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Ecological memory modifies the cumulative impact of recurrent climate extremes

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Climate change is radically altering the frequency, intensity and spatial scale of severe weather events, such as heatwaves, droughts, floods and fires[1]. As the time interval shrinks between recurrent shocks[2–5], the responses of ecosystems to each new disturbance are increasingly likely to be contingent on the history of other recent extreme events. Ecological memory—defined as the ability of the past to influence the present trajectory of ecosystems[6,7]—is also critically important for understanding how species assemblages are responding to rapid changes in disturbance regimes due to anthropogenic climate change[2,3,6–8]. Here, we show the emergence of ecological memory during unprecedented back-to-back mass bleaching of corals along the 2,300 km length of the Great Barrier Reef in 2016, and again in 2017, whereby the impacts of the second severe heatwave, and its geographic footprint, were contingent on the first. Our results underscore the need to understand the strengthening interactions among sequences of climate-driven events, and highlight the accelerating and cumulative impacts of novel disturbance regimes on vulnerable ecosystems.

Changes through time are fundamental to the study of ecology and evolution, yet our understanding of the contemporary condition of ecosystems often discounts the role of non-equilibrial dynamics and history[6,9]. Emerging theoretical frameworks and models point to the important effects of time lags and memory, as the enduring influences of past experiences and changing conditions unfold over time[7]. For example, the responses of ecosystems during ecological succession, and the evolution of life history traits, are key legacy effects of the history of recurrent disturbances[2]. On most coral reefs, for instance, where recurrent tropical cyclones have historically been the most significant external disturbance[10], regional- and global-scale bleaching of corals has become a major additional agent of mortality of reef-building corals in recent decades[5,11]. Here, we document how ecological memory of severe coral bleaching on the Great Barrier Reef in 2016[12] subsequently transformed the response of corals to heat stress during a second marine heatwave in 2017. We show further that the geographic pattern of heat exposure in 2016 had a lingering impact on the spatial footprint of bleaching along the 2,300 km length of the world's largest reef system during the subsequent heatwave one year later—history has a geographic signal. Our results demonstrate the need to understand the combined, interactive effects of sequences of recurrent climate-related disturbances at a hierarchy of spatial scales, and the critical role of recent history for predicting ecological outcomes in an era of rapid global change.

The response of corals to heat stress during the second of two unprecedented back-to-back bleaching events on the Great Barrier Reef was markedly different from the first. Heat stress—measured from satellites as degree heating weeks (DHW; °C-weeks)—was greater in 2017 on 79.9% of individual reefs ($n = 3,863$ reefs; Fig. 1a and Supplementary Fig. 1), yet despite the higher and/or longer-lasting summer sea surface temperatures, the surviving corals were more resistant in 2017 to a recurrence of bleaching compared with the previous year (Fig. 1b and Supplementary Fig. 2). Specifically, in 2016, an exposure of 4–5 °C-weeks elicited a 50% probability of severe bleaching (affecting >30% of corals), but in 2017 the same 50% response occurred at a much higher level of heat exposure of 8–9 °C-weeks. In comparison, an exposure of 8–9 °C-weeks in 2016 was associated with a >90% probability of severe bleaching (Fig. 1b). Furthermore, the bleaching response curves in 2017 (in response to the severity of the second heatwave) were contingent on the history of heat exposure in 2016, with the shift being progressively greater depending on the severity of heat stress in the first event (Fig. 1c). For example, reefs exposed to 9 °C-weeks in 2017 had only a 14% probability of re-bleaching if they had experienced 9 °C-weeks in 2016, compared with almost 100% for reefs that were exposed to 0 or 3 °C-weeks in 2016 (Fig. 1c).

In 2016, the most intense heat exposure and bleaching occurred in the northern third of the Great Barrier Reef (Supplementary Video 1), whereas in 2017 the central region was the most severely affected (Supplementary Fig. 3). Consequently, the back-to-back bleaching has cumulatively extended along close to two-thirds of the Great Barrier Reef, while the southernmost region escaped with little or no bleaching in both episodes. Of the 606 individual reefs that were surveyed in both bleaching events, 22.3% bleached severely twice, 21.8% bleached severely in 2016 but not 2017, 9.2% bleached severely in 2017 but not 2016, and 46.7% (overwhelmingly in the south, and on offshore far northern reefs) escaped severe bleaching in both years (Supplementary Fig. 3b). The back-to-back heatwaves bring the total number of mass bleaching events on the Great Barrier Reef to four over the past two decades (in 1998, 2002, 2016 and 2017). Of the 171 reefs that have been assessed by aerial surveys during all 4 events, only 7% have escaped bleaching entirely since 1998, and 61% have been severely bleached (>30% of colo-

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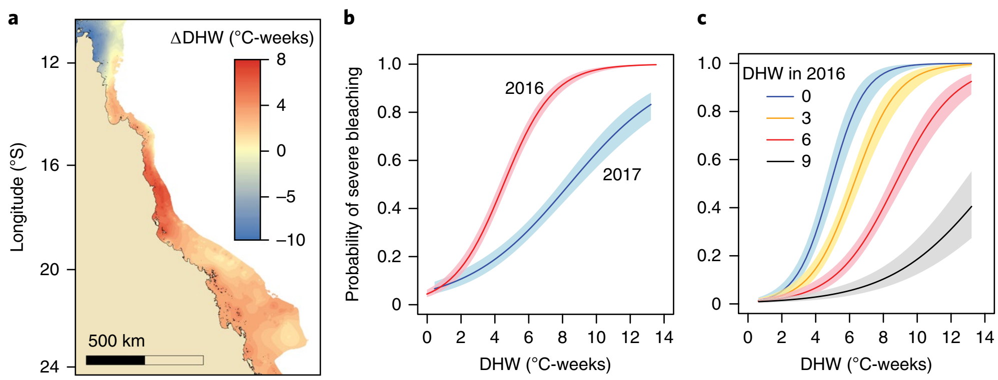

Fig. 1 | The bleaching response of corals on the Great Barrier Reef was diminished in a second summer heatwave, despite higher exposure to heat stress. a, Change in cumulative heat exposure on the Great Barrier Reef, measured on 3,863 individual reefs by satellites as DHW, in 2017 compared with 2016. Red indicates greater exposure in 2017, while blue indicates less. **b**, Bleaching response curves, with 95% confidence limits (shading), in two consecutive years. The *x* axis shows the heat exposure in 2016 (red) and 2017 (blue). The *y* axis is the probability of severe bleaching (affecting >30% of corals) calculated from aerial bleaching scores ($n=1,135$ reefs in 2016, and 742 in 2017). **c**, Bleaching response curves in 2017, explained by DHW in 2017 and its interaction with DHW in 2016, for reefs with 4 different levels of heat exposure: 0, 3, 6 and 9 °C-weeks in 2016.

nies affected) at least once. So far, the cumulative footprint of severe bleaching extends throughout most of the northern and central regions, and along the 2,300 km coastline of the Great Barrier Reef (Supplementary Fig. 4).

The severity of bleaching in different regions along the Great Barrier Reef in 2017 was contingent on the geographic pattern of heat exposure and bleaching in 2016, revealing the emergence of a spatial pattern of ecological memory (Fig. 2). We used the bleaching threshold fitted from the 2016 event (red curve in Fig. 1b) to predict the expected 2017 bleaching from the DHW exposure in the second year, then mapped the location of reefs that were predicted to not bleach severely in 2017 but actually did, or that were expected to bleach but did not. This analysis reveals strikingly different outcomes in 2017 for the northern, central and southern regions of the reef (Fig. 2), depending on the severity of heat exposure in both 2016 and 2017.

The northern region bleached much less in 2017 compared with 2016, even on individual reefs that had the same severe 8–13 °C-week exposure in both summers (Supplementary Fig. 3). The prediction error distribution in a model that predicted the 2017 bleaching event based on the heat stress experienced in 2017, but using the fitted bleaching response curve from 2016, is strongly skewed in the northern Great Barrier Reef (Fig. 2a), because of the erroneous prediction of a high probability of bleaching that did not actually occur. Reefs exhibiting this apparent resistance to bleaching in 2017 (coloured blue in Fig. 2b) were widely distributed throughout the region, across the full spectrum of environmental conditions, from nearshore to the outer edge of the continental shelf, and spanning a latitudinal extent of close to 700 km. A plausible mechanism for less bleaching in the second event is the observed mass mortality of heat-sensitive coral species caused by the unprecedented intensity of heat stress in 2016 (Fig. 3a and Supplementary Video 2), which sharply increased the proportion of more resistant, heat-tolerant colonies in 2017[11]. The hardier corals that were bleached relatively mildly in 2016 subsequently regained their colour during the ensuing winter, then bleached moderately again when heat stress recurred in 2017 (Fig. 3a).

In the central region, heat exposure and the severity of bleaching were both sharply higher in the second year (Fig. 1a and Supplementary Fig. 3). However, a model predicting the level of bleaching in 2017, based on the fitted 2016 bleaching threshold, showed that the observed bleaching in the central region during the second event was indistinguishable from the amount expected, in stark contrast with the strong historical pattern further north (Fig. 2a). Consequently, the distribution of prediction errors was symmetrical for the central region (Fig. 2a), indicating that the bleaching responses to heat exposure in 2017 were very similar to the responses in 2016. In 2016, the central region experienced relatively moderate warming and bleaching, and in contrast with the northern Great Barrier Reef, only a small loss of <10% of corals occurred[12]. Therefore, central populations of heat-susceptible corals remained intact and vulnerable in 2017 (Fig. 1a and Supplementary Fig. 3). Any acclimation that may have occurred in central populations, in response to moderate heat exposure in 2016, was apparently swamped by the extreme marine heatwave in the following year (Supplementary Fig. 3a).

In the southern Great Barrier Reef, less bleaching than predicted occurred in 2017 despite the corals being exposed to higher heat stress during the second year (Figs. 1,2b and 3b). Consequently, the predicted error distribution was asymmetrical, and intermediate between the central and northern regions (Fig. 2a). In 2016, reefs that were exposed to 4 °C-weeks, on average, had a 50% chance of bleaching severely (Fig. 1b). In 2017, 24.9% of the reefs we resampled in the southern region ($n=346$) experienced >4 °C-weeks, yet only 9.5% bleached, consistent with a shift in the response curve (Fig. 1b). Although the historical effect was weaker compared with the north (Fig. 2), it is plausible that the earlier experience of low levels of heat stress in 2016 improved the chances of corals escaping a bleaching response in 2017 throughout the southern region. The historical effect we observed (Fig. 2) is consistent with a variety of potential mechanisms for acclimation and adaptation of corals and their symbionts to recurrent heat stress events[13–15].

The spatial correspondence between heat exposure (DHW) and patterns of bleaching on individual reefs along and across the Great Barrier Reef (Supplementary Fig. 3) was weaker in 2017 than in 2016 because of the confounding effect of the ecological memory of heating, bleaching and mortality one year earlier. Severe bleaching in 2016 was predicted correctly for 83% of reefs by a generalized linear model (GLM), based on satellite-derived DHW at a resolution of 5 km. However, in 2017, DHW explained the occurrence of severe bleaching in only 69% of cases, consistent with the divergent responses to heat stress of reefs in the central versus northern and southern regions (Fig. 2a). A key finding is that the model fit for 2017 was substantially improved by incorporating DHW scores for 2016 as well as 2017, from 69 to 82% (for 606 reefs that were assessed in both years), indicating that bleaching

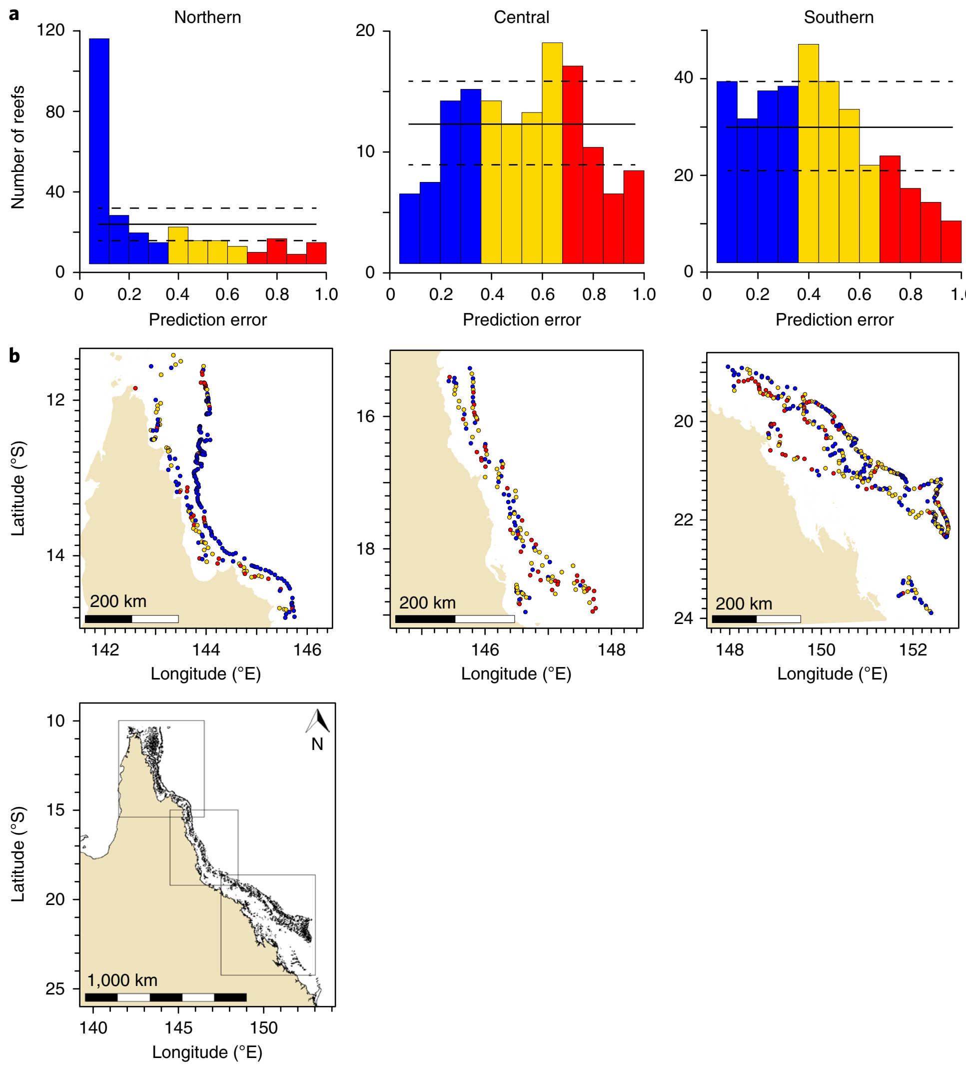

Fig. 2 | Ecological memory of the 2016 bleaching event unfolds differently in the northern, central and southern Great Barrier Reef. a. Histograms of standardized errors in predicting the 2017 bleaching event based on the 2016 response curve, in northern, central and southern regions of the Great Barrier Reef. A reef erroneously predicted to bleach with a high probability has a value close to 0, and a reef erroneously predicted as very unlikely to bleach has a value close to 1. The prediction errors are colour coded as blue (0, 0.333), gold (0.333, 0.667) and red (0.667, 1). The null expectation is for a uniform distribution of standardized residuals (solid horizontal line) and 95% confidence intervals on this null expectation are depicted with dashed horizontal lines. **b**. Maps of standardized model prediction errors showing the locations of reefs ($n=742$) and the degree to which the 2016 bleaching model (red curve in Fig. 1b) overestimated actual 2017 bleaching (blue reefs), correctly estimated 2017 bleaching (gold) and underestimated 2017 bleaching (red). The boundaries of the northern, central and southern regions are indicated in the larger-scale map.

in 2017 was influenced by the ecological memory of heat exposure 1 year earlier. The remaining unexplained variation (18%) is likely to be attributable to measurement errors in the satellite DHW metric and the bleaching scores, and to variation in the light, cloud cover, wind, rainfall and hydrodynamic conditions experienced by individual reefs.

In summary, the outcome of the global heatwave on the Great Barrier Reef in 2017 depended not only on the heat stress of that year, but was also contingent on the history of heat exposure and the physiological and ecological responses experienced one year earlier. We show that recurrent bleaching in 2017 was less than expected for a given level of heat stress for hundreds of reefs, depending on the nature of experiences in the recent past, and that history consequently had a discernible geographic footprint (Fig. 2). Potential mechanisms for generating large-scale contingencies from multiple events include acclimatization[16,17], a re-assortment of symbiotic zooxanthellae, bacteria or other symbionts[18,19], increased vulnerability in corals injured or weakened by previous disturbances[20–22], and/or a shift in species composition due to differential survival before a subsequent event[11,12,23,24].

The unprecedented back-to-back bleaching of corals on the Great Barrier Reef, predominantly in the north in 2016, followed by the central region in 2017 (Supplementary Fig. 3b), creates a new set of legacies that will unfold in coming decades. For example, the recovery of corals is likely to be slow because of the unprecedented loss of adult brood stock and the presence of many millions of dead, unstable coral skeletons that are poor substrates for the persistence of new recruits (Fig. 3a). In the longer term, the ecological resilience of coral reefs to global warming will be challenged by the growing misalignment between coral life-histories (an evolutionary legacy strongly influenced by the return times of cyclones (Fig. 3c)) and the emergence of a radically different disturbance regime that now includes frequent, regional-scale mass bleaching events (Supplementary Fig. 3). Furthermore, based on

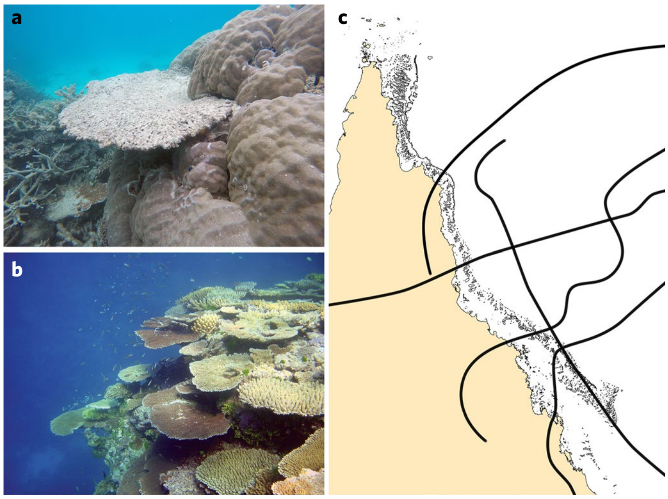

Fig. 3 | Legacy effects of multiple disturbance. a, Disproportionate loss of abundant, susceptible tabular and branching *Acropora* corals on northern reefs in 2016, compared with more resistant mound-shaped *Porites*, increased community resistance to recurrent bleaching in 2017. **b**, Corals in the southern Great Barrier Reef remained unbleached and dominated by *Acropora* in 2017, despite higher levels of heat exposure than in 2016. **c**, Map of the Great Barrier Reef showing the tracks of 5 severe tropical cyclones that peaked at either category 4 or 5 in the past decade (2008–2017). Coral life-histories are an evolutionary legacy of the history of recurrent cyclones. Contemporary mass-bleaching events, including the unprecedented back-to-back events in 2016 and 2017, represent a radical shift in historical disturbance regimes, causing a misalignment between the frequency of disturbances and the capacity of corals to recover. Photo credits: **a**, J.T.K.; **b**, G.T.

our investigation of recurrent heatwaves and coral bleaching in 2016 and 2017, we conclude that it is no longer feasible to understand fully the consequence of an individual climate-driven event in isolation from other disturbances that occur before and afterwards. Rather, because of the increasing frequency of climate-driven disturbances[4,5], it is imperative now more than ever to scrutinize sequences of multiple disturbance events to reveal the complex role of ecological memory, and its geographical extent.

Online content

Any methods, additional references, Nature Research reporting summaries, source data, statements of data availability and associated accession codes are available at https://doi.org/10.1038/s41558-018-0351-2.

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Author contributions

The study was conceptualized and led 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, analysis and graphics. J.T.K. and T.P.H. conducted the aerial bleaching surveys in 2016 and 2017. Underwater assessments and ground-truthing of aerial scores were performed by A.H.B., A.S.H., M.O.H., M.S.P. and G.T. S.F.H., C.M.E., G.L. and W.S. provided satellite data on heat stress. S.R.C. and M.J. contributed statistical and modelling expertise.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary information is available for this paper at https://doi.org/10.1038/s41558-018-0351-2.

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Methods

We measured the bleaching responses of corals exposed to a broad spectrum of heat exposures in each of two consecutive marine heatwaves, throughout the Great Barrier Reef in the summers of 2016 and 2017. Mass bleaching is a stress response by corals following their exposure to marine heatwaves, disrupting their symbiotic relationship with zooxanthellae, causing a loss of colour. We conducted aerial surveys of individual reefs ($n = 1{,}135$ reefs in 2016, and 742 in 2017, of which 606 were common to both years) at an elevation of approximately 150 m, using light fixed-wing aircraft and a helicopter. The reefs extended throughout the Great Barrier Reef, from the coast to the edge of the continental shelf up to 250 km offshore, and along 14° of latitude[25]. We followed the same methodology used earlier in aerial assessments of bleaching in 1998 and 2002[26], in which each reef was assigned by visual assessment to one of 5 categories of bleaching severity: (0) <1% of corals bleached; (1) 1–10%; (2) 10–30%; (3) 30–60%; and (4) >60% of corals bleached. We confirmed the accuracy of the aerial scores by underwater ground-truthing in 2016 on 104 reefs along the Great Barrier Reef that exhibited the full spectrum of bleaching[25]. The aerial bleaching scores for each year are shown in Supplementary Fig. 3b as heat maps (stretch type: histogram equalize) using inverse distance weighting (power: 2, cell size: 1,000, search radius: variable, 100 points) in ArcGIS 10.2.1.

Maximum accumulated heat exposure throughout the Great Barrier Reef in 2016 and 2017 was quantified at 5 km resolution, using the NOAA Coral Reef Watch version 3 DHW metric (Supplementary Figs. 1 and 3a), which incorporated both the temperature anomaly above the long-term summer maximum, and the duration[27]. DHW is the most accurate metric currently available for predicting large-scale bleaching[25,28] and subsequent mortality[12]. Geographic patterns of maximum DHW values are presented in Supplementary Fig. 3a as a heat map of the Great Barrier Reef for each year (stretch type: histogram equalize) using inverse distance weighting (power: 2, cell size: 1,000, search radius: variable, 100 points) in ArcMap 10.2.1. The difference between the cumulative heat exposure in both years is shown in Fig. 1a, indicating that sea surface temperatures in 2017 were generally hotter and/or longer lasting. Widespread bleaching began 2–3 weeks earlier in 2017 than in 2016, in mid-February, consistent with the earlier onset of heat stress[28]. A significant weather event also occurred in each summer: severe tropical cyclone Winston crossed Fiji on 20 February 2016, before moving to the southern Great Barrier Reef as a rain depression with persistent cloud cover, reducing sea temperatures in late February and early March, and curtailing bleaching in the south. In the following summer, severe tropical cyclone Debbie crossed the southern Great Barrier Reef at approximately 20° S on 27–28 March 2017. However, the resulting wind, cloud and rain was 4–6 weeks too late and too far south to moderate the second bout of severe bleaching. Cyclone Debbie is the southernmost cyclone trajectory in Fig. 3c.

We used the aerial bleaching scores in each year to test for a shift in the bleaching response of corals to heat exposure in 2016 versus 2017 (Fig. 1b). We fit a GLM with binomial error structure, using DHW as the explanatory variable and the level of bleaching as the binomial response (that is, whether a reef was severely bleached (aerial score categories 3 and 4) or not (categories 0–2)). Coral assemblages with bleaching scores of category 2 or lower generally regained their colour following each bleaching event, whereas corals in category 3, and especially category 4, had high levels of mortality[12]. Categories 0–2 versus 3–4 provided a viable split of the data: in 2016, 55% of surveyed reefs ($n = 1{,}135$) had a bleaching score of 3–4, compared with 33% in 2017 ($n = 742$) (Supplementary Fig. 2). Alternative binning splits of bleaching scores (0 versus 1–4, 0–1 versus 2–4 and 0–3 versus 4) yielded similar results, despite more uneven splits of the data (that is, the severity of bleaching was significantly correlated with DHW and the threshold shifted upwards in 2017 (as in Fig. 1b)).

To evaluate the goodness of fit of the models to the data, we compared the observed residuals with the quantiles of a null distribution of residuals generated by simulation from the fitted models[29]. Because this approach compares observed versus expected quantiles, the null expectation is for a uniform distribution of residual quantiles (standardized residuals)[28]. Inspection of the standardized residuals from our GLMs supported this null expectation (one-sample Kolmogorov–Smirnov test: $D = 0.041$, $P = 0.17$ for the 2017 model; and $D = 0.019$, $P = 0.81$ for the 2016 model). In our analyses, a standardized residual value close to 0 indicates that the model predicted severe bleaching in 2017 with a high probability, while this did not actually occur. Conversely, a standardized residual near 1 indicates that severe bleaching occurred even though the model fit implied such bleaching to be highly unlikely.

To further investigate the deviation of the pattern of bleaching responses to heat exposure in 2017 from 2016, we mapped the extent to which the model that was fitted to the 2016 data could predict actual occurrences of severe bleaching in 2017. Here, we used the 2016 bleaching response curve (shown in red in Fig. 1b) to predict bleaching in 2017 given the observed DHW exposure for 742 reefs surveyed for bleaching in 2017. We generated predicted quantiles for this 2017-from-2016 prediction model, and we used them to produce 'standardized prediction error' values in the same way that we generated standardized residuals for our other models. We termed these standardized prediction errors, rather than standardized residuals, because they represent genuine out-of-sample prediction (using a model calibrated from 2016 data to predict bleaching in 2017). We mapped geographical variation in the prediction errors (Fig. 2) for each of three regions distinguished by differences in their history of heat exposure: the northern region (from approximately 10–15° S) that experienced the most extreme heat exposure in 2016; the central region (15–19° S) that was moderately exposed in 2016 compared with extreme heat stress in 2017; and the south (19–24° S), where minor bleaching occurred in both years. In addition, we investigated how the footprints of heat exposure in the previous year affected the bleaching responses in 2017. We fitted the GLM model with binomial error structure as we did with the 2017 data (blue line in Fig. 1b), but with the addition of an interaction term between DHW values from 2016 and 2017 (Fig. 1c, which shows specific DHW values in 2016 of 0, 3, 6 and 9 °C-weeks). In this model, we omitted a fixed effect of 2016 DHW, to ensure that all thresholds had the same intercept at 0 °C-weeks.

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

Data availability

Source data are available online at the Tropical Data Hub (https://tropicaldatahub.org/).

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☒	☐	For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
☒	☐	For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
☐	☒	Estimates of effect sizes (e.g. Cohen's d, Pearson's r), indicating how they were calculated
☒	☐	Clearly defined error bars *State explicitly what error bars represent (e.g. SD, SE, CI)*

Our web collection on statistics for biologists may be useful.

Software and code

Policy information about availability of computer code

Data collection	n/a
Data analysis	R code for statistical analysis (version R3.5.1). ArcGIS (ArcMap 10.2.1) for graphical interpolation of data

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors/reviewers upon request. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Research guidelines for submitting code & software for further information.

Data

Policy information about availability of data

All manuscripts must include a data availability statement. This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A list of figures that have associated raw data
- A description of any restrictions on data availability

Source data are available online at the Tropical Data Hub, https://tropicaldatahub.org/.

Field-specific reporting

Please select the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

☐ Life sciences ☐ Behavioural & social sciences ☒ Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see nature.com/authors/policies/ReportingSummary-flat.pdf

Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	Reefs were surveyed from the air, during two bleaching events throughout the Great Barrier Reef
Research sample	1135 reefs in 2016, 742 in 2017. 606 common in both years
Sampling strategy	Reefs were selected at random along the length of the Great Barrier Reef
Data collection	Collected and recorded during aerial survey (TPH and JTK)
Timing and spatial scale	Eight days of aerial surveys during the peak of the bleaching events. March - April 2016. March - April 2017
Data exclusions	No data were excluded
Reproducibility	n/a
Randomization	Reefs were selected at random along the length of the Great Barrier Reef
Blinding	n/a

Did the study involve field work? ☒ Yes ☐ No

Field work, collection and transport

Field conditions	Low tide and low wind conditions, during the peak of the bleaching
Location	Great Barrier Reef along 14 degrees of latitude
Access and import/export	n/a
Disturbance	n/a

Reporting for specific materials, systems and methods

Materials & experimental systems

n/a	Involved in the study	
☒	☐	Unique biological materials
☒	☐	Antibodies
☒	☐	Eukaryotic cell lines
☒	☐	Palaeontology
☒	☐	Animals and other organisms
☒	☐	Human research participants

Methods

n/a	Involved in the study	
☒	☐	ChIP-seq
☒	☐	Flow cytometry
☒	☐	MRI-based neuroimaging