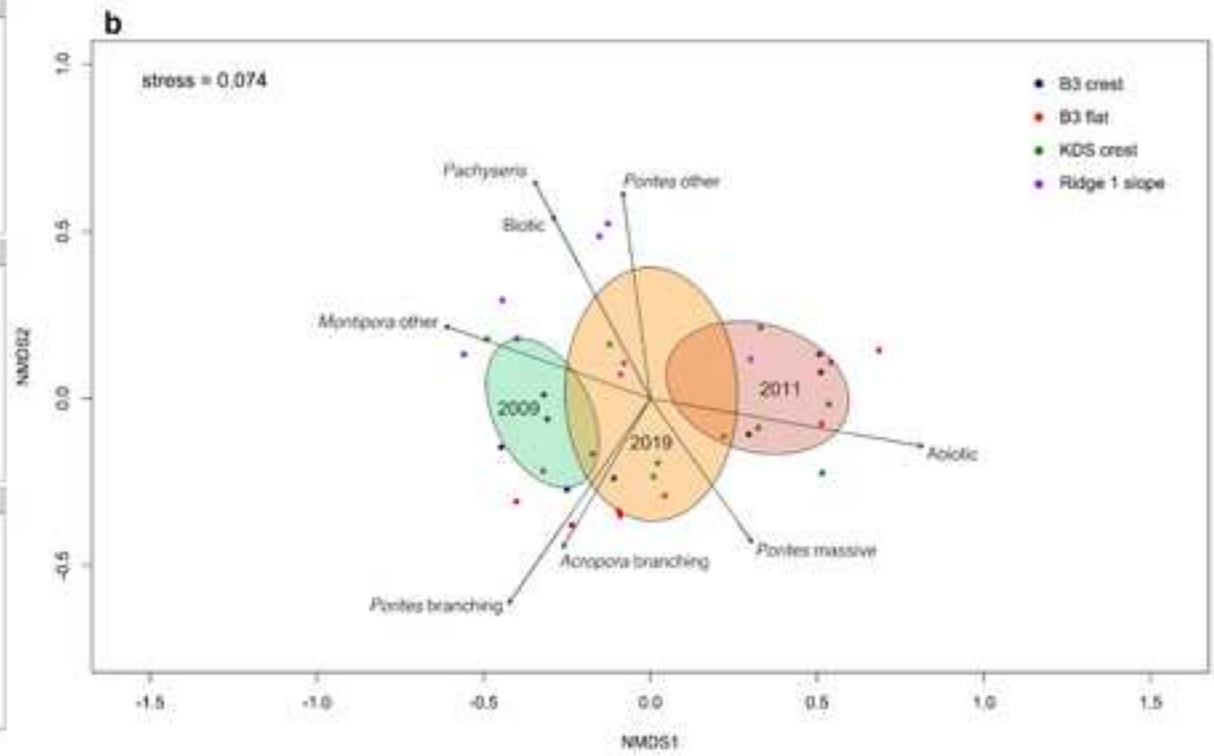
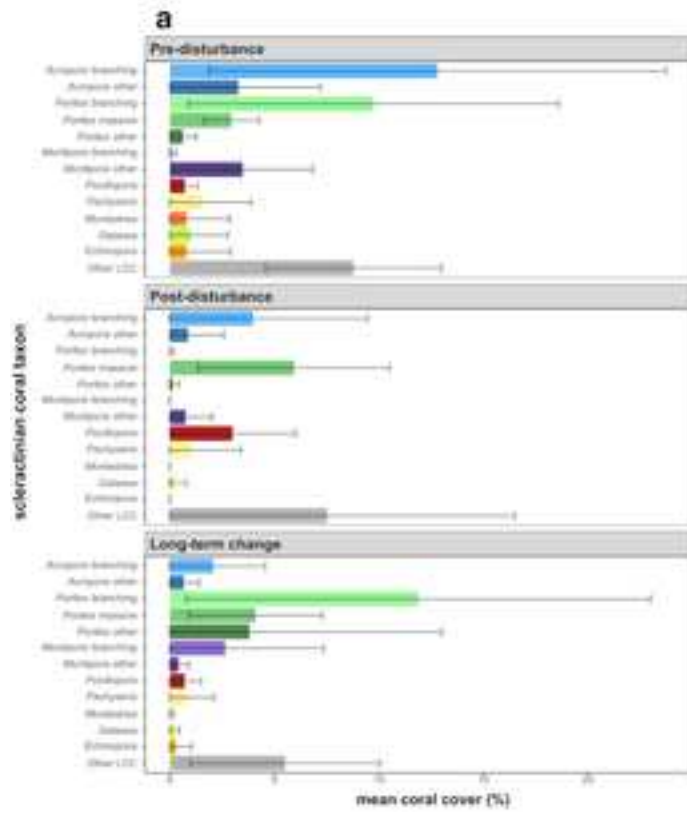
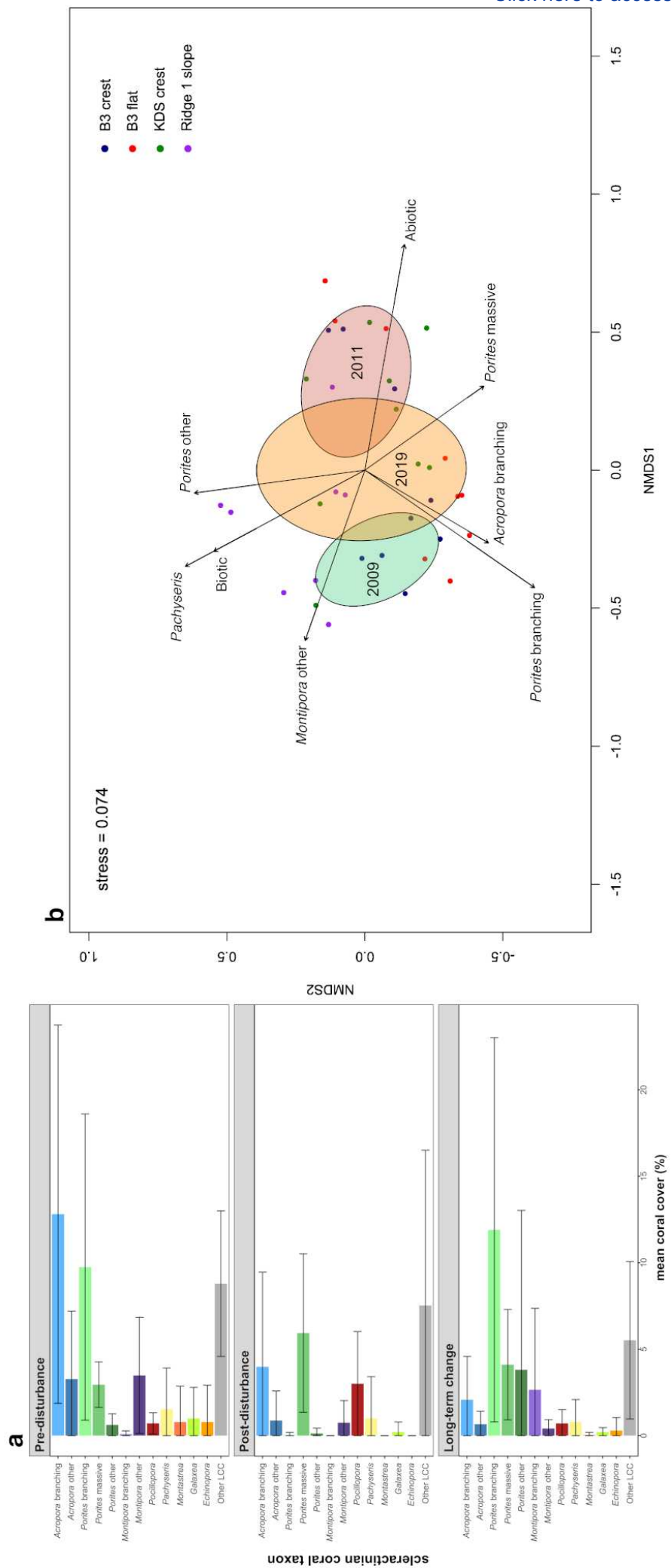


Fig5







## RESULTS TABLES

**Table 1**

Model	Model Type	Testing	Model Formula
A) BA <sub>gp2</sub>	Generalised-poisson	Effect of <i>TP</i> on BA	BA <sub>pts</sub> ~ offset(log(TR <sub>pts</sub> )) + TP * Site + ReefZone + (1   Year), family = genpois, data = modelsdf
B) OBC <sub>gp2</sub>	Generalised-poisson	Effect of <i>TP</i> on OBC	OBC <sub>pts</sub> ~ offset(log(TR <sub>pts</sub> )) + TP * Site + ReefZone + (1   Year), family = genpois, data = modelsdf

**Legend:** 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).

**Table 2**

<i>Acropora</i> (Model A)			
	Chisq	Df	Pr (>Chisq)
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 ***
Other branching corals (Model B)			
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

**Legend:** 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. 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.

**Table 3**

<b>Branching <i>Acropora</i></b>				
	<b>Sum Sq</b>	<b>Df</b>	<b>F value</b>	<b>Pr(&gt;F)</b>
Year	290.5	1	18.643	1.821e-05 ***
Residuals	10158.3	652		
<b>Other branching corals</b>				
Year	60.7	1	2.2675	0.1326
Residuals	17466.2	652		

---

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

**Legend:** 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 between year and OBC.

**Table 4**

<b>Pre-disturbance</b>				
	<b>Sum Sq</b>	<b>Df</b>	<b>F value</b>	<b>Pr(&gt;F)</b>
<b>Branching <i>Acropora</i></b>				
lm(formula = Year ~ BAperc, data = modelsdf, subset = (Period == "PreDist"))				
Year	0.814	1	0.5088	0.4768
Residuals	236.846	148		
<b>Other branching corals</b>				
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>				
<b>Branching <i>Acropora</i></b>				
lm(formula = Year ~ BAperc, data = modelsdf, subset = (Period == "PostDist"))				
Year	17.28	1	2.5662	0.1099
Residuals	3036.64	451		
<b>Other branching corals</b>				
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

**Legend:** 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.