

1 **Synchronous behavioural shifts in reef fishes linked to mass coral bleaching**

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19 **Mass coral bleaching causes population declines and mortality of coral reef species¹ yet**
20 **its impacts on behaviour are largely unknown. Here, we unite behavioural theory with**
21 **community ecology to test whether bleaching-induced mass mortality of corals can**
22 **cause consistent changes in the behaviour of coral-feeding fishes. We documented 5,259**
23 **encounters between individuals of 38 *Chaetodon* (butterflyfish) species on 17 reefs**
24 **within the central Indo-Pacific, of which 3,828 were repeated on 10 reefs both before**
25 **and after the global coral bleaching event in 2016. Aggression between butterflyfishes**
26 **decreased by two-thirds following large-scale coral mortality, despite no significant**
27 **change in fish abundance or community composition. Pairwise encounters were most**
28 **likely to be aggressive between obligate corallivores and on reefs with high coral cover.**
29 **After bleaching, the proportion of preferred *Acropora* corals in the diet decreased**
30 **significantly (up to 85% fewer bites), with no increase in overall bite rate to compensate**
31 **for the loss of these nutritionally-rich corals. The observed reduced aggression at low**
32 **resource levels due to nutritional deficit follows the predictions of the economic theory**
33 **of aggressive behaviour^{2,3}. Our results reveal synchronous changes in behaviour in**
34 **response to coral mortality. Such changes could potentially disrupt territories⁴, leading**
35 **to reorganisation of ecological communities.**

36 Coral mortality following mass bleaching events caused by global warming has
37 reshaped coral reef ecosystems around the world⁶⁻⁹. Effects of coral mortality cascade
38 through the ecosystem, leading to decreased abundance or local extinction of coral-dependent
39 species, and subsequent re-organisation of ecological communities⁷. Despite the prevalence
40 of these changes, the underlying mechanisms remain unclear. One mechanism that could be
41 important yet is unresolved is the role of individual behaviour in altering population
42 dynamics or community structure^{10,11}. In particular, interference behaviour between

43 individual fish of different species is widespread and implicated in population abundance,
44 species co-existence, and geographical range shifts¹¹⁻¹³.

45 Laboratory experiments suggest that fish behaviour can be mediated by environment.
46 However, these experiments are overwhelmingly focused on the direct effects of water
47 temperature and acidification e.g.,¹⁴, despite the more immediate threat from on-going loss of
48 coral¹⁵. Moreover, these experiments focus on the short-term responses of only a handful of
49 species to single stressors in aquaria isolated from community interactions. Despite their
50 simplicity, these experiments yield contrasting results^{16,17}, hindering our ability to forecast
51 the consequences of coral mortality on reef communities in nature. While field experiments
52 are more likely to capture the complexity of natural systems¹⁸, they are not amenable to
53 manipulation at large geographical scales. An alternative approach is to combine large-scale
54 natural experiments in a macroecological framework. In this way, we can move beyond site-
55 contingent results and test whether fish behaviour responds in a consistent way to disturbance
56 across reefs *despite* variation in biogeographic history, environmental conditions and biotic
57 context.

58 Mass bleaching events reduce resource availability for fishes that rely on corals for
59 food e.g., butterflyfishes (*Chaetodon* spp.). Theory predicts that aggression among
60 individuals should be highest at intermediate resource availability, due to the trade-off
61 between resource value and the relative energetic cost of resource defence². Depending on
62 the availability of resources prior to disturbance, the probability of aggression, and the extent
63 of resource (e.g., coral) loss, two possible outcomes of reduced resource availability on
64 aggression are possible. First, reduced coral availability could increase fish aggression due to
65 enhanced value of the rarer resource. Second, reduced coral availability could decrease
66 aggression because nutritional deficits intensify the relative energetic cost of resource
67 defence, reducing resource holding potential^{2,19}. Distinguishing between these possibilities is

68 necessary to provide mechanistic predictions of the impacts of coral bleaching effects on reef
69 fishes.

70 Here, we report on observations of 5,259 encounters between individuals of 38
71 species of *Chaetodon* (butterflyfishes) before and after the global coral bleaching event in
72 2015-2016. Encounters were recorded over 11,740 minutes (2,348 five-minute observations)
73 at 17 reefs nested within five regions of the central Indo-Pacific (Fig. 1; see Supplementary
74 Table 1 for sample sizes per reef). We used this uniquely powerful dataset to examine
75 behavioural change in response to abrupt reductions in resource availability, a critical
76 determinant of aggressive behaviour^{2,19}.

77 To determine the effect of resource availability on butterflyfish aggression, we
78 followed a focal fish for five minutes and recorded as an encounter every conspecific that
79 came within 1 m of that individual²⁰. Encounters were categorised as passive when there was
80 no observed change in behaviour, or aggressive when one or both individuals engaged in
81 display or chasing behaviour. By comparing behaviour before and after bleaching, we
82 explicitly examine the consequences of coral mortality on the probability of aggressive
83 behaviour. Whilst behavioural data were collected only once from both Bali (before
84 bleaching, although coral cover was collected before and after) and Aceh (after, although fish
85 abundance and coral cover were collected before and after), we include these data to
86 determine whether behaviour fits expectations from other reefs, and to inform our general
87 model of the predictors of fish aggression.

88 Bleaching-induced mortality resulted in the loss of 18% - 65% of initial standing coral
89 cover across 12 reefs in four of the regions for which we had coral cover data both before and
90 after the bleaching events (Christmas Island, Iriomote, Aceh, Bali; Fig. 1). Despite some
91 bleaching, there was no coral mortality in the fifth region, Luzon, which provided a natural
92 control. On reefs with high coral mortality, the probability of aggressive encounters between

93 heterospecific butterflyfishes decreased from 0.15 ± 0.02 (95% confidence interval) to 0.05
94 ± 0.01 (Fig. 2a,b; across species Supplementary Fig. 1) and for conspecifics decreased from
95 0.66 ± 0.08 to 0.45 ± 0.08 (Fig. 2c, d). Because we generally sampled reefs at similar times of
96 year, we infer that the decrease in the probability of aggressive encounters is due to coral
97 mortality rather than seasonal differences or phenological effects. Luzon, which did not
98 experience coral mortality, had the largest seasonal difference between surveys (six months
99 between samples; mean water temperature: before = $27.06^\circ\text{C} \pm 0.56$, after = $29.34^\circ\text{C} \pm 0.47$)
100 but the smallest change in aggression (heterospecifics from 0.14 ± 0.03 to 0.18 ± 0.03 ;
101 conspecifics from 0.70 ± 0.13 to 0.55 ± 0.13 ; note the overlapping 95% confidence intervals).
102 Such consistent behavioural change on multiple reefs across a large geographic extent in
103 response to a natural experiment provides strong support that high coral mortality led to
104 decreased aggression.

105 To further test whether coral cover, rather than alternative factors, triggered the
106 decrease in aggression, we generated a Bayesian hierarchical model to predict whether
107 outcomes of pairwise encounters between individual fish were aggressive or passive.
108 Conspecific aggression is linked to territorial defence, where mated pairs aggressively defend
109 a set of coral colonies²¹. In contrast, heterospecific aggression is associated with dietary
110 overlap, where dominant competitors gain priority access to preferred prey species²⁰.
111 Consequently, we model conspecific and heterospecific encounters separately.

112 The probability of heterospecific encounters rises with increased coral cover (median
113 = 0.97, 95% Credible Interval = 0.61-1.36; Fig. 3a). In addition, aggression was more likely
114 during encounters between pairs of obligate corallivores (median = 1.07, 95% CI = 0.78-
115 1.37; Fig. 3a) than between pairs that included facultative corallivores or non-coral
116 invertivores. These results support the hypothesis that interspecific aggression is an adaptive

117 response to resource competition^{22,23}. Phylogenetic relatedness (median = -0.11, 95% CI = -
118 0.23-0.01; Fig. 3a) and body size ratios between species were poor predictors of
119 heterospecific aggression (median = 0.13, 95% CI = -0.02-0.27; Fig. 3a), offering little
120 support for the notion that closely-related similar species should interact more aggressively
121 than distantly-related dissimilar species^{16,25}. The failure of temperature to predict aggression
122 suggests that the effect of metabolic relationships²⁴ are small relative to resource availability,
123 and also indicates that changes in water temperature that might arise from seasonal
124 differences are relatively unimportant. Similarly, outcomes of conspecific encounters were
125 predicted most strongly by coral cover (within 90% credible interval), while body size, diet
126 and water temperature contributed minimally (Fig. 3b).

127 Feeding comparisons amongst corallivorous butterflyfishes before and after bleaching
128 suggest that nutritional deficit offers an explanation for the differences in aggression. Many
129 corallivorous butterflyfish prefer corals in the genus *Acropora*, because they provide more
130 energy per foraging effort than do other coral taxa^{6,25}, yet *Acropora* corals are highly
131 susceptible to bleaching²⁶. Foraging by corallivorous butterflyfishes on *Acropora* species
132 after bleaching was 71% lower than before bleaching at Iriomote, and 85% lower than before
133 at Christmas Island, whilst at Luzon, which did not experience coral mortality, foraging on
134 *Acropora* was only 7% lower. The reduction in foraging on *Acropora* species was
135 particularly noticeable in the highly specialised corallivores (*C. trifascialis* and *C.*
136 *baronessa*), which are also the most aggressive species. The largest shifts in foraging on
137 *Acropora* were observed around Christmas Island, which also had the largest reduction in
138 aggression (Fig. 4; for proportions by time and species with confidence intervals, see
139 Supplementary Fig. 2). Moreover, individuals did not compensate for the loss of nutritious
140 *Acropora* in their diets by feeding more intensely on other less nutritious coral genera
141 because the overall bite rate did not increase after bleaching (one-tailed paired Wilcoxon

142 signed rank tests: Luzon, $V = 15$, $p = 1$; Iriomote, $V = 35$, $p = 0.936$; Christmas Island, $V =$
143 19 , $p = 0.969$; Fig. 5). The observed reduction in butterflyfish aggression is therefore
144 consistent with the hypothesis that energetic deficit caused by decreased resource availability
145 after coral bleaching leads to reduced aggression.

146 Aggression can also be influenced by changes in the density of competing
147 individuals: more individuals lead to increased probability of encounter by Brownian motion,
148 the random movement of individuals, alone²⁸. Here, the density of *Chaetodon* spp. did not
149 change significantly from pre- to up to 12 months post-bleaching ($V = 36$, $p = 0.831$;
150 Supplementary Fig. 3). This result is consistent with time lags of up to five years between
151 coral mortality and declines in butterflyfish abundance^{1,29}. Lampuuk (Aceh) and Eisvold
152 (Christmas Island) reefs did decrease in butterflyfish density (Supplementary Fig. 3).
153 However, both heterospecific and conspecific aggression for these reefs were strongly
154 positively associated with coral cover in the Bayesian regression model (95% confidence
155 intervals for group intercept overlap zero), consistent with the hypothesis that coral mortality
156 has led to reduced aggression probabilities on these reefs regardless of density effects on
157 encounter rates.

158 While declines in the abundance of butterflyfishes might be anticipated over longer
159 time-scales as body condition deteriorates^{1,30}, subtle shifts in the abundance of a few key
160 species might be sufficient to cause reduced aggression. The two most aggressive species –
161 *C. trifascialis*, and the sister species complex *C. baronessa/C. triangulum* are expected to be
162 particularly vulnerable to coral cover loss²⁰. Encounters involving *C. trifascialis* and *C.*
163 *baronessa/C. triangulum* reduced from 44% to 28% following the bleaching, yet the
164 probability of aggression within those encounters mirrored the broader pattern, decreasing by
165 39% for *C. trifascialis* and 79% for *C. baronessa/C. triangulum* (Supplementary Fig. 4).
166 Moreover, the abundance of these species did not change (*C. baronessa/C. triangulum*

167 $V=1.5$, $p = 0.586$; *C. trifascialis* $V=14$, $p = 0.106$), and overall species composition of the
168 butterflyfish communities was not significantly different between survey times ($F_{1,9} = 1.27$,
169 $R^2 = 0.02$, $p = 0.278$). Consequently, the reduced aggression observed was not caused
170 directly by shifts in abundance or composition of the butterflyfish community.

171 Our results show that mass coral mortality caused by increased water temperatures
172 during the 2015-2016 global bleaching event⁹ led to the depletion of food resources, and
173 subsequent nutritional deficit offers a plausible explanation for the decreased aggressive
174 behaviour amongst butterflyfishes within the central Indo-Pacific. More broadly, aggression
175 is an important mediator of competitive interactions within ecological communities³¹;
176 therefore, behavioural changes could help explain the time lag leading to the well-
177 documented patterns of reduced abundance, local extinctions and altered species composition
178 after bleaching¹ by initiating detrimental yet sub-lethal conditions. For instance, reduced
179 aggression could indicate the breakdown of territories among butterflyfishes⁴ as individuals
180 roam further to obtain enough resources^{27,32}, rendering investment in aggressive defence too
181 costly and potentially causing a shift from interference to exploitative competition. At the
182 community scale, as resource availability declines and becomes uneconomical to defend,
183 previously aggressive coral specialists cease to be the dominant competitive species. Altered
184 competitive hierarchies can influence community co-existence relationships as the “rules of
185 engagement” are rewritten^{2,12,34} and territorial breakdown could lead to dampened dispersal
186 among reefs³³, together altering metacommunity dynamics. Additionally, although
187 behavioural flexibility can increase survival over the short-term it can also create ecological
188 traps in the longer-term if the disturbance endures¹¹, as is the case for mass coral mortality.
189 Identifying behavioural change at an early-stage could provide a potential early warning of
190 population and community shifts. We suggest that application of a macroecological approach
191 to behaviour more broadly across taxa and ecosystems can move us towards greater

192 understanding of how animal behaviour will be disrupted in the face of on-going global
193 environmental change and identify previously under-appreciated mechanisms that could
194 underpin the structure and dynamics of ecological communities in an ever-changing world.

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299 **AUTHOR CONTRIBUTIONS**

300 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.,
301 A.H.B., E.S.W. and A.S.H. collected the data; N.F. provided fieldwork support; S.A.K.
302 analysed the data and wrote the manuscript with contributions from all authors.

303

304 **FIGURE LEGENDS**

305 **Fig. 1.** Change in coral cover before and after the 2016 coral bleaching events at each field
306 region across replicate belt transects at depths 1-5 m. Boxplot lines are the median coral
307 cover, boxes range from 25th to 75th percentile. Mean loss of coral cover on reefs was
308 significant both with and without the inclusion of Luzon (paired Wilcoxon signed rank test,
309 all reefs: $V = 122$, $p = 0.003$; reefs excluding Luzon: $V = 78$, $p < 0.001$) and not for Luzon
310 only (paired Wilcoxon signed rank test, $V = 0$, $p = 0.125$).

311

312 **Fig. 2.** Probability of encounters resulting aggression before and after bleaching.
313 Heterospecific (a,b) and conspecific (c,d) aggression across reefs ($n = 17$; b,d) nested within
314 regions (a,c) was recorded both before (black outline) and after (no outline) the 2016
315 bleaching events. Data were resampled 1,000 times within regions to obtain bootstrapped
316 estimates of uncertainty around the median owing to variable sample sizes. Both
317 heterospecific (paired Wilcoxon signed rank test: $V = 21$, $p = 0.031$) and conspecific (paired
318 Wilcoxon signed ranks test: $V = 21$, $p = 0.031$) aggression decreased significantly when the
319 control region (Luzon) was not included. Note that Bali and Aceh are not directly comparable
320 but fit the trend from reefs surveyed at two points in time. Zero values are due to no
321 aggressive interactions being observed, rather than missing data.

322

323 **Fig. 3.** Influence of biotic and abiotic factors on the probability of aggression following
324 encounters. Central dots indicate median point estimate for the highest posterior density, thin
325 lines are 95% credible intervals and thick lines are 80% credible intervals from Bayesian
326 hierarchical regression analysis for heterospecific (a) and conspecific (b) encounters.
327 Comparisons among diet categories are indicated with obligate = obligate corallivore,

328 facultative = facultative corallivore, non = non-corallivore; reference category was that with
329 the largest sample size: obligate - facultative.

330

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

337

338 **Fig. 5.** Total bite rate (i.e., all coral genera) before and after bleaching for each species at
339 each region, and overall for each region. Bite rate has been maintained or reduced across all
340 species and regions, except *C. argentatus* at Iriomote. This result provides compelling
341 support for our hypothesis that reduced aggression was a result of nutritional deficit: a lower
342 proportion of bites on *Acropora* accompanied by the same bite rate as before coral mortality
343 would supply less nutrition overall.

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348 **METHODS**

349 Field Sites

350 We recorded abundance of 38 *Chaetodon* spp., hard coral cover, and behavioural
351 observations in five regions across the central Indo-Pacific (Fig. 1, Supplementary Table 1):
352 Christmas Island (Indian Ocean; 105.6°E, 10.4°S), Bali (Indonesia; 115.6°E, 8.4°S), Aceh
353 (Indonesia; 95.1-95.3°E, 5.4–5.9°S), Iriomote (Japan; 123.7°E, 24.4°N) and Luzon (the
354 Philippines; 120.8°E, 13.7°N). Reefs were surveyed up to 12 months before and/or 12
355 months after the global mass bleaching event reached that region, at a similar time of year
356 when possible (see Supplementary Table 1 for survey dates). Different survey dates between
357 regions were largely due to differences in the timing of the bleaching events and logistical
358 constraints associated with conducting field research across a large geographical extent whilst
359 maintaining consistent survey protocol and observers. All regions except Luzon are contact
360 zones between Indian and Pacific Ocean *Chaetodon* species, chosen to maximise the number
361 of species we were able to observe and the potential for aggression. At each location, we
362 surveyed three to four reefs resulting in a total of 17 sampled reefs (Supplementary Table 1).
363 To ensure, as far as possible, that different individuals were sampled, reefs were separated by
364 >1 km and interspersed with non-reef patches (corallivorous butterflyfish territories are
365 generally <0.2 km² ³⁵). A similar number of focal individuals were observed on each reef
366 (Supplementary Table 1).

367

368 Data collection

369 *Chaetodon* abundance & coral cover. We quantified the abundance of butterflyfishes with 50
370 x 5 m belt transects and the cover of hard corals (*Scleractinia*) was recorded every 0.5 m
371 along 50 m point intercept transects. At least three transects were deployed at each of two
372 depths (1 and 5 m) at each reef where possible to capture the abundance of *Chaetodon* spp.

373 and coral cover at the depths we observed encounters. Exceptions included Blue Lagoon
374 (Bali, 2 transects at 5 m), Eisvold (Christmas Island, 5 m only) and Million Dollar Bommie
375 (Christmas Island, 5 m only). All transects on Acehnese reefs were restricted to 1 m depth
376 because remote locations prevented use of SCUBA equipment. Fish and coral surveys were
377 conducted along the same transects, with the coral surveyor trailing the fish surveyor and
378 recording benthic cover.

379

380 *Aggression.* Observations were made on snorkel or SCUBA depending on depth and
381 visibility using a well-established protocol^{19,36}. Following an acclimation period (~ 1 minute)
382 to check that the individual was responding naturally (i.e., feeding), focal individuals were
383 followed at a distance of 2-4 m for 5 minutes. Many *Chaetodon* species occur in pairs and no
384 aggressive interactions were recorded among partners, so only one individual per pair was
385 observed to avoid dependence. An encounter was recorded when a congeneric came within 1
386 m of the focal animal. At this distance, we assumed the individuals were aware of each
387 other's presence and had the potential to interact. The outcome of each encounter was
388 recorded as passive if no discernible change in behaviour was elicited in either individual, or
389 aggressive if one or both individuals engaged in display or chase behaviour²⁰. There is strong
390 evidence that these displays can be attributed to aggression over food resources¹⁹, and paired
391 individuals, which comprised the vast majority of our target individuals, were highly unlikely
392 to engage in courtship displays with individuals outside of their pair²⁰. We used a U-shaped
393 search pattern to ensure as far as possible that we did not observe the same individual or pair
394 as the focal animal more than once. Contextual variables were recorded for each observation:
395 date, time, weather, water temperature, and observer identity. As far as possible, we tried to
396 observe every individual (pair) present on the reef. To ensure observation data were
397 standardised, each new observer was trained by an experienced observer (either JPH or SK)

398 until recorded data were identical. Manual recording captures fish chase behaviour better than
399 video recording³⁷ and *Chaetodon* spp. are not sensitive to diver presence³⁸.

400

401 *Feeding.* We used the same protocols for selecting and following a focal fish as for
402 aggression. Over three minute observation periods, we recorded the substrate from which
403 each bite was taken, identifying hard corals to species following Pratchett³⁹.

404

405 Statistical analysis

406 *Coral cover, fish abundance, fish community composition.* We tested whether hard coral
407 cover had declined significantly following the 2016 coral bleaching events with a paired
408 Wilcoxon signed rank test for reefs with before and after data. Changes in *Chaetodon* spp.
409 abundance were examined with a Wilcoxon signed ranks test paired by reefs before and after
410 bleaching, and changes in community composition with a PERMANOVA using Bray-Curtis
411 dissimilarity and 9999 permutations using the function `adonis` in the `vegan` package⁴⁰. The
412 assumption of dispersion similarity at both times necessary for this test was met (`betadispers`
413 function, average distance to median; before = 0.494, after = 0.502).

414

415 *Change in aggression probabilities and feeding.* Mean aggression probabilities for each reef
416 were compared before (n=13) and after (n=9) bleaching using a paired Wilcoxon signed
417 ranks test. Because our sampling protocol may lead to some pseudo-replication (i.e., ‘focal
418 individuals’ can be ‘encountered individuals’ in another observation), which can over-
419 estimate significance, we focus on the effect size. To explore uncertainty in aggression
420 probabilities around varying sample sizes of behavioural observations across reefs, we
421 bootstrapped the encounters within each reef by resampling with replacement 1000 times and
422 generated boxplots of bootstrapped values.

423 To determine the change in feeding behaviour, we first calculated the mean
424 proportion of bites on *Acropora* spp. across individuals within each species (plotted in Fig. 4,
425 Fig. S3). To determine whether bite rate increased after bleaching, we conducted one-tailed
426 paired Wilcoxon signed rank tests at each region with before and after feeding data (i.e.,
427 Luzon, Iriomote, Christmas Island)

428

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

437 To test the influence of abiotic factors, both models also included water temperature
438 to the nearest 1°C (measured *in situ*) at the time of the observation and coral cover at each
439 reef during the relevant survey. Although structural complexity can also be an important
440 factor affecting reef fish communities and behaviour, we were unable to include this as a
441 predictor due to lack of data. However, we do not believe structural complexity would drive
442 the aggression changes we observe because coral mortality caused by biological impacts,
443 such as bleaching or crown-of-thorns (as opposed to physical e.g., cyclones), is not generally
444 followed by a loss of complexity for between 4-10 years after the event (Pratchett et al 2008).

445 Diet was classified as obligate corallivore, facultative corallivore or non-coral
446 invertivore²⁶. Phylogenetic relatedness was represented by branch length between each
447 species pair in the phylogeny⁴¹, calculated with the ape package v.4.1⁴². Body sizes were

448 based on maximum length recorded for each species in FishBase (www.fishbase.org,
449 downloaded 20th July 2017). *Chaetodon andamanensis* and *C. triangulum* were missing from
450 the phylogenetic tree and, therefore, were excluded from further analysis, reducing the data
451 by 82 encounters.

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

460 We used weakly informative priors to constrain the coefficients of the predictors and
461 the intercept. Continuous predictors were centred on zero and scaled to have a standard
462 deviation of one, and we used a prior of a normal distribution with mean 0 and standard
463 deviation of 1, which assumes large coefficients are unlikely. This assumption is particularly
464 useful in complex models that struggle to converge in a frequentist framework. Here, larger
465 standard deviations on the prior distribution led to very high rejection rates for the initial
466 parameter values. Priors for the correlation matrix of the hierarchical groups were Gamma
467 distributions with shape and scale parameters set to one⁴³.

468 Models were implemented in RStanArm v.2.14.1⁴³ with the No-U-Turn Sampler
469 (NUTS) variant of the Hamiltonian Monte Carlo (HMC) algorithm because it is highly
470 efficient at sampling parameter space, automates fine tuning of HMC, deals well with
471 correlated parameters, and provides robust inference⁴⁴. We ran four chains with 2000
472 iterations, discarding the first of 1000 iterations as a burn-in period. The target average

473 proposal acceptance probability was set to 0.995 to avoid divergent transitions. We verified
474 chain convergence with \hat{R} (converged if ≤ 1.1) and visual inspection of the chains and
475 autocorrelation plots. We tested for collinearity in the model by quantifying the Pearson
476 correlation between all MCMC chains across parameter pairs. Models met assumptions
477 (cross-correlation between chain values for predictors < 0.6 , Supplementary Fig. 5-6) and
478 performed well.

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

484

485 **DATA AVAILABILITY**

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

488

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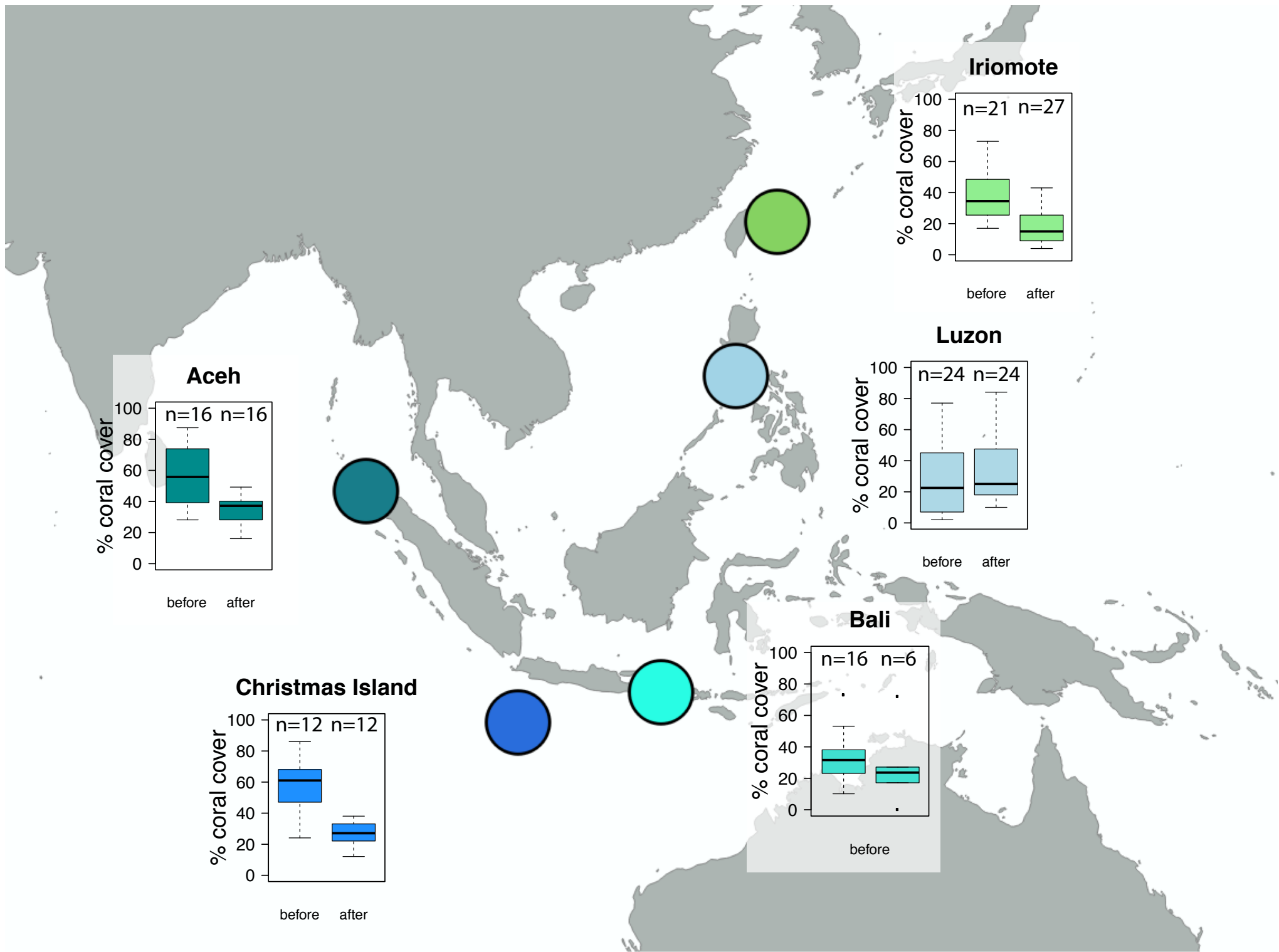
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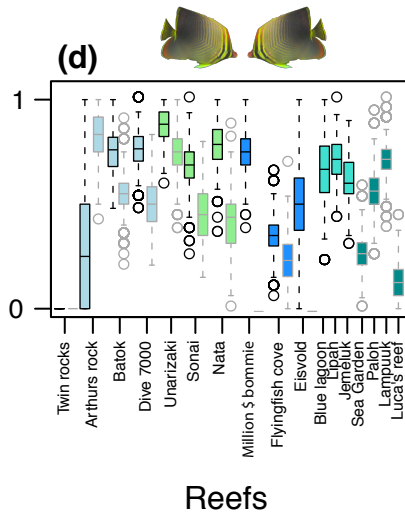
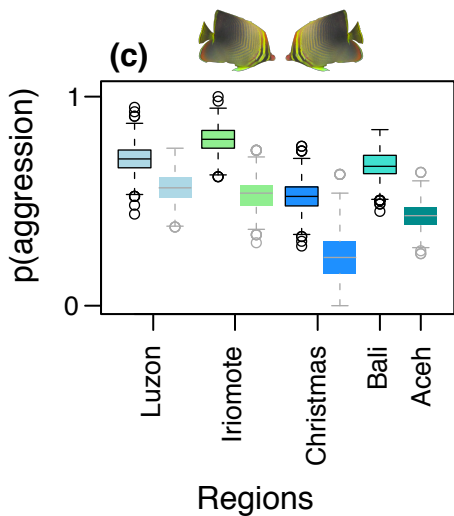
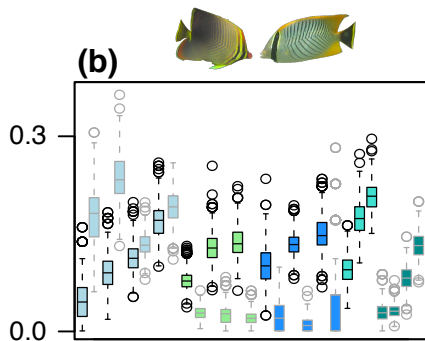
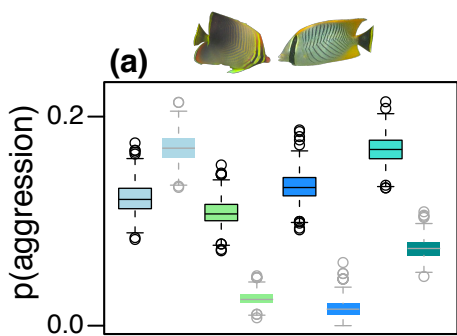
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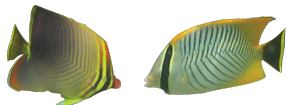
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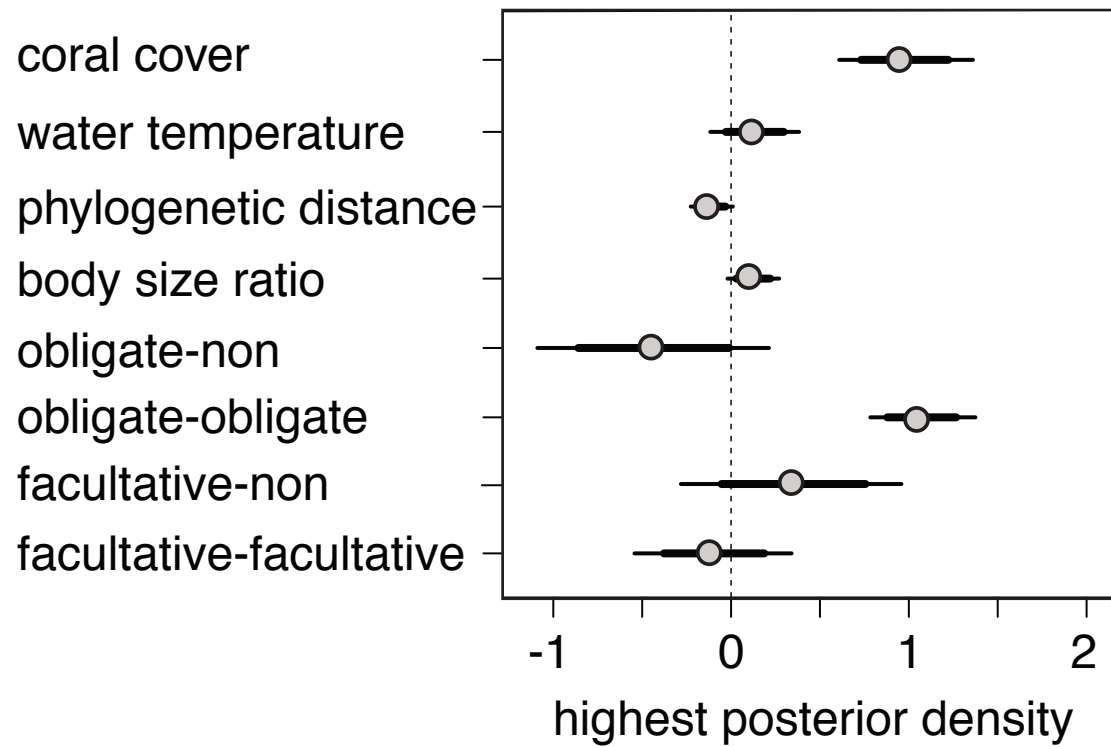


 before bleaching

 after bleaching



(a)



(b)

