LETTER

https://doi.org/10.1038/s41586-018-0041-2

Global warming transforms coral reef assemblages

Terry P. Hughes[1]*, James T. Kerry[1], Andrew H. Baird[1], Sean R. Connolly[1,2], Andreas Dietzel[1], C. Mark Eakin[3], Scott F. Heron[3,4,5], Andrew S. Hoey[1], Mia O. Hoogenboom[1,2], Gang Liu[3,4], Michael J. McWilliam[1], Rachel J. Pears[6], Morgan S. Pratchett[1], William J. Skirving[3,4], Jessica S. Stella[6] & Gergely Torda[1,7]

Global warming is rapidly emerging as a universal threat to ecological integrity and function, highlighting the urgent need for a better understanding of the impact of heat exposure on the resilience of ecosystems and the people who depend on them[1]. Here we show that in the aftermath of the record-breaking marine heatwave on the Great Barrier Reef in 2016[2], corals began to die immediately on reefs where the accumulated heat exposure exceeded a critical threshold of degree heating weeks, which was 3–4 °C-weeks. After eight months, 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. Fast-growing staghorn and tabular corals suffered a catastrophic die-off, transforming the three-dimensionality and ecological functioning of 29% of the 3,863 reefs comprising the world's largest coral reef system. Our study bridges the gap between the theory and practice of assessing the risk of ecosystem collapse, under the emerging framework for the International Union for Conservation of Nature (IUCN) Red List of Ecosystems[3], by rigorously defining both the initial and collapsed states, identifying the major driver of change, and establishing quantitative collapse thresholds. The increasing prevalence of post-bleaching mass mortality of corals represents a radical shift in the disturbance regimes of tropical reefs, both adding to and far exceeding the influence of recurrent cyclones and other local pulse events, presenting a fundamental challenge to the long-term future of these iconic ecosystems.

Extreme weather events due to anthropogenic global warming are rapidly emerging as major contemporary threats to almost all ecosystems[1]. On coral reefs, severe heatwaves trigger episodes of mass bleaching[4–7], which occur 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 the bleaching is severe and the recovery time of their symbionts is prolonged[8,9]. However, the relationship between heat exposure, bleaching and the initial and longer term mortality of different taxa is not well understood or quantified. Although the concept of winners versus losers has been widely applied to describe inter-specific differences in the degree of bleaching[10–14], predicting the definitive losers, namely those 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, to our knowledge, examined the quantitative relationship between a broad range of heat exposures and the response of coral assemblages. Establishing the shape of this response curve is essential for identifying the critical levels of heat exposure that trigger bleaching and mass mortality, and for predicting the amount of heat exposure that could drive a transformation in species composition and the widespread collapse of ecological functions. Here, we examine geographical patterns of heat exposure and the resultant mortality of coral assemblages along the 2,300 km length of the Great Barrier Reef, following the record-breaking marine heatwave of 2016[2]. We show that taxonomic patterns of bleaching did not predict the identity of the corals that ultimately died, that many corals succumbed immediately from heat stress, and that others died more slowly following the depletion of their zooxanthellae. The die-off of corals drove a radical shift in the composition and functional traits of coral assemblages on hundreds of individual reefs, transforming large swaths of the Great Barrier Reef from mature and diverse assemblages to a highly altered, degraded system.

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 almost no heat-stress mortality occurring further south (Fig. 1a and Extended Data Figs. 1–3). The geographical footprint and intensity of the coral die-off (Fig. 1a) closely matched the observed north–south pattern in accumulated heat (Fig. 1b), measured as satellite-derived degree heating weeks (DHW in °C-weeks), a commonly used measurement that incorporates both the duration and intensity of heat stress[15,16]. The 5-km-resolution DHW values (Fig. 1b) were significantly correlated with independently estimated losses of corals (Fig. 1a; $r^2 = 0.50$, $P < 0.001$, $n = 1{,}156$ reefs). In the northern, 700-km-long section of the Great Barrier Reef (from 9.5–14.5 °S), in which 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, throughout the entire Great Barrier Reef, including the southern third, in which the 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, localized damage that typically occurs on reef sites within the track of a severe tropical cyclone[17].

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 temperature extremes in March 2016, many millions of corals died quickly in the northern third of the Great Barrier Reef over a period of only 2–3 weeks (Fig. 2a). These widespread losses were not due to the attrition of corals that slowly starved because they failed to regain their symbionts[9]. Rather, temperature-sensitive species of corals began to die almost immediately in locations that were exposed to heat stress of more than 3–4 °C-weeks (Figs. 1b, 2a). The amount of initial mortality increased steadily with increasing heat exposure ($r^2 = 0.50$, $P < 0.001$, $n = 63$ reefs); on reefs which were exposed to less than 4 °C-weeks, fewer than 5% of the corals died, whereas an initial median loss of 15.6% of corals was recorded on reefs with 4–8 °C-weeks exposure, and a median loss of 27.0% of corals at locations that experienced 8 °C-weeks or more (Fig. 2a). Across the entire Great Barrier Reef, 34.8% of individual reefs experienced at least 4 °C-weeks, and 20.7% of reefs were exposed to 8 °C-weeks or more of accumulated heat stress in 2016 (Fig. 1b). The amount of initial mortality at the peak of summer varied strikingly among different groups of corals (Extended Data Fig. 4a).

[1]Australian Research Council Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, Queensland, Australia. [2]College of Science and Engineering, James Cook University, Townsville, Queensland, Australia. [3]Coral Reef Watch, US National Oceanic and Atmospheric Administration, College Park, MD, USA. [4]Global Science & Technology, Inc., Greenbelt, MD, USA. [5]Marine Geophysical Laboratory, Physics Department, James Cook University, Townsville, Queensland, Australia. [6]Great Barrier Reef Marine Park Authority, Townsville, Queensland, Australia. [7]Australian Institute of Marine Science, Townsville, Queensland, Australia. *e-mail: terry.hughes@jcu.edu.au

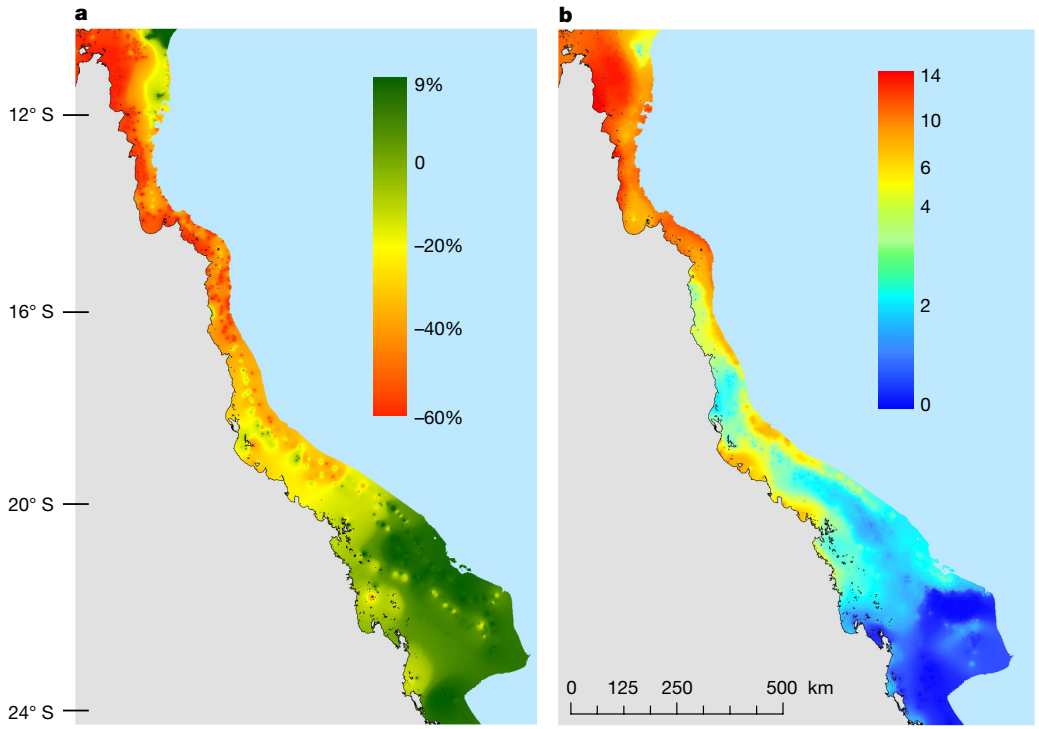


Fig. 1 | Large-scale spatial patterns in change in coral cover and in heat exposure on the Great Barrier Reef, Australia. a, Change in coral cover between March and November 2016. **b**, Heat exposure, measured in DHW (in °C-weeks) in the summer of 2016. Map template is provided by Geoscience Australia (© Commonwealth of Australia (Geoscience Australia) 2018).

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. Less than 1% of surviving colonies 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 percentage of corals that were initially bleached (Fig. 2b; $r^2 = 0.51$, $P < 0.001$, $n = 63$ reefs). Specifically, reefs that experienced less than 25% bleaching in March typically had almost no loss of cover after eight months (Fig. 2b). By 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 also intensified with increasing levels of heat exposure (DHW) experienced by each reef ($r^2 = 0.44$, $P < 0.001$, $n = 63$ reefs; Fig. 2c). Consequently, we recorded almost no loss of coral cover for reefs exposed to 0–3 °C-weeks, compared to a 40% decline at 4 °C-weeks, 66% for 8 °C-weeks, and extreme declines of > 80% for exposures of 9 °C-weeks or more. The nonlinear responses to heat exposure varied significantly among coral taxa (Extended Data Figs. 5, 6), illustrating a spectrum of survivorship 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 more than 60% of colonies), as illustrated by a non-metric multi-dimensional scaling (nMDS) analysis (Fig. 3). The abundances of all categories of corals

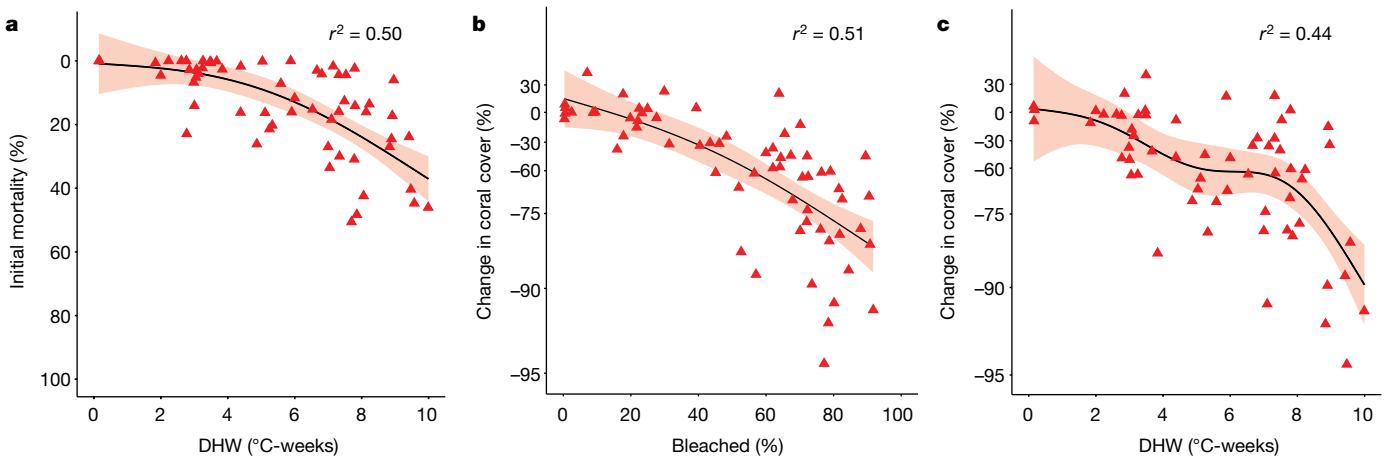


Fig. 2 | The initial and longer term response of coral assemblages to heat exposure. Regression curves were fitted using generalized additive models, with 95% confidence limits (ribbons). Data points represent individual reefs. **a**, Initial coral mortality measured at the peak of bleaching ($n = 63$ reefs), versus the heat exposure each reef experienced (satellite-based DHW (in °C-weeks)). **b**, Longer term change in coral cover ($\log_{10}$) between March and November 2016 on 63 individual reefs, versus the initial amount of bleaching recorded underwater. **c**, Longer term change in coral cover ($\log_{10}$) between March and November 2016, versus heat exposure (DHW) on the same individual reefs.

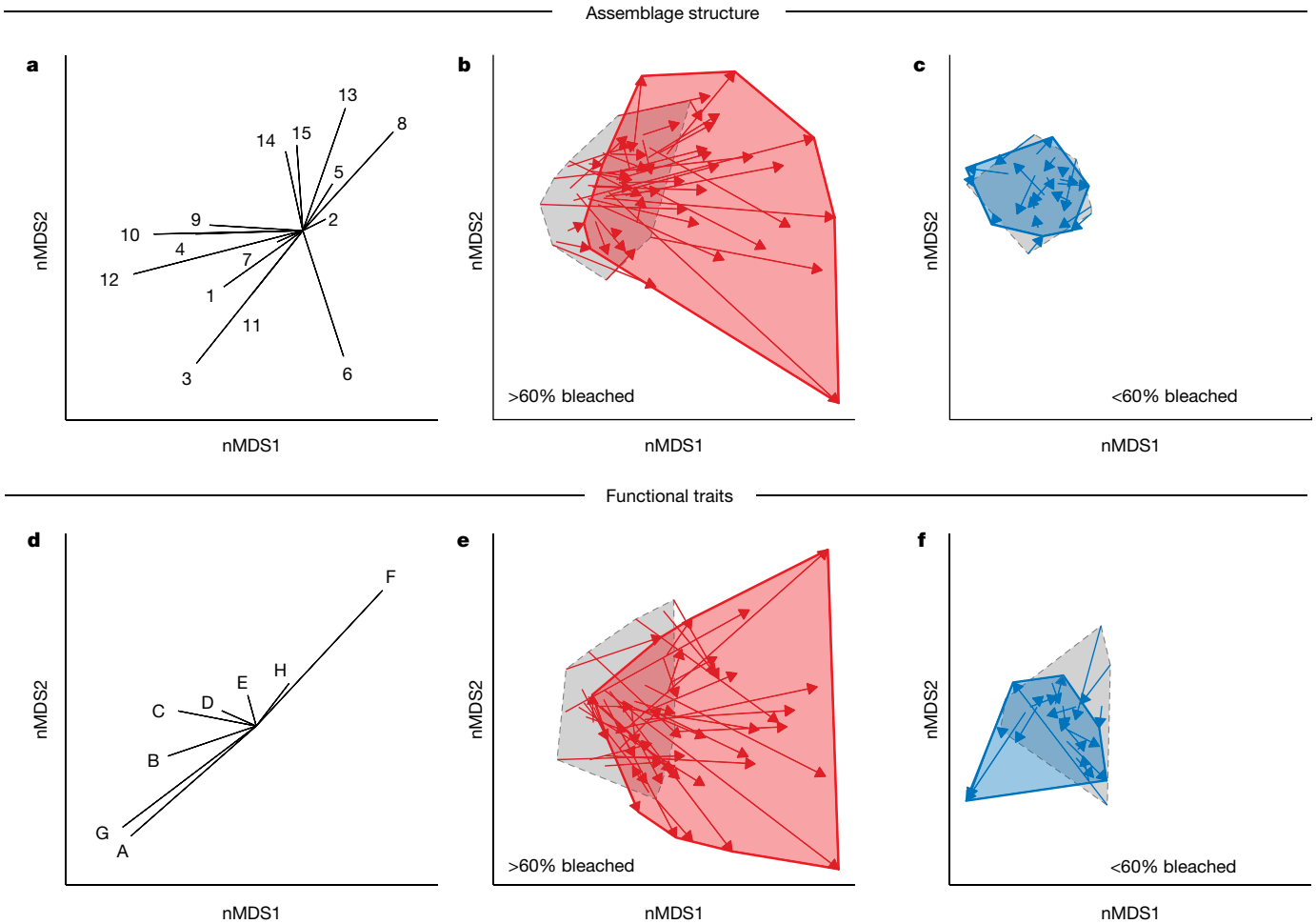


Fig. 3 | Changes in assemblage structure and functional traits of corals following mass bleaching. a–c, nMDS analyses of shifts in coral assemblages between March and November 2016. **a**, Fifteen nMDS vectors indicate the responses of individual taxa: 1, other *Acropora*; 2, favids; 3, *Isopora*; 4, *Montipora*; 5, Mussidae; 6, other *Pocillopora*; 7, *Pocillopora damicornis*; 8, Poritidae; 9, *Seriatopora hystrix*; 10, staghorn coral (*Acropora* spp.); 11, *Stylophora pistillata*; 12, tabular coral (*Acropora* spp.); 13, soft corals; 14, other scleractinia; 15, other sessile fauna (see Methods). **b**, The grey polygon bounds the ordination space occupied by coral assemblages on each reef in March. 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, $n = 43$ reefs) after eight months (in November), bounded by the red polygon. **c**, Blue arrows connect the before–after pairs of data points for each location on reefs ($n = 20$) that were moderately (< 60% bleached), bounded by the grey (March) and blue polygons (November). **d–f**, nMDS analyses of shifts in assemblage trait composition between March and November 2016 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 (see Methods and Extended Data Table 1). **e**, The shift in abundance-weighted trait space coordinates for coral assemblages over eight months for reefs with > 60% bleaching. **f**, The shift in abundance-weighted trait space coordinates for coral assemblages on reefs with < 60% bleaching.

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 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 minor (0–30%) bleaching (Fig. 3c).

The response of coral assemblages on reefs exposed to a broad range of heat stress, ranging from 0 to 10 °C-weeks, was strikingly nonlinear (Fig. 4). The changes in assemblage structure after eight months (measured as the Euclidean distance between before and after compositions on each reef; Fig. 3b, c) were small on reefs that were exposed to less than 6 °C-weeks, whereas reefs subjected to more than 6 °C-weeks lost over 50% of their corals (Fig. 2c) and shifted markedly 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 more than 6 °C-weeks during the 2016 bleaching event, and 20.7% (800 reefs) were exposed to more than 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 less than 6 °C-weeks were located predominantly in the southern half of the Great Barrier Reef, and in a narrow northern patch at the outer edge of the continental shelf where temperature anomalies in 2016 above the local long-term summer maximum were small (Fig. 1b).

The abrupt, regional-scale shift in coral assemblages has also radically reduced the abundance and diversity of species traits that facilitate key ecological functions (Fig. 3d, e and Extended Data Tables 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 over 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, branching and tabular species that are important providers of three-dimensional habitat, to a depauperate assemblage dominated by taxa

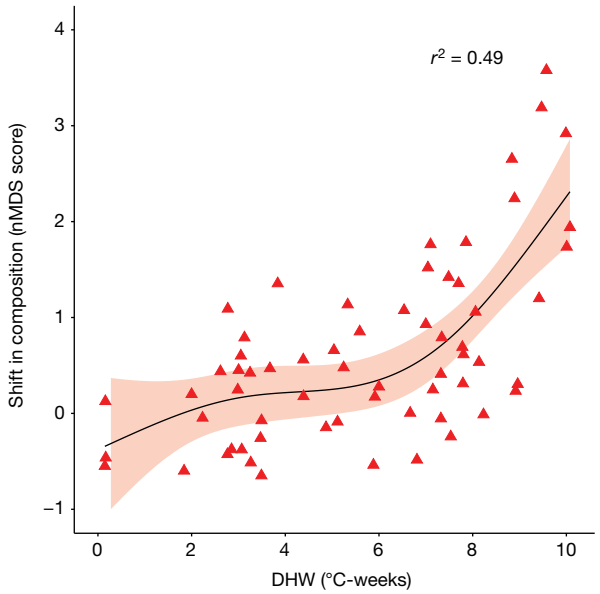


Fig. 4 | Change in coral assemblages in response to heat exposure. The regression curve is fitted using a generalized additive model, with 95% confidence limits. Each data point represents the shift in composition ($n = 63$ reefs), based on the Euclidean distance in a non-metric multi-dimensional scaling analysis of assemblages on individual reefs sampled at the peak of bleaching and eight months later. Heat exposure for each reef was measured as satellite-derived DHW (in °C-weeks).

with simpler morphological characteristics and slower growth rates. By 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 1,000 km-scale transformation 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 are accompanied with guidance that a DHW exposure of 4 °C-weeks is expected to cause significant bleaching, and 8 °C-weeks may also result in mortality of corals[15,16,18]. Similarly, a model for predicting the locations of resilient reefs on the Great Barrier Reef assumed that coral mortality starts to occur only once thermal exposure exceeds 6 °C-weeks[19]. However, we show that substantial mortality occurred on the Great Barrier Reef in 2016 well below 6 °C-weeks, beginning instead at 3–4 °C-weeks, and with typical losses exceeding 50% at 4–5 °C-weeks (Fig. 2c). Furthermore, the threshold that 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 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[20,21]. Second, the replacement of dead corals by larval recruitment and subsequent colony growth will take at least a decade even for fast-growing, highly fecund corals, such as species of *Acropora*, *Pocillopora*, *Seriatopora* and *Stylophora*[22,23]. The success of future recruitment will depend on 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[24]. Third, 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. The recurrence of mass bleaching during the recovery period will be critical, in view of the global rise in the frequency of bleaching events[4–6].

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 Ocean[4]. Furthermore, the Great Barrier Reef experienced severe bleaching again in early 2017, causing additional extensive damage[25,26]. The most likely scenario, therefore, is that coral reefs throughout the tropics will continue to degrade over the current century until climate change stabilizes[7,27], 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 (Figs. 1, 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 ecosystems, reinforcing the need for risk assessment of ecosystem collapse[3], especially if global action on climate change fails to limit warming to 1.5–2 °C above the pre-industrial base-line.

Online content

Any Methods, including any statements of data availability and Nature Research reporting summaries, along with any additional references and Source Data files, are available in the online version of the paper at https://doi.org/10.1038/s41586-018-0041-2.

Received: 24 August 2017; Accepted: 16 March 2018;
Published online: 18 April 2018

1. IPCC. *Climate Change 2014: Impacts, Adaptation, and Vulnerability* (eds Field, C. B. et al.) (Cambridge Univ., Cambridge, 2014).
2. Australian Bureau of Meteorology. 2016 marine heatwave on the Great Barrier Reef. http://www.bom.gov.au/environment/doc/marine-heatwave-2016.pdf (2016).
3. Bland, L. M. et al. Developing a standardized definition of ecosystem collapse for risk assessment. *Front. Ecol. Environ.* **16**, 29–36 (2018).
4. Hughes, T. P. et al. Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. *Science* **359**, 80–83 (2018).
5. Heron, S. F., Maynard, J. A., van Hooidonk, R. & Eakin, C. M. Warming trends and bleaching stress of the World's coral reefs 1985–2012. *Sci. Rep.* **6**, 38402 (2016).
6. Donner, S. D., Rickbeil, G. J. M. & Heron, S. F. A new, high-resolution global mass coral bleaching database. *PLoS ONE* **12**, e0175490 (2017).
7. Hughes, T. P. et al. Coral reefs in the Anthropocene. *Nature* **546**, 82–90 (2017).
8. Baird, A. H. & Marshall, P. A. Mortality, growth and reproduction in scleractinian corals following bleaching on the Great Barrier Reef. *Mar. Ecol. Prog. Ser.* **237**, 133–141 (2002).
9. Baker, A. C., Glynn, P. W. & Riegl, B. Climate change and coral reef bleaching: an ecological assessment of long-term impacts, recovery trends and future outlook. *Estuar. Coast. Shelf Sci.* **80**, 435–471 (2008).
10. Marshall, P. A. & Baird, A. H. Bleaching of corals on the Great Barrier Reef: differential susceptibilities among taxa. *Coral Reefs* **19**, 155–163 (2000).
11. Loya, Y. et al. Coral bleaching: the winners and the losers. *Ecol. Lett.* **4**, 122–131 (2001).
12. Hughes, T. P. et al. Climate change, human impacts, and the resilience of coral reefs. *Science* **301**, 929–933 (2003).
13. Swain, T. D. et al. Coral bleaching response index: a new tool to standardize and compare susceptibility to thermal bleaching. *Glob. Change Biol.* **22**, 2475–2488 (2016).
14. Hughes, T. P. et al. Global warming and recurrent mass bleaching of corals. *Nature* **543**, 373–377 (2017).
15. Eakin, C. M. et al. Caribbean corals in crisis: record thermal stress, bleaching, and mortality in 2005. *PLoS ONE* **5**, e13969 (2010).
16. Liu, G. et al. Reef-scale thermal stress monitoring of coral ecosystems: new 5-km global products from NOAA Coral Reef Watch. *Remote Sens.* **6**, 11579–11606 (2014).
17. Beeden, R. et al. Impacts and recovery from severe tropical cyclone Yasi on the Great Barrier Reef. *PLoS ONE* **10**, e0121272 (2015).
18. Kayanne, H. Validation of degree heating weeks as a coral bleaching index in the northwestern Pacific. *Coral Reefs* **36**, 63–70 (2017).
19. Hock, K. et al. Connectivity and systemic resilience of the Great Barrier Reef. *PLoS Biol.* **15**, e2003355 (2017).
20. Muller, E. M. et al. Bleaching increases likelihood of disease on *Acropora palmata* (Lamarck) in Hawksnest Bay, St. John, US Virgin Islands. *Coral Reefs* **27**, 191–195 (2008).
21. Miller, J. et al. Coral disease following massive bleaching in 2005 causes 60% decline in coral cover on reefs in the US Virgin Islands. *Coral Reefs* **28**, 925–937 (2009).
22. Kayanne, H., Harii, S., Ide, Y. & Akimoto, F. Recovery of coral populations after the 1998 bleaching on Shiraho Reef, in the southern Ryukyus, NW Pacific. *Mar. Ecol. Prog. Ser.* **239**, 93–103 (2002).

23. Gilmour, J. P., Smith, L. D., Heyward, A. J., Baird, A. H. & Pratchett, M. S. Recovery of an isolated coral reef system following severe disturbance. *Science* **340**, 69–71 (2013).
24. Webster, N. S., Soo, R., Cobb, R. & Negri, A. P. Elevated seawater temperature causes a microbial shift on crustose coralline algae with implications for the recruitment of coral larvae. *ISME J.* **5**, 759–770 (2011).
25. Hughes, T. P. & Kerry, J. T. Back-to-back bleaching has now hit two-thirds of the Great Barrier Reef. *The Conversation* https://theconversation.com/back-to-back-bleaching-has-now-hit-two-thirds-of-the-great-barrier-reef-76092 (2017).
26. Great Barrier Reef Marine Park Authority. Final report: 2016 coral bleaching event on the Great Barrier Reef. http://elibrary.gbrmpa.gov.au/jspui/bitstream/11017/3206/1/Final-report-2016-coral-bleaching-GBR.pdf (2017).
27. Hartmann, D. L. et al. in *Climate Change 2013: The Physical Science Basis*. (eds Stocker, T.F. et al.) 159–254 (IPCC, Cambridge Univ. Press, Cambridge, 2013).

Acknowledgements We acknowledge support from the Australian Research Council's Centre of Excellence Program and a Laureate Fellowship to T.P.H., from the Great Barrier Reef Marine Park Authority, and from the US National Oceanic and Atmospheric Administration. The scientific results and conclusions, as well as any views or opinions expressed herein, are those of the authors and do not necessarily reflect the views of NOAA or the US Department of Commerce. We thank T. Simpson, who provided 225 aerial scores of bleaching from the Torres Strait; M. Jacobson for assistance with statistical programming; members of the Australian National Coral Bleaching Taskforce, marine park managers and rangers, and 30 student volunteers, who participated in extensive field studies on the Great Barrier Reef throughout 2016.

Author contributions The study was conceptualized by T.P.H., who also wrote the first draft of the paper. All authors contributed to writing subsequent drafts. J.T.K. coordinated data compilation, analyses and graphics. Aerial bleaching surveys were conducted by T.P.H. and J.T.K. Underwater bleaching and mortality censuses were undertaken by A.H.B., A.D., A.S.H., M.O.H., M.J.M., R.J.P., M.S.P., J.S.S. and G.T. C.M.E., S.F.H., G.L. and W.J.S. provided satellite data on heat stress. M.J.M. undertook the functional trait analysis and S.R.C. provided statistical advice and modelled loss of coral cover among different taxa.

Competing interests The authors declare no competing interests.

Additional information
Extended data is available for this paper at https://doi.org/10.1038/s41586-018-0041-2.
Supplementary information is available for this paper at https://doi.org/10.1038/s41586-018-0041-2.
Reprints and permissions information is available at http://www.nature.com/reprints.
Correspondence and requests for materials should be addressed to T.P.H.
Publisher's note: Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

METHODS

Initial mortality and heat stress. We used aerial surveys, conducted in March–April 2016, to measure the geographical 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 °S to 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%; 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[14,28].

We assessed underwater the initial mortality of different taxa due to heat stress, at the same time as the aerial surveys, on 63 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 $10 \times 1\,m^2$ 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; 6, recently dead. The dead colonies, which had suffered whole-colony mortality, were white with fully intact fine-scale skeletal features, typically still had patches of rotting coral tissue and were experiencing the initial week or two of colonization by filamentous algae, features which distinguished them from corals that had 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 DHW metric[16]. DHW values are presented in Fig. 1b as a heat map (stretch type: histogram equalize) using inverse distance weighting (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 the 63 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 Great Barrier Reef during the March–November 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 Fig. 2 and Extended Data Fig. 1, changes in coral cover are presented as percentages calculated from the log-scale.

We compared the initial and final composition of corals using a non-metric multi-dimensional scaling (nMDS) analysis 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 fifteen groups 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* and *A. valida*); favids (that is, species and genera from the formerly recognized family Faviidae: *Cyphastrea*, *Favia*, *Favites*, *Goniastrea*, *Leptastrea*, *Montastrea* and *Platygyra*); Mussidae (*Lobophyllia* and *Symphyllia*); *Isopora* (*I. palifera* and *I. cuneata*); other *Pocillopora* (*P. meandrina* and *P. verrucosa*); other sessile animals (sponges, tunicates, molluscs); *Porites* (*P. annae* and *P. lobata*); *Montipora* (*M. foliosa*, *M. grisea*, *M. hispida*, *M. montasteriata* and *M. tuberculosa*); staghorn *Acropora* (*A. florida*, *A. intermedia*, *A. microphthalma*, *A. muricata* and *A. robusta*); soft corals (alcyonaceans and zooanthids); tabular *Acropora* (*A. cytherea*, *A. hyacinthus* and *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, which provided the best spatial resolution (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 (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 total coral cover on 110 reefs (Extended Data Fig. 2), including the 63 reefs that were re-censused for change in composition. 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 replicate reefs surveyed within each of eight sectors of the Great Barrier Reef Marine Park and the Torres Strait), 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 DHW and observed change in cover (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 Figs. 2 and 3) yielded consistent results with Fig. 1a—a 29.0% and 27.7% decline, respectively, after eight months.

Differential mortality among coral taxa. To estimate how exposure to heat (measured as 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. We excluded from the analysis observations with zero initial coral cover of a particular taxonomic group. Change in coral cover was transformed before analysis by calculating the $log\left(\frac{C_f+\epsilon}{C_i+\epsilon}\right)$ where C_f and C_i were the final and initial coral cover, respectively, and ϵ was the minimum observed value of coral cover. 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 (that is, there was a random effect of taxonomic group on the slope). To illustrate these differences, Extended Data Fig. 5 plots the estimated slope of the coral cover response variable 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, 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[29], 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, except for *Montipora* and *Porites*, for which we used the mean score across the reef crest species that 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:

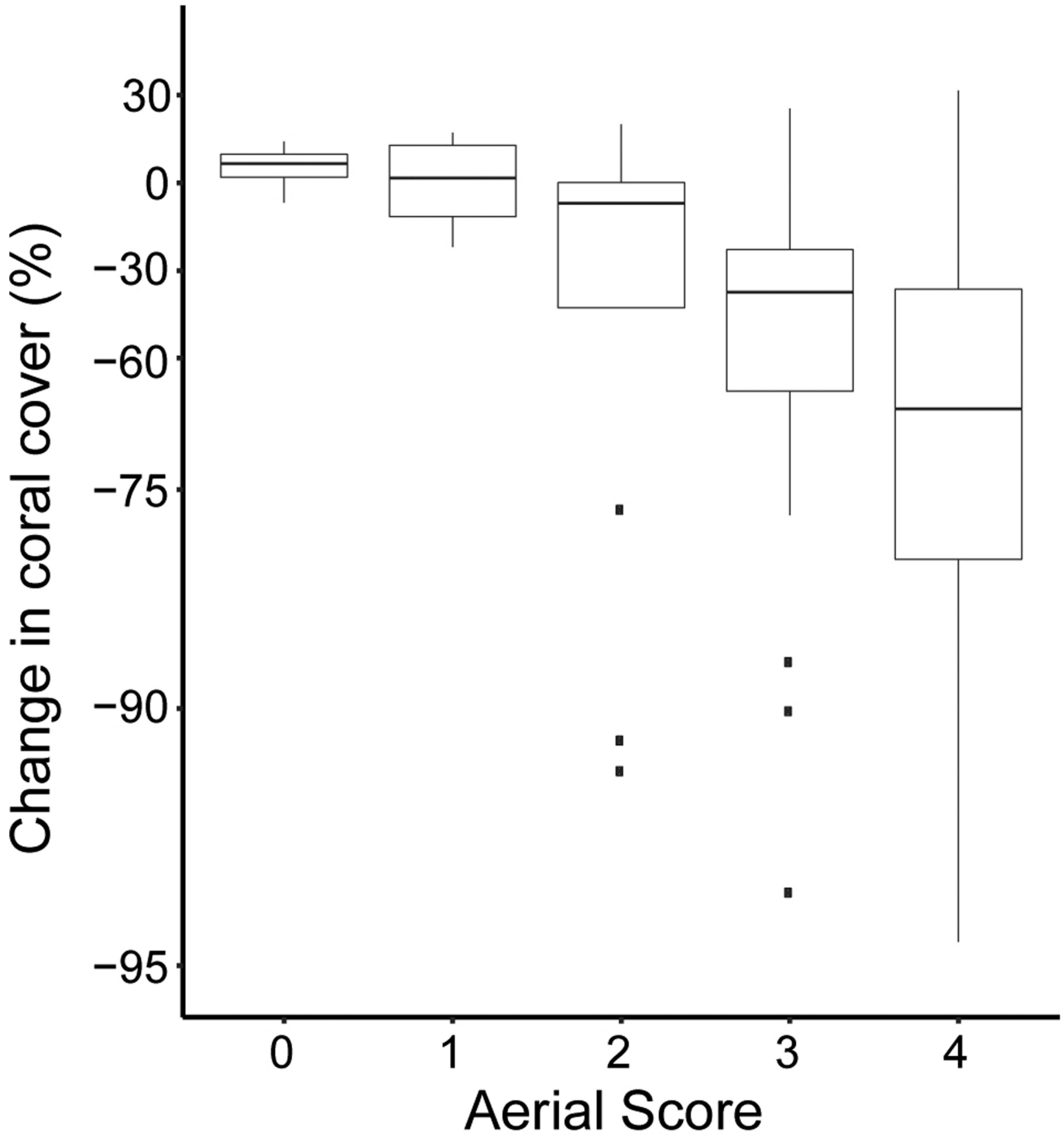
$$\mathrm{CWM} = \sum_{i=1}^{n} a_i \mathrm{trait}_i$$

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 visualize the overall shift in functional composition, we used a nMDS analysis based on a Bray–Curtis dissimilarity 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.

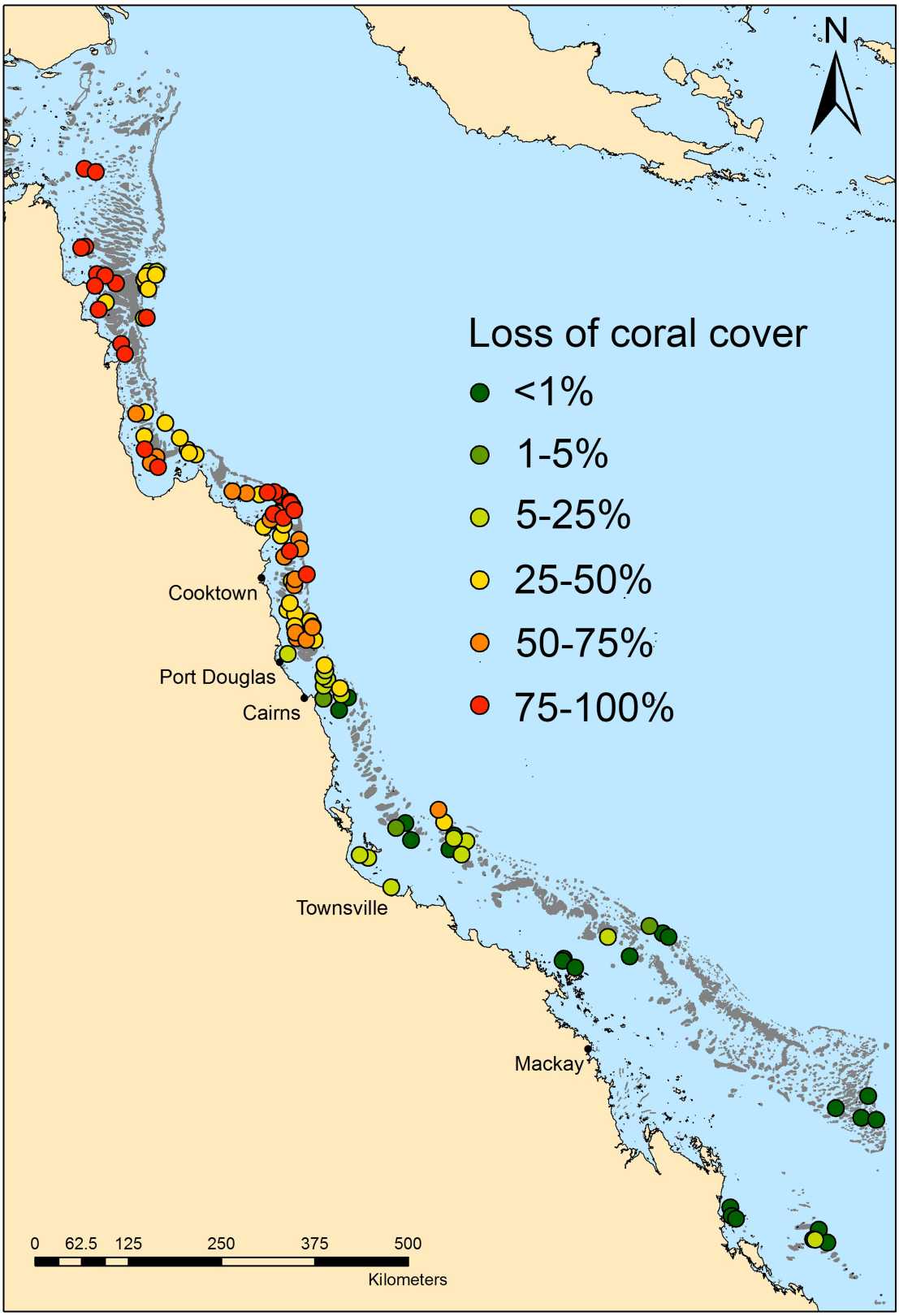
Reporting Summary. Further information on experimental design is available in the Nature Research Reporting Summary linked to this paper.

Data availability. All heat exposure data used in this study are publicly available from the US National Oceanic and Atmospheric Administration. Source data for coral bleaching, mortality and abundances are available online at the Tropical Data Hub: https://doi.org/10.4225/28/5a725ee7548a7.

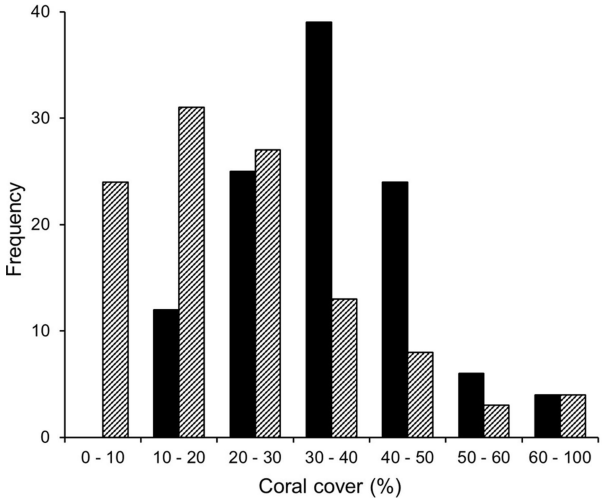
28. Hughes, T. P., Kerry, J. T. & Simpson, T. Large-scale bleaching of corals on the Great Barrier Reef. *Ecology* **99**, 501 (2017).
29. Madin, J. S. et al. The Coral Trait Database, a curated database of trait information for coral species from the global oceans. *Sci. Data* **3**, 160017 (2016).



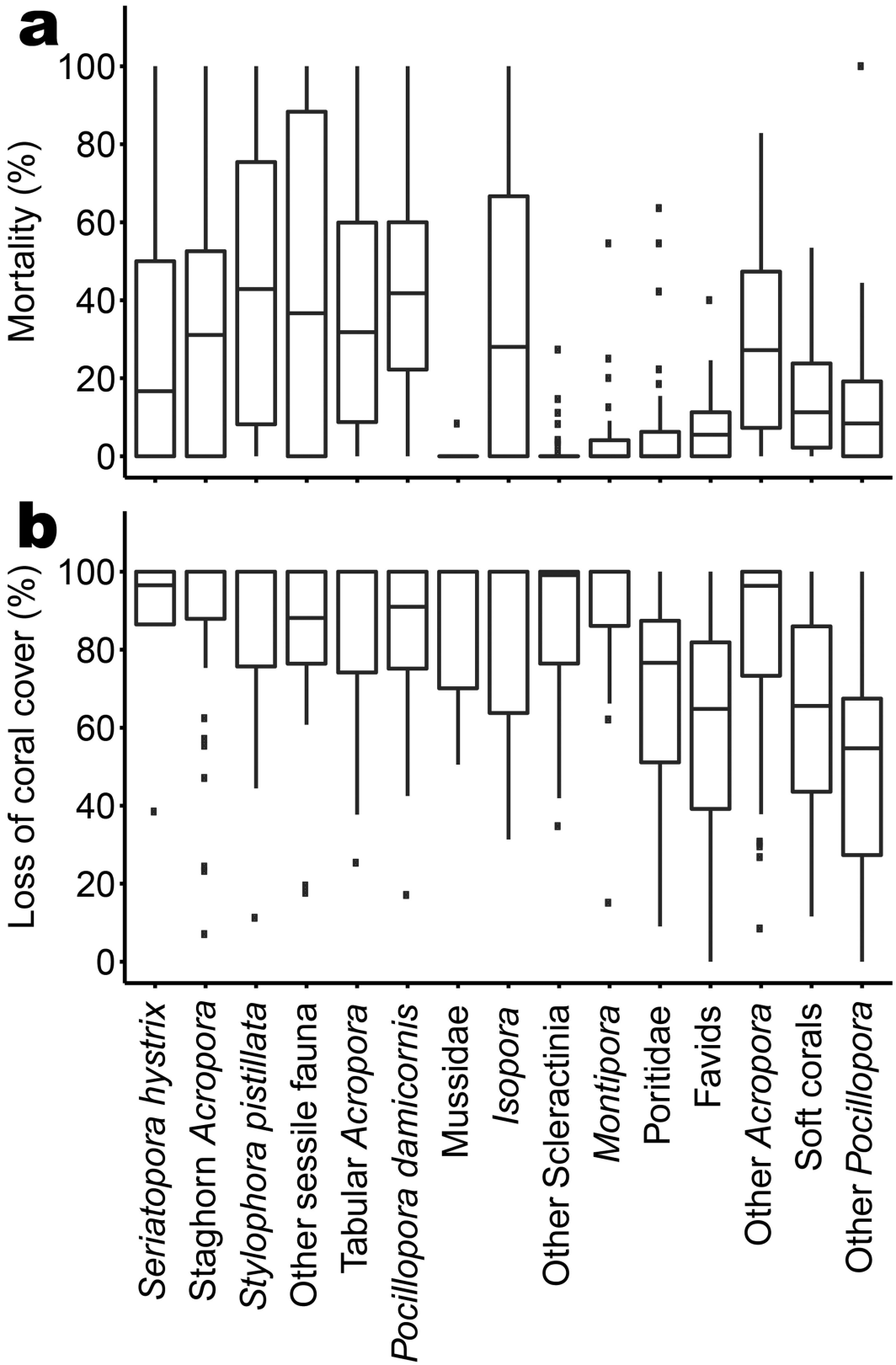
Extended Data Fig. 1 | Relationship between aerial bleaching scores and change in coral cover. Aerial scores of bleaching on the *x* axis are: 0 (< 1% of colonies bleached), 1 (1–10%), 2 (10–30%), 3 (30–60%) and 4 (60–100%). Change in coral cover on the *y* axis was measured in situ between March and November 2016 on 98 reefs that were also scored from the air. Box plots are shown for each aerial category, showing median values (horizontal lines), boxes for values in the 25th–75th percentiles, vertical lines for values less than the 25th percentile and greater than the 75th, and data points for outliers. Medians were used when calibrating change in cover for each aerial category (see Fig. 1a).



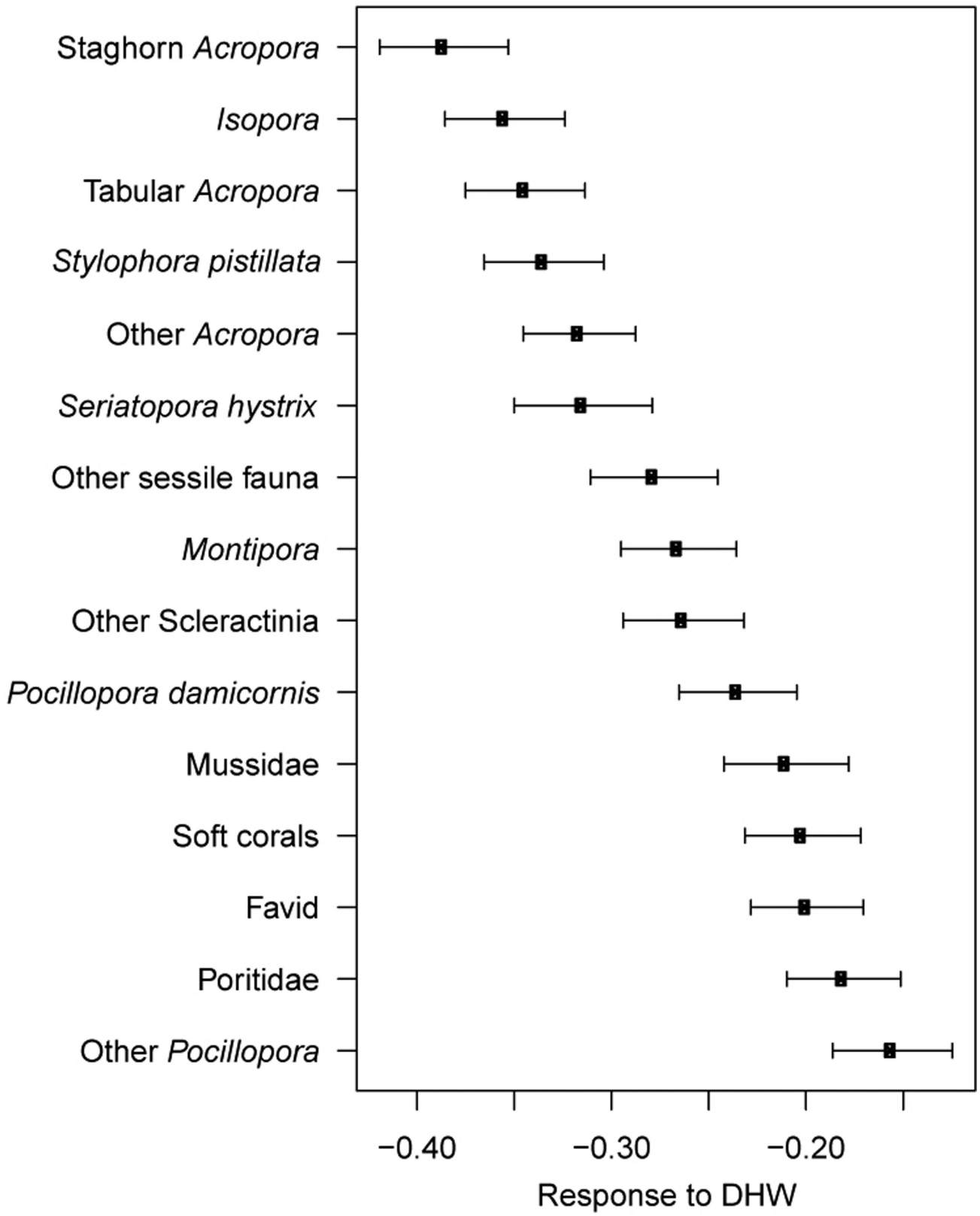
Extended Data Fig. 2 | Loss of coral cover along the Great Barrier Reef in 2016. Losses, measured on 110 reefs between March and November 2016, range from 0 (dark green) to 100% (1–5% (green), 5–25% (light green), 25–50% (yellow), 50–75% (orange) and 75–100% (red)). Map template is provided by Geoscience Australia (Commonwealth of Australia (Geoscience Australia) 2018).



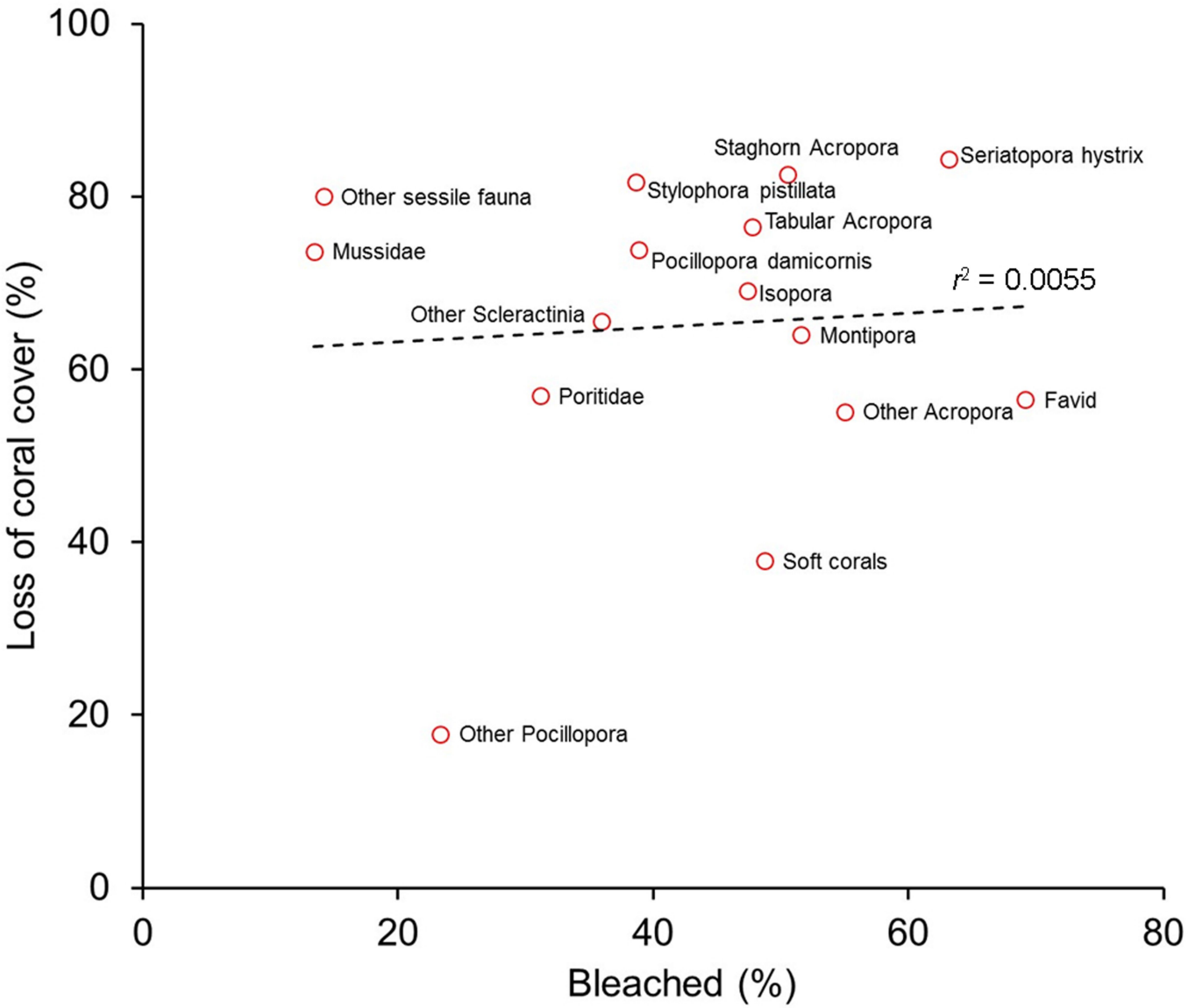
Extended Data Fig. 3 | Shifts in coral cover following coral bleaching. The frequency distribution of coral cover on 110 reefs, measured in March 2016 (solid bars) and again in November 2016 (hashed bars). Reef locations are shown in Extended Data Fig. 2.



Extended Data Fig. 4 | Mortality rates differ among coral taxa. Box plots are shown for each taxon, showing median mortality (horizontal lines), boxes for the middle two quartiles, vertical lines for the first and fourth quartiles, and data points for outliers. **a**, The initial mortality of corals recorded on belt transects on 43 reefs with > 60% bleaching. **b**, Longer term loss of cover for taxonomic categories recorded between March and November 2016 on the 43 remeasured reefs with > 60% bleaching. Taxa in **a** and **b** are plotted in rank order along the *x* axis, from highest to lowest decreases in mean cover between March and November 2016.



Extended Data Fig. 5 | Differential sensitivity of coral taxa to temperature stress. Sensitivity is estimated from the loss of cover on 63 reefs for different groups of corals between March and November 2016, 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 DHW (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 Fig. 6 | Bleaching extent is unrelated to mortality. The regression shows the relationship between the levels of bleaching by individual coral taxa on severely bleached reefs (where > 60% of all colonies were affected, $n = 43$ reefs), and their subsequent loss of cover eight months later. The non-significant 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

Spawners release eggs and sperm that fertilize externally, whereas brooders release internally fertilized planulae larvae.

nature research

Corresponding author(s): Terry Hughes

☐ Initial submission ☐ Revised version ☒ Final submission

Life Sciences Reporting Summary

Nature Research wishes to improve the reproducibility of the work that we publish. This form is intended for publication with all accepted life science papers and provides structure for consistency and transparency in reporting. Every life science submission will use this form; some list items might not apply to an individual manuscript, but all fields must be completed for clarity.

For further information on the points included in this form, see Reporting Life Sciences Research. For further information on Nature Research policies, including our data availability policy, see Authors & Referees and the Editorial Policy Checklist.

Experimental design

1. Sample size

   Describe how sample size was determined.

   No statistical methods were used to predetermine sample size of experimental treatments - the study was observational (non-manipulative). For aerial scoring of bleaching, a sample size of 1,156 reefs was sufficient to map bleaching throughout the Great Barrier Reef, and to demonstrate a statistically significant correlation ($p < 0.001$) with a satellite-based measures of heat exposure on each reef. For underwater observations, a sample size of 63 reefs was sufficient to demonstrate relationships between heat exposure, bleaching and mortality (all with $p<0.001$)

2. Data exclusions

   Describe any data exclusions.

   No data were excluded

3. Replication

   Describe whether the experimental findings were reliably reproduced.

   The study is observational rather than experimental. See #1 for justification of sample sizes.

4. Randomization

   Describe how samples/organisms/participants were allocated into experimental groups.

   There were no experimental treatments. Therefore, reefs were selected randomly from throughout the Great Barrier Reef to assess their condition.

5. Blinding

   Describe whether the investigators were blinded to group allocation during data collection and/or analysis.

   There were no experimental treatments. Therefore, investigators were not blinded to allocation during experiments and outcome assessment.

Note: all studies involving animals and/or human research participants must disclose whether blinding and randomization were used.

6. Statistical parameters

   For all figures and tables that use statistical methods, confirm that the following items are present in relevant figure legends (or in the Methods section if additional space is needed).

n/a	Confirmed	
☐	☒	The exact sample size (*n*) for each experimental group/condition, given as a discrete number and unit of measurement (animals, litters, cultures, etc.)
☐	☒	A description of how samples were collected, noting whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
☒	☐	A statement indicating how many times each experiment was replicated
☐	☒	The statistical test(s) used and whether they are one- or two-sided (note: only common tests should be described solely by name; more complex techniques should be described in the Methods section)
☐	☒	A description of any assumptions or corrections, such as an adjustment for multiple comparisons
☐	☒	The test results (e.g. *P* values) given as exact values whenever possible and with confidence intervals noted
☐	☒	A clear description of statistics including central tendency (e.g. median, mean) and variation (e.g. standard deviation, interquartile range)
☐	☒	Clearly defined error bars

See the web collection on statistics for biologists for further resources and guidance.

Software

Policy information about availability of computer code

7. Software

Describe the software used to analyze the data in this study.	R coding for statistical analysis. ArcGIS (ArcMap) for graphical interpolation of data

For manuscripts utilizing custom algorithms or software that are central to the paper but not yet described in the published literature, software must be made available to editors and reviewers upon request. We strongly encourage code deposition in a community repository (e.g. GitHub). *Nature Methods* guidance for providing algorithms and software for publication provides further information on this topic.

Materials and reagents

Policy information about availability of materials

8. Materials availability

Indicate whether there are restrictions on availability of unique materials or if these materials are only available for distribution by a for-profit company.	No unique materials were used

9. Antibodies

Describe the antibodies used and how they were validated for use in the system under study (i.e. assay and species).	No antibodies were used

10. Eukaryotic cell lines

a. State the source of each eukaryotic cell line used.	No cell lines were used
b. Describe the method of cell line authentication used.	No cell lines were used
c. Report whether the cell lines were tested for mycoplasma contamination.	No cell lines were used
d. If any of the cell lines used are listed in the database of commonly misidentified cell lines maintained by ICLAC, provide a scientific rationale for their use.	No cell lines were used

Animals and human research participants

Policy information about studies involving animals; when reporting animal research, follow the ARRIVE guidelines

11. Description of research animals

Provide details on animals and/or animal-derived materials used in the study.	No animals were used

Policy information about studies involving human research participants

12. Description of human research participants

Describe the covariate-relevant population characteristics of the human research participants.	Study did not involve human research participants