Global warming transforms coral reef assemblages

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Global warming is rapidly emerging as the most prominent threat to the ecological integrity of the world’s coral reefs[1-4], highlighting the need for a better understanding of the impact of heat exposure on the resilience of reef ecosystems and the people who depend on them. Here we reveal the non-linear responses of coral assemblages to a wide array of heat exposures, which arises as their resistance to low levels of stress is increasingly exceeded at higher exposures, resulting in a catastrophic collapse of coral abundances and functions. In the aftermath of the record-breaking marine heatwave on the Great Barrier Reef in 2016[5], corals began to die immediately where accumulated heat stress exceeded a critical threshold of 3-4 °C-weeks (Degree Heating Weeks). After eight months, sites exposed to 4-10 °C-weeks lost between 40% and 90% of their coral cover. An exposure of 6 °C-weeks or more drove an unprecedented, regional-scale shift in the composition of coral assemblages, reflecting markedly divergent responses to heat stress by different taxa. These abrupt shifts have transformed the three-dimensionality and ecological functioning of 29% of the 3,863 reefs comprising the world’s largest coral reef system. In the northern third of the Great Barrier Reef, where temperature anomalies in 2016 were the most extreme, the collapse of all major coral taxa is unlikely to be fully reversed in the foreseeable future because of the increasing frequency of marine heatwaves[6]. Post-bleaching mass mortality of corals represents a radical shift in the disturbance regimes of tropical reefs, adding to but far exceeding the impact of recurrent cyclones and other local events, representing a fundamental challenge to the long-term future of these iconic ecosystems.

Marine heatwaves due to global warming have triggered pan-tropical bleaching of corals in 1998, 2010 and 2015/2016[6], and acute thermal stress is rapidly emerging as the most widespread threat to the world's coral reefs[2-4,7]. Bleaching occurs when the relationship between corals and their photosynthetic symbionts (zooxanthellae, *Symbiodinium* spp.) breaks down, turning the coral pale. Bleached corals are physiologically damaged and nutritionally compromised, and they can die if bleaching is severe and recovery of their symbionts is prolonged[8,9]. However, the relationships between heat exposure and the subsequent mortality of different taxa is not well understood or quantified. While the concept of winners versus losers has been widely applied to describe inter-specific differences in the degree of bleaching[11-14], predicting the definitive losers, namely the corals that fail to regain their colour and ultimately die following heat stress, is key to understanding how climate change affects biodiversity, species composition and ecosystem function. To date, no study has examined the quantitative relationship between a broad range of heat exposures and the response of coral assemblages. The shape of this response curve is essential for identifying critical levels of heat exposure when the initial resistance of different taxa is overcome, and for predicting what further amount of heat exposure could drive a transformation in species composition and ecological functions. Here, we examine geographic patterns of heat exposure and differential mortality of coral taxa along the 2,300 km length of the Great Barrier Reef, arising during the record-breaking marine heatwave of 2016[5]. We show that taxonomic patterns of bleaching did not predict the identity of the ultimate losers that died, that many corals succumbed immediately from heat stress as well as more slowly following the depletion of their zooxanthellae, and that heat stress drove a radical shift in the composition and functional traits of coral assemblages on hundreds of individual reefs, transforming large swaths of the remote northern third of the Great Barrier Reef from mature and diverse assemblages to a new, degraded system. This altered ecosystem is unlikely to have sufficient time to recover to its original pre-bleaching configuration in the face of future, recurrent climate-driven disturbances.

The 2016 bleaching event triggered an unprecedented loss of corals on the northern third of the Great Barrier Reef, and to a lesser extent, the central third, with virtually no heat-stress mortality occurring further south (Fig. 1a, Extended Data Fig. 1, 2). The geographic footprint and intensity of the coral die-off (Fig. 1a) closely matched by the observed north-south pattern in accumulated heat (Fig. 1b), measured as satellite-derived Degree Heating Weeks (DHW, °C-weeks), a widely-used measure that incorporates both the duration and intensity of heat stress[15]. The 5 km-resolution DHW values (Fig. 1b) were significantly correlated with the independently-estimated losses of corals on 1,156 reefs (Fig. 1a; $r^2 = 0.50$, $p < 0.001$). In the northern, 700 km-long section of the Great Barrier Reef (from 9.5-14.5°S), where the heat exposure was the most extreme, 50.3% of the coral cover on reef crests was lost within eight months (Fig. 1b). More broadly, in the 1,200 km extent of the northern and central regions where the bleaching had occurred in March (from 9.5-19.5°S), the decrease by November was 38.2%, and throughout the entire Great Barrier Reef, including the southern third of the Reef where heat exposure was minimal (Fig. 1b), the cover of corals declined by 30.0% between March and November 2016. In comparison, the massive loss of corals from the 2016 marine heatwave was an order of magnitude greater and more widespread than the patchier damage that typically occurs on reefs sites within the track of a severe tropical cyclone[16].

At the scale of individual reefs, the severity of coral mortality was also highly correlated with the amount of bleaching, and with the level of heat exposure (Fig. 2). Initially, at the peak of temperatures extremes in March 2016, many tens of millions of corals died quickly in the northern half of the Great Barrier Reef over a period of just 2-3 weeks (Fig. 2a). These widespread losses were not due to slow attrition of corals that failed to regain their symbionts. Rather, thermally-sensitive species of corals began to die almost immediately where they were exposed to heat stress of >4°C-weeks (Fig. 1b, Fig. 2a). The amount of initial mortality increased steadily with increasing heat exposure ($r^2 = 0.50$, $p < 0.001$); where the exposure was <4° C-weeks, fewer than 5% of the corals died, whereas we recorded an initial median loss of 15.6% of corals on reefs with 4-8 °C-weeks exposure, and a median loss of 27.0% of corals at locations that experienced $\geq$8 °C-weeks (Fig. 2a). Across the entire Great Barrier Reef, 34.8% of individual reefs experienced $\geq$4 °C-weeks, and 20.7% of reefs were exposed to $\geq$8 °C-weeks DHW (Fig. 1a). The amount of initial mortality at the peak of summer varied strikingly among different groups of corals, and was highest for *Pocillopora damicornis,* two species of *Isopora*, *Stylophora pistillata,* and staghorn *Acropora* (Extended Data Figure 4a).

During the ensuing Austral winter, the bleached corals in the northern and central Great Barrier Reef either slowly regained their colour and survived, or they continued to die at unprecedented levels. Only a handful, <1%, remained bleached after eight months. The severity of the longer-term loss of corals, measured *in situ* as the decline in coral cover between March and November, was accurately predicted by the percent of corals that were initially bleached (Fig. 2b; $r^2 = 0.51$, $p < 0.001$). Specifically, reefs that experienced less than 25% bleaching in March typically had almost no loss of cover after eight months (Fig. 2b). In contrast, above this threshold, the loss of coral cover increased progressively, indicating that fewer of the bleached corals survived. Furthermore, the longer-term loss of coral cover accelerated with increasing levels of heat exposure of each reef (DHW, $r^2 = 0.44$, $P < 0.001$; Fig. 2c). Consequently, we recorded almost no loss of coral cover for reefs exposed to 0-3 °C-weeks, compared with a 40% decline at 4° C-weeks, 66% for 8 °C-weeks, and extreme declines of >80% for exposures of $\geq$9 °C-weeks. The non-linear responses to heat exposure varied significantly among coral taxa (Extended Data Fig. 5), illustrating a spectrum of surivorship among winners versus losers, driving a radical shift in species composition.

Post-bleaching mortality has disproportionately transformed the assemblage structure and functional diversity of corals on reefs that experienced high levels of bleaching (affecting >60% of colonies), as illustrated by a non-metric multi-dimensional scaling (nMDS) analysis (Fig. 3). The abundances of all categories of corals decreased to varying degrees on these heavily bleached reefs, shown by the orientation of the nMDS vectors (Fig. 3a) and the directional shift in the before-after assemblages (Fig. 3b). Tabular and staghorn *Acropora*, *Seriatopora hystrix* and *Stylophora pistillata* - fast-growing, three-dimensional, weedy species that dominate many shallow Indo-Pacific reefs – all declined by >75% (Extended Data Fig. 4b). In contrast to the radical shifts on heavily bleached reefs, assemblages changed very little between March and November on reefs that experienced moderate (30-60%) or little (0-30%) bleaching. On these reefs, the nMDS analysis of before and after assemblages shows that shifts in composition were small and multi-directional (Fig. 3c).

The response curve of coral assemblages exposed to a range of heat exposures, from 0-10^{o}C-weeks, (measured as the Euclidean distance between before and after compositions on each reef (Fig. 3b, c)), is strikingly non-linear (Fig. 4). The changes in assemblage structure after eight months were small on reefs that were exposed to DHW <6 °C-weeks, whereas reefs subjected to >6 °C-weeks lost >50% of their corals (Fig. 2c) and shifted dramatically in composition (Fig. 4). Satellite-derived DHW data indicate that 28.6% of the 3,863 reefs comprising the Great Barrier Reef experienced thermal exposures of >6° C-weeks during the 2016 bleaching event, and 20.7% (800 reefs) were exposed to >8 °C-weeks (Fig. 1). Individual reefs with this severity of heat exposure have undergone an unprecedented ecological collapse, extending southwards from Papua New Guinea for up to 1,000 km (Fig.

1). Reefs that were exposed to <6 °C-weeks were located predominantly in the southern half of the Great Barrier Reef, and in a small northern patch at the outer edge of the continental shelf where temperature anomalies in 2016 above the long-term summer maximum were small (Fig. 1b).

The abrupt, geographic-scale shift in coral assemblages has also radically reduced the abundance and diversity of species traits that facilitate key ecological functions (Fig. 3d-e, Extended Data Table 1, 2). A before-after analysis of the multi-dimensional trait space of coral assemblages, weighted by the absolute abundance of taxa contributing to each trait, reveals a transformation in the functional-trait composition of assemblages on heavily bleached reefs (affecting >60% of colonies) in the eight month period after March 2016 (Fig. 3e). In most cases, reefs shifted away from the dominance of fast-growing, three-dimensional, branching and tabular species with dense skeletons, to a depauperate assemblage dominated by taxa with simpler morphological characteristics and slower growth rates. In contrast, on less-bleached reefs the weighted abundances of functionally important traits typically showed small gains (Fig. 3f).

In conclusion, our analyses show that acute heat stress from global warming is a potent driver of a geographic-scale collapse of coral assemblages, affecting even the most remote and well-protected reefs within an iconic World Heritage Area. Forecasts of coral bleaching made continuously by the US National Oceanic and Atmospheric Administration (NOAA) are accompanied with guidance that a DHW exposure of 4° C-weeks usually results in significant bleaching, and 8 °C-weeks may also cause mortality of corals[1,15,17]. We show here that substantial mortality occurred on the Great Barrier Reef in 2016 well below 8 °C-weeks (beginning at 3-4 °C-weeks, Fig. 2c), and that the resistance of coral assemblages to heat exposure increasingly collapsed above 6 °C-weeks, triggering large-scale shifts in the composition and ecological functions of reefs (Fig. 3). The threshold we have identified for the breakdown of assemblage structure, approximately 6 °C-weeks (Fig. 4), was transgressed in 2016 throughout most of the northern, as well as much of the central, region of the Great Barrier Reef (Fig. 1). The prospects for a full recovery to the pre-bleaching coral assemblages before the next major bleaching event are poor, for several reasons. First, many of the surviving coral colonies continue to die slowly even after recovery of their algal symbionts, because they have lost extensive patches of tissue, are injured and fragmented, and because corals weakened by bleaching are susceptible to subsequent outbreaks of disease[18,19]. Secondly, the replacement of dead corals by larval recruitment and subsequent colony growth will take at least a decade for weedy corals, such as species of *Acropora, Pocillopora, Seriatopora* and *Stylophora*[10,20,21]. The success of future recruitment will depend upon an adequate supply of larvae from lightly bleached locations, the rapid break down of many millions of dead coral skeletons to provide a more enduring and stable substrate for settling larvae, and the availability of suitable settlement cues and conditions for survival of juvenile corals[22]. Thirdly, for longer-lived, slow-growing species, the trajectory of replacement of dead corals on heavily damaged reefs will be far more protracted, almost certainly decades longer than the return-times of future bleaching events[7]. The recurrence of mass bleaching during the recovery period will be critical, in view of the global increase in the frequency of bleaching events which are increasingly occurring throughout all phases of El Niño Southern Oscillation cycles[6].

The 2015-2016 global bleaching event is a watershed for the Great Barrier Reef, and for many other severely affected reefs elsewhere in the Indo-Pacific[6]. Furthermore, the Great Barrier Reef experienced severe bleaching again in early 2017, causing additional extensive damage[23,24]. The most likely scenario, therefore, is that coral reefs throughout the tropics will continue to degrade over the current century until climate change stabilises[4,25], allowing remnant populations to reorganize into novel, heat-tolerant reef assemblages. The 2016 marine heatwave has triggered the initial phase of that transition on the northern, most-pristine region of the Great Barrier Reef (Fig. 4), changing it forever as the intensity of global warming continues to escalate. The large-scale loss of functionally-diverse corals is a harbinger of further radical shifts in the condition and dynamics of all marine ecosystems, especially if global action on climate change fails to limit warming to +1.5°C above the pre-industrial base-line.

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Author contributions The study was conceptualized by TPH who also wrote the first draft of the paper. All authors contributed to writing subsequent drafts. JTK coordinated data compilation, analyses and graphics. Aerial bleaching surveys were conducted by TPH and JKT. Underwater bleaching and mortality censuses were undertaken by AHB, AD, ASH, MOH, MMcW, RJP, MSP, JSS and GT. CME, SFH, GL, and WJS provided satellite data on heat stress. MMcW undertook the functional trait analysis, and SRC provided statistical advice and modelled loss of coral cover among different taxa.

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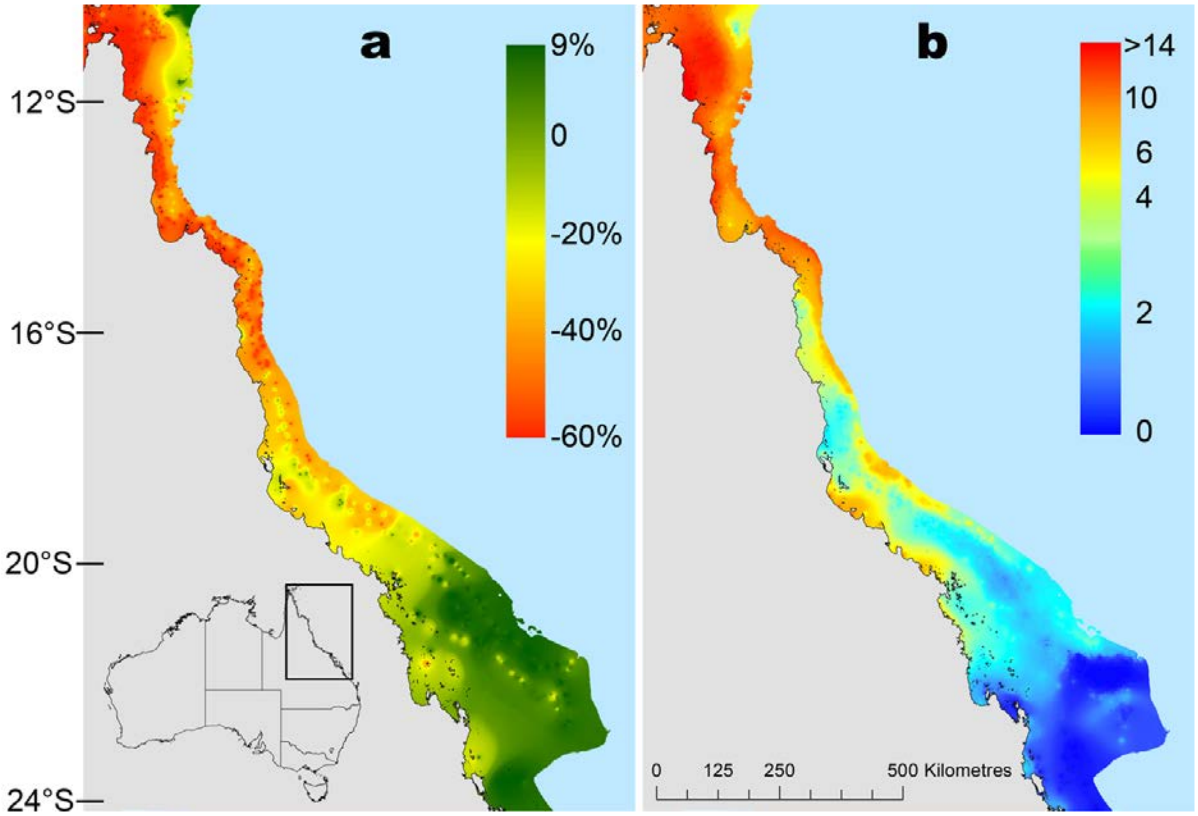


Figure 1. Large-scale spatial patterns in change in coral cover and in heat exposure on the Great Barrier Reef, Australia. (a) Change in coral cover between March and November 2016. (b) Heat exposure, measured as Degree Heating Weeks (DHW, ^{o}C-weeks) in the summer of 2016.

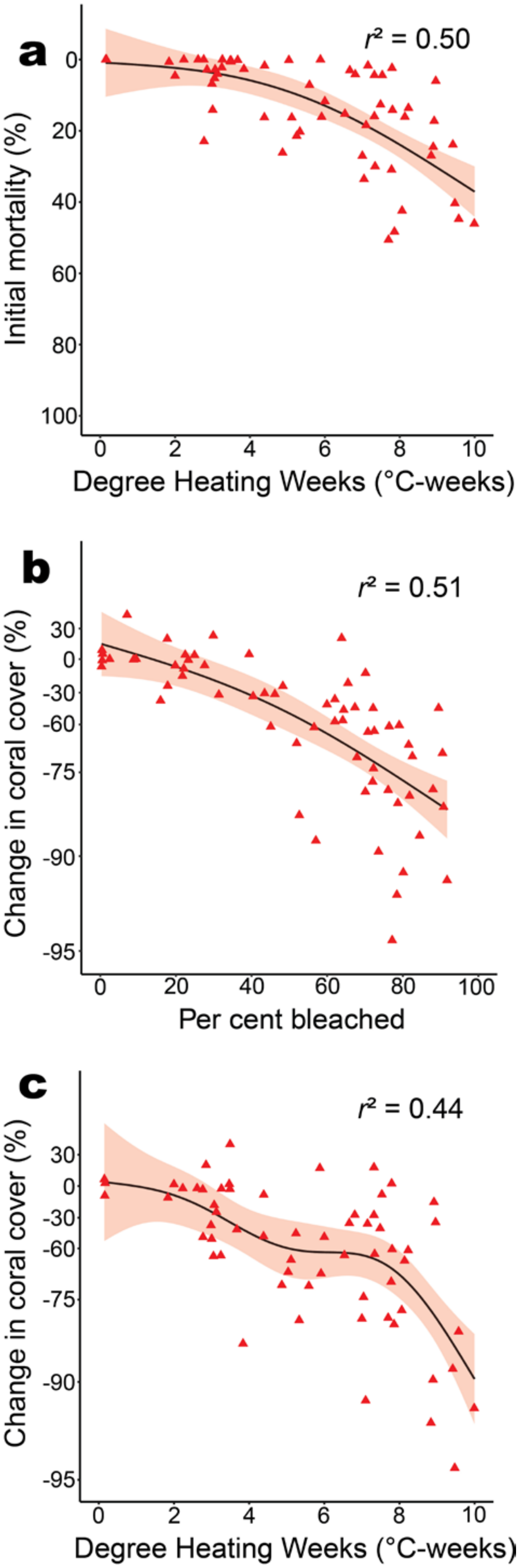

a
$r^2 = 0.50$
Initial mortality (%)
0
20
40
60
80
100
0
2
4
6
8
10
Degree Heating Weeks (°C-weeks)
b
$r^2 = 0.51$
Change in coral cover (%)
30
0
-30
-60
-75
-90
-95
0
20
40
60
80
100
Per cent bleached
c
$r^2 = 0.44$
Change in coral cover (%)
30
0
-30
-60
-75
-90
-95
0
2
4
6
8
10
Degree Heating Weeks (°C-weeks)

Figure 2. The initial and longer-term response of coral assemblages to heat exposure. Regression curves are fitted using Generalised Additive Models (GAMs), with 95% confidence limits (ribbons). Data points represent individual reefs. (a) Initial coral mortality measured at the peak of bleaching, versus the heat exposure each reef experienced (satellite-based Degree Heating Weeks, DHW, °C-Weeks). (b) Longer-term change in coral cover between March and November 2016 on individual reefs, versus the initial amount of bleaching recorded underwater. (c) Longer-term change in coral cover between March and November 2016, versus heat exposure (DHW) on individual reefs.

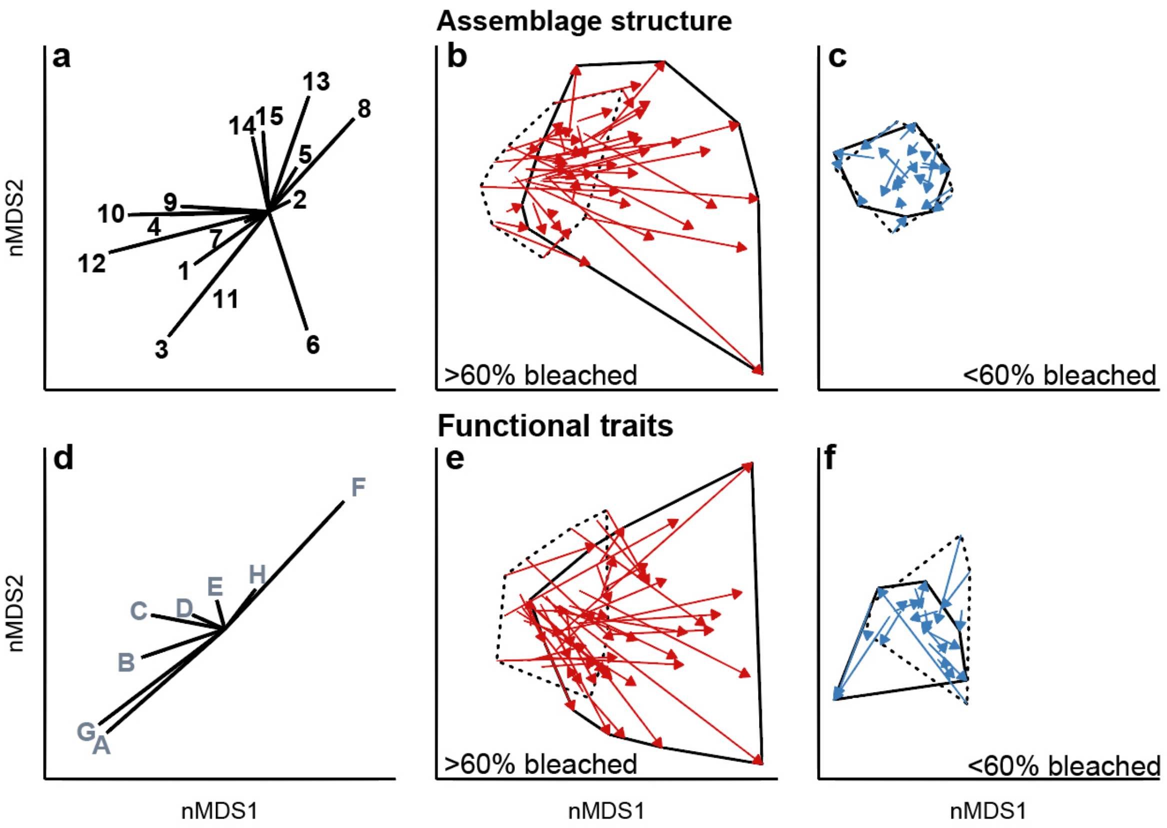


Figure 3. Changes in assemblage structure and functional traits of corals following mass bleaching. (a-c) A non-metric multi-dimensional scaling (nMDS) analysis of shifts in coral assemblages between March and November 2016. (a) Fifteen nMDS vectors indicate the responses of individual taxa: (1) Other *Acropora*, (2) Favids, (3) *Isopora*, (4) *Montipora*, (5) Mussidae, (6) Other *Pocillopora*, (7) *Pocillopora damicornis*, (8) Poritidae, (9) *Seriatopora hystrix*, (10) Staghorn *Acropora*, (11) *Stylophora pistillata*, (12) Tabular *Acropora*, (13) Soft corals, (14) Other Scleractinia, and (15) Other sessile fauna. (b) Polygons indicate ordination space that was initially occupied by coral assemblages on each reef in March (dotted line) and again eight months later (solid line). Red arrows connect the before-after pairs of data points for each location to show changes in composition on severely bleached reefs (>60% of colonies bleached) after eight months. (c) Blue arrows connect the before-after pairs of data points for each location on reefs that were lightly or moderately (<60%) bleached. (d-f) An nMDS analysis of shifts in assemblage trait composition between March and November at

the same locations. (d) The eight vectors indicate the absolute contribution of traits to coral assemblages: (A) Surface area to volume ratio, (B) Growth rate, (C) Colony size, (D) Skeletal density, (E) Colony height, (F) Corallite width, (G) Interstitial space size, (H) Reproductive mode. (e) The shift in abundance-weighted trait space co-ordinates for coral assemblages over eight months for reefs with >60% bleaching. (f) The shift in abundance-weighted trait space co-ordinates for coral assemblages on reefs with <60% bleaching.

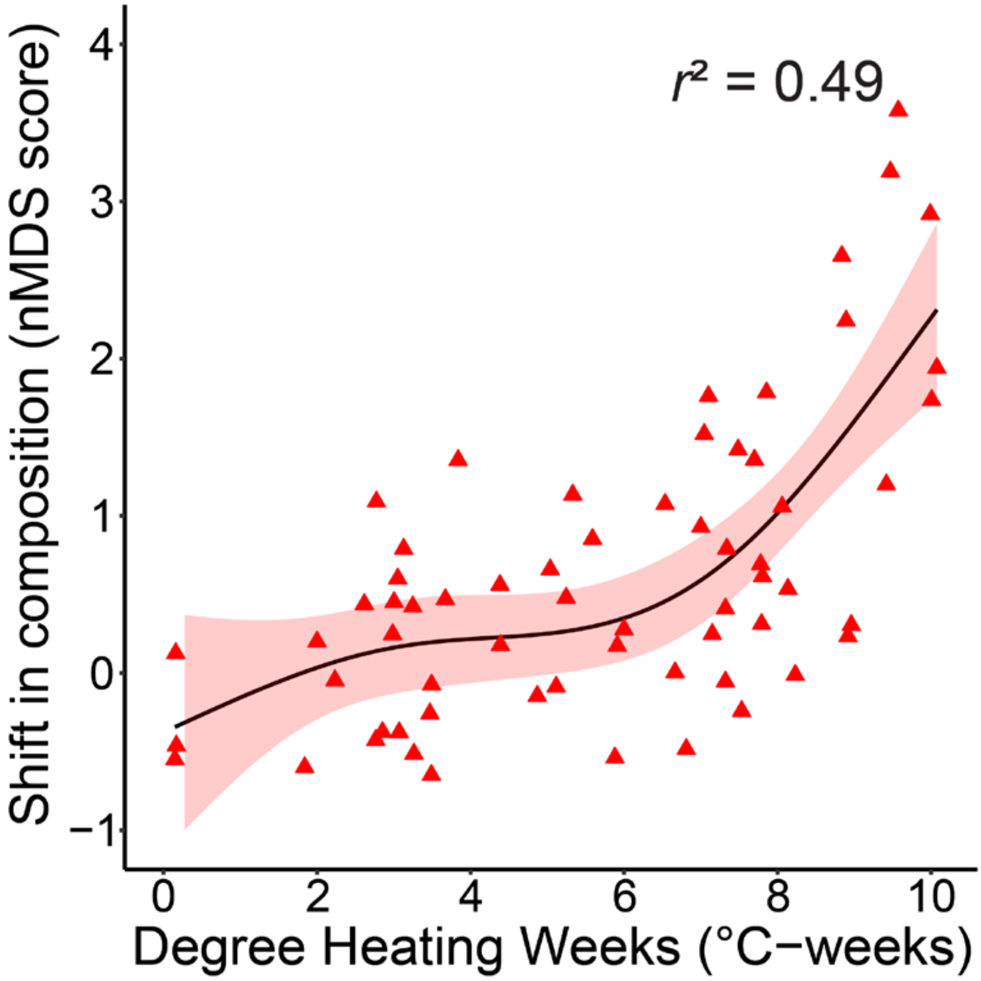


Figure 4. Change in coral assemblages in response to heat exposure. Regression curve is fitted using a Generalised Additive Model (GAM), with 95% confidence limits. Each data point represents the shift in composition, based on the Euclidean distance in a non-metric multi-dimensional scaling analysis of assemblages on individual reefs sampled at the peak of bleaching and eight months later. Heat exposure for each reef is measured as satellite-derived Degree Heating Weeks (DHW, °C-weeks).

Methods

Initial mortality and heat stress

We used aerial surveys, conducted in March/April 2016, to measure the geographic extent and severity of bleaching on the Great Barrier Reef, and subsequently converted the bleaching scores into mortality estimates (Fig. 1a) using a calibration curve based on underwater measurements of coral losses (Extended Data Fig. 1). The aerial surveys were conducted throughout the Great Barrier Reef Marine Park and the Torres Strait between Australia and Papua New Guinea, from the coast of Queensland to the outermost reefs, and along the entire Reef from latitudes 9.5-23.5°S. Each of 1,156 individual reefs was scored into one of five bleaching categories: (0) less than 1% of corals bleached, (1) 1-10%, (2) 10-30%, (3) 30-60%, and (4) more than 60% of corals bleached. The accuracy of the aerial scores was ground-truthed by measuring the extent of bleaching underwater on 104 reefs, also during March/April 2016[14, 25].

We assessed underwater the initial mortality of different taxa due to heat stress, at the same time as the aerial surveys, on 83 reefs that spanned the full spectrum of heat exposures and bleaching. On each reef, the extent of bleaching and mortality on individual coral colonies was measured at two sites using five 10 x 1 m belt transects placed on the reef crest at a depth of 2 m. We identified each colony (at the species or genus level) and recorded a categorical bleaching score for each one (n = 58,414 colonies): (1) no bleaching, (2) pale, (3) 1-50% bleached, (4) 51-99% bleached, (5) 100% bleached, and (6) recently dead. The dead colonies had suffered whole-colony mortality, were white with fully intact fine-scale skeletal features, typically still had patches of rotting coral tissue, and they were experiencing the initial week or two of colonization by filamentous algae, features which distinguished them from corals that died earlier. The timing of our initial underwater censuses, at the peak of the bleaching in

March/April 2016, was critical for identifying corals that were dying directly from heat stress, and for measuring the baseline composition of the assemblages.

Heat stress on the Great Barrier Reef in 2016 was quantified at 5 km resolution, using the NOAA Coral Reef Watch version 3 Degree Heating Week (DHW) metric[15]. DHW values are presented in Fig. 1b as a heat-map (Stretch type: Histogram Equalize) using inverse distance weighting (IDW; Power: 2, Cell Size: 1000, Search Radius: variable, 100 points) in ArcMap 10.2.1.

Longer term mortality

To measure longer-term coral loss (decrease in coral cover after eight months) and its relationship to the level of bleaching and heat exposure, we also conducted detailed before-after assessments of taxon-specific abundances by re-visiting 63 of the 83 reefs. We measured abundances in March/April and eight months later at the same locations in October/November, allowing us to compare changes in coral cover for 15 ecologically and taxonomically distinct components of benthic assemblages, on reefs exposed to a broad spectrum of heat stress. These measurements were conducted at the same two geo-referenced sites per reef, on reef crests at a depth of 2 m, using five 10 m long line-intercept transects per site. There were no cyclones or flood events on the GBR during the dry-season period (Austral Winter) in 2016. Unbleached reefs typically showed small increases in cover due to growth, which we included in the regression analyses. Analysis of change in coral cover was undertaken using the $\log_{10}$-transformed ratio of final to initial cover. To improve readability of Figure 2 and Extended Data Figure 1, changes in coral cover are presented as percentages calculated from the log-scale.

We compared the initial and final composition of corals using non-metric multi-dimensional scaling (nMDS) based on a Bray-Curtis similarity matrix of square-root transformed data, and quantified the shift over time using the Euclidean distance between before-after assemblages at each location. We then estimated the relationship between the shift in composition at each reef versus the level of heat exposure experienced there (Fig. 4). To include all species, the majority of which are too rare to analyse individually, we pooled them into 15 ecologically cohesive groups depending on their morphology, life history, and taxonomy. Three of the 15 are ubiquitous species or species complexes: *Pocillopora damicornis, Seriatopora hystrix*, and *Stylophora pistillata*. In each of the multi-species groups, the dominant species or genera on reef crests were: Other *Acropora* (*A. gemmifera, A. humilis, A. loripes, A. nasuta, A. secale, A. tenuis, A. valida*); Favids (i.e. species and genera from the formerly recognized Family Faviidae - *Cyphastrea, Favia, Favites, Goniastrea, Leptastrea, Montastrea, Platygyra*); Mussidae (*Lobophyllia, Symphyllia*); *Isopora* (*I. palifera, I. cuneata*); Other *Pocillopora* (*P. meandrina, P. verrucosa*); Other sessile animals (sponges, tunicates, molluscs); *Porites* (*P. annae, P. lobata*); *Montipora* (*M. foliosa, M. grisea, M. hispida, M. montasteriata, M. tuberculosa*); Staghorn *Acropora* (*A. florida, A. intermedia, A. microphthalma, A. muricata, A. robusta*); Soft Corals (alcyonaceans, zooanthids); and Tabular *Acropora* (*A. cytherea, A. hyacinthus, A. anthocercis*).

We calculated longer-term mortality for all species combined at the scale of the entire Great Barrier Reef in three ways, all of which yielded consistent results. The first approach (Fig. 1a) was based on a comparison of the observed loss of total coral cover on 63 reefs that extend along the entire Great Barrier Reef measured underwater between March and November, with aerial bleaching scores of the same locations in March/April (Extended Data Fig. 1). This calibration allowed us to convert the aerial scores of bleaching that we recorded for 1,156 reefs into mortality estimates for each of the five aerial score categories, and to map the geographic footprint of losses of corals throughout the Great Barrier Reef (Fig. 1a). The spatial patterns of coral decline (Fig. 1a) are presented as a heat-map of the calibrated scores

(Stretch type: Histogram Equalize) using inverse distance weighting (IDW; Power: 2, Cell Size: 1000, Search Radius: variable, 100 points) in ArcMap 10.2.1.

The second methodology for estimating large-scale mortality is independent of aerial surveys of bleaching, and based on the loss of coral cover on 110 reefs (Extended Data Fig. 2). The median cover on these reefs declined between March and November from 34% to 20% (Extended Data Fig. 3). For method two, the observed loss of coral cover was averaged for each of eight sectors of the Great Barrier Reef Marine Park and the Torres Strait (Extended Data Fig. 2), corrected for differences in reef area for each sector based on GIS data provided by the Great Barrier Reef Marine Park Authority, and then summed to calculate the total loss. For method three, we used the fitted relationship between satellite-derived Degree Heating Weeks and observed change in cover (63 reefs; Fig. 2c) to score the losses or gains on all 3,863 individual reefs comprising the Great Barrier Reef, and averaged the total. These two alternative approaches for estimating large-scale loss of cover, both based on before-after underwater surveys (Extended Data Fig. 2, Extended Data Fig. 3) yielded consistent results with Fig, 1a – a 27.7 and 29.0% decline, respectively, after 8 months.

Differential mortality among coral taxa

To estimate how exposure to heat (measured as Degree Heating Weeks, DHW) affects loss of cover differentially among taxa we used a linear mixed effects model. The fixed effect was DHW, and we allowed for a random effect of taxonomic grouping on both the intercept and slope of the relationship between coral cover change and DHW. Coral cover change was measured as log(final % cover + 0.0002) minus log(initial % cover+0.0002) (0.0002 was the smallest observed value in the data set). Also, we excluded from the analysis observations with zero initial coral cover of a particular taxonomic group. This treatment of the data yielded the best agreement between the residuals and the model’s statistical assumptions. The estimated random effect on intercepts was approximately zero, so we eliminated it from our final model. Thus, in the final model, there was a common intercept, but differences between taxa in sensitivity to DHW (i.e., there was a random effect of taxonomic group on the slope). To illustrate these differences, Extended data Fig. 5 plots the estimated slope of coral cover change for each taxon versus DHW as the overall mean effect of DHW plus the taxon-specific random effect. Conditional standard errors plotted in Extended data Fig. 5 are the standard errors on each random effect.

Shifts in functional traits

To calculate how differential mortality affected the mix of traits in the coral assemblages, we scored eight traits for 12 of the 15 functional groupings (excluding Soft Corals, Other Scleractinia, and Other Sessile Fauna, Extended Data Tables 1 and 2). We chose traits that are likely to influence ecosystem functions. For example, corals with fast growth rates and high skeletal density strongly influence calcification, colony shape affects photosynthesis and the provision of three-dimensional habitat, and the size of corallites is a measure of heterotrophy. The traits were scored using the Coral Trait Database[27], with the exception of colony size which we measured directly for each group on reef crests using the geometric mean of intercept lengths for each taxon from our initial transects. For multi-species groups, the traits were generally identical for all species. Otherwise, for *Montipora* and *Porites*, we used the mean score across the reef crest species we encountered. To measure the depletion of traits based on changes in absolute abundances between March and November (Fig. 3e-f), we used a community weighted mean (CWM) analysis of each trait:

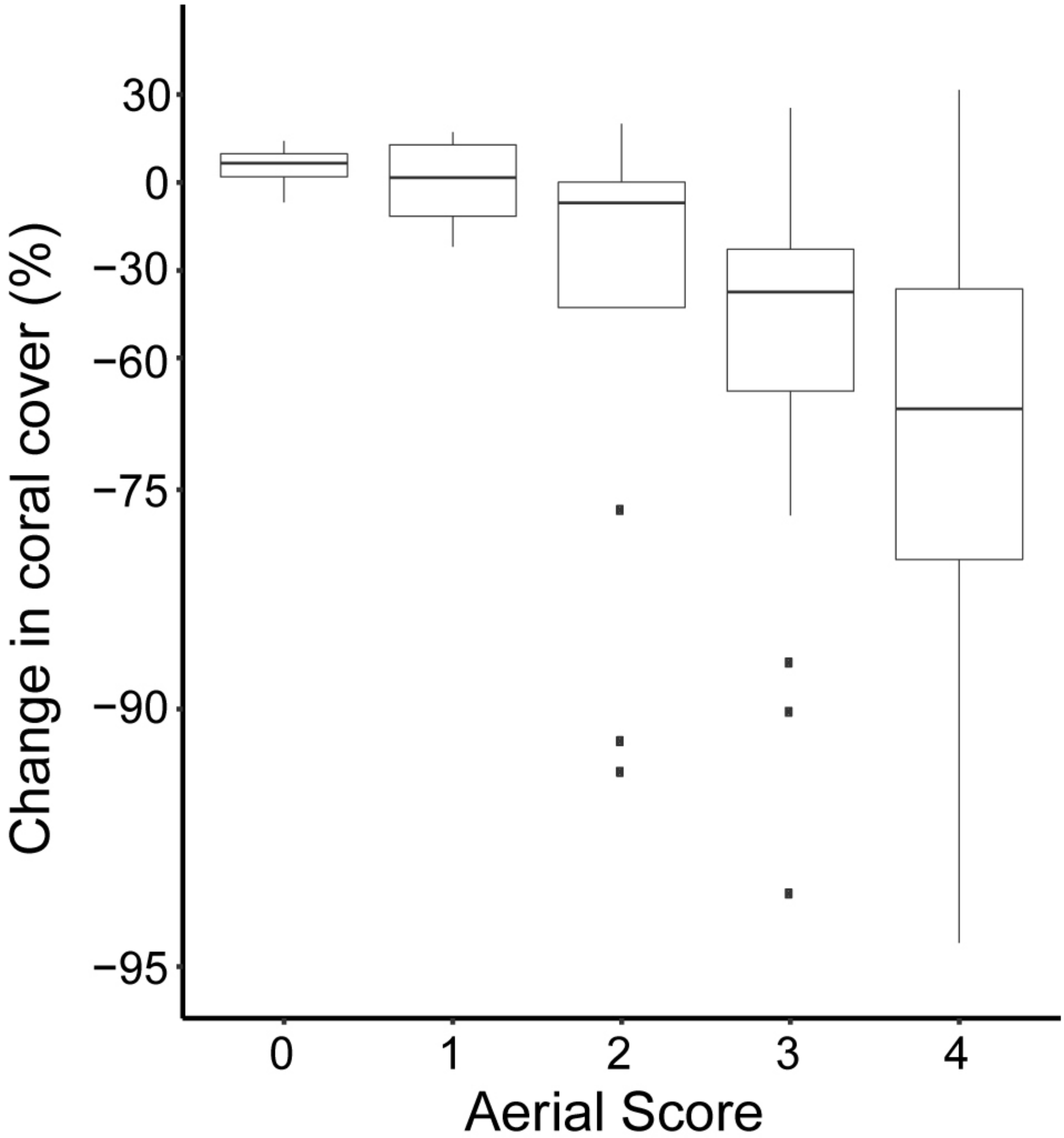
$$CWM = \sum_{i=1}^{n} a_i \; trait_i$$

where a_i is the abundance of coral taxa i and $trait_i$ is the trait value of coral taxa i. This metric provides a trait value for each reef weighted by the total abundance of each taxa. To visualise the overall shift in functional composition, we used a non-metric multi-dimensional scaling analysis (nMDS) based on a Bray-Curtis similarity matrix of square-root transformed data for each trait community weighted mean, creating a multi-dimensional trait space in which reefs are positioned according to the value and abundance of critical traits.

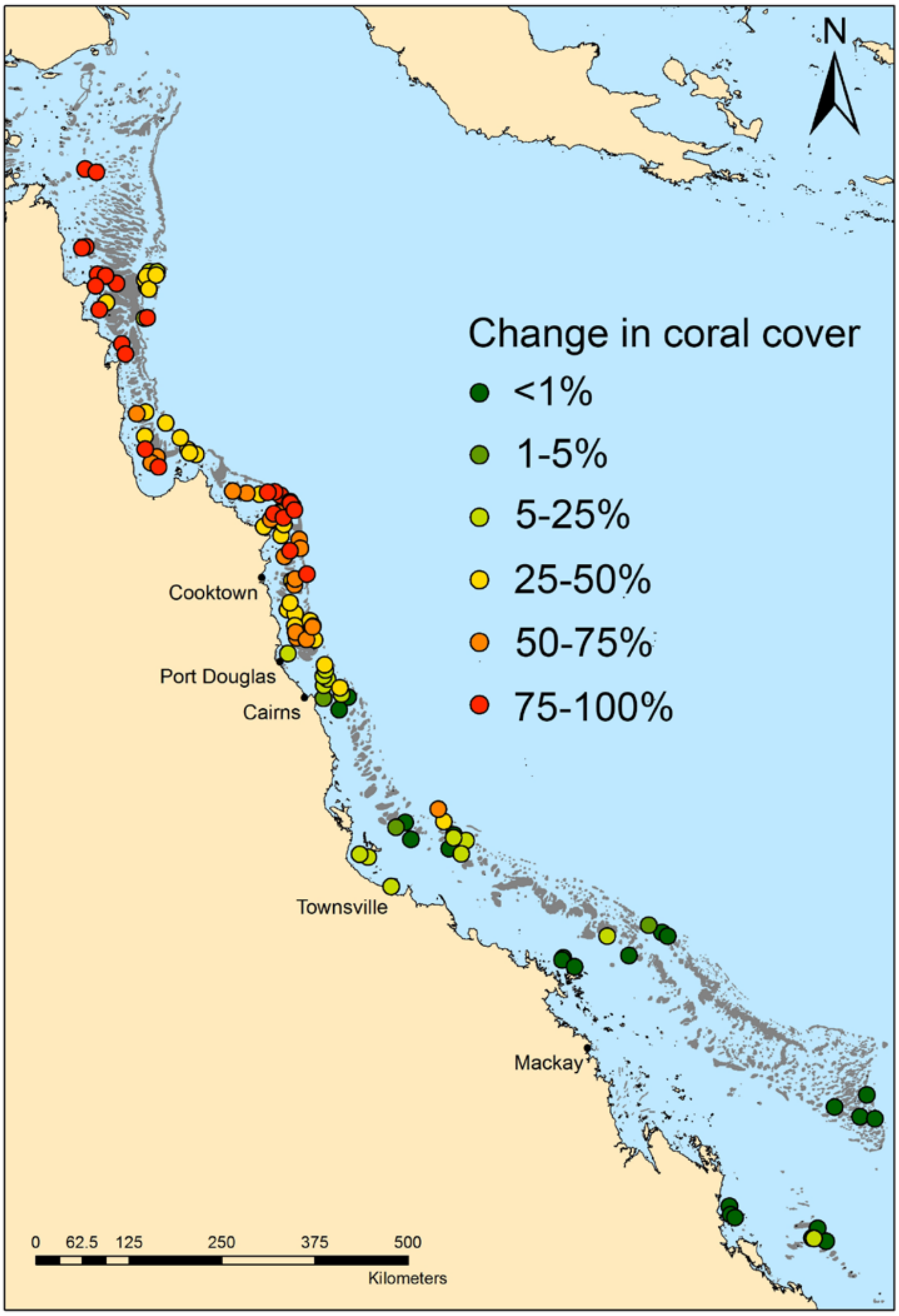
Additional References

26. Hughes, T.P., J.T. Kerry, T. Simpson. Large-scale bleaching of corals on the Great Barrier Reef. Ecology Data Papers http://onlinelibrary.wiley.com/doi/10.1002/ecy.2092/full
27. Madin, J. S., *et al.* The Coral Trait Database, a curated database of trait information for coral species from the global oceans. *Scientific data* **3** (2016).

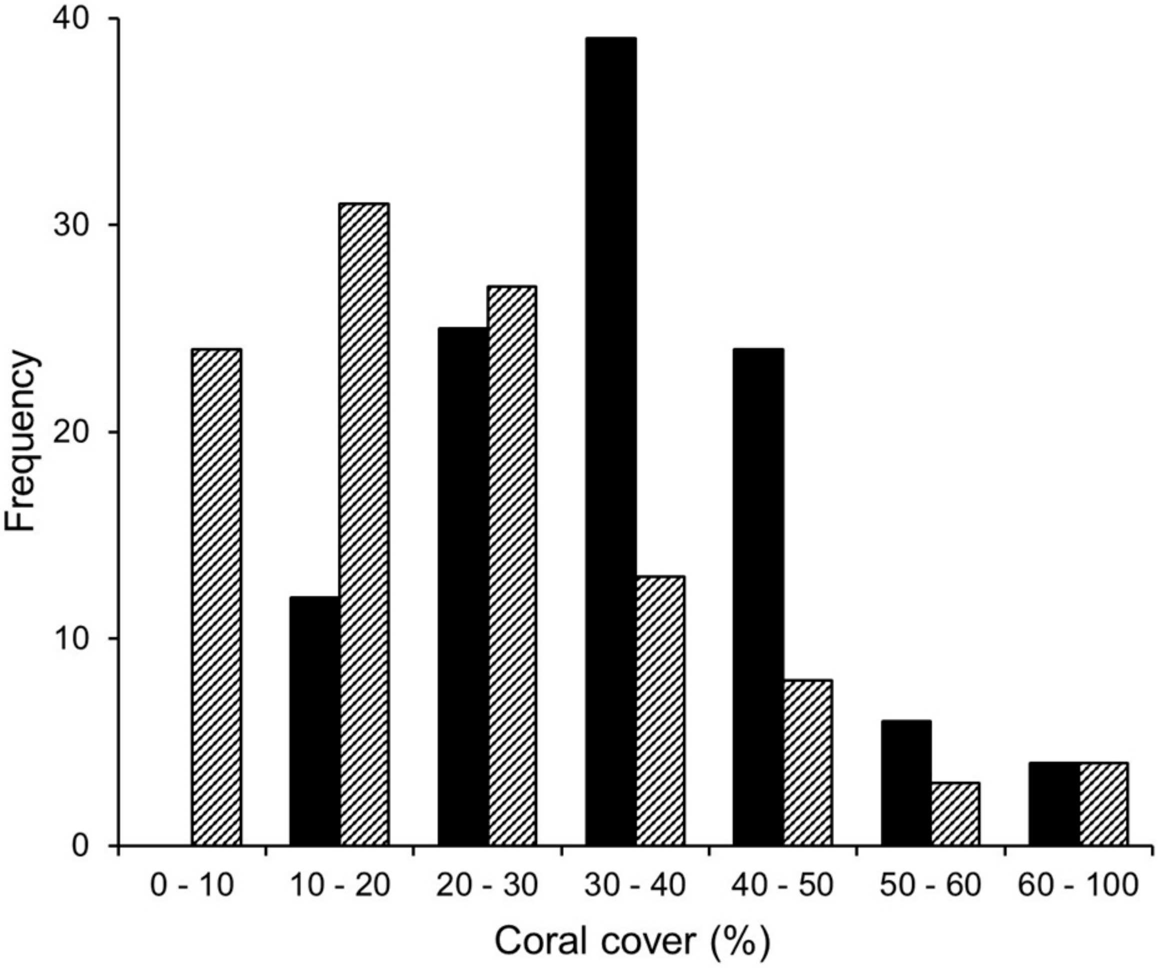
EXTENDED DATA



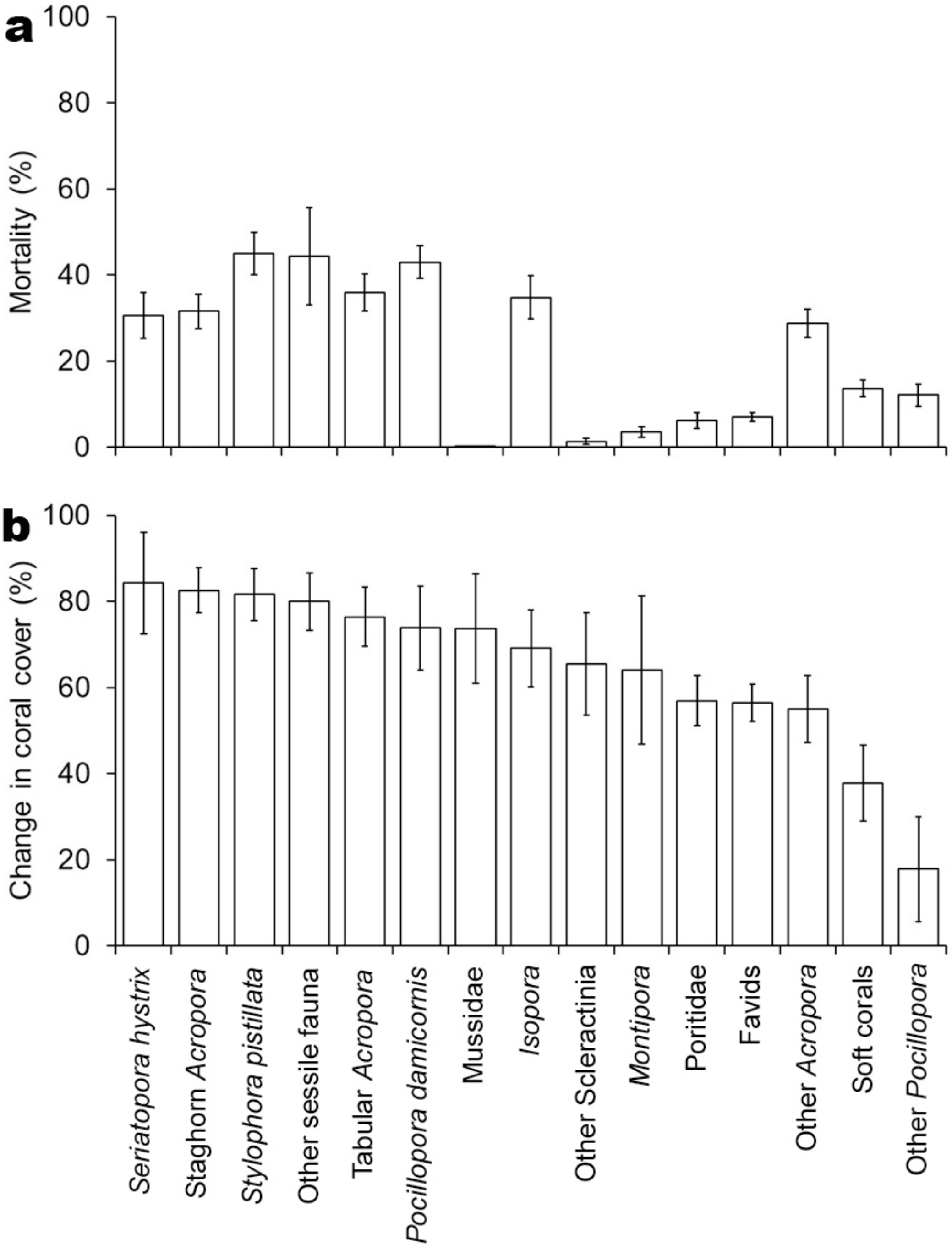
Extended Data Figure 1. Calibration of loss of corals on reefs with different amounts of bleaching. Aerial scores of bleaching on the x-axis are: 0 (<1% of colonies bleached), 1 (1-10%), 2 (10-30%), 3 (30-60%) and 4 (60-100%). Change in coral cover on the y-axis was measured *in situ* between March and November on reefs that were also scored from the air. Boxplots are shown for each aerial category, showing median values (horizontal lines), boxes for the middle two quartiles, vertical lines for the 1st and 4th quartiles, and data points for outliers. Medians were used when calibrating change in cover for each aerial category (see Fig. 1a).



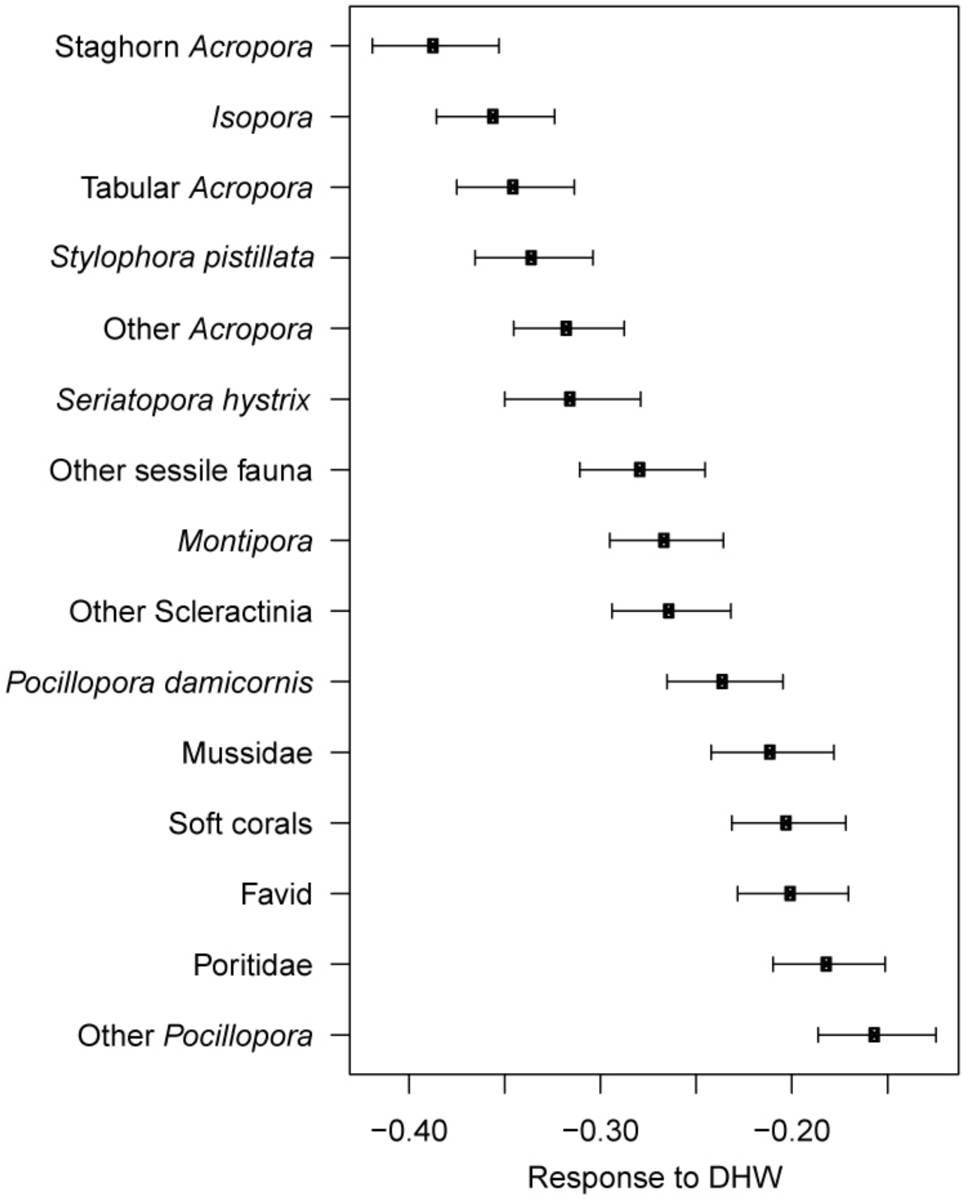
Extended Data Figure 2. Map of loss of coral cover on 110 reefs that were surveyed underwater in 2016. Losses between March and November range from zero (dark green), to 1-5% (green), 5-25% (light green), 25-50% (yellow), 50-75% (orange) and 75-100% (red).



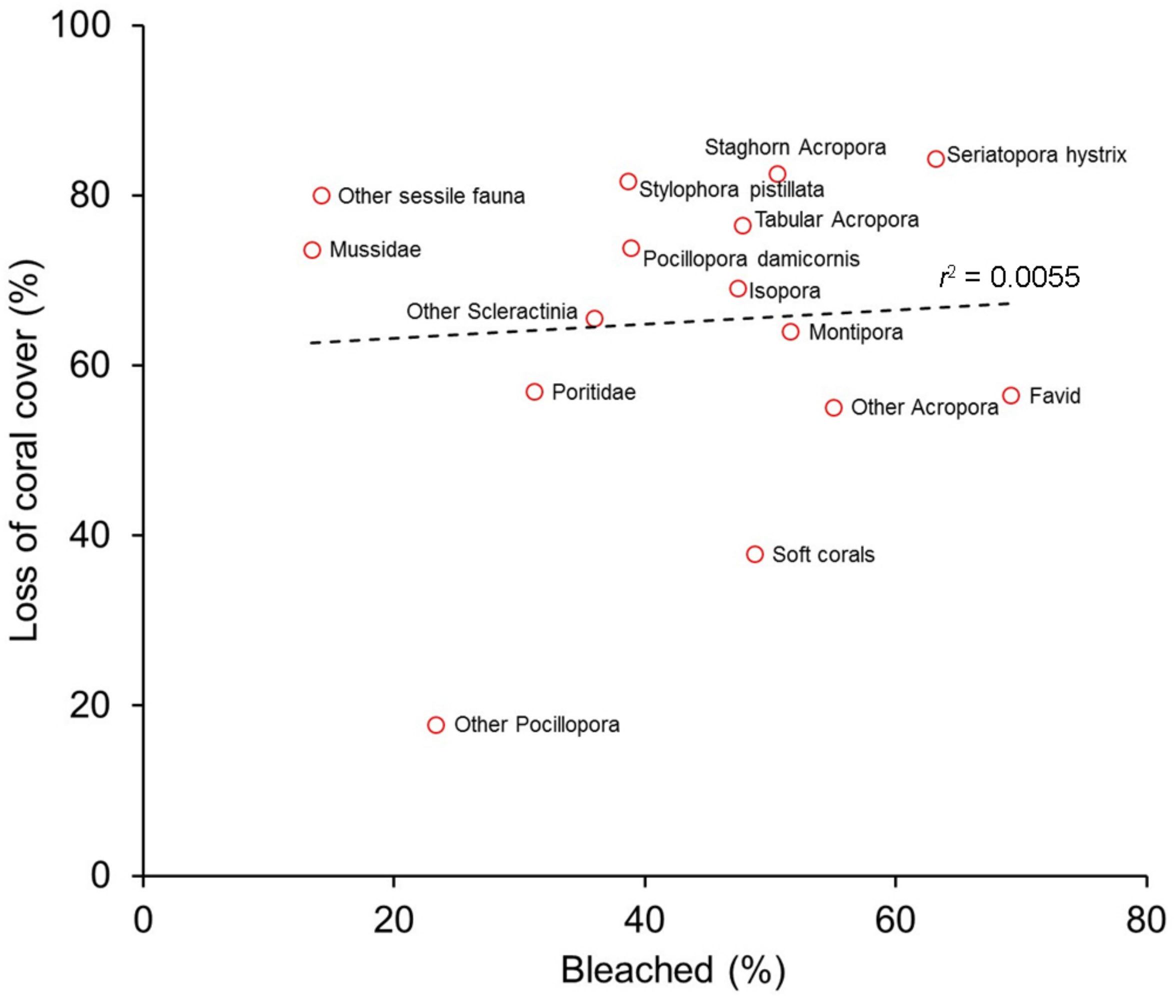
Extended Data Figure 3. A frequency distribution of coral cover on 110 reefs, measured between March (solid bars) and November (hashed bars). Reef locations are shown in Extended Data Fig. 2.



Extended Data Figure 4. Mortality rates differ among taxa and increase over time. (a) The initial mortality of corals recorded on belt transects on 83 reefs with >60% bleaching (b) Longer-term average loss of cover for taxonomic categories recorded between March and November on 63 re-censused reefs with >60% bleaching. Taxa are plotted in rank order along the x-axis from high to low decreases in cover, with a spectrum of relative winners on the right and losers to the left. Error bars are one standard error.



Extended Data Figure 5. Differential sensitivity of coral taxa to temperature stress, illustrated by the estimated loss of cover for different groups of corals between March and November as a function of heat exposure (DHW). The horizontal axis is the slope of the relationship between the log-ratio of final and initial coral cover (response variable) and degree-heating weeks (explanatory variable). Values plotted for each taxonomic grouping (ordered from most sensitive to least sensitive) are random effects estimates, with conditional standard errors.



Extended Data Figure 6. The relationship between the levels of bleaching by individual coral taxa on severely bleached reefs (>60% of all colonies affected), and their subsequent loss of cover eight months later. The weak correlation indicates that the winners-losers spectrum of bleaching among taxa is a poor predictor of which ones ultimately die.

Extended Data Table 1. Eight traits of coral species and their key functional roles.

Trait	**Trait scores**	**Reef function**
Growth rate	In mm/year: 0-10 (1), 10-20 (2), 20-40 (3), 40-60 (4), >60 (5).	Carbonate framework accretion; reef regeneration
Skeletal density	In g/cm^3: <1 (1), 1-1.4 (2), 1.4-1.7 (3), 1.7-2 (4), >2 (5)	Carbonate framework accretion
Corallite width	In mm: <1 (1), 1-2 (2), 2-5 (3), 5-15 (4) ; <15 (5)	Filter feeding; nutrient capture
Interstitial space size	(1-5) Based on morphological categories.	Habitat provision
Colony height	(1-5) Based on morphological categories.	Carbonate framework accretion; habitat provision
Surface area to volume ratio	(1-5) Based on morphological categories	Primary productivity; nutrient cycling
Colony size	Rank (1-12) measured from reef crest transects	Carbonate framework accretion; habitat provision
Reproductive mode	Brooders (1), Mixed (2), Spawners (3)	Reef connectivity and regeneration

Extended Data Table 2. Trait scores for each of 12 groups of corals.

Taxon	Corallite size	Growth rate	Colony size	Skeletal density	Colony height	Tissue area	Interstitial space size	Reproductive mode
Bushy *Acropora*	2	3	7	3	3	5	3	Spawner
Favids	4	1	4	3	2	1	1	Spawner
Isopora	2	2	10	3	2	2	1	Brooder
Montipora	2	3	9	5	1	1	1	Spawner
Mussidae	5	1	3	2	2	1	1	Spawner
Other *Pocillopora*	1	3	8	3	3	4	3	Spawner
Pocillopora damicornis	1	3	2	4	2	4	3	Brooder
Poritidae	2	2	6	2	4	1	1	Mix
Seriatopora hystrix	1	3	1	5	2	3	3	Brooder
Staghorn *Acropora*	2	5	11	4	5	3	5	Spawner
Stylophora pistillata	2	3	5	4	2	3	3	Brooder
Tabular *Acropora*	2	4	12	4	3	5	5	Spawner