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Abstract

Environmental anomalies that trigger adverse physiological responses and mortality are occurring with increasing frequency due to climate change. At species' range peripheries, environmental anomalies are particularly concerning because species often exist at their environmental tolerance limits and may not be able to migrate to escape unfavourable conditions. Here, we investigated the bleaching response and mortality of 14 coral genera across high-latitude eastern Australia during a global heat stress event in 2016. We evaluated whether the severity of assemblage-scale and genus-level bleaching responses was associated with cumulative heat stress and/or local environmental history, including long-term mean temperatures during the hottest month of each year (SST_{LTMAX}), and annual fluctuations in water temperature (SST_{VAR}) and solar irradiance ($PARZ_{VAR}$). The most severely-bleached genera included species that were either endemic to the region (*Pocillopora aliciae*) or rare in the tropics (e.g. *Porites heronensis*). *Pocillopora* spp., in particular, showed high rates of immediate mortality. Bleaching severity of *Pocillopora* was high where SST_{LTMAX} was low or $PARZ_{VAR}$ was high, whereas bleaching severity of *Porites* was directly associated with cumulative heat stress. While many tropical *Acropora* species are extremely vulnerable to bleaching, the *Acropora* species common at high latitudes, such as *A. glauca* and *A. solitaryensis*, showed little incidence of bleaching and immediate mortality. Two other regionally-abundant genera, *Goniastrea* and *Turbinaria*, were also largely unaffected by the thermal anomaly. The severity of assemblage-scale bleaching responses was poorly explained by the environmental parameters we examined. Instead, the severity of assemblage-scale bleaching was associated with local differences in species abundance and taxon-specific bleaching responses. The marked taxonomic disparity in bleaching severity, coupled with high mortality of high-latitude endemics, point to climate-driven simplification of assemblage structures and progressive homogenisation of reef functions at these high-latitude locations.

INTRODUCTION

The distribution of global biodiversity is undergoing substantial modifications as climate change accelerates and environmental anomalies become more frequent and severe (Butchart et al., 2010; Cheung et al., 2009; Parmesan & Yohe, 2003; Sala et al., 2000). One such climate-driven reconfiguration of global biodiversity during interglacial periods is linked to the propensity for cold-adapted species to migrate further toward the poles or to contract their distributions to range cores and for warm-adapted species to move toward range peripheries or to pursue *ex situ* refugia. This phenomenon, also termed 'tropicalisation' of high-latitude communities, is prevalent in both geological (Gavin et al., 2014; Greenstein & Pandolfi, 2008; Stewart, Lister, Barnes, & Dalen, 2010) and contemporary records (Chen, Hill, Ohlemuller, Roy, & Thomas, 2011; Parmesan & Yohe, 2003; Vergés et al., 2019; Wernberg et al., 2016), highlighting the significance of high-latitude regions in the persistence of many species under climate change. Interestingly, introduction of tropical species into high-latitude communities is not the only driver of contemporary changes in high-latitude community compositions. Climate-mediated changes in species interactions following the introduction of vagrant species into high-latitude communities (Kumagai et al., 2018; Smale et al., 2019; Vergés et al., 2019; Visser, 2008) and local rearrangements of species abundance (Tuckett, de Bettignies, Fromont, & Wernberg, 2017) can outweigh the direct influence of species range shifts on the changes in contemporary high-latitude community compositions. As such, understanding of the direct effects of progressive warming (e.g. gradual influx of tropical species), as well as the indirect effects of climate-mediated changes in species interactions and niche availability (e.g. the persistence and proliferation of resident high-latitude species) is fundamental to predicting changes in high-latitude communities.

While the tropicalisation of high-latitude communities is primarily driven by the direct and

indirect effects of progressive warming, acute thermal anomalies impose punctuated stress events that further alter the dynamics of resident high-latitude species (Smale et al., 2019). A common trend observed among high-latitude marine communities under progressive warming is a regime shift in foundation species from cold-adapted macroalgae to scleractinian corals (Kumagai et al., 2018; Smale et al., 2019; Vergés et al., 2014; 2019). Notwithstanding their increasing abundances, scleractinian corals at high-latitudes are also vulnerable to acute heat stress. Similar to tropical corals, high-latitude corals suffer coral bleaching under thermal conditions that exceed long-term local averages (Celliers & Schleyer, 2002; Cook, Logan, Ward, Luckhurst, & Berg, 1990; Dalton & Carroll, 2011). The impacts of bleaching in the tropics have been well-documented over the past three decades, and recent increases in the frequency of mass bleaching events have caused large-scale mortality among corals on tropical reefs (Hughes et al., 2017). While high-latitude coral assemblages along the coasts of Australia, the Atlantic, Japan, and South Africa have also experienced varying degrees of bleaching in previous years, the overall frequency of mass bleaching events has been considerably lower than in the tropics (Abdo, Bellchambers, & Evans, 2012; Celliers & Schleyer, 2002; Cook et al., 1990; Dalton & Carroll, 2011; Harrison, Dalton, & Carroll, 2011; Hongo & Yamano, 2013; Loya et al., 2001; Schleyer, Kruger, & Celliers, 2008).

Similar to tropical reefs (Hughes et al., 2018b), bleaching at high-latitudes is characterised by taxonomic differences in bleaching susceptibility and mortality, which can lead to changes in assemblage structure (Dalton & Carroll, 2011; Floros et al., 2004; Hongo & Yamano, 2013; Loya et al., 2001). Unfortunately, high-latitude regions are predicted to experience greater heat stress than the tropics over the coming decades (Hobday & Pecl, 2013; Wu et al., 2012), which is likely to result in increasingly frequent and intense regional bleaching events (Heron, Maynard, van Hooidonk, & Eakin, 2016; van Hooidonk, Maynard, & Planes, 2013; van

128   Hooidonk et al., 2016). However, unlike their tropical counterparts, poleward range shifts

129   and/or expansions are unlikely for many high-latitude coral species because suitable habitats

130   are progressively unavailable toward the poles, such as in the high-latitude east coast of

131   Australia and South Africa (Harriott & Banks, 2002; Schleyer et al. 2018; but see Booth &

132   Sears, 2018; Greenstein & Pandolfi, 2008; Richards et al., 2016). Similar to other flora and

133   fauna (Jablonski, 2008; Parmesan, 2006), many high-latitude corals may therefore contract

134   their geographic ranges and be more prone to extinction as their habitats become unsuitable

135   under climate change and/or they are unable to compete with incoming vagrant species.

136   Understanding the effects of punctuated stress events (e.g. thermal anomalies leading to

137   bleaching) on high-latitude coral assemblages provides critical insights into the emerging

138   changes in high-latitude community configurations over the coming decades.

139

140   In this study, we focus on the scleractinian coral assemblages of high-latitude coastal eastern

141   Australia that harbour diverse yet spatially patchy coral assemblages (Dalton & Roff, 2013;

142   Harriott & Banks, 2002; Sommer et al., 2017). These assemblages are inhabited by a subset of

143   species from the nearby, tropical Great Barrier Reef (GBR) to the north, and by subtropical

144   specialists that are either rare in the tropics or endemic to the region (Baird, Hoogenboom, &

145   Huang, 2017; Schmidt-Roach, Miller, & Andreakis, 2013; Veron, 2000). These coral

146   assemblages are increasingly susceptible to environmental stress as bleaching and disease

147   outbreaks are becoming more common under climate change (Dalton & Carroll, 2011; Dalton,

148   Godwin, Smith, & Pereg, 2010). During one of the harshest heat stress events recorded in the

149   region, the northern and central GBR suffered severe bleaching in 2016 (Hughes et al., 2017).

150   Here, we assess the impact of this heat stress event on the high-latitude coral assemblages

151   across 22 locations extending south of the GBR. Specifically, we investigate the relative

152   contributions of cumulative heat stress and local environmental history to the severity of

153 assemblage-scale and taxon-specific bleaching responses. Further, we quantify the importance

154 of taxonomic composition to assemblage-scale bleaching severity measurements. Lastly, we

155 discuss how taxonomic variability in bleaching vulnerability and immediate mortality, coupled

156 with geographic patterns in species composition, may lead to a reorganisation of high-latitude

157 coral assemblages. Together, the findings from this study improve our knowledge of the

158 vulnerability of high-latitude corals under climate change.

159

160 **MATERIALS AND METHODS**

161 **Bleaching surveys and response metrics**

162 We surveyed a total of 8,952 coral colonies across 22 sites along the subtropical east coast of

163 Australia spanning 26°S to 31°S (Fig. 1) between April and May 2016, using rapid underwater

164 assessment methods described below. The timing of our April survey coincided with the peak

165 of heat stress at 19 of the survey sites. Three additional sites (Black Rock, Cook Island, and

166 Julian Rocks) were surveyed in May, within six weeks of maximum heat stress. At each site, a

167 1 m^2 quadrat was placed every 5 m along three or four 25 m belt transects, laid at a depth

168 between 3 and 13 m depending on the topography and depth profile of each location. In each

169 quadrat, all coral colonies were identified to the genus level. Recent changes to the

170 nomenclature of regional species (Table S1) included divisions and synonymy of a few genera

171 (Arrigoni et al., 2016; Budd, Fukami, Smith, & Knowlton, 2012; Huang, Benzoni, Arrigoni, et

172 al., 2014a; Huang, Benzoni, Fukami, et al., 2014b). Members of the synonymised genera

173 showed minimal bleaching severity and no immediate mortality, suggesting negligible impact

174 of taxonomic updates on bleaching patterns found among the synonymised genera (Table S2).

175 The health of each colony was visibly assessed *in situ* and scored as a categorical variable with

176 five levels: (0) no visible bleaching, (1) 1-20% of the colony bleached, (2) 21-50% bleached,

177 (3) 51-80% bleached, and (4) 81-100% bleached. Pigmentation patterns of a coral can differ

178 depending on environmental conditions and location (Brown, Dunne, Ambarsari, Le Tissier,

179 & Satapoomin, 1999; Fitt, McFarland, Warner, & Chilcoat, 2000; Wallace, Fellegara, Muir, &

180 Harrison, 2009). Therefore, signs of pigmentation, such as a mottled or pale appearance, were

181 not included in the bleaching severity measurements, providing a conservative estimate of

182 bleaching responses. Coral colonies were scored as 'recently dead' (i.e. immediate post-

183 bleaching mortality) when live tissue was lost completely from the skeleton and an initial

184 colonisation of turf algae was evident.

185

186 The severity of the bleaching response for each coral genus was calculated for each survey

187 replicate as the weighted mean of the five health assessment categories (0-4, detailed above),

188 adjusted by the proportion of coral colonies in each category (i.e. bleaching index – measure

189 of taxon-specific bleaching response; modified from McClanahan, Baird, Marshall, &

190 Toscano, 2004; Eq. 1);

191 $$Bleaching\ index\ (BI) = \frac{1}{n-1} \sum_{i=0}^{n-1} \left(\frac{i * x_i}{X} \right), where\ X = \sum_{i=0}^{n-1} x_i \quad (Eq.\ 1)$$

192 where n is the number of health assessment categories ($n = 5$ in this study), with an increase in

193 the category value (i) indicating an increase in bleaching severity, and x_i is the number of coral

194 colonies in the ith category. A bleaching index value of 0 indicates none of the colonies are

195 affected by bleaching, and a value of 1 indicates that all colonies within a genus were affected

196 under the highest severity category. To obtain an estimate of site-level bleaching severity, we

197 used the site susceptibility index (SSI – measure of assemblage-scale bleaching response) that

198 considers the regional BI of each genus and weights the relative abundance of each genus

199 present at a specific site (modified from McClanahan et al., 2007b; Eq. 2);

200 $$Site\ susceptibility\ index\ (SSI) = \sum_{i=1}^{n} \frac{(\mu_{BI_i} * x_i) * 100}{X}, where\ X = \sum_{i=1}^{n} x_i \quad (Eq.\ 2)$$

201   where n is the number of taxa (i.e. genera) present at a site, μ_{BI_i} is the mean bleaching index for

202   the ith taxon across the region, and x_i is the number of coral colonies for the ith genus at the site.

203   Unlike the bleaching index, the site susceptibility index does not have a maximum positive

204   value limit. Higher SSI values indicate higher assemblage-scale susceptibility, and 0 SSI

205   suggests no colonies at the site were affected, irrespective of the taxonomic composition of the

206   assemblage.

207

208   **Environmental data**

209   To examine the effects of local-scale variability in cumulative heat stress and of long-term

210   environmental parameters on assemblage-scale and taxon-specific bleaching responses, we

211   compiled a suite of remote sensing satellite data. The Degree Heating Week (DHW) metric

212   was used as a measure of heat stress and calculated using version 3.1 of the NOAA Coral Reef

213   Watch dataset at 5 km spatial resolution (Liu et al., 2014). The conventional DHW metric

214   accumulates SST anomalies exceeding 1°C above the long-term maximum of the monthly

215   mean (MMM) climatology (hereafter DHW_{1C}). To assess the potential effect of low-magnitude

216   heat stress, we also computed DHW with the same MMM climatology, but without the 1°C

217   filter (hereafter DHW_{0C}; van Hooidonk & Huber, 2009). For any given heat stress event,

218   DHW_{0C} is greater than DHW_{1C} as it includes contributions when SST exceeds the MMM by

219   less than 1°C. We compared temperature measurements between remote sensing satellite and

220   *in situ* logger data (present at seven sites) to assess the robustness of our heat stress

221   measurements and long-term environmental parameters obtained from satellite data. Our

222   analysis showed that the satellite data provided robust approximations of *in situ* thermal

223   conditions (site-specific Pearson's correlation coefficients between satellite and logger were

224   between 0.88 and 0.92, with all p-values < 0.001; Fig. S1; Table S3).

225

226 Long-term environmental parameters derived from remote sensing satellite data included long-

227 term means of the hottest month of each year, and annual variability in thermal conditions and

228 solar irradiance. These parameters were selected based on experimental and *in situ* evidence in

229 the literature that showed their direct influence on bleaching severity (Brown, Dunne, Goodson,

230 & Douglas, 2002; Hoegh-Guldberg, 1999; Lesser, Stochaj, Tapley, & Shick, 1990;

231 McClanahan, Maina, Moothien-Pillay, & Baker, 2005). Long-term mean water temperature of

232 the hottest month of each year between 1985 and 2015 (hereafter SST_{LTMAX}) was used as a

233 measure of the upper-bound thermal conditions at each site. Using the same sea surface

234 temperature (SST) data, variability in thermal conditions (hereafter SST_{VAR}) was calculated as

235 the long-term mean of the standard deviation of annual SST. Further, we calculated annual

236 variation in solar irradiance (hereafter $PARZ_{VAR}$) as the long-term mean of the standard

237 deviation of annual photosynthetically active radiation (PAR) between 2002 and 2015. The

238 amount of PAR reaching the benthos decreases with depth and with increasing turbidity (Read,

239 Rose, Winslow, & Read, 2015), and we adjusted the PAR values at each site accordingly (i.e.

240 PARZ; Pierson, Kratzer, Strömbeck, & Håkansson, 2008; Eq. 3);

$$PARZ = PAR_0 * e^{(-K490 * Z)} \text{ (Eq. 3)}$$

242 where *PAR₀* is PAR on the surface, *K490* is the diffuse attenuation coefficient (a measure of

243 turbidity), and *Z* is the survey depth at each site. SST_{VAR} and $PARZ_{VAR}$ are particularly relevant

244 for high-latitude reefs because the monthly and seasonal fluctuations of these parameters are

245 greater in high-latitude regions than most locations in the tropics (Beger, Sommer, Harrison,

246 Smith, & Pandolfi, 2014; Malcolm, Davies, Jordan, & Smith, 2011; Sommer, Beger, Harrison,

247 Babcock, & Pandolfi, 2018). SST_{LTMAX} and SST_{VAR} were calculated using version 3.1 of the

248 NOAA Coral Reef Watch dataset at 5 km spatial resolution (Liu et al., 2014). PAR and K490

249 data were obtained from the Global Moderate Resolution Imaging Spectroradiometer (MODIS)

250 Aqua Satellite products at 4 km resolution (Parkinson, 2003).

251

Data analyses

Assemblage-scale bleaching response

Before examining the effects of environmental parameters and taxonomic composition on assemblage-scale bleaching responses, we first checked for multicollinearity of environmental parameters using Pearson's correlation coefficient and variance inflation factor (VIF) with cut-offs of $r = \pm 0.65$ and $VIF = 2$, respectively (Craney & Surles, 2007; Gordon, 2015). DHW_{1C} showed a higher VIF value and larger Pearson's correlation coefficients with other environmental variables than those exhibited by DHW_{0C}. Therefore, DHW_{0C} was used in all our models (Fig. S2; Table S4). Subsequently, we evaluated a variety of variable combinations using the widely applicable information criterion (WAIC) and leave-one-out cross-validation (LOO) to select the final model (Table S5; Vehtari, Gelman, & Gabry, 2017). The final model included DHW_{0C}, SST_{LTMAX}, SST_{VAR}, and $PARZ_{VAR}$ as independent environmental parameters. VIF and model selection criteria were computed using the 'usdm' (Naimi, Hamm, Groen, Skidmore, & Toxopeus, 2014) and 'loo' (Vehtari et al., 2017) packages. All modelling and analyses in this study were conducted in R (R Core Team 2018).

We used hierarchical Bayesian generalised linear models with student's t-distribution to assess the effects of heat stress, long-term environmental parameters, and the relative abundance of each taxon in an assemblage on regional assemblage-scale (SSI) bleaching responses. To account for spatial autocorrelation stemming from geographic clustering of survey sites, survey site location was included as a random effect after categorisation into seven groups based on geographic proximity and shelf position: Inner Moreton Bay, Outer Moreton Bay, Northern New South Wales, Inshore Solitary Islands, Mid-shelf Solitary Islands, Offshore Solitary Islands, and Central New South Wales (see Table S6 for detailed site information). Models

were executed in Stan (Carpenter et al., 2017) with weakly informative normal priors assigned

for beta parameters and gamma priors for degrees of freedom. All Stan models were called

from R using the 'rstan' package (Stan Development Team 2018). Each model was run with

four chains of 20,000 iterations; the first 10,000 iterations were discarded as warm-up, and all

subsequent iterations were sampled. We examined all chains for model convergence, the

adequacy of warm-up, and autocorrelation (Fig. S3). The Gelman-Rubin diagnostic ($\hat{R}$)

compares the variance of each chain to the compiled variance of all chains, and values under

1.001 are desirable to ensure appropriate chain convergence (Gelman & Shirley, 2011). $\hat{R}$

values for all parameters of the assemblage-scale response models were equal to or below 1.

Model fits were summarised using the highest posterior density (HPD) interval as the credible

interval, and median point estimates for all chains were computed.

Taxon-specific bleaching responses

Taxonomic variability in overall bleaching severity across our survey sites was tested by

comparing the bleaching index (BI) of the five most abundant genera (*Acropora*, *Goniastrea*,

Pocillopora, *Porites*, and *Turbinaria*) using an analysis of variance (ANOVA) and Tukey's

post-hoc test. We also used generalised additive models (GAM) to test whether the taxon-

specific BI was linked to the relative proportion of 'recently dead' colonies (i.e. immediate

mortality). *Goniastrea* and *Turbinaria* were excluded from the mortality analysis as they

suffered no or negligible mortality (*Goniastrea*: no mortality; *Turbinaria*: one colony mortality

across all survey sites). GAMs were run using the 'mgcv' package in 'R' (Wood, 2011).

The influence of heat stress and long-term environmental parameters on the taxon-specific

bleaching index (BI) was examined using a hierarchical Bayesian beta regression model with

logit link. The taxon-specific response model was restricted to the same five most abundant

13

genera and executed in Stan (Carpenter et al., 2017), with weakly informative normal priors

assigned for beta parameters and gamma priors for the dispersion parameter. In addition to the

geographic group random effect in the assemblage-scale models (Table S6), survey site

locations were included as a second random effect nested in geographic group to account for

survey replicates within the same site. The taxon-specific BI values were transformed using a

data range compression method (Smithson & Verkuilen, 2006) to preserve crucial information

in zero (no bleaching) values. The taxon-specific response model was run with the same

number of chains, iterations, and warm-up as the assemblage-scale response models (model

diagnostics – Fig. S4). $\hat{R}$ values for all parameters of the taxon-specific response model were

equal to or below 1.

Inferring Bayesian results

Estimated model coefficients (β coefficients) indicate the modelled effect of a given predictor

on bleaching severity. Positive and negative β coefficients suggest corresponding strength of

positive or negative correlation between a given predictor variable (environmental parameter,

relative abundance of taxa) and the response variable (bleaching severity). The HPD intervals

reflect the distribution of β coefficients (i.e. distribution of modelled effects of a predictor on

bleaching severity) that is supported by the data. A high precision of β coefficients leads to a

high probability density and narrow posterior distribution of β coefficients, whereas low

precision of β coefficients results in low probability density and wide posterior distribution of

β coefficients.

Spatial patterns of coral bleaching impacts

To examine spatial patterns of taxon-specific bleaching severity and their subsequent impacts

on local assemblage structures, we examined the correlation between taxon-specific bleaching

326   severity of the five most abundant genera and latitude, as well as the correlation between their

327   relative abundances and latitude using Pearson's correlation coefficient. The Coffs Harbour

328   region has the most extensive high-latitude coral assemblages along the east coast of Australia,

329   whereas assemblages elsewhere in the region are generally more patchy in their distribution

330   with considerably lower coral cover (Fig. 1; Dalton & Roff, 2013; Harriott, Smith, & Harrison,

331   1994; Harriott & Banks, 2002). To examine whether the disproportionate concentration of

332   survey sites near Coffs Harbour skewed spatial patterns of bleaching severity and assemblage

333   compositions, we conducted a sensitivity test. A random number of survey replicates were

334   selected from the survey sites near Coffs Harbour and were combined with survey replicates

335   from other sites. Subsequently, these combined site datasets were used to test correlations

336   between taxon-specific bleaching index (BI) of the five most abundant genera and latitude, as

337   well as their relative abundances and latitude. This process was repeated 1,000 times and

338   summary statistics of the iterations were used to infer statistical significance of the correlations

339   between taxon-specific bleaching severity and latitude, and between relative abundance and

340   latitude.

341

342   **RESULTS**

343   **Assemblage-scale bleaching response**

344   The environmental parameters explored here did not capture the observed differences in

345   assemblage-scale bleaching severity (Site susceptibility index – SSI; Fig. 2a; Table S7). In

346   particular, estimated model coefficients for all environmental parameters were centred near

347   zero with wide posterior density intervals, indicating that these parameters were poorly

348   associated with the patterns of assemblage-scale bleaching responses. Model residuals also

349   showed no gradient pattern between all bivariate environmental variable combinations,

350   indicating that two-way interactive effects between tested environmental variables also were

351   unrelated to assemblage-scale bleaching severity (Fig. S5). In contrast, the variation in

352   taxonomic composition among assemblages was linked to the site susceptibility index (SSI).

353   The relative abundance of *Pocillopora,* in particular, was strongly associated with SSI (Fig. 2b;

354   Table S8). SSI was higher at sites where *Pocillopora* was more abundant. Posterior density

355   intervals of β coefficients for other genera, including regionally common *Acropora*, *Goniastrea*,

356   *Porites*, and *Turbinaria*, were wide and crossed zero, indicating an unlikely association

357   between the relative abundance of these genera and assemblage-scale bleaching severity.

358

359   **Taxon-specific bleaching responses**

360   Taxon-specific bleaching severity and immediate mortality were strikingly different among the

361   five most abundant genera (Fig. 3; Table S9; Table S10). Among the five most abundant genera,

362   *Pocillopora* and *Porites* were significantly more susceptible to bleaching than *Acropora*,

363   *Goniastrea*, and *Turbinaria* (Fig. 3a; Table S9). Despite the similarity in the bleaching index

364   (BI) values of the two severely impacted genera, they differed in patterns of mortality; mortality

365   rose as BI increased for *Pocillopora*, whereas mortality and BI were not correlated for *Porites*

366   (Fig. 3d; Fig. 3e; Table S10). *Acropora*, *Goniastrea*, and *Turbinaria* also had similar degrees

367   of bleaching to one another, and exhibited little or no bleaching (Fig. 3a; Table S9) or mortality

368   (Fig. 3b; Fig. 3c; Fig. 3f; Table S10).

369

370   The taxon-specific bleaching severity (BI) was associated with environmental predictors, yet

371   the specific predictors that affected bleaching severity responses differed among genera (Fig.

372   4; Table S11). Bleaching worsened with increasing heat stress (DHW) for *Porites* (Fig. 4a),

373   whereas *Pocillopora* bleached more at sites where water temperature was historically cooler

374   (SST$_{LTMAX}$; Fig. 4b), or experienced higher fluctuations in annual solar irradiance (PARZ$_{VAR}$;

375   Fig. 4d). The bleaching severities of *Pocillopora* and *Porites* were not linked to the annual

376 variation in historical water temperature (SST$_{VAR}$; Fig. 4c). Contrary to the clear associations

377 between bleaching severity and environmental parameters found among *Pocillopora* and

378 *Porites*, bleaching severities of *Acropora*, *Goniastrea*, and *Turbinaria* were not correlated with

379 any of the examined environmental parameters. Overall absolute model residuals were low for

380 *Acropora*, *Goniastrea*, and *Turbinaria,* whereas *Pocillopora* and *Porites* showed considerably

381 higher absolute model residuals without a notable pattern between all bivariate environmental

382 variable combinations (Figure S6).

383

384 **Spatial patterns of bleaching severity**

385 The geographic pattern in bleaching severity (BI) and the relative effect of bleaching on local

386 populations differed among genera (Fig. 5; Fig. S7; Fig. S8; Table S12). Overall, the severity

387 of bleaching response for the genus *Acropora* was minimal and did not vary across latitude

388 (Table S12; mean r = -0.26, R^2 = 0.07, p = 0.12), while the relative proportion of *Acropora* in

389 assemblages declined toward higher latitudes (Fig. 5a; mean r = -0.55, R^2 = 0.3, p < 0.01).

390 Bleaching severity of *Goniastrea* declined toward higher latitudes (Fig. 5b; mean r = -0.54, R^2

391 = 0.29, p < 0.01), without a corresponding change in relative abundance (Fig. 5a). Bleaching

392 was also less severe for *Turbinaria* toward higher latitudes (Fig. 5d; mean r = -0.46, R^2 = 0.21,

393 p < 0.01), yet its relative contribution to the total species assemblage increased with latitude

394 (Fig. 5a; mean r = 0.56, R^2 = 0.32, p < 0.01). In contrast, bleaching severity for *Pocillopora*

395 increased with latitude (Fig. 5c; mean r = 0.51, R^2 = 0.27, p < 0.01), without a significant

396 change in its relative abundance across latitude (Fig. 5a; mean r = 0.23, R^2 = 0.06, p = 0.12).

397 There was no correlation between bleaching severity (Table S12; mean r = 0.002, R^2 = 0.004,

398 p = 0.85) or relative abundance and latitude for *Porites* (Fig. 5a; mean r = 0.32, R^2 = 0.12, p =

399 0.08).

400

DISCUSSION

Analysis of the spatial and taxonomic patterns of coral bleaching allows us to identify specific coral taxa or assemblages vulnerable to climate change and to predict future configurations of coral assemblages (Hughes et al., 2018a; 2018b; Loya et al., 2001; van Woesik, Sakai, Ganase, & Loya, 2011). Our findings highlight that in high-latitude eastern Australia, assemblage-scale patterns of coral bleaching are heavily influenced by local abundance of a regionally common genus sensitive to heat stress, *Pocillopora*, instead of environmental gradients. Further, the clear distinction in taxon-specific bleaching severity and immediate mortality, coupled with spatial patterns of taxon-specific bleaching responses and abundances, may lead to simplification of assemblage structures and gradual homogenisation of reef functions.

The importance of taxonomic composition in assemblage-scale bleaching responses

Bleaching among the high-latitude coral assemblages along eastern Australia was initiated by record heat stress in early 2016 (Fig. S9). Nevertheless, regional variability in the severity of assemblage-scale bleaching responses (SSI – site susceptibility index) was poorly explained by cumulative heat stress (Degree Heating Weeks) and long-term environmental conditions. While remote sensing satellite data provided robust estimates of the regional variation in water temperature (Fig. S1; Table S3), they were unlikely to capture fine temporal- and spatial-scale variation in environmental conditions due to their coarser measurement scales than *in situ* loggers (e.g. Castillo & Lima, 2010). It is plausible that these fine temporal- and spatial-scale environmental parameters might include predictors that are better able to explain the observed patterns of assemblage-scale bleaching severity, such as local high-frequency temperature variability (Safaie et al., 2018).

425   Interestingly, the severity of assemblage-scale bleaching responses was associated with the

426   relative abundance of *Pocillopora*, a genus that is highly susceptible to heat stress (Fig. 3; Loya

427   et al., 2001; Marshall & Baird, 2000; McClanahan et al., 2004; van Woesik et al., 2011). By

428   definition, assemblage-scale bleaching metrics (e.g. SSI, Eq. 2) are influenced by both species

429   abundances and their respective bleaching responses. Severe bleaching of a single, locally

430   dominant species in an assemblage can produce a comparable SSI value (or an assemblage-

431   scale percentage of bleached corals) to another assemblage where many different species

432   experienced mild bleaching. As such, assemblage-scale metrics can be difficult to interpret or

433   may poorly explain the bleaching dynamics for coral assemblages characterised by high

434   variation in community structure. The close linkage between the abundance of bleaching-

435   susceptible taxa and assemblage-scale bleaching severity thus highlights the limitations of

436   assemblage-scale bleaching metrics and supports the idea that assessments of bleaching impact

437   should consider spatial variation in community composition and taxon-specific (e.g. species-

438   or genus-specific) bleaching responses (Marshall & Baird, 2000; Fitt, Brown, Warner, &

439   Dunne, 2001; Safaie et al., 2018).

440

441   **Taxon-specific environmental drivers of bleaching severity responses**

442   Contrary to the overall lack of association between environmental parameters and assemblage-

443   scale bleaching severity (SSI), taxon-specific bleaching (BI) patterns for *Porites* and

444   *Pocillopora* showed clear linkages to environmental parameters. Interestingly, *Porites* was the

445   only genus whose bleaching severity escalated with heat stress (Fig. 4a). *Porites* species with

446   massive growth forms are generally considered to be less sensitive to bleaching (Loya et al.,

447   2001; Marshall & Baird, 2000; McClanahan et al., 2004), yet encrusting *Porites* species, such

448   as those abundant along the high-latitude eastern Australia and at other high-latitude regions,

449   can be vulnerable to heat stress and susceptible to bleaching (Dalton & Carroll, 2011; van

450 Woesik et al., 2011). On the other hand, patterns of bleaching severity for *Pocillopora* were

451 best explained by long-term environmental conditions. Specifically, prior exposure to warm

452 temperature (SST_{LTMAX}) and low variability in solar irradiance ($PARZ_{VAR}$) reduced the severity

453 of bleaching. These patterns are consistent with previous findings, in which long-term exposure

454 to higher temperature was linked to a reduction in acute responses to heat stress (Brown et al.,

455 2002; Brown & Dunne, 2016; Griffin, Bhagooli, & Weil, 2006; Woolsey, Keith, Byrne,

456 Schmidt-Roach, & Baird, 2015). A recent study on *Pocillopora* also highlighted that

457 experimental transplantation of coral colonies from low to high fluctuations in PAR increased

458 the sensitivity of corals to heat stress (Sampayo et al., 2016). While previous studies indicated

459 that exposure to fluctuating water temperature might enhance thermal tolerance (McClanahan,

460 Ateweberhan, Muhando, Maina, & Mohammed, 2007a; Woolsey et al., 2015), we found that

461 fluctuation in annual water temperature had little effect on taxon-specific bleaching severity.

462 This lack of correlation between fluctuation in water temperature and taxon-specific bleaching

463 severity may be due to the narrower range of SST_{VAR} across our survey sites (< 2.4°C)

464 compared to the previously reported experimental threshold for biological responses among

465 regional corals (+4°C; Woolsey et al., 2015).

466

467 Patterns of bleaching severity for *Acropora*, *Goniastrea*, and *Turbinaria* were not linked to any

468 of the explored environmental parameters. The genus *Acropora* contains numerous tropical

469 species that tend to suffer severe bleaching and mortality during mass bleaching events

470 (Goreau, McClanahan, Hayes, & Strong, 2000; Hughes et al., 2019; Marshall & Baird, 2000;

471 McClanahan et al., 2004). However, our findings showed that high-latitude *Acropora* species,

472 such as *A. glauca* and *A. solitaryensis*, were resistant to heat stress. Low sensitivity to bleaching

473 among high-latitude *Acropora* spp. has also been reported in other parts of the globe,

474 highlighting distinctive bleaching resilience among high-latitude members of this genus

475 (Celliers & Schleyer, 2002; van Woesik et al., 2011; but see Hongo & Yamano, 2013). Overall,

476 the variability in taxon-specific bleaching responses under the same environmental conditions

477 observed across our study sites supports the notion that mild to moderate bleaching episodes

478 can identify locally/regionally resistant (e.g. *Goniastrea*, *Turbinaria*, and high-latitude

479 *Acropora* spp.) and vulnerable (e.g. *Pocillopora* and regional encrusting *Porites* spp.) taxa

480 (Hughes et al., 2017, 2018b; Loya et al., 2001; Marshall & Baird, 2000; van Woesik et al.,

481 2011). However, the distinction between bleaching tolerant and susceptible taxa likely varies

482 in space and with environmental conditions, such as local environmental history and

483 microhabitats (Safaie et al., 2018), and biological factors, including species identity, traits

484 (Mizerek, Baird, & Madin, 2018), and the presence of locally adapted genotypes (Bay &

485 Palumbi, 2014; LaJeunesse, Reyes-Bonilla, & Warner, 2007). Long-term studies that examine

486 taxon-specific bleaching mechanisms over a broad spatial scale are therefore needed to

487 understand shifts in ecosystem dynamics under climate change.

488

489 **Regional implications of taxonomic variability in bleaching impact and abundance**

490 Against the backdrop of species migrations (Baird, Sommer, & Madin, 2012) and

491 tropicalisation of high-latitude marine ecosystems (Smale et al., 2019; Vergés et al., 2014;

492 2019; Wernberg et al., 2016), taxon-specific bleaching, mortality, and spatial abundance

493 patterns have the potential to broadly affect ecosystem structure and functioning (Hughes et

494 al., 2003; 2018b; Pandolfi, Connolly, Marshall, & Cohen, 2011; Stuart-Smith, Brown,

495 Ceccarelli, & Edgar, 2018). While both *Pocillopora* and *Porites* experienced severe bleaching,

496 bleaching severity was only linked to immediate mortality of *Pocillopora* (Fig. 3d). Post-

497 bleaching mortality data from the Solitary Islands showed that the immediate mortality pattern

498 of *Pocillopora* observed in this study worsened, and *Pocillopora* suffered significant declines

499 in abundance (Cant et al. 2018). In contrast, *Turbinaria* was the only genus that experienced

mild bleaching, was more abundant at higher latitudes, and did not suffer severe bleaching or mortality (Fig. 3f; Cant et al. 2018). These patterns suggest that recurrent bleaching and mortality events may lead to increased dominance of *Turbinaria* and declines of *Pocillopora* on high-latitude reefs, especially if the capacity for population recovery is affected by the severity of bleaching (Hughes et al., 2019).

On tropical coral reefs, changes in assemblage composition following disturbance are largely a function of other tropical taxa filling gaps in physical space vacated by vulnerable taxa (Stuart-Smith et al., 2018). On high-latitude reefs, loss of vulnerable taxa potentially creates opportunities for thermally-resilient local/regional taxa and incoming tropical taxa that benefit from warming temperatures at high latitudes, thereby introducing new sets of life-history traits to the ecosystem (Beger et al., 2014; Greenstein & Pandolfi, 2008; Sommer et al., 2018). For example, corals on tropical coral reefs exhibit diverse growth forms and create complex three-dimensional frameworks, whereas corals on high-latitude reefs tend to have more uniform or less diverse morphologies (Sommer, Harrison, Beger, & Pandolfi, 2014), generally resulting in structurally less complex coral framework toward higher latitudes (DeVantier, De'Ath, Turak, Done, & Fabricius, 2006; Mizerek, Baird, Beaumont, & Madin, 2016). Therefore, loss of species in high-latitude assemblages and replacement by tropical taxa could not only lead to a change in the assemblage composition, but also result in a significant shift in habitat complexity. However, the growth of structurally complex tropical taxa at high-latitudes may be inhibited by chemical conditions increasingly less conducive to calcification with climate change (e.g. ocean acidification; van Hooidonk, Maynard, Manzello, & Planes, 2014) or by oceanographic conditions particularly unfavourable for corals with complex morphologies (e.g. strong wave actions; Harriott & Banks, 2002). Such conditions may hamper the poleward range expansion of tropical corals, in which case, the marked disparity in taxon-specific

22

525 bleaching severity and mortality will likely lead to proliferation of resident bleaching-resistant

526 corals and a homogenisation of assemblages, which in turn can impair ecosystem functioning

527 (Clavel, Julliard, & Devictor, 2011; McKinney & Lockwood, 1999).

528

529 **Outlook and conclusion**

530 The resilience of coral reefs to environmental anomalies is rapidly weakening as corals are

531 exposed to extreme conditions more frequently, and their capacity to rebound is declining

532 (Heron et al., 2016; Hughes et al. 2019; van Hooidonk et al., 2013; van Woesik et al., 2011).

533 While high-latitude reefs have been considered as potential climate refugia for tropical corals

534 under climate change (Beger et al., 2014; Riegl, 2003; but see Lybolt et al., 2011), our findings

535 suggest that resident high-latitude corals are also vulnerable to thermal anomalies, potentially

536 without suitable *ex situ* climate refugia equivalent to those of tropical corals (Harriott & Banks,

537 2002; Schleyer et al., 2018). The levels of heat stress measured among subtropical assemblages

538 were relatively low (DHW_{0C} of 4-9°C-weeks) compared to those recorded in the tropics during

539 the same time period of 2016 (up to DHW_{1C} of 12°C-weeks; Hughes et al., 2017). Nonetheless,

540 bleaching was prevalent throughout the region and resulted in severe bleaching of two abundant

541 genera, *Pocillopora* and *Porites*. This is particularly concerning because some representatives

542 of these genera are endemic species (*Pocillopora aliciae* Schmidt-Roach et al., 2013) or rare

543 in the tropics (*Porites heronensis* Veron, 1985). Loss of endemic or locally abundant taxa is

544 more than a simple loss of biodiversity as it can undermine ecosystem processes (e.g. energy

545 flow), deprive the ecosystem of novel ecological interactions (Bailey, Wooley, Lindroth, &

546 Whitham, 2006; Gorman, Potts, Schweitzer, & Bailey, 2014; Valiente-Banuet et al., 2015), and

547 incur a critical loss in evolutionary history for the taxonomic group (Huang & Roy, 2013; 2015).

548 The degree of changes in the ecological functions of high-latitude coral assemblages, and the

549 ability of high-latitude areas to act as climate refugia for tropical taxa will depend upon

550 recovery patterns of bleaching-susceptible regional taxa, range expansion rates of tropical taxa,

551 the relative strength of competitive advantages that resident high-latitude corals possess over

552 the ability of tropical corals to colonise the rocky substrates in the subtropics, and the frequency

553 and magnitude of recurrent environmental anomalies. Importantly, our mechanistic

554 understanding of coral bleaching, and efforts to predict the future of reefs are nullified under

555 extreme and unprecedented thermal conditions (Hughes et al., 2017), making the reduction of

556 global warming an urgent priority.

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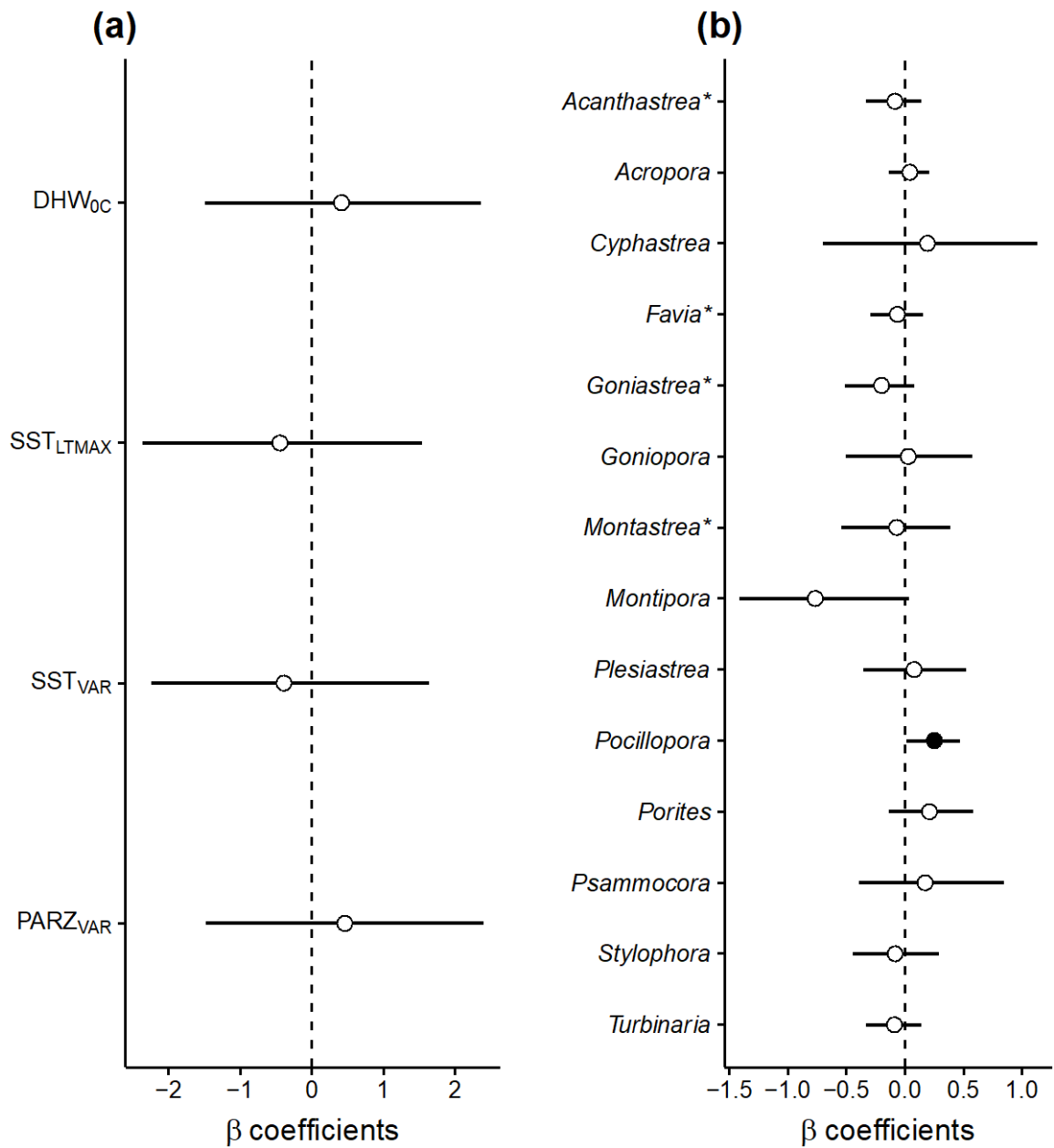
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FIGURE CAPTIONS
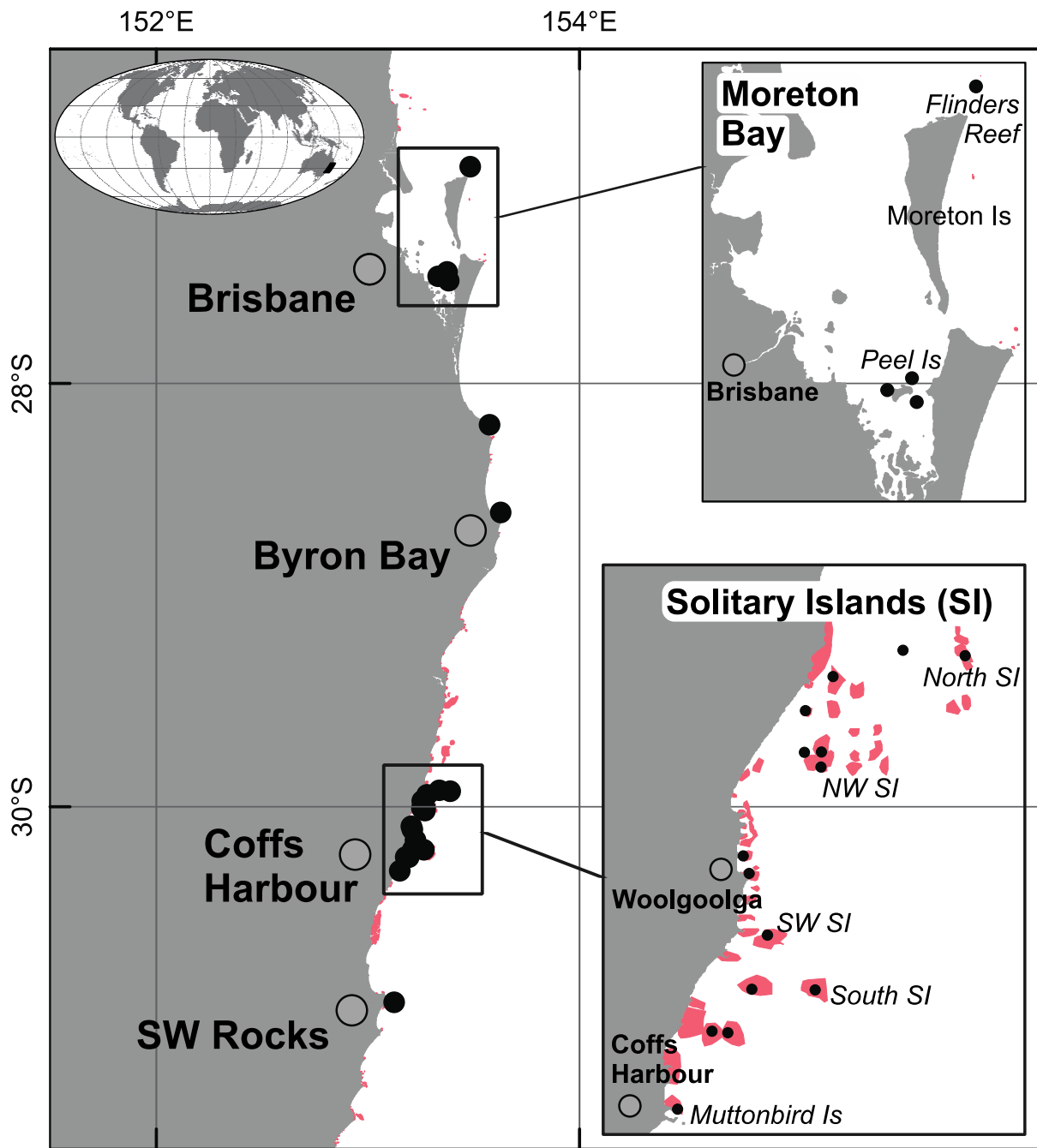
Figure 1. Survey locations along the subtropical east coast of Australia spanning 26°S to 31°S. Black dots mark the location of each survey site and red polygons indicate the known presence of coral assemblages.

Figure 2. The effects of (a) environmental variables and (b) taxonomic composition on assemblage-scale bleaching severity. Points indicate the median of the 95% highest posterior density (HPD) intervals of β coefficients, and horizontal lines indicate the 95% HPD intervals. Statistical significance is inferred where the 95% HPD interval does not intersect 0 and is annotated with a closed symbol. A positive β coefficient represents a positive association and a negative β coefficient indicates a negative association between assemblage-scale bleaching
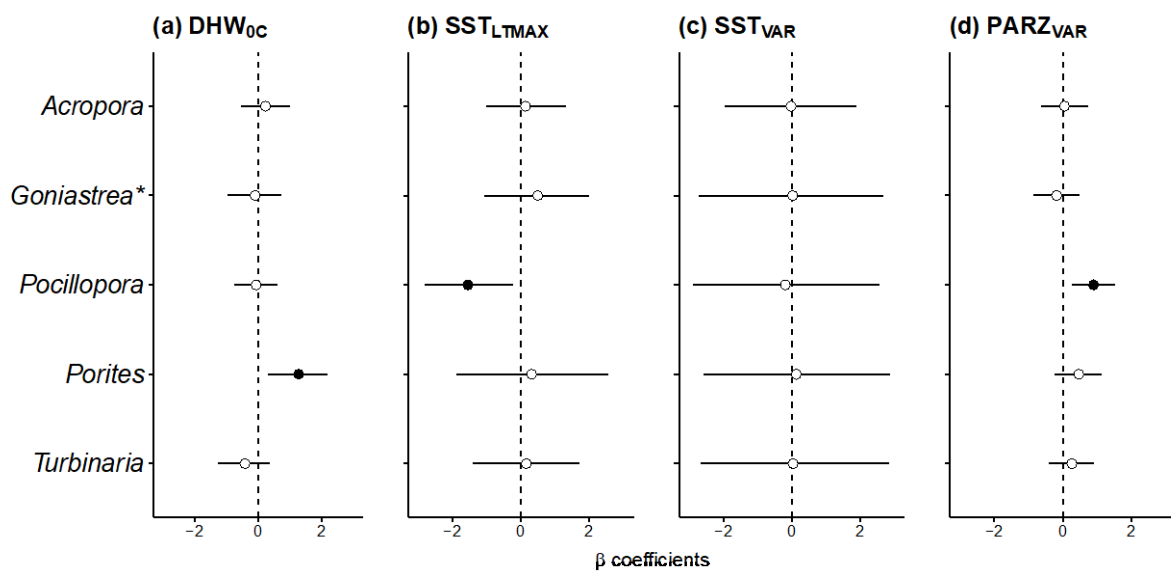
severity (SSI) and (a) an environmental variable or (b) relative abundance of a genus. The

genera annotated with an asterisk have undergone a recent taxonomic revision (Table S1).

876
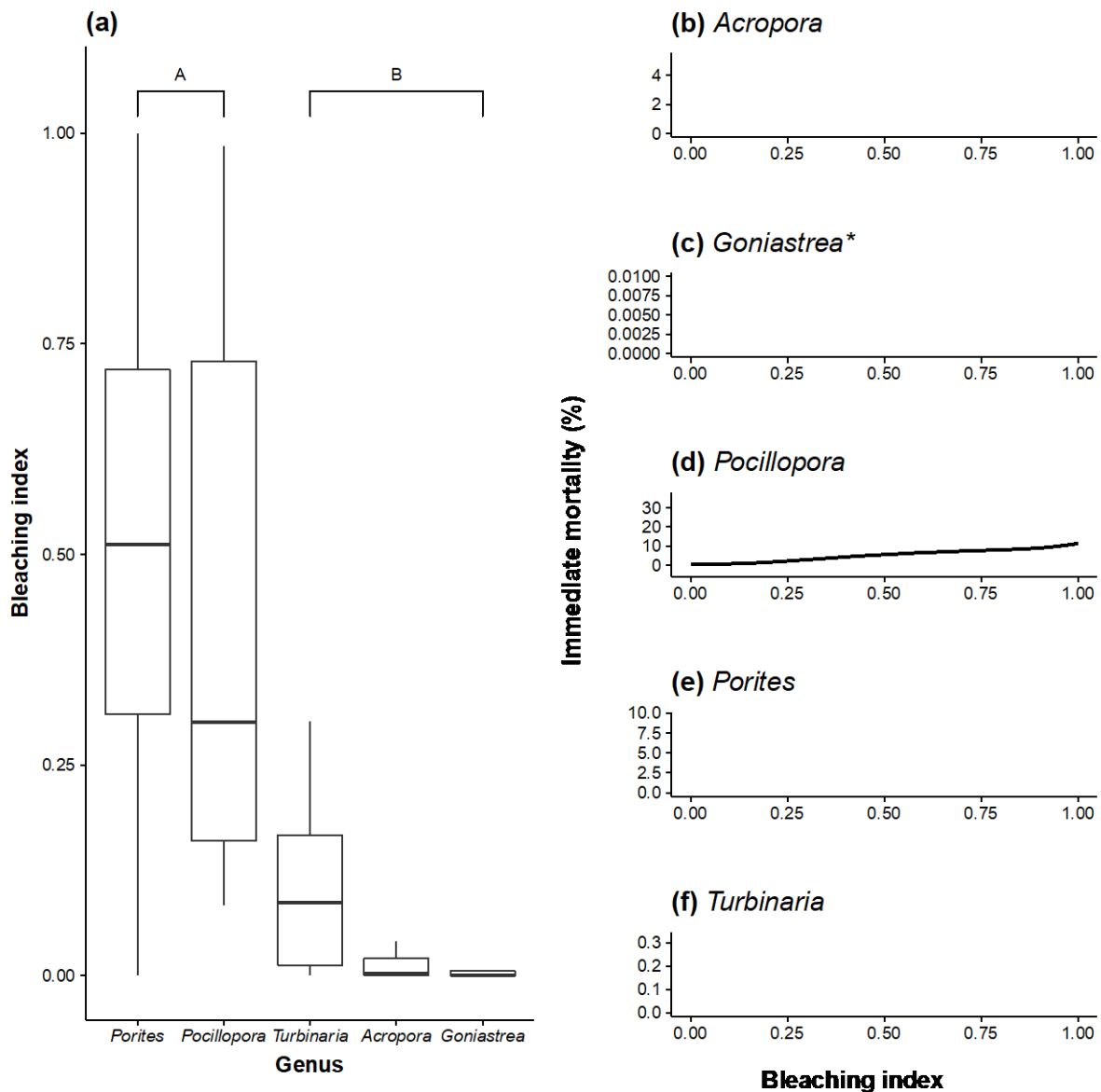
878 **Figure 3.** Intergeneric variability in (a) bleaching index (BI) and (b-f) the relationship between

879 bleaching index (BI) and immediate mortality for *Acropora*, *Goniastrea**, *Pocillopora*, *Porites*,

880 and *Turbinaria*. The genera in (a) are grouped based on statistical similarity in bleaching index

881 (brackets A and B). The box plots illustrate interquartile ranges of BI for each genus, whiskers

882 indicate minimum and maximum values not exceeding 1.5 times below and above the first and

third quartiles (i.e. Tukey's boxplot) and dots indicate outliers. (b-f) Each dot represents the

mean BI and immediate mortality for the taxon at each of the survey sites. Horizontal and

vertical lines represent 95% confidence intervals for the mean values. Splines were estimated

using generalised additive models with only significant relationships shown, and the shaded

areas represent 95% confidence intervals (Table S10). Note the figures (b-f) are on different y-

axis scales.

Figure 4. The effect of environmental variables on taxon-specific bleaching severity for: (a)

Degree Heating Weeks (DHW_{0C}), (b) long-term mean water temperature of hottest month of

each year (SST_{LTMAX}), (c) long-term mean of annual fluctuations in water temperature

(SST_{VAR}), and (d) long-term mean of annual fluctuation in solar irradiance ($PARZ_{VAR}$). Points

indicate the median of the 95% highest posterior density (HPD) intervals of β coefficients, and

lines indicate the 95% HPD intervals. Statistical significance is annotated with a closed symbol.

A positive β coefficient represents a positive association and a negative β coefficient indicates

a negative association between an environmental variable and taxon-specific bleaching severity

(BI).
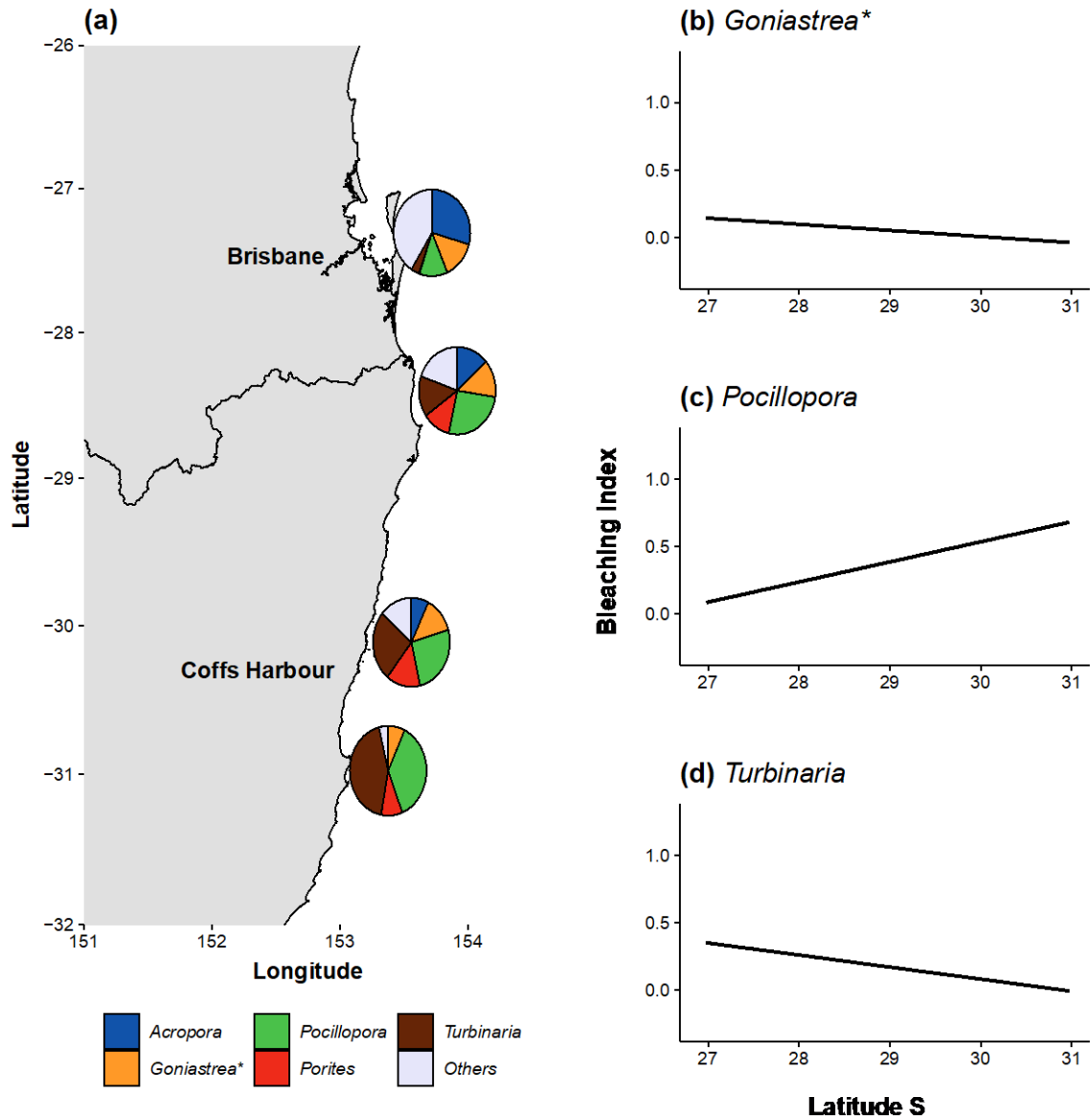
Figure 5. (a) The relative contribution of the five most abundant genera (*Acropora*, *Goniastrea**, *Pocillopora*, *Porites*, and *Turbinaria*) and all remaining genera (Others) to assemblage composition across latitude. Sites are grouped based on geographic proximity for graphical purposes. Direct correlation between relative abundance and latitude can be found in Table S12. (b)-(d) The bleaching index (BI) for three of the five most abundant genera across latitude. Each point represents the mean BI for a survey site. Vertical lines are 95% confidence

908   intervals for the mean BI values. The slope of regressions indicates the relationship between

909   latitude and BI. Only statistically significant relationships are depicted.