

# Synchronous behavioural shifts in reef fishes linked to mass coral bleaching

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**Mass coral bleaching causes population declines and mortality of coral reef species<sup>1</sup> yet its impacts on behaviour are largely unknown. Here, we unite behavioural theory with community ecology to test whether bleaching-induced mass mortality of corals can cause consistent changes in the behaviour of coral-feeding fishes. We documented 5,259 encounters between individuals of 38 *Chaetodon* (butterflyfish) species on 17 reefs within the central Indo-Pacific, of which 3,828 were repeated on 10 reefs both before and after the global coral bleaching event in 2016. Aggression between butterflyfishes decreased by two-thirds following large-scale coral mortality, despite no significant change in fish abundance or community composition. Pairwise encounters were most likely to be aggressive between obligate corallivores and on reefs with high coral cover. After bleaching, the proportion of preferred *Acropora* corals in the diet decreased significantly (up to 85% fewer bites), with no increase in overall bite rate to compensate for the loss of these nutritionally rich corals. The observed reduced aggression at low resource levels due to nutritional deficit follows the predictions of the economic theory of aggressive behaviour<sup>2,3</sup>. Our results reveal synchronous changes in behaviour in response to coral mortality. Such changes could potentially disrupt territories<sup>4</sup>, leading to reorganization of ecological communities.**

Coral mortality following mass bleaching events caused by global warming has reshaped coral reef ecosystems around the world<sup>5–8</sup>. Effects of coral mortality cascade through the ecosystem, leading to decreased abundance or local extinction of coral-dependent species, and subsequent reorganization of ecological communities<sup>6</sup>. Despite the prevalence of these changes, the underlying mechanisms remain unclear. One mechanism that could be important yet is unresolved is the role of individual behaviour in altering population dynamics or community structure<sup>9,10</sup>. In particular, interference behaviour between individual fish of different species is widespread and implicated in population abundance, species coexistence and geographical range shifts<sup>10–12</sup>.

Laboratory experiments suggest that fish behaviour can be mediated by environment. However, these experiments are overwhelmingly focused on the direct effects of water temperature and acidification (for example, ref. <sup>13</sup>), despite the more immediate threat from ongoing loss of coral<sup>14</sup>. Moreover, these experiments focus on the short-term responses of only a handful of species to single

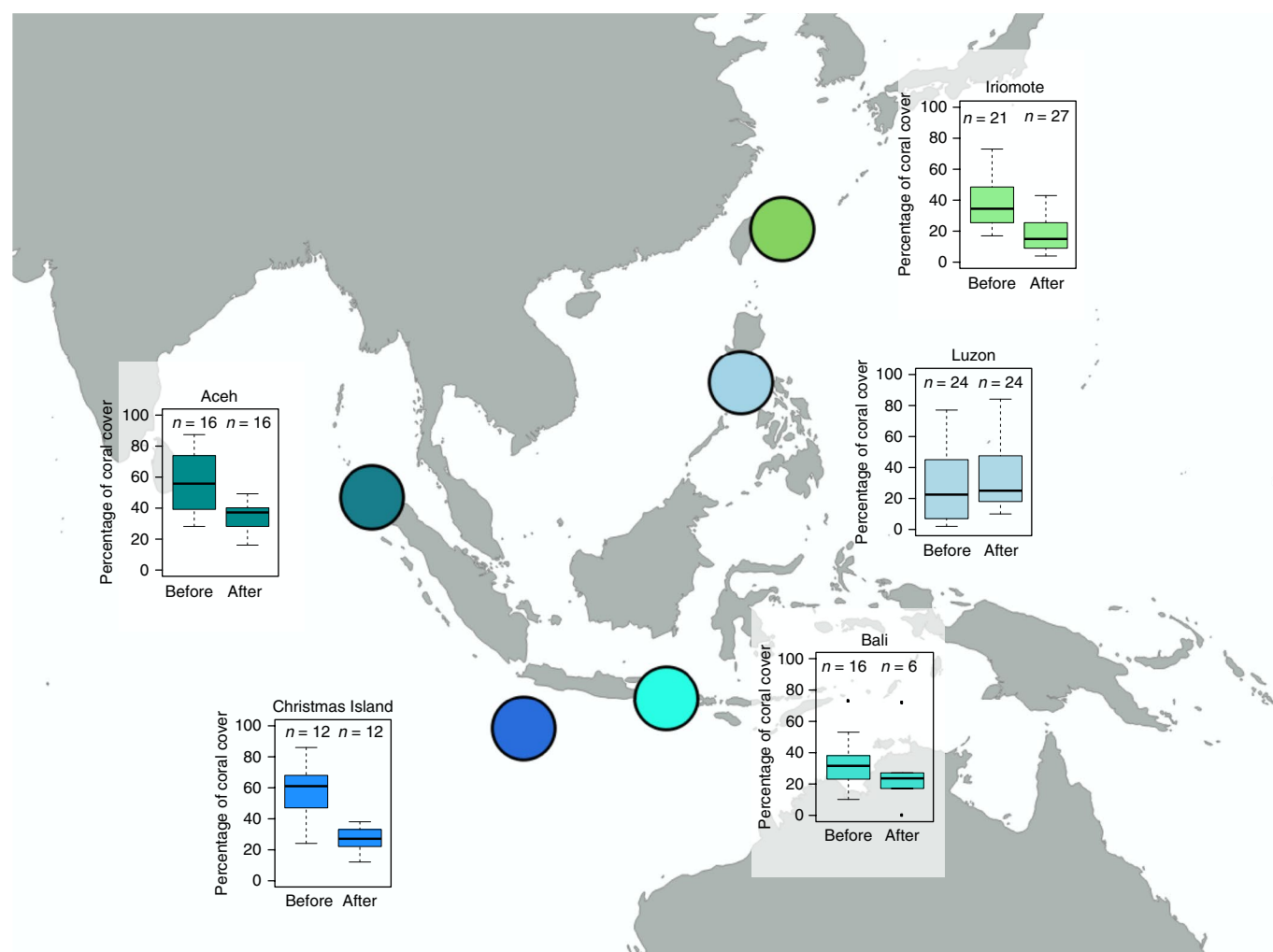
stressors in aquaria isolated from community interactions. Despite their simplicity, these experiments yield contrasting results<sup>15,16</sup>, hindering our ability to forecast the consequences of coral mortality on reef communities in nature. While field experiments are more likely to capture the complexity of natural systems<sup>17</sup>, they are not amenable to manipulation at large geographical scales. An alternative approach is to combine large-scale natural experiments in a macro-ecological framework. In this way, we can move beyond site-contingent results and test whether fish behaviour responds in a consistent way to disturbance across reefs despite variation in biogeographic history, environmental conditions and biotic context.

Mass bleaching events reduce resource availability for fishes that rely on corals for food, such as butterflyfishes (*Chaetodon* spp.). Theory predicts that aggression among individuals should be highest at intermediate resource availability, due to the trade-off between resource value and the relative energetic cost of resource defence<sup>2</sup>. Depending on the availability of resources before disturbance, the probability of aggression, and the extent of resource (for example, coral) loss, two possible outcomes of reduced resource availability on aggression are possible. First, reduced coral availability could increase fish aggression due to enhanced value of the rarer resource. Second, reduced coral availability could decrease aggression because nutritional deficits intensify the relative energetic cost of resource defence, reducing resource holding potential<sup>2,18</sup>. Distinguishing between these possibilities is necessary to provide mechanistic predictions of the impacts of coral bleaching effects on reef fishes.

Here, we report on observations of 5,259 encounters between individuals of 38 species of *Chaetodon* (butterflyfishes) before and after the global coral bleaching event in 2015–2016. Encounters were recorded over 11,740 minutes (2,348 five-minute observations) at 17 reefs nested within 5 regions of the central Indo-Pacific (Fig. 1; see Supplementary Table 1 for sample sizes per reef). We used this uniquely powerful data set to examine behavioural change in response to abrupt reductions in resource availability, a critical determinant of aggressive behaviour<sup>2,18</sup>.

To determine the effect of resource availability on butterflyfish aggression, we followed a focal fish for five minutes and recorded as an encounter every conspecific that came within 1 m of that individual<sup>19</sup>. Encounters were categorized as passive when there was no observed change in behaviour, or aggressive when one or both individuals engaged in display or chasing behaviour. By comparing

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**Fig. 1 | Change in coral cover before and after the 2016 coral bleaching events at each field region across replicate point intercept transects at depths 1–5 m.** The boxplot lines are the median coral cover, the boxes range from the 25th to the 75th percentile. Mean loss of coral cover on reefs was significant both with and without the inclusion of Luzon (paired Wilcoxon signed rank test, all reefs:  $V=122$ ,  $P=0.003$ ; reefs excluding Luzon:  $V=78$ ,  $P<0.001$ ) and not for Luzon alone (paired Wilcoxon signed rank test,  $V=0$ ,  $P=0.125$ ).

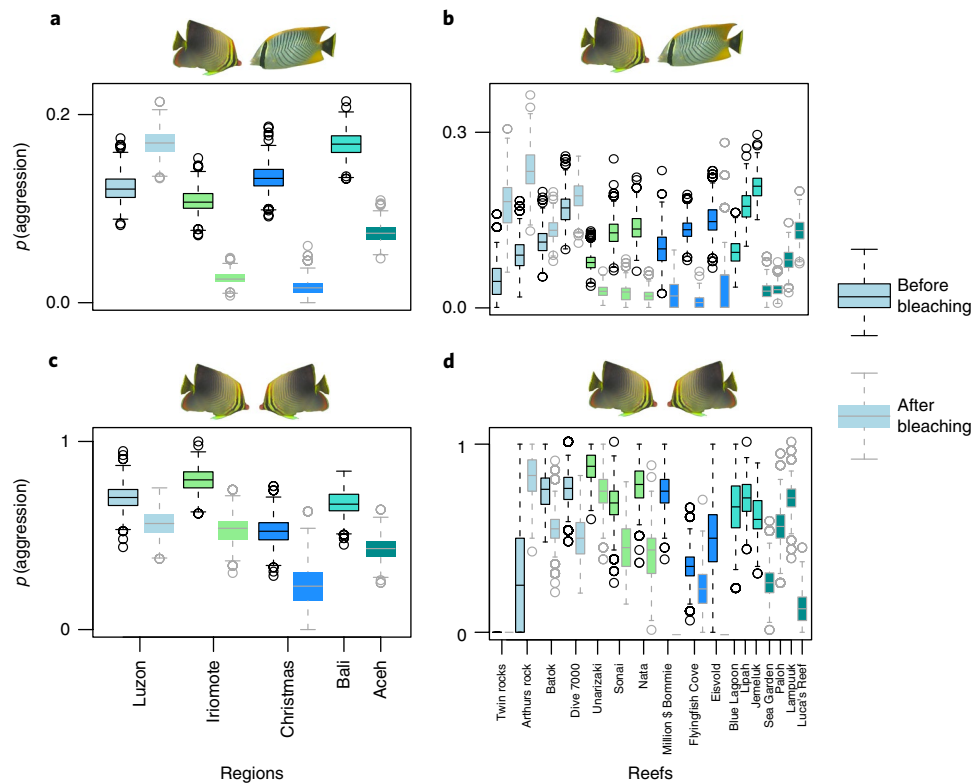
behaviour before and after bleaching, we explicitly examine the consequences of coral mortality on the probability of aggressive behaviour. Whilst behavioural data were collected only once from both Bali (before bleaching, although coral cover was collected before and after) and Aceh (after, although fish abundance and coral cover were collected before and after), we include these data to determine whether behaviour fits expectations from other reefs, and to inform our general model of the predictors of fish aggression.

Bleaching-induced mortality resulted in the loss of 18%–65% of initial standing coral cover across 12 reefs in 4 of the regions for which we had coral cover data both before and after the bleaching events (Christmas Island, Iriomote, Aceh and Bali; Fig. 1). Despite some bleaching, there was no coral mortality in the fifth region, Luzon, which provided a natural control. On reefs with high coral mortality, the probability of aggressive encounters between heterospecific butterflyfishes decreased from  $0.15 \pm 0.02$  (95% confidence interval) to  $0.05 \pm 0.01$  (Fig. 2a,b; across species Supplementary Fig. 1) and for conspecifics decreased from  $0.66 \pm 0.08$  to  $0.45 \pm 0.08$  (Fig. 2c,d). As we generally sampled reefs at similar times of year, we infer that the decrease in the probability of aggressive encounters is due to coral mortality rather than seasonal differences or phenological effects. Luzon, which did

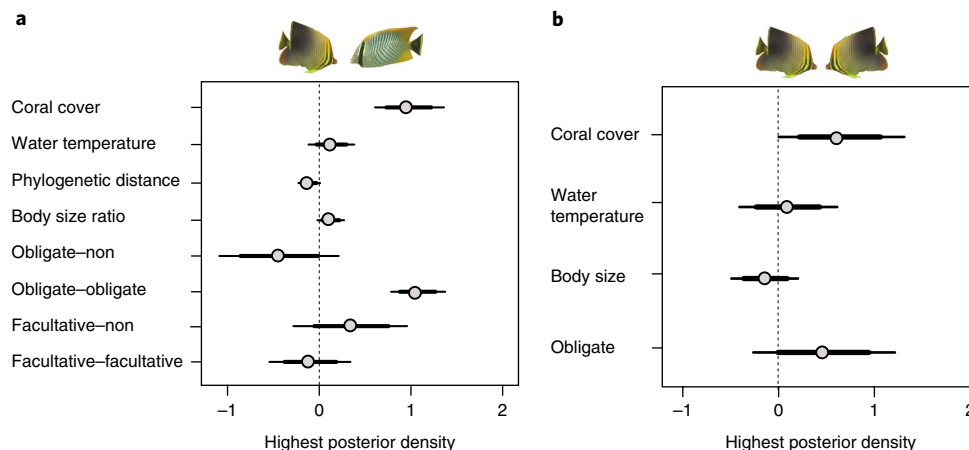
not experience coral mortality, had the largest seasonal difference between surveys (6 months between samples; mean water temperature: before =  $27.06^\circ\text{C} \pm 0.56$ , after =  $29.34^\circ\text{C} \pm 0.47$ ) but the smallest change in aggression (heterospecifics from  $0.14 \pm 0.03$  to  $0.18 \pm 0.03$ ; conspecifics from  $0.70 \pm 0.13$  to  $0.55 \pm 0.13$ ; note the overlapping 95% confidence intervals). Such consistent behavioural change on multiple reefs across a large geographic extent in response to a natural experiment provides strong support that high coral mortality led to decreased aggression.

To further test whether coral cover, rather than alternative factors, triggered the decrease in aggression, we generated a Bayesian hierarchical model to predict whether outcomes of pairwise encounters between individual fish were aggressive or passive. Conspecific aggression is linked to territorial defence, where mated pairs aggressively defend a set of coral colonies<sup>20</sup>. In contrast, heterospecific aggression is associated with dietary overlap, where dominant competitors gain priority access to preferred prey species<sup>19</sup>. Consequently, we model conspecific and heterospecific encounters separately.

The probability of heterospecific encounters rises with increased coral cover (median = 0.97, 95% credible interval = 0.61–1.36; Fig. 3a). In addition, aggression was more likely during encounters



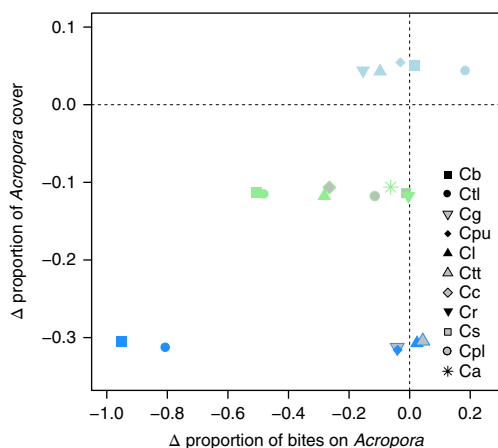
**Fig. 2 | Probability of encounters resulting aggression before and after bleaching. a–d,** Heterospecific (**a,b**) and conspecific (**c,d**) aggression across reefs ( $n=17$ ; **b,d**) nested within regions (**a,c**) was recorded both before (black outline) and after (no outline) the 2016 bleaching events. Data were resampled 1,000 times within regions to obtain bootstrapped estimates of uncertainty around the median owing to variable sample sizes. Both heterospecific (paired Wilcoxon signed rank test:  $V=21$ ,  $P=0.031$ ) and conspecific (paired Wilcoxon signed rank test:  $V=21$ ,  $P=0.031$ ) aggression decreased significantly when the control region (Luzon) was not included. The boxplot lines are the median coral cover, the boxes range from the 25th to the 75th percentile, dashed lines are whiskers ( $1.5 \times \text{IQR}$ ), open circles are outliers. Note that Bali and Aceh are not directly comparable but fit the trend from reefs surveyed at two points in time. Zero values are due to no aggressive interactions being observed, rather than missing data.



**Fig. 3 | Influence of biotic and abiotic factors on the probability of aggression following encounters. a,b,** The central dots indicate the median point estimate for the highest posterior density, the thin lines are 95% credible intervals and the thick lines are 80% credible intervals from Bayesian hierarchical regression analysis for heterospecific (**a**) and conspecific (**b**) encounters. Comparisons among diet categories are indicated by en dashes, and the reference category was that with the largest sample size (obligate–facultative). Obligate, obligate corallivore; facultative, facultative corallivore; non, non-corallivore.

between pairs of obligate corallivores (median=1.07, 95% confidence interval (CI)=0.78–1.37; Fig. 3a) than between pairs that included facultative corallivores or non-coral invertivores. These results support the hypothesis that interspecific aggression is an

adaptive response to resource competition<sup>21,22</sup>. Phylogenetic relatedness (median=−0.11, 95% CI=−0.23–0.01; Fig. 3a) and body size ratios between species were poor predictors of heterospecific aggression (median=0.13, 95% CI=−0.02–0.27; Fig. 3a), offering



**Fig. 4 | Change in *Acropora* spp. cover against change in the proportion of bites on *Acropora* spp. for obligate and facultative corallivores.** The data were recorded at Luzon (light blue), Iriomote (green) and Christmas Island (dark blue), before and after coral bleaching. Cb, *Chaetodon baronessa*; Ctl, *C. trifascialis*; Cl, *C. lunulatus*; Cpu, *C. punctatofasciatus*; Cr, *C. rafflesii*; Cc, *C. citrinellus*; Cs, *C. speculum*; Cpl, *C. plebeius*; Ca, *C. argentatus*; Cg, *C. guttatissimus*; Ctt, *C. trifasciatus*.

little support for the notion that closely related similar species should interact more aggressively than distantly related dissimilar species<sup>2,23</sup>. The failure of temperature to predict aggression suggests that the effect of metabolic relationships<sup>24</sup> is small relative to resource availability, and also indicates that changes in water temperature that might arise from seasonal differences are relatively unimportant. Similarly, outcomes of conspecific encounters were predicted most strongly by coral cover (within 90% credible interval), while body size, diet and water temperature contributed minimally (Fig. 3b).

Feeding comparisons amongst corallivorous butterflyfishes before and after bleaching suggest that nutritional deficit offers an explanation for the differences in aggression. Many corallivorous butterflyfish prefer corals in the genus *Acropora*, because they provide more energy per foraging effort than do other coral taxa<sup>25</sup>, yet *Acropora* corals are highly susceptible to bleaching<sup>26</sup>. Foraging by corallivorous butterflyfishes on *Acropora* species after bleaching was 71% lower than before bleaching at Iriomote, and 85% lower than before at Christmas Island, whilst at Luzon, which did not experience coral mortality, foraging on *Acropora* was only 7% lower. The reduction in foraging on *Acropora* species was particularly noticeable in the highly specialized corallivores (*C. trifascialis* and *C. baronessa*), which are also the most aggressive species. The largest shifts in foraging on *Acropora* were observed around Christmas Island, which also had the largest reduction in aggression (Fig. 4; for proportions by time and species with confidence intervals, see Supplementary Fig. 2). Moreover, individuals did not compensate for the loss of nutritious *Acropora* in their diets by feeding more intensely on other less nutritious coral genera because the overall bite rate did not increase after bleaching (one-tailed paired Wilcoxon signed rank tests: Luzon,  $V = 15$ ,  $P = 1$ ; Iriomote,  $V = 35$ ,  $P = 0.936$ ; Christmas Island,  $V = 19$ ,  $P = 0.969$ ; Fig. 5). The observed reduction in butterflyfish aggression is therefore consistent with the hypothesis that energetic deficit caused by decreased resource availability after coral bleaching leads to reduced aggression.

Aggression can also be influenced by changes in the density of competing individuals: more individuals lead to increased probability of encounter by Brownian motion, the random movement of individuals, alone<sup>27</sup>. Here, the density of *Chaetodon* spp. did not change significantly from pre- to up to 12 months post-bleaching ( $V = 36$ ,  $P = 0.831$ ; Supplementary Fig. 3). This result is consistent with time

lags of up to five years between coral mortality and declines in butterflyfish abundance<sup>1,28</sup>. Lampuuk (Aceh) and Eisvold (Christmas Island) reefs did decrease in butterflyfish density (Supplementary Fig. 3). However, both heterospecific and conspecific aggression for these reefs were strongly positively associated with coral cover in the Bayesian regression model (95% confidence intervals for group intercept overlap zero), consistent with the hypothesis that coral mortality has led to reduced aggression probabilities on these reefs regardless of density effects on encounter rates.

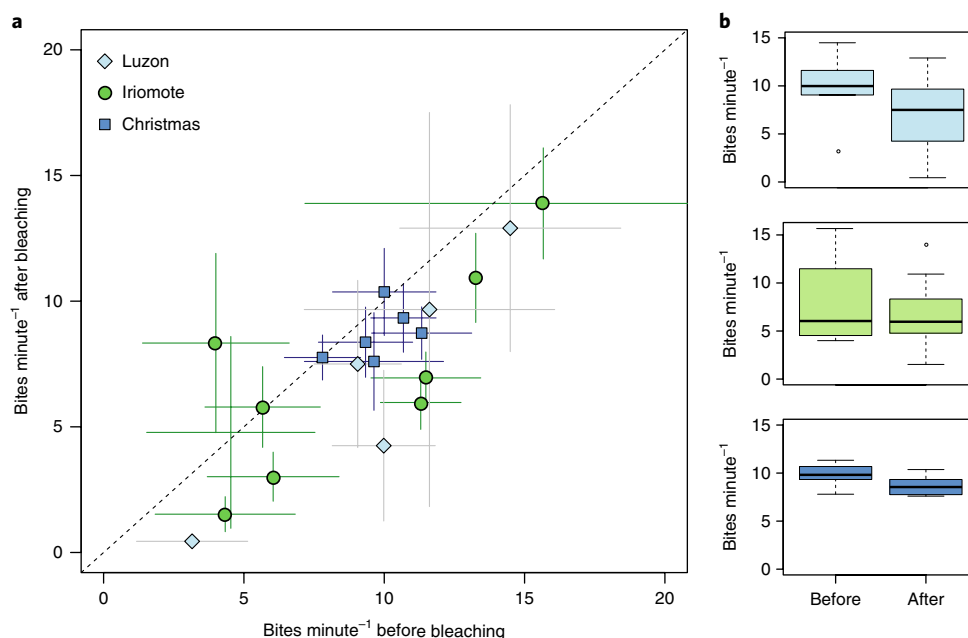
While declines in the abundance of butterflyfishes might be anticipated over longer timescales as body condition deteriorates<sup>1,29</sup>, subtle shifts in the abundance of a few key species might be sufficient to cause reduced aggression. The two most aggressive species—*C. trifascialis*, and the sister species complex *C. baronessa*/*C. triangulum*—are expected to be particularly vulnerable to coral cover loss<sup>19</sup>. Encounters involving *C. trifascialis* and *C. baronessa*/*C. triangulum* reduced from 44% to 28% following the bleaching, yet the probability of aggression within those encounters mirrored the broader pattern, decreasing by 39% for *C. trifascialis* and 79% for *C. baronessa*/*C. triangulum* (Supplementary Fig. 4). Moreover, the abundance of these species did not change (*C. baronessa*/*C. triangulum*  $V = 1.5$ ,  $P = 0.586$ ; *C. trifascialis*  $V = 14$ ,  $P = 0.106$ ), and overall species composition of the butterflyfish communities was not significantly different between survey times ( $F_{1,9} = 1.27$ ,  $R^2 = 0.02$ ,  $P = 0.278$ ). Consequently, the reduced aggression observed was not caused directly by shifts in abundance or composition of the butterflyfish community.

Our results show that mass coral mortality caused by increased water temperatures during the 2015–2016 global bleaching event<sup>8</sup> led to the depletion of food resources, and subsequent nutritional deficit offers a plausible explanation for the decreased aggressive behaviour amongst butterflyfishes within the central Indo-Pacific. More broadly, aggression is an important mediator of competitive interactions within ecological communities<sup>30</sup>; therefore, behavioural changes could help explain the time lag leading to the well-documented patterns of reduced abundance, local extinctions and altered species composition after bleaching<sup>1</sup> by initiating detrimental yet sub-lethal conditions. For instance, reduced aggression could indicate the breakdown of territories among butterflyfishes<sup>4</sup> as individuals roam further to obtain enough resources<sup>31,32</sup>, rendering investment in aggressive defence too costly and potentially causing a shift from interference to exploitative competition. At the community scale, as resource availability declines and becomes uneconomical to defend, previously aggressive coral specialists cease to be the dominant competitive species. Altered competitive hierarchies can influence community coexistence relationships as the ‘rules of engagement’ are rewritten<sup>2,11,33</sup> and territorial breakdown could lead to dampened dispersal among reefs<sup>34</sup>, together altering metacommunity dynamics. Moreover, although behavioural flexibility can increase survival over the short-term, it can also create ecological traps in the longer-term if the disturbance endures<sup>10</sup>, as is the case for mass coral mortality. Identifying behavioural change at an early stage could provide a potential early warning of population and community shifts. We suggest that application of a macroecological approach to behaviour more broadly across taxa and ecosystems can move us towards greater understanding of how animal behaviour will be disrupted in the face of ongoing global environmental change and identify previously under-appreciated mechanisms that could underpin the structure and dynamics of ecological communities in an ever-changing world.

### 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/s41558-018-0314-7>





**Fig. 5 | Mean bite rate (all coral genera) before and after bleaching for each species at each region, and overall for each region. a,** Bite rate has been maintained or reduced across all species and regions, except *C. argentatus* at Iriomote. This result provides compelling support for our hypothesis that reduced aggression was a result of nutritional deficit: a lower proportion of bites on *Acropora* accompanied by the same bite rate as before coral mortality would supply less nutrition overall. Lines are 95% confidence intervals around the mean, and overlap of 95% CIs with dashed line indicates no change in bite rate. **b,** Overall in each region, bite rate has either decreased or been maintained. Boxplot lines are the median coral cover, the boxes range from the 25th to the 75th percentile, dashed lines are whiskers (1.5 × IQR), open circles are outliers.

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### Author contributions

S.A.K. designed the study with input from J.-P.A.H., A.H.B. and N.J.S.; S.A.K., J.-P.A.H., A.H.B., E.S.W. and A.S.H. collected the data; N.F. provided fieldwork support; S.A.K. analysed the data and wrote the manuscript with contributions from all authors.

### Competing interests

The authors declare no competing interests.

### Additional information

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## Methods

**Field sites.** We recorded abundance of 38 *Chaetodon* spp., hard coral cover and behavioural observations in 5 regions across the central Indo-Pacific (Fig. 1 and Supplementary Table 1): Christmas Island (Indian Ocean; 105.6°E, 10.4°S), Bali (Indonesia; 115.6°E, 8.4°S), Aceh (Indonesia; 95.1–95.3°E, 5.4–5.9°S), Iriomote (Japan; 123.7°E, 24.4°N) and Luzon (the Philippines; 120.8°E, 13.7°N). Reefs were surveyed up to 12 months before and/or 12 months after the global mass bleaching event reached that region, at a similar time of year when possible (see Supplementary Table 1 for survey dates). Different survey dates between regions were largely due to differences in the timing of the bleaching events and logistical constraints associated with conducting field research across a large geographical extent whilst maintaining consistent survey protocol and observers. All regions except Luzon are contact zones between Indian and Pacific Ocean *Chaetodon* species, chosen to maximize the number of species we were able to observe and the potential for aggression. At each location, we surveyed 3 to 4 reefs resulting in a total of 17 sampled reefs (Supplementary Table 1). To ensure, as far as possible, that different individuals were sampled, reefs were separated by >1 km and interspersed with non-reef patches (corallivorous butterflyfish territories are generally <0.2 km<sup>2</sup>; ref.<sup>35</sup>). Similar numbers of focal individuals were observed on each reef (Supplementary Table 1).

**Data collection.** *Chaetodon* abundance and coral cover. We quantified the abundance of butterflyfishes with 50 × 5 m belt transects and the cover of hard corals (*Scleractinia*) was recorded every 0.5 m along 50 m point intercept transects. At least three transects were deployed at each of two depths (1 and 5 m) at each reef where possible to capture the abundance of *Chaetodon* spp. and coral cover at the depths we observed encounters. Exceptions included Blue Lagoon (Bali, 2 transects at 5 m), Eisvold (Christmas Island, only 5 m) and Million Dollar Bommie (Christmas Island, only 5 m). All transects on Acehnese reefs were restricted to 1 m depth because remote locations prevented use of SCUBA equipment. Fish and coral surveys were conducted along the same transects, with the coral surveyor trailing the fish surveyor and recording benthic cover.

**Aggression.** Observations were made on snorkel or SCUBA depending on depth and visibility using a well-established protocol<sup>19,36</sup>. Following an acclimation period (~1 minute) to check that the individual was responding naturally (that is, feeding), focal individuals were followed at a distance of 2–4 m for five minutes. Many *Chaetodon* species occur in pairs and no aggressive interactions were recorded among partners, so only one individual per pair was observed to avoid dependence. An encounter was recorded when a congeneric came within 1 m of the focal animal. At this distance, we assumed the individuals were aware of each other's presence and had the potential to interact. The outcome of each encounter was recorded as passive if no discernible change in behaviour was elicited in either individual, or aggressive if one or both individuals engaged in display or chase behaviour<sup>19</sup>. There is strong evidence that these displays can be attributed to aggression over food resources, and paired individuals, which comprised the vast majority of our target individuals, were highly unlikely to engage in courtship displays with individuals outside of their pair<sup>19</sup>. We used a U-shaped search pattern to ensure as far as possible that we did not observe the same individual or pair as the focal animal more than once. Contextual variables were recorded for each observation: date, time, weather, water temperature and observer identity. As far as possible, we tried to observe every individual (pair) present on the reef. To ensure observation data were standardized, each new observer was trained by an experienced observer (either J.-P.A.H. or S.A.K.) until recorded data were identical. Manual recording captures fish chase behaviour better than video recording<sup>37</sup> and *Chaetodon* spp. are not sensitive to diver presence<sup>38</sup>.

**Feeding.** We used the same protocols for selecting and following a focal fish as for aggression. Over three-minute observation periods, we recorded the substrate from which each bite was taken, identifying hard corals to species following Pratchett<sup>39</sup>.

**Statistical analysis.** *Coral cover, fish abundance and fish community composition.* We tested whether hard coral cover had declined significantly following the 2016 coral bleaching events with a paired Wilcoxon signed rank test for reefs with before and after data. Changes in *Chaetodon* spp. abundance were examined with a Wilcoxon signed rank test paired by reefs before and after bleaching, and changes in community composition were examined with a PERMANOVA using Bray–Curtis dissimilarity and 9,999 permutations using the function *adonis* in the *vegan* package<sup>40</sup>. The assumption of dispersion similarity at both times necessary for this test was met (betadispers function, average distance to median; before = 0.494, after = 0.502).

**Change in aggression probabilities and feeding.** Mean aggression probabilities for each reef were compared before ( $n=13$ ) and after ( $n=9$ ) bleaching using a paired Wilcoxon signed rank test. As our sampling protocol may lead to some pseudo-replication (that is, 'focal individuals' can be 'encountered individuals' in another observation), which can overestimate significance, we focus on the effect size.

To explore uncertainty in aggression probabilities around varying sample sizes of behavioural observations across reefs, we bootstrapped the encounters within each reef by resampling with replacement 1,000 times and generated boxplots of bootstrapped values.

To determine the change in feeding behaviour, we first calculated the mean proportion of bites on *Acropora* spp. across individuals within each species (plotted in Fig. 4 and Supplementary Fig. 3). To determine whether bite rate increased after bleaching, we conducted one-tailed paired Wilcoxon signed rank tests at each region with before and after feeding data (that is, Luzon, Iriomote and Christmas Island).

**Predictors of aggression.** To identify which hypothesized factors could plausibly predict when an encounter between two individuals of the same or different species would result in aggression, we formulated two Bayesian hierarchical logistic regression models: one model for heterospecific, and one model for conspecific encounters. For the heterospecific models, three predictor variables were based on pairwise species level traits of the two encountering individuals: phylogenetic relatedness, body size ratio and diet categories. For conspecific models, pairwise information was not required because both individuals possess the same species characteristics, so we used only species diet and body size.

To test the influence of abiotic factors, both models also included water temperature to the nearest 1 °C (measured in situ) at the time of the observation and coral cover at each reef during the relevant survey. Although structural complexity can also be an important factor affecting reef fish communities and behaviour, we were unable to include this as a predictor due to lack of data. However, we do not believe structural complexity would drive the aggression changes we observe because coral mortality caused by biological impacts, such as bleaching or crown-of-thorns (as opposed to physical, for example, cyclones), is not generally followed by a loss of complexity for between 4–10 years after the event<sup>1</sup>.

Diet was classified as obligate corallivore, facultative corallivore or non-coral invertivore<sup>25</sup>. Phylogenetic relatedness was represented by branch length between each species pair in the phylogeny<sup>41</sup>, calculated with the *ape* package v.4.1<sup>42</sup>. Body sizes were based on maximum length recorded for each species in FishBase ([www.fishbase.org](http://www.fishbase.org), downloaded 20 July 2017). *Chaetodon andamanensis* and *C. triangulum* were missing from the phylogenetic tree and, therefore, were excluded from further analysis, reducing the data by 82 encounters.

We grouped observations at three nested hierarchical levels. At the lowest level, encounters were grouped by observation to account for the repeated measures design whereby a single individual could have experienced multiple encounters. Second, we grouped observations by reef to account for site-level variation not captured by our abiotic variables. Last, we grouped reefs by region to account for differences in climate, historical biogeography or other unmeasured variables. To minimize collinearity amongst dummy variables necessary to include nominal data, we chose the category with the largest number of samples as the reference category.

We used weakly informative priors to constrain the coefficients of the predictors and the intercept. Continuous predictors were centred on zero and scaled to have a standard deviation of 1, and we used a prior of a normal distribution with mean 0 and standard deviation of 1, which assumes large coefficients are unlikely. This assumption is particularly useful in complex models that struggle to converge in a frequentist framework. Here, larger standard deviations on the prior distribution led to very high rejection rates for the initial parameter values. Priors for the correlation matrix of the hierarchical groups were Gamma distributions with shape and scale parameters set to 1 (ref.<sup>43</sup>).

Models were implemented in RStanArm v.2.14.1<sup>43</sup> with the No-U-Turn Sampler variant of the Hamiltonian Monte Carlo algorithm because it is highly efficient at sampling parameter space, automates fine-tuning of the Hamiltonian Monte Carlo, deals well with correlated parameters and provides robust inference<sup>44</sup>. We ran 4 chains with 2,000 iterations, discarding the first 1,000 iterations as a burn-in period. The target average proposal acceptance probability was set to 0.995 to avoid divergent transitions. We verified chain convergence with  $\hat{R}$  (converged if  $\leq 1.1$ ) and visual inspection of the chains and autocorrelation plots. We tested for collinearity in the model by quantifying the Pearson correlation between all Markov chain Monte Carlo chains across parameter pairs. Models met assumptions (cross-correlation between chain values for predictors <0.6; Supplementary Figs. 5 and 6) and performed well.

Models were not strongly influenced by grouping variables (that is, region, reef, focal fish), indicating that the results were consistent and general among regions of the central Indo-Pacific regardless of the survey locations, survey times or species pools. The only exception was Paloh reef in Aceh, where the aggression probability overall was lower than that found at other reefs.

## Data availability

The data that support the findings of this study are available from the corresponding author upon request.

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n/a

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R software for statistical analysis v.3.3.0 with package RStanArm v.2.14.1. Code to implement analyses was written by the authors.

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## Ecological, evolutionary & environmental sciences study design

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Study description	We recorded 5,259 encounters between individuals of 38 species of Chaetodon (butterflyfishes) before and after the global coral bleaching event in 2015-2016. Encounters were recorded over 11,740 minutes (2,348 five-minute observations) at 17 reefs nested within five regions of the central Indo-Pacific. Data were analysed with a combination of non-parametric statistics and Bayesian hierarchical regression analysis.
Research sample	38 species of fish in the genus Chaetodon were observed
Sampling strategy	We aimed to observe at least 10 encounters between each species pair combination at each field site. However, in the case of the less abundant species, we observed as many individuals as we could locate. Sample sizes were also constrained by the maximum number of individuals that could be observed during our field trips as it was important to the research to include different locations to enable us to identify consistent patterns of behaviour. We used a U-shaped search pattern to ensure as far as possible that we did not observe the same individual or pair as the focal animal more than once.
Data collection	Aggression observations: we followed a focal fish for five minutes and recorded as an encounter every conspecific that came within 1 m of that individual. Encounters were categorised as passive when there was no observed change in behaviour, or aggressive when one or both individuals engaged in display or chasing behaviour. Feeding observations: we used the same protocols for selecting and following a focal fish as for aggression. Over three minute observation periods, we recorded the substrate from which each bite was taken, identifying hard corals to species following Pratchett. Chaetodon abundance & coral cover: we quantified the abundance of butterflyfishes with 50 x 5 m belt transects and the cover of hard corals (Scleractinia) was recorded every 0.5 m along 50 m point intercept transects at each of two depths (1 and 5 m). Fish and coral surveys were conducted along the same transects, with the coral surveyor trailing the fish surveyor and recording benthic cover.
Timing and spatial scale	Iriomote, Japan: 25th June - 10th July 2016; 12th July - 23rd July 2017 Luzon, Philippines: 20th March - 10th April 2016; 9th October - 21st October 2016 Christmas Island, Indian Ocean: 12th September - 28th September 2015; 25th June - 10th July 2017 Bali, Indonesia: 5th November - 26th November 2015; 21st June - 22nd June 2016 Aceh, Indonesia: 18th February - 23rd February 2016; 2nd - 13th February 2017
Data exclusions	As reported in our Methods, two species were excluded from the regression analysis because phylogenetic data were not available for them. These species contributed <1% of the total samples.
Reproducibility	The observations and the natural experiment was replicated across multiple geographic regions.
Randomization	This is not relevant because we take advantage of a natural experiment so randomization was possible.
Blinding	Blinding was not possible for fieldwork.
Did the study involve field work?	<input checked="" type="checkbox"/> Yes <input type="checkbox"/> No

## Field work, collection and transport

Field conditions	Field work took place at depths of 1 m - 5 m in benign sea conditions on tropical coral reefs. Longitude and latitude of each individual reef are reported in Supplementary Table 1 and are located in the central Indo-Pacific.
Location	See above
Access and import/export	At each location we worked with local researchers and institutions to ensure we had the necessary permissions. Our study involved no invasive methods, only observations.
Disturbance	No disturbance was caused by the study.

## Reporting for specific materials, systems and methods

## Materials &amp; experimental systems

n/a	Involved in the study
<input checked="" type="checkbox"/>	<input type="checkbox"/> Unique biological materials
<input checked="" type="checkbox"/>	<input type="checkbox"/> Antibodies
<input checked="" type="checkbox"/>	<input type="checkbox"/> Eukaryotic cell lines
<input checked="" type="checkbox"/>	<input type="checkbox"/> Palaeontology
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## Methods

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<input checked="" type="checkbox"/>	<input type="checkbox"/> Flow cytometry
<input checked="" type="checkbox"/>	<input type="checkbox"/> MRI-based neuroimaging

## Animals and other organisms

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Laboratory animals

The study did not involve laboratory animals

Wild animals

38 species of fish in the genus Chaetodon were observed. Individual age range is estimated at 1 - 7 years based on known longevity of these species.

Field-collected samples

The study did not involve samples collected from the field.