

## **Transformation of coral communities subjected to an unprecedented heatwave is modulated by local disturbance**

**Authors:** Julia K. Baum<sup>1,2\*</sup>, Danielle C. Claar<sup>1,3</sup>, Kristina L. Tietjen<sup>1</sup>, Jennifer M.T. Magel<sup>1,4</sup>,  
Dominique G. Maucieri<sup>1</sup>, Kim M. Cobb<sup>5</sup>, Jamie M. McDevitt-Irwin<sup>1,6</sup>

<sup>1</sup>Department of Biology, University of Victoria, PO BOX 1700 Station CSC, Victoria, British Columbia, V8W 2Y2, Canada.

<sup>2</sup>Hawaii Institute of Marine Biology, University of Hawaii, Kaneohe, HI, 96744, USA.

<sup>3</sup>School of Aquatic and Fisheries Sciences, University of Washington, Seattle, WA, USA.

<sup>4</sup>Department of Forest and Conservation Sciences, University of British Columbia, 2424 Main Mall, Vancouver, British Columbia, V6T 1Z4, Canada.

<sup>5</sup>School of Earth and Atmospheric Sciences, Georgia Institute of Technology, Atlanta, GA, USA.

<sup>6</sup>Hopkins Marine Station, Stanford University, 120 Ocean View Blvd, CA, 93950, USA.

\*Corresponding Author: Julia K. Baum, Tel: (250) 858-9349, Email: [baum@uvic.ca](mailto:baum@uvic.ca)

**Corals are imminently threatened by climate change-amplified marine heatwaves. Yet how to conserve reef ecosystems faced with this threat remains unclear, since protected reefs often seem equally or more susceptible to thermal stress as unprotected ones. Here, we disentangle this apparent paradox, revealing that the relationship between reef disturbance and heatwave impacts depends upon the focal scale of biological organization. We document a heatwave of unprecedented duration that culminated in an 89% loss of coral cover. At the community level, losses hinged on pre-heatwave community structure, with sites dominated by competitive corals—which were predominantly protected from local disturbance—undergoing the greatest losses. In contrast, at the species level, survivorship of individual coral colonies typically decreased as local disturbance intensified, illustrating that underlying chronic disturbances can impair resilience to thermal stress at this scale. Our study advances understanding of the relationship between climate change and local disturbance, knowledge of which is crucial for coral conservation this century.**

## 30 INTRODUCTION

Marine heatwaves threaten the persistence of tropical scleractinian corals (1–3), and with them  
32 the biologically diverse ecosystems these foundational reef-building species support. Corals are  
particularly vulnerable to temperature anomalies, with increases of only 1°C capable of  
34 disrupting their obligate symbiosis with the photosynthetic dinoflagellate microalgae (family  
Symbiodiniaceae (1)) that normally fuel them, causing the coral animal to expel its symbionts  
36 and bleach (4, 5). Prolonged bleaching typically leads to coral starvation and mortality (5).  
Although climate change has long been recognized as a serious threat to tropical corals (6–8), the  
38 recent preponderance of marine heatwaves—persistent anomalously warm ocean temperatures  
(9)—has shifted focus from the threats posed by gradually rising temperatures and ocean  
40 acidification (8) to these punctuated disturbances (1, 3). Already, three global coral bleaching  
events triggered by El Niño-fueled marine heatwaves (1997–1998; 2010; 2014–2017) have  
42 caused devastating coral losses (10, 11). Climate change models project that both the intensity  
and frequency of marine heatwaves will increase in the coming decades (1, 3), such that many of  
44 the world’s coral reefs are predicted to undergo annual bleaching events by mid-century (12).  
None of these events will, however, occur in isolation. On almost all reefs, climate change is  
46 superimposed on a suite of chronic local anthropogenic disturbances (13)—ranging from coastal  
development and associated pollution and reef sedimentation to overexploitation, destructive  
48 fishing practices, and disease—that have already significantly altered coral communities through  
reductions in coral cover and changes to community composition, with largely unknown  
50 consequences for species and ecosystem resilience to thermal stress.

52 Given the intensification of marine heatwaves and the ubiquity of local anthropogenic  
disturbances on coral reefs, there is an urgent need to understand how these stressors interact  
54 (14). Yet to date, few coral bleaching studies have explicitly examined multiple stressors (15).  
Chronic local anthropogenic disturbance might mediate coral reef responses to thermal stress,  
56 either increasing susceptibility—as documented for massive corals on the Mesoamerican Reef  
following the 1998 El Niño (16, 17)—or conversely enhancing resilience, if disturbances have  
58 already eliminated the most vulnerable coral species, leaving behind only the hardiest species  
(18)—as documented on Kenyan reefs (19). Alternatively, exposure to chronic local disturbance  
60 may have no effect, with thermal stress impacting corals irrespective of underlying protection, as  
found recently on the Great Barrier Reef (20). The degraded state of most modern reefs is widely  
62 acknowledged (8, 13, 21, 22), and as managers seek to understand how to manage coral reefs  
under climate change, one might expect that examination of multiple stressors would be common  
64 practice in modern coral reef research. However, when we systematically reviewed studies  
reporting on the effects of recent marine heatwaves (2014–2021)—a period that includes six of  
66 the seven hottest years on record—we found that only 10% ( $n = 20/194$ ) had explicitly tested if  
local anthropogenic disturbance (or conversely, local protection) influenced heat stress effects on  
68 corals (fig. S1, supp. data S1). Approximately half of those that did ( $n = 9/20$ ) reported a positive  
effect of protection and increased survival of corals during heat stress events, while 40% ( $n =$   
70  $8/20$ ) reported no effect and 15% ( $n = 3/20$ ) of studies stated that protection reduced coral  
resilience to heat stress. Conflicting evidence amongst the few bleaching studies that have tested  
72 for the effects of local anthropogenic disturbance, and the overall lack of attention to this  
fundamental aspect of modern coral reefs, impedes understanding of how best to manage these  
74 ecosystems in a warming world.

How coral reefs are transformed by climate change this century will depend not only on their  
76 exposure to thermal stress and local anthropogenic disturbance but also on the sensitivity and  
response capacity of individual coral species to these stressors (23–25). Coral sensitivity to  
78 thermal stress is determined by biological traits, such as tissue thickness (26), and physiological  
tolerance, which is influenced by factors including the type and abundance of the coral colony’s  
80 obligate algal endosymbionts (27–30). Response capacity, in turn, may reflect species-specific  
propensity for acclimatization (e.g., the flexibility to switch or shuffle symbionts or to upregulate  
82 host thermal stress responses) and adaptation (e.g., selection for traits of either the host or  
symbionts that confer a fitness advantage under stressful conditions) (28, 31, 32). Interspecific  
84 differences in sensitivity to thermal stress have long been recognized (23, 26, 33), with ‘winners’  
generally able to either avoid bleaching during thermal stress or recover from it after warming  
86 subsides, and ‘losers’ tending to bleach and die quickly in response to warming (34). Since  
environmental filtering is stronger under stressful conditions (35–37), reefs increasingly stressed  
88 by marine heatwaves may lose diversity and converge towards simpler assemblages as ‘losers’  
are eliminated from the species pool. However, because repeated heatwaves may turn some  
90 ‘winners’ into ‘losers’ and vice versa (38), questions remain about how corals with different  
sensitivities will respond to heatwaves of increasing frequency, duration and intensity. Which  
92 corals will endure in communities will also depend upon whether species exhibit positive or  
negative co-tolerance to thermal stress and local anthropogenic disturbance (35, 39). Predicting  
94 future reef states thus requires not only accounting for underlying anthropogenic disturbances but  
also understanding interspecific variability in survivorship through heatwaves. To date, however,  
96 most heatwave studies have focused on quantifying coral bleaching, a symptom of thermal  
stress, rather than coral mortality, a fundamental parameter required to quantify the demographic

98 effects of such events. This disconnect reflects the challenge of quantifying coral mortality,  
which under the strictest standards requires following individual colonies over time, and at  
100 minimum requires quantifying coral cover before and after a heatwave, as opposed to bleaching  
assessments which require only a single site visit. Although bleaching may be an accurate proxy  
102 for mortality in short heatwaves, during prolonged events that are becoming the norm, for corals  
that either bleach quickly and die (and hence are unlikely to be recorded in the bleached state) or  
104 those that can persist in a bleached state for prolonged periods, it will not (40).

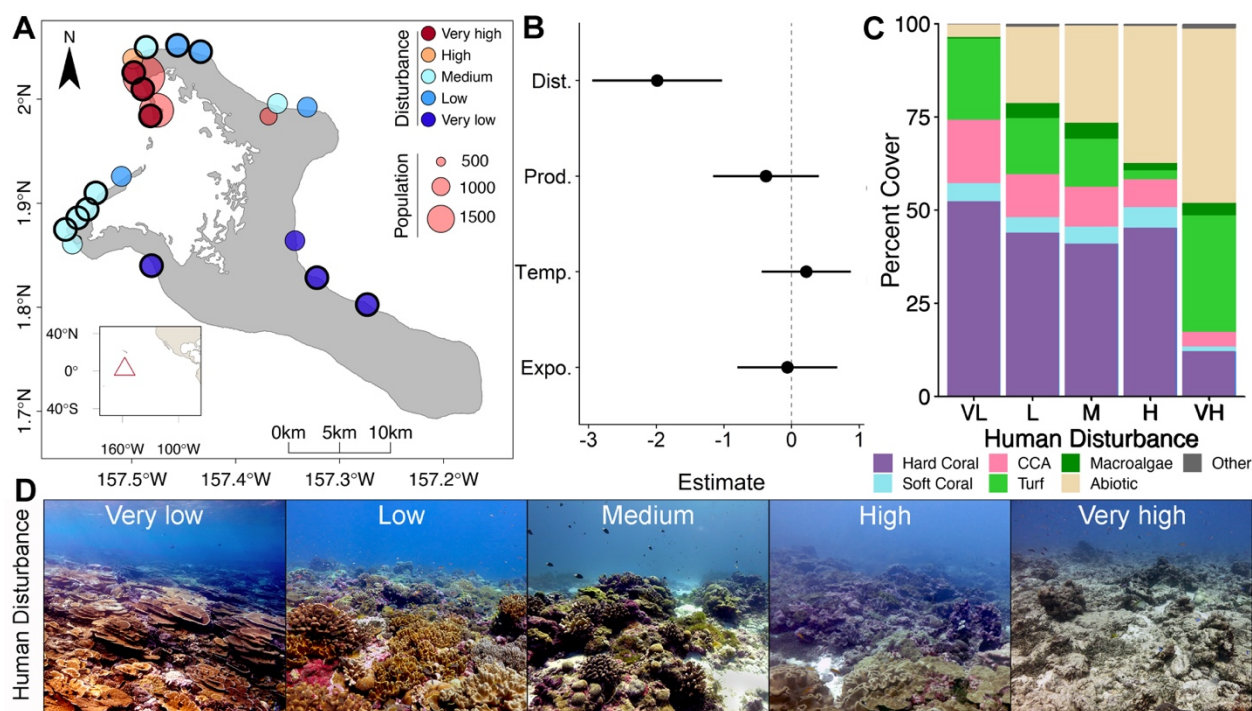
106 Here, we took advantage of the ecosystem-scale natural experiment created at the epicenter of  
the 2015–2016 El Niño, the central equatorial Pacific Ocean, where prolonged heat stress  
108 blanketed a spatial gradient of chronic local anthropogenic disturbance on the world’s largest  
atoll, Kiritimati. We quantified thermal stress around the atoll using high-precision *in situ*  
110 temperature loggers and satellite data. Our primary objective was to evaluate if protection from  
local disturbance modulates the impacts of stress on corals. We sought to examine this question  
112 both at the community level (i.e., amongst coral species) and at the species level (i.e., for  
individual coral species). In addition, we evaluated if coral bleaching, the most commonly  
114 recorded reef metric during heatwaves, accurately predicts coral mortality. Thus, over the course  
of nine expeditions (2013–2017) before, during, and after the heatwave, at sites exposed to  
116 varying levels of local disturbance (Fig. 1, A and D, fig. S2, S3), we quantified coral community  
composition and bleaching (n > 250,000 points from 94 photo surveys) and, in one of the largest  
118 longitudinal studies of individual corals to date (41), tracked the fate of > 850 individual coral  
colonies.

120

## RESULTS

### 122 **Prolonged heat stress superimposed on reefs spanning a local disturbance gradient**

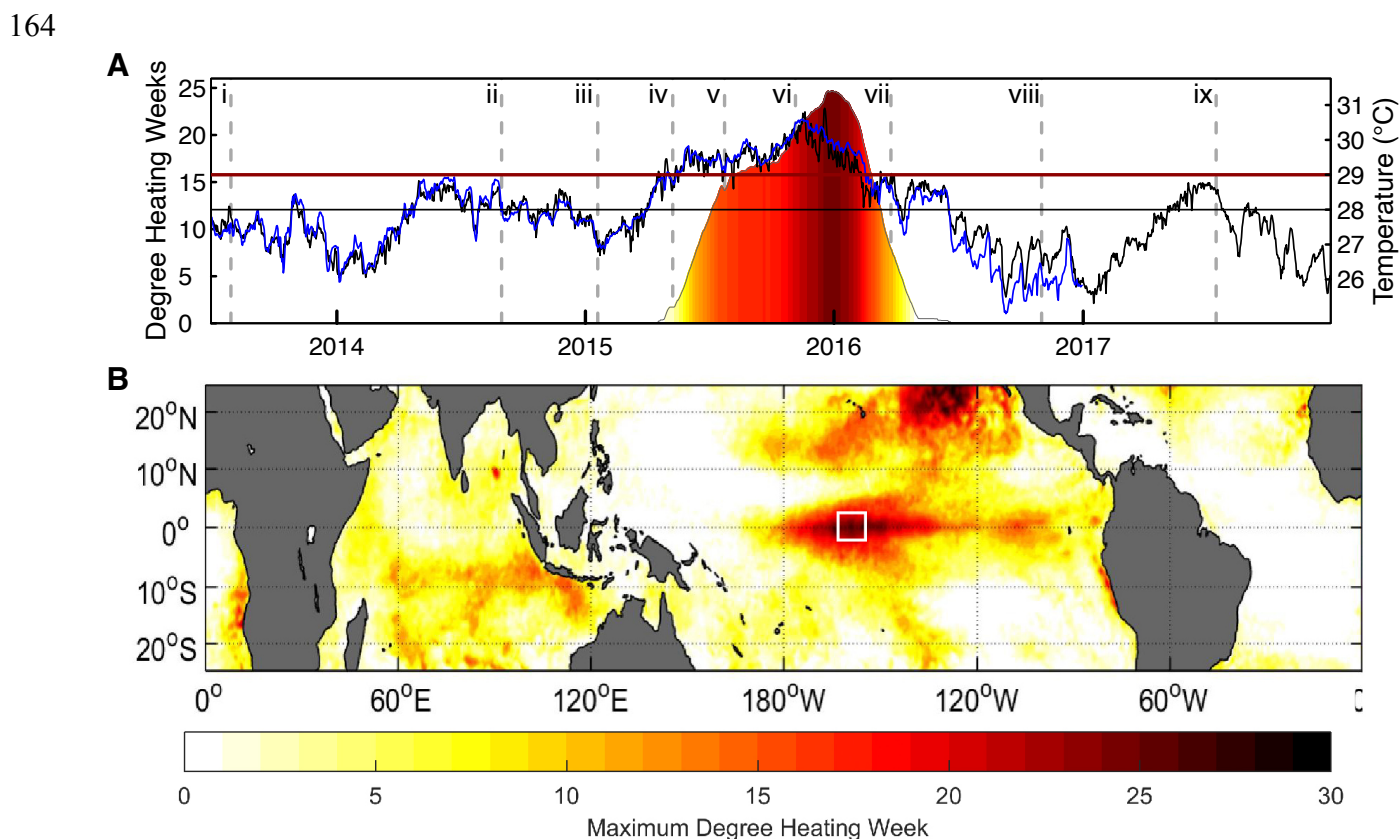
Prior to the El Niño, benthic communities varied dramatically across the atoll's forereefs, with  
124 sites ranging from a high of 62.7% hard coral cover to a low of only 1.6% (Fig. 1). Chronic local  
human disturbance (fig. S2, S3, table S1; detailed in Supplementary Materials), including  
126 dredging and pollution, was the primary determinant of these differences, with coral cover  
declining significantly as local disturbance increased ( $z = -4.063$ ,  $P < 0.001$ ; Fig. 1B). Abiotic  
128 factors, including oceanographic productivity, site exposure (windward versus sheltered), and  
sea surface temperature, did not significantly influence coral cover amongst sites (Fig. 1B, table  
130 S2). Reefs far from villages, with very low exposure to chronic local human disturbance, were  
amongst the most pristine remaining on the planet before the heatwave, with almost three-  
132 quarters of their benthos composed of hard and soft corals and beneficial crustose coralline algae  
(mean =  $52.4 \pm 13.2\%$  (SD) hard coral cover) (Fig. 1C). In contrast, reefs exposed to the highest  
134 levels of local human disturbance had little hard coral cover ( $12.2 \pm 17.3\%$ ), with most of the  
benthic community composed of turf algae ( $31.3 \pm 18.6\%$ ), sediment ( $28.4 \pm 15.5\%$ ), sand ( $11.9$   
136  $\pm 3.2\%$ ), and rubble ( $5.1 \pm 1.7\%$ ) (Fig. 1C). The effects of different intensities of chronic human  
disturbance on reef states were strikingly evident visually prior to the El Niño-induced heatwave  
138 (Fig. 1D).



140 **Fig. 1. Reef communities across a gradient of chronic human disturbance, prior to thermal**  
 142 **stress.** (A) Reef sites on Kiritimati (central equatorial Pacific Ocean) at which coral community  
 144 structure and individually tagged coral colonies (sites encircled in black) were tracked over the  
 146 course of the 2015–2016 El Niño; (B) parameter estimates and 95% confidence intervals for  
 148 factors examined (Dist. = local human disturbance, Prod. = net primary productivity, Temp. =  
 150 temperature, Expo. = wave exposure) for their influence on hard coral cover prior to thermal  
 stress; (C) mean community composition (CCA = crustose coralline algae; turf = turf algae;  
 abiotic = sediment, sand, rubble) of the forereef benthos amongst sites, classified by their  
 exposure to chronic local human disturbance; (D) photos of the coral reef communities prior to  
 the El Niño, at sites representing each of the atoll's levels of local human disturbance.

As the epicenter of the 2015–2016 El Niño, Kiritimati's coral reefs experienced a sustained  
 152 heatwave (Degree Heating Weeks (DHW, °C-weeks) > 0) for approximately one year (Fig. 2).  
 Heat stress started accumulating on 17 April 2015 and exceeded 4 °C-weeks (NOAA's Coral  
 154 Reef Watch (CRW) Bleaching Alert 1) from 28 May 2015 until 13 April 2016; DHWs > 0  
 persisted until 17 July 2016 (Fig. 2A). Accumulated heat stress rapidly exceeded both NOAA's  
 156 CRW Bleaching Alert Level 2 threshold (8 °C-weeks) and its 12 °C-weeks threshold, reaching  
 an unprecedented level (> 24.7 °C-weeks; Fig. 2A, table S3) by January 2016. Heat stress was

158 remarkably consistent around the atoll, varying by a maximum of only 4.3% (1.08 °C-weeks)  
across sites over the course of the event (fig. S4, table S3). Maximum temperature anomalies  
160 ranged across sites from 2.83°C to 3.05°C above the reef's normal maximum monthly mean  
(MMM) temperature during the event (table S3). The heat stress sustained by Kiritimati's reefs  
162 during this El Niño far exceeds that at any other time point from the recent past for which there  
are records (fig. S5).



166 **Fig. 2. Thermal stress at the epicenter of the 2015–2016 El Niño.** (A) *In situ* (blue line) and  
168 satellite (black line; from NOAA (42)) temperature on Kiritimati's reefs, with maximum  
monthly mean (MMM) temperature and bleaching threshold for reference (black and red  
170 horizontal lines, respectively; from NOAA CRW (Coral Reef Watch) (43)); all right axis. Color  
shows cumulative heat stress on Kiritimati as degree heating weeks (DHW, °C-weeks; left axis),  
172 from NOAA CRW (43). Dashed vertical lines denote the timing of expeditions prior to (i–iv),  
during (v–vii), and after (vii–ix) the event. (B) Global heat stress on coral reefs during the 2015–  
174 2016 El Niño (May 2015–June 2016) from NOAA CRW, with white box denoting Kiritimati's  
location at the epicenter of the heat stress during this event. Color (scale at bottom) indicates  
176 maximum thermal stress (°C-weeks).

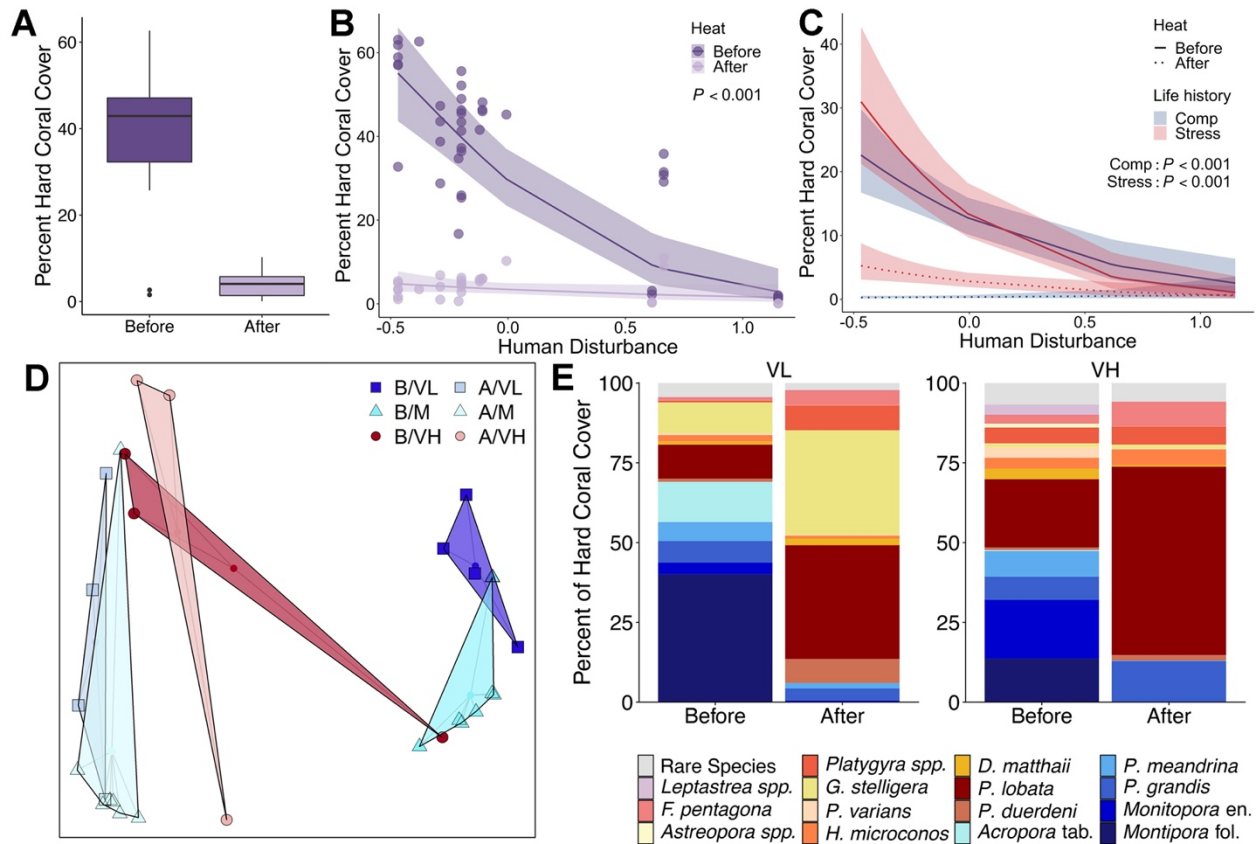


178 **Prolonged heatwave impacts primarily reflect differences in coral community composition**

180 The exceptional heat stress unleashed on Kiritimati during the 2015–2016 El Niño caused  
staggering coral mortality, culminating in an overall estimated loss of  $89.3 \pm 7.1\%$  of the  
182 forereef's hard coral cover (Fig. 3A, 4). Consistency in thermal stress around the atoll meant that  
DHW was not a significant factor explaining variability in overall hard coral cover amongst sites  
184 ( $z = -0.447$ ,  $P = 0.655$ ; table S4). Nor was bleaching prevalence early in the heatwave (fig. S6)  
related to the final overall loss of coral cover in the community ( $z = -0.633$ ,  $P = 0.527$ ). Instead,  
186 we found that heat stress period (i.e., before vs. after the event;  $z = 18.096$ ,  $P < 0.001$ ) and local  
disturbance ( $z = -5.146$ ,  $P < 0.001$ ) were both significant predictors of coral cover. The  
188 interaction between local disturbance and heat stress period was also significant, indicative of the  
absolute loss of corals being much greater at minimally disturbed sites than at those exposed to  
190 very high disturbance (Fig. 3B), which resulted in the strong inverse relationship between coral  
cover and local disturbance being completely eroded by the end of the heatwave ( $z = 6.538$ ,  $P <$   
192  $0.001$ ; slope =  $-0.73$ , 95% CI:  $-1.66$ – $0.21$ ; Fig. 3B, table S4). Relative coral cover losses also  
tended to be greater with lower local disturbance: on average, minimally disturbed sites  
194 underwent an estimated  $91.9 \pm 1.9\%$  decline in coral cover, ending the heatwave with only  $4.7 \pm$   
 $1.5\%$  coral cover, while sites exposed to very high levels of local disturbance—which already  
196 had depressed levels of coral cover—declined by a further  $64.6 \pm 15.1\%$ , ending the heatwave  
with only  $3.89 \pm 4.6\%$  coral cover (Fig. 3B, 4). However, this difference in relative coral cover  
198 losses was not quite statistically significant ( $t = -3.1124$ ,  $P = 0.09$ ), likely due to variable losses  
at the high local disturbance sites. Reef-building corals were replaced primarily by turf algae,  
200 which rapidly overgrew the dead coral, and at some sites also by macroalgae (Fig. 4, fig. S7).

202

204



206 **Fig. 3. Impact of a prolonged heatwave on coral community composition.** (A) Overall  
 208 change in hard coral cover across all sites from before to after the 2015–2016 El Niño on  
 210 Kiritimati (sites as in Fig. 1A); model predictions of the effect of local human disturbance on  
 212 percent coral cover before versus after the heatwave for (B) the overall coral community and (C)  
 214 stress-tolerant (red) and competitive (blue) corals; (D) PCoA plots of coral assemblage structure  
 216 before (B) and after (A) the event at very low (VL), medium (M), and very high (VH) levels of  
 local human disturbance; and (E) comparison of average coral community composition across  
 sites exposed to very low disturbance versus those exposed to very high levels of disturbance,  
 before and after the heatwave (stress-tolerant species in shades of red – yellow, competitive  
 species in blues).

218

220

222

224

226



228

230

232

234



236

238

240

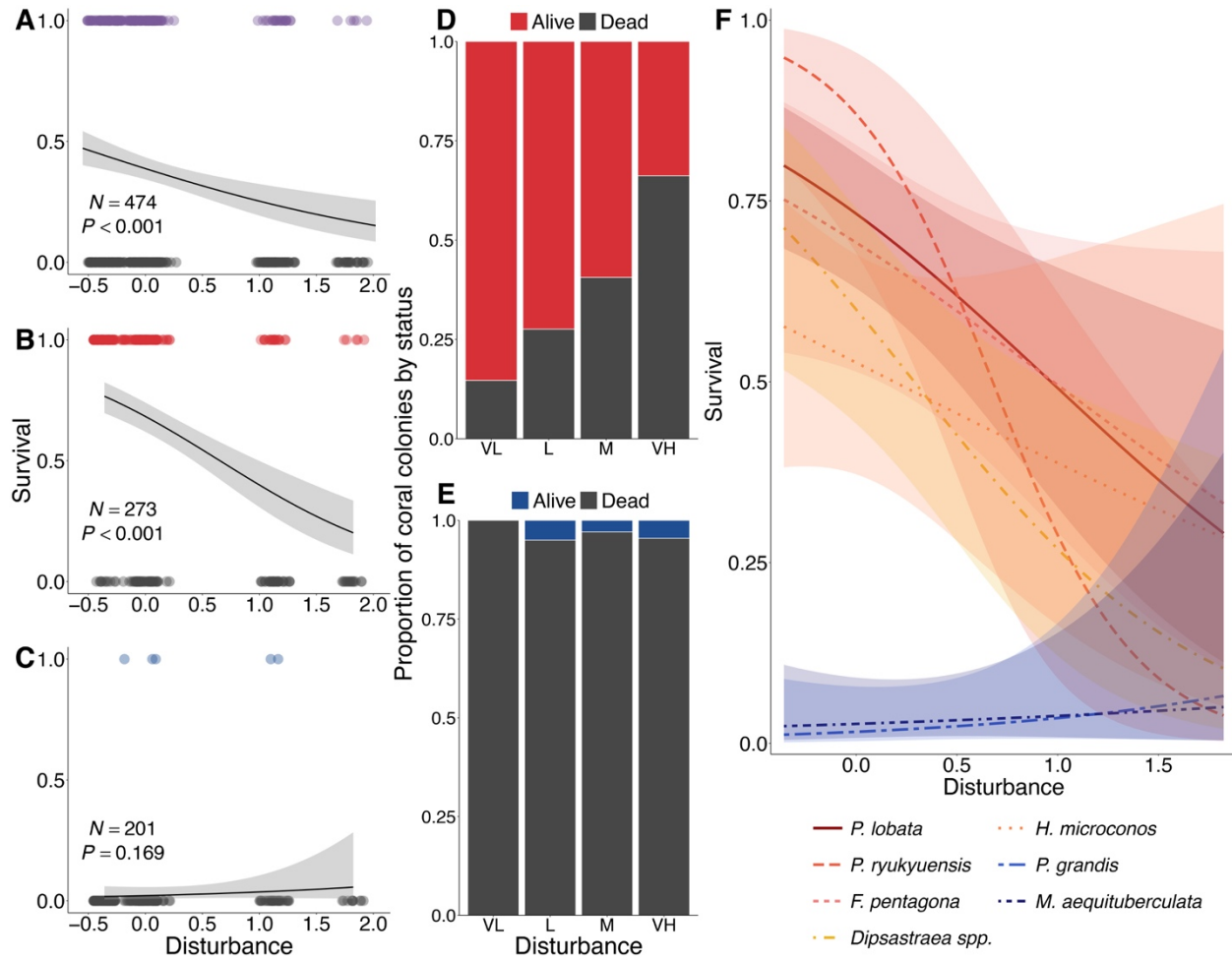
242

**Fig. 4. Transformation of a minimally disturbed coral reef by a heatwave of unprecedented duration. (A) Before (July 2015) and (B) after (July 2017) the 2015–2016 El Niño-induced mass coral mortality event at one site (VL1) with very low exposure to chronic local stressors on Kiribati. Virtually all coral in (B) is dead and overgrown by turf algae. Photo credits: (A) Kieran Cox, University of Victoria and (B) Kristina Tietjen, University of Victoria.**

244

We hypothesized that differences in coral cover loss across the local disturbance gradient reflected distinct coral communities, comprised of species with variable thermal stress tolerances, found at different disturbance levels. Examining these coral communities revealed

246 that not only did community composition vary with disturbance prior to the heatwave  
(PERMANOVA,  $pseudo-F = 4.4$ ,  $P < 0.001$ ; Fig. 3D, dark shaded polygons), but that it also  
248 changed significantly as a result of it (PERMANOVA,  $pseudo-F = 15.3$ ,  $P = 0.002$ ), with sites  
exposed to very low or medium local disturbance experiencing greater turnover than those  
250 exposed to very high disturbance (PERMANOVA,  $pseudo-F = 3.9$ ,  $P = 0.022$ ; Fig. 3D).  
Underlying this change was the loss of corals with a competitive life history strategy, namely all  
252 large tabulate and corymbose *Acropora* at very low local disturbance sites (100% loss) and all  
foliose *Montipora* at very low and medium local disturbance sites (100% loss; Fig. 3E, 4).  
254 Models testing the relationship between pre-heatwave community composition and coral cover  
showed that sites dominated by ‘competitive’ corals were more strongly impacted by the  
256 heatwave than those dominated by ‘stress-tolerant’ corals ( $z = -3.169$ ,  $P = 0.002$ ; fig. S8).  
Moreover, separate models of competitive and stress-tolerant coral cover revealed that while the  
258 cover of both life histories decreased significantly due to the heatwave (competitive:  $z = -13.252$ ,  
 $P < 0.001$ ; stress-tolerant:  $z = -12.293$ ,  $P < 0.001$ ; Fig. 3C, table S4), the degree of change was  
260 substantially greater for competitive corals ( $96.8 \pm 4.8\%$ ) than for stress-tolerant ones ( $78.7 \pm$   
 $10.5\%$ ;  $t = -6.8807$ ,  $P < 0.001$ ). We also found that, unlike for overall hard coral cover, the  
262 magnitude of thermal stress at each site ( $^{\circ}\text{C}$ -weeks) was statistically significantly related to the  
cover of both competitive and stress-tolerant corals; however, its effect size was much smaller  
264 than that of local disturbance or heat stress period (Table S4).



266

**Fig. 5. Survival of n = 475 individually tracked colonies throughout the heatwave.** Logistic regressions of coral survival versus disturbance for: (A) all coral colonies, (B) stress-tolerant (red) species, (C) competitive (blue) species, and (F) all coral colonies, with species modelled as a fixed effect, in a two-way interaction with local disturbance; bar plots of coral colony survival by local disturbance level for (D) stress-tolerant and (E) competitive coral species.

272

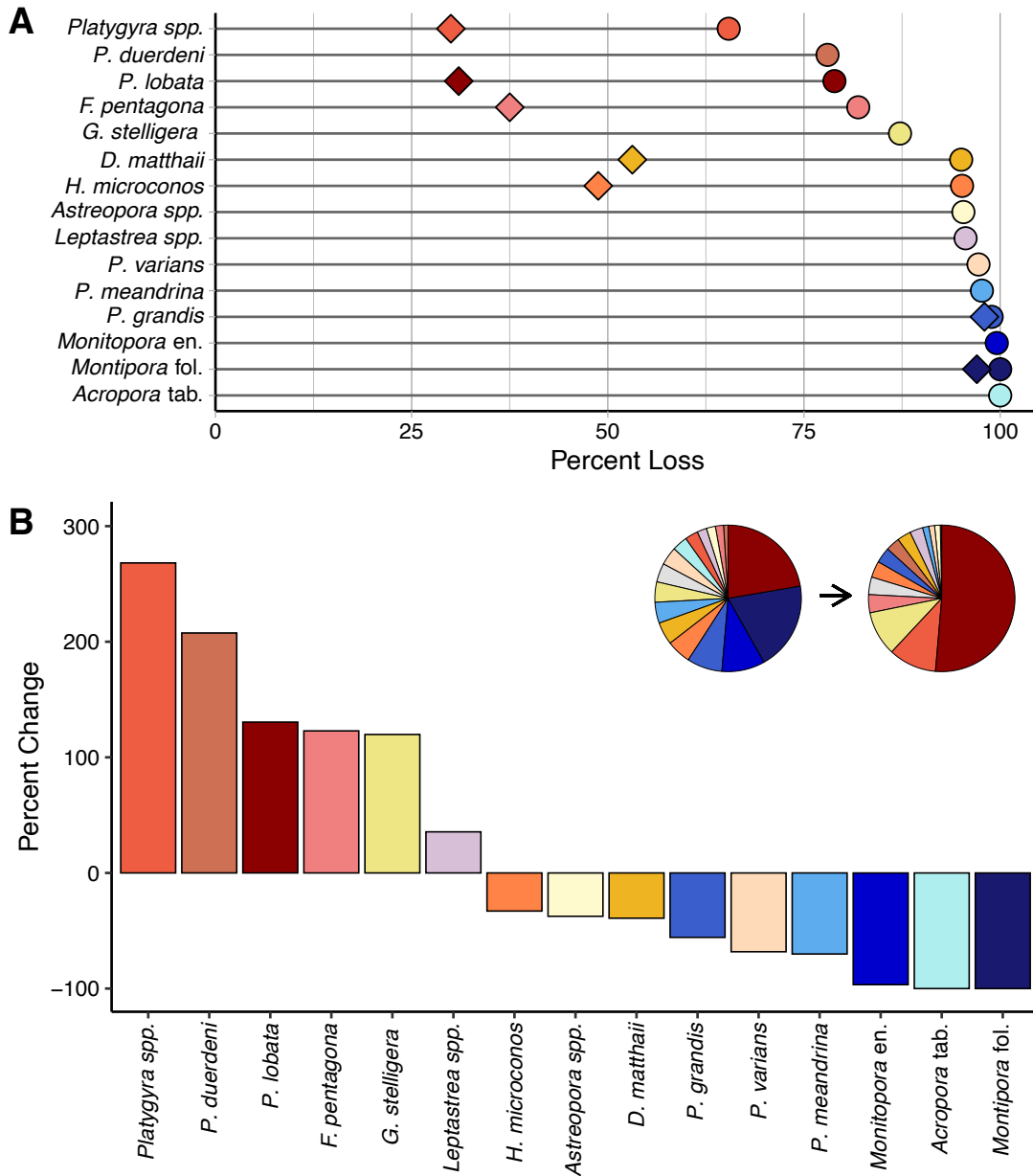
### 274 Chronic local disturbance can exacerbate heatwave impacts on individual coral species

276 In contrast to the observed changes at the community level, at the species level we found a clear  
 278 signal of the negative influence of chronic local disturbance on coral survival through prolonged  
 heat stress (Fig. 5; fig. S9). Examining a representative sample of the same seven coral species  
 across sites showed a significant negative relationship between local disturbance and coral

280 survival ( $z = -3.79$ ,  $P < 0.001$ ; Fig. 5A, table S5). This signal became clearer when distinguishing  
between life history strategies, with survival of the stress-tolerant coral species strongly  
282 negatively related to local disturbance (Fig. 5, B, D and F) while that of the competitive coral  
species showed no relationship with disturbance, namely because these colonies were so  
284 sensitive to the heat stress that few of them survived (Fig. 5, C, E, and F; 2.0% survival for  
*Pocillopora grandis*; 2.97% for *Montipora aequituberculata*). Individually, each stress-tolerant  
286 coral species exhibited an inverse relationship between survival and local disturbance, with the  
massive corals *Platygyra ryukyuensis* and *Porites lobata* exhibiting the steepest relationships (an  
288 estimated 95% and 80% survival at very low sites, and 4% and 29% survival at very high sites  
for the two species, respectively) and *Hydnophora microconos* the shallowest (58% survival at  
290 very low sites to 28% survival at very high sites) (Fig. 5F, Fig. S9, S10, Table S5). Survivorship  
of the two competitive species each showed weakly positive, but non-significant, relationships  
292 with local disturbance, with mortality at all sites exceeding 97.5% (Fig. 5F, Fig. S9, S10).  
Bleaching prevalence early in the heatwave was not related to the ultimate survival of any coral  
294 species ( $P > 0.69$ ) (Figs. S11, 12).

### 296 **Emergent winners and losers**

Given strong interspecific differences in survival, certain coral species emerged from this  
298 unprecedented heatwave as winners, while others were clear losers (Fig. 6). All of the  
competitive coral species were losers, having each lost over 97.5% of their cover (Fig. 6A). In  
300 contrast, the winners were all stress-tolerant coral species that underwent smaller losses in cover  
(65.4% to 87.2% for the five biggest ‘winners’) and thus increased considerably in their relative  
302 proportion of coral cover (Fig. 6). Notably, the massive coral *Porites* spp., which was already the



304 **Fig. 6. Interspecific variation in prolonged heat stress impacts on corals.** (A) Overall change  
 306 in percent cover of individual coral taxa (circles) for the 15 taxa comprising the greatest  
 proportion of benthic cover prior to the heatwave, ordered from least to greatest cover loss;  
 308 overall percent colony mortality for the seven individually tracked coral species is overlaid  
 (diamonds). (B) Percent change in proportion of overall coral cover, from before to after the  
 310 heatwave, ordered left to right from species that underwent the greatest proportional gains  
 ('winners') to the greatest proportional loss ('losers'). Inset pie charts show species composition  
 312 of the overall coral assemblage before (left) and after (right) the heatwave (grey = rare species).  
 See table S6 for taxonomic and other details.

314

most common coral prior to the heatwave, underwent more than a two-fold relative increase,  
316 such that over half of the atoll's remaining coral community is now comprised of this one slow-  
growing, stress-tolerant species (Fig. 6B). Although two other corals—*Platygyra* spp. and  
318 *Pavona duerdeni*—had even greater proportional gains, because they were initially relatively  
rare, they still comprised only a small proportion of the coral community at the end of the  
320 heatwave (10.6% and 3.1%, respectively; Fig. 6B). Finally, substantially lower rates of colony  
mortality than coral cover loss for the five individually tracked stress-tolerant species reflects the  
322 fact that while many colonies sustained partial mortality during the heatwave, a portion of the  
colony was still alive at the end of it (Fig. 6A).

324

## DISCUSSION

326 Despite the urgent need to leverage all available solutions for enhancing coral reef resilience to  
thermal stress in the face of escalating climate change, it has been unclear if protecting reefs  
328 from underlying local anthropogenic disturbance helps or hinders in this regard. Our study sheds  
new light on this debate. Tracking whole coral communities and individual species exposed to  
330 consistent thermal stress, but different levels of underlying local anthropogenic disturbance,  
clarified that the relationship between local anthropogenic disturbance and climate resilience  
332 varies qualitatively across biological scales. At the community level, we found that reefs exposed  
to high levels of chronic local anthropogenic disturbance fared better through a prolonged  
334 heatwave than those shielded from local disturbance, an outcome driven by differences in the  
coral community composition amongst sites. In contrast, when comparing survival rates within  
336 individual coral species, the predominant relationship for those species that were not eradicated  
by the heatwave was one of declining survivorship as local disturbance increased. These findings



338 have implications for managing and restoring coral reefs as climate change-driven marine  
heatwaves continue to intensify.

340

### **Winners and losers in prolonged heatwaves**

342 Overall, we documented mass coral mortality (89% hard coral cover loss) arising from a  
heatwave that persisted for a remarkable ten months unabated. At its peak, heat stress  
344 accumulated to 25 °C-weeks (degree heating weeks), a level that had not previously been  
anticipated to occur on any reef until mid-century (26). Its occurrence 35 years earlier than  
346 predicted underscores how rapidly climate change is advancing (1, 2, 9). Although corals  
typically exhibit high interspecific variability in their sensitivity to thermal stress (33), a  
348 heatwave this extreme might have been expected to overwhelm the tolerance of even the most  
resilient species, resulting in high mortality rates across the board. Instead, we found that  
350 interspecific coral cover losses still varied widely, from the complete loss of tabular *Acropora*  
and foliose *Montipora* to a loss of only 65% in the stress-tolerant mounding coral *Platygyra* spp.  
352 Mortality rates for the individual colonies we tracked were also highly variable across species,  
but with lower mortality rates for the stress-tolerant species because many of the colonies of  
354 these species had surviving corallites, thus potentially paving the way for their recovery. Only on  
nearby tiny Jarvis Island was thermal stress more extreme (maximum 31.58 °C-weeks) during  
356 this heatwave (44, 45). There, reefs underwent an estimated >98% decline in hard coral cover,  
with severe losses of *Montipora* spp. (100%), *Pocillopora* spp. (>90%), and *Pavona* spp. (~85%)  
358 recorded in the surveyed areas (45, 46). Together, these results illustrate that extremely  
prolonged heatwaves will still have ‘winners’ and ‘losers’, such that these events will cause not  
360 only dramatic coral losses but also substantial changes in community composition.

## **Influence of local anthropogenic disturbance on coral survival**

362 In species-specific models of the influence of exposure to chronic local anthropogenic  
disturbance on coral resilience to thermal stress, we detected an inverse relationship for those  
364 species with ‘stress-tolerant’ life histories. Survivorship of all stress-tolerant species was at least  
twice as high at sites sheltered from local stressors compared to those with the highest exposure,  
366 and over 10 times as high for that with the strongest inverse relationship, *Platygyra ryukyuensis*.  
Increased coral sensitivity to thermal stress is, we expect, most likely attributable to the  
368 diminished water quality at the most highly disturbed sites. On Kiritimati, raw sewage and  
pollution inputs have resulted in increased turbidity and sedimentation (Fig. S3) and greater  
370 concentrations of bacteria, virus-like particles, and potential pathogens in the water column at  
these sites (47, 48). Previous studies have shown that low water quality can change the coral  
372 microbiome (49–51), and microbiome analyses of subsets of our tracked corals prior to the  
heatwave showed increased bacterial diversity at highly disturbed sites (52). Such changes can  
374 have knock-on effects for coral physiology and survivorship even in the absence of warming  
(53), which may then be exacerbated during heatwave events. Poor water quality, as with other  
376 environmental stressors, can also lead to changes in coral–algal symbioses (54–56), which may  
then influence coral resilience to subsequent thermal stress. Indeed, an analysis of our tracked  
378 *Platygyra ryukyuensis* colonies revealed that distinct *Symbiodiniaceae* genera across the  
disturbance gradient were linked to coral survival during heat stress (57). Although the  
380 mechanism underlying the relationship between coral survival and local disturbance remains  
unclear for the other stress-tolerant corals we tracked—and may differ across species—we  
382 suggest that it likely results from distinct coral microbiomes, and their associated physiological  
traits, found across the disturbance gradient. We attribute the failure to detect an effect of local

384 disturbance on coral resilience to thermal stress in our two competitive coral species to their  
extremely high mortality. A recent study of a less severe heatwave, on Moorea, French  
386 Polynesia, showed that bleaching severity was significantly increased by local nitrogen pollution  
in the competitive coral genera *Acropora* and *Montipora* (58). Overall, these results suggest that  
388 impairment of coral resilience to thermal stress by local stressors may be a general phenomenon,  
and at least deserves increased research and management attention.

390  
Strikingly, however, these species-level results stand in contrast to our own community-level  
392 results, and previous studies, which have suggested that local disturbance enhances coral reef  
resilience to thermal stress. Over a decade ago, Côte and Darling (59) argued that this would be  
394 the case for coral reefs exposed to, and altered by, local stressors, because the most sensitive  
coral species would already have been eliminated, leaving behind a more stress-tolerant  
396 community. That is, if organisms exhibit co-tolerance to stressors (or, conversely, co-sensitivity)  
such that they respond similarly to them, then the combined effects of the stressors may be  
398 antagonistic, resulting in a response that is less than the sum of their individual effects (14, 39,  
60). Although such a response is not a given, with multiple stressors also sometimes eliciting  
400 synergistic or additive responses, it appears not uncommon on reefs exposed to local stressors  
and global climate change. Darling et al. (19) found that while the stress-tolerant corals that  
402 dominated fished reefs in Kenya prior to the 1998 El Niño were barely impacted by the  
bleaching event, reefs in no-take reserves had more diverse coral assemblages, including many  
404 corals with competitive life-history traits that exhibited co-sensitivity to fishing and bleaching,  
and incurred heavy losses. More recently, Cannon et al. (61) showed that central Pacific reefs in  
406 the Gilbert Islands that were exposed to higher levels of chronic local pressure were dominated

by a coral species tolerant of nutrient loading and turbidity and were subsequently less impacted  
408 during a bleaching event than nearby reefs with fewer local pressures. At Kiritimati's highest  
disturbance sites, we found that of the competitive coral species, *Acropora* were completely  
410 absent, and while some encrusting *Montipora* persisted, only a few colonies of the foliose form  
(common in less disturbed sites) were recorded. Thus, the 'positive' effect of local disturbance  
412 reflects different community compositions and the variable thermal sensitivities of the coral  
species that dominate disturbed reef communities, rather than there being a mechanism by which  
414 local disturbance itself enhances coral resilience to thermal stress.

416 More difficult to reconcile with either our species- or community-level findings are studies  
reporting that coral responses occur irrespective of local protection, influenced only by the reef's  
418 exposure to thermal stress (18). In surveys of the Great Barrier Reef Marine Park during the  
2016 marine heatwave, for example, Hughes et al. (20) documented severe bleaching on reefs in  
420 each of the park's types of management zones, and concluded that local management of water  
quality and fishing pressure had little to no influence on coral resistance to extreme heat.

422 Similarly, a study in one of Indonesia's oldest marine parks during the same heatwave found that  
management zone made no difference to coral losses (62). More recently, Baumann et al.'s (63)  
424 global meta-analysis tested the relationship between human influence and coral resilience and  
concluded that reefs isolated from human pressures are not more resilient to climate change,  
426 noting that even the world's most remote reefs bear the impacts of intense marine heatwaves. We  
concur that at broad spatial scales, exposure to thermal stress will be highly variable across the  
428 considered reefs, and this may well be the primary determinant of reef impacts; remote reefs are  
not immune to high thermal stress exposure levels. Such an emphasis on current and future

430 thermal stress exposures has proven useful when considering future thermal refugia for coral  
reefs, as in the ‘50 Reefs’ conservation prioritization (64, 65). At finer spatial scales, however,  
432 where thermal stress exposure is the same (or very similar) across reefs, a corollary of the  
conclusion that coral responses are (or appear to be) the same irrespective of protection is that  
434 coral sensitivities and response capacities to thermal stress must be the same across the  
protection levels. We can envision only a few means by which these conditions could be met: 1)  
436 corals are exposed to similar conditions inside and outside the protected area, such that the  
communities do not differ. This is likely to be the case in some areas where MPAs either have  
438 inadequate enforcement or have not been established long enough for coral recovery to have  
occurred within the MPA; 2) exposures to thermal stress across protection levels were not  
440 actually equal; 3) failure to detect different impacts due to insufficient power, or measuring  
bleaching at only a single time point such that the full ecological impacts of the event were not  
442 quantified; or 4) the coral communities differed because of the stressor, but the coral species in  
the different areas had equal sensitivities and response capacities to heat stress. Scenarios one to  
444 three do not imply that local disturbance has no effect on coral resilience to thermal stress, and  
the high interspecific variability in thermal tolerance makes the latter scenario unlikely.

446  
Considering our results together across scales suggests that, although local anthropogenic  
448 disturbance can result in the loss of sensitive coral species such that the remaining community is  
more tolerant to subsequent thermal stress, when comparing ‘apples with apples’—that is, the  
450 same species across different levels of local anthropogenic disturbance—there is clear evidence  
that local disturbance can impair survival. Thus, while there is compelling recent evidence that  
452 coral reef recovery following bleaching events may not be aided by reef protection (18), our

study suggests that previous conflicting results pertaining to coral community resilience to  
454 thermal stress can be resolved through consideration of biological scale.

#### 456 **Coral bleaching does not foretell demographic impacts of prolonged heatwaves**

Our repeated reef surveys during an extended bleaching event also provide an empirical test of  
458 the relationship between coral bleaching and mortality. Given the many challenges associated  
with conducting *in-situ* assessments of coral bleaching events—including the need to marshal  
460 resources quickly when heatwaves arise, the limited reef area that can be assessed by divers, and  
the complexities of accessing remote reefs—rapid reef surveys at a single time point during a  
462 heatwave are often used to assess ecological impacts. But whereas bleaching incidence may be a  
reliable indicator of diminished coral fitness (given that it can lead to decreased coral growth and  
464 reproduction), the capacity of corals to recover from bleaching means that it may not accurately  
foretell coral mortality, and hence the demographic impacts of heatwaves. Indeed, we found no  
466 relationship between bleaching prevalence and subsequent mortality levels in any of our tagged  
coral species. Instead, we found that the species with the highest bleaching incidence early in the  
468 event (*Platygyra ryukyuensis* and *Favites pentagona*) had amongst the lowest mortality, while a  
species with very low bleaching incidence (*Pocillopora grandis*) suffered near complete  
470 mortality (Figs. 6A, S11, S12); results were similar for our benthic community data. Mismatches  
between bleaching and mortality could arise if certain coral species can resist the onset of  
472 bleaching more than others, but then only persist in a bleached state for a short period (40, 66).  
Such mismatches will be more likely in the prolonged heatwaves that are predicted to become  
474 more common under climate change (40, 67), thus highlighting the need for increased sampling  
during these events to accurately gauge demographic impacts. As the capacity to use satellite-

476 derived data to accurately monitor coral bleaching increases, these sources could help to  
overcome this challenge.

478

### **Coral reef recovery from prolonged heatwaves unlikely under climate change**

480 We posit that coral reef recovery from prolonged heatwaves is increasingly unlikely, because of  
long ecosystem recovery times and the diminishing interval between successive heatwaves under  
482 climate change (68, 69). On Kiritimati, our sampling up until three years after the end of the  
heatwave (2019, prior to the onset of COVID-19) revealed new juvenile corals and regrowth of  
484 colonies that had experienced partial mortality, which together resulted in some increase in  
overall coral cover but still left the ecosystem a long way from full recovery. Long-term studies  
486 of coral reefs from the Indian and Pacific Oceans following the major 1998 El Niño found that  
recovery of hard coral cover typically took more than a decade and involved substantial turnover  
488 of community composition, with ‘recovered’ reefs tending to have lower coral diversity and be  
dominated by fast-growing corals (70–73). Recovered reefs in Moorea, for example, are now  
490 dominated by ‘fields’ of weedy *Pocillopora*, while recovering reefs in the Seychelles became  
dominated by fast-growing, branching *Acropora* corals (74). Reef recovery following mass  
492 bleaching events is also not guaranteed. Following the 1998 El Niño, over 40% of surveyed reefs  
in the Seychelles underwent regime shifts to fleshy macroalgae (73). Those that were on a  
494 recovery trajectory, which had high coral cover prior to the 1998 El Niño, still had not fully  
recovered by 2014, and although full recovery was projected to be complete within 17 to 29  
496 years (74), progress was nullified by Seychelles’ 2016 bleaching event (75). Such outcomes are  
increasingly likely with climate change (68). Thus, as with many reefs, full recovery of  
498 Kiritimati’s reefs now seems unlikely.

Persistence of coral reefs throughout the 21<sup>st</sup> century will be dictated almost entirely by the  
500 extent to which greenhouse gas emissions are reduced (67). Our study shows that prolonged  
heatwaves under climate change will not only significantly reduce coral cover but also transform  
502 coral community composition. Diminishing intervals between recurrent heatwaves will leave  
most reefs with insufficient time to recover (68). Emissions reductions that only limit warming to  
504 2°C are projected to result in the loss of virtually all coral reefs (99%), whereas if warming is  
limited to 1.5°C, losses could be limited to between 70% and 90% (67, 76). Under such dire  
506 conditions, strategies additional to GHG emissions reductions that can reliably enhance coral  
resistance to, or recovery from, marine heatwaves should be broadly deployed. Yet, the efficacy  
508 and scalability of the potential options remains uncertain. Our study provides evidence that coral  
species' resilience to thermal stress is enhanced as local anthropogenic stressors are reduced.  
510 These findings imply that alleviating local stressors—such as by improving water quality, which  
is likely one of the most tractable options for reef managers—could not only benefit natural coral  
512 reefs but also aid coral restoration efforts, improving the odds of success for the individual coral  
species that are out-planted on reefs. With much still to learn about the interactions between  
514 multiple stressors on coral reefs, we encourage researchers to explicitly incorporate local  
stressors into future studies of marine heatwave impacts on coral reefs. In addition to urgent  
516 reductions in greenhouse gas emissions, evidence-based local management actions that are both  
scalable and durable are urgently needed as a means of increasing the odds of persistence for  
518 these imperiled ecosystems under climate change.



## MATERIALS AND METHODS

### 520 **Literature survey**

We conducted a systematic review of the primary literature to quantify the extent to which field  
522 studies assessing the impacts of recent marine heatwaves (i.e., 2014 to 2021) on corals quantified  
underlying local anthropogenic disturbance at their study site and tested for an effect of them on  
524 coral outcomes through the heat stress event. On 9 September 2021, we conducted a search for  
papers published between 2015 and 2021 using all databases on the Web of Science, with the  
526 following search terms: (“coral\*”) AND (“mortal\*” OR “bleach\*” OR “cover\*” OR “health\*”) AND (“El Niño” OR “El Nino” OR “ENSO” OR “heat\*” OR “thermal stress” OR  
528 (“temperature” AND “anomal\*”) OR “bleaching event”). We evaluated each of the n = 721  
papers returned from this search, reviewing the titles, abstracts, and method sections, to first  
530 determine if the paper examined corals during a heatwave between 2014 and the present day; we  
excluded papers describing lab-based studies or heatwaves prior to 2014. Additionally, we added  
532 n = 10 papers that were not returned from this search but were known to quantify the effects of a  
heatwave between 2014 and the present day. The remaining n = 184 papers that met our criteria  
534 were classified based upon if the study included an anthropogenic disturbance (searching for  
“anthropogenic”, “human”, “disturbance”, “stressor”, “cumulative effects” or “protection”) and  
536 if the study analyzed or made conclusions about the effect of anthropogenic disturbances. We  
also noted the type of disturbance (e.g., fishing, pollution), if the study included sites without  
538 disturbance as a control, the coral sampling method (e.g., randomized quadrats, etc.), as well as  
the frequency of sampling before, during, and after the heatwave event.

540

## Study site

542 Situated in the central equatorial Pacific Ocean at the center of the Niño 3.4 region (a designation  
used to quantify El Niño presence and strength) (77), Kiritimati (Christmas Island) is the world's  
544 largest atoll by landmass (388 km<sup>2</sup>, 150 km in perimeter). Coral reefs are exposed to vastly  
different levels of chronic local human disturbance depending on their location around the atoll  
546 (Fig. 1A). Human impacts—including pollution from sewage outflow and an oil company, major  
infrastructure (i.e., a pier), and fishing pressure on the forereef—are densely concentrated on the  
548 northwest coast, where the two main villages are located and the majority of the population  
resides (Fig. 1A, table S1). In contrast, reefs on the atoll's north, east, and south coasts are  
550 minimally impacted (Figs. 1, S2; detailed in Supplementary Materials) (78, 79).

We quantified the intensity of chronic local human disturbance at each forereef site  
552 (described below in Field Methods), as in (57, 80), using two spatial data sources: 1) the number  
of people residing within 2 km of each site, as a proxy for localized impacts, based upon the  
554 Government of Kiribati's 2015 population census data for each village on Kiritimati (81); 2)  
subsistence fishing pressure, quantified through detailed semi-structured interviews conducted  
556 with heads of household in each of the atoll's villages in 2013 (82) and represented using a  
kernel density function as a measure of its intensity at each site. We combined these data with  
558 equal weight to create a quantitative metric of chronic local human disturbance at each site (table  
S1). This metric correlated strongly with sedimentation, turbidity, and bacterial loads, three other  
560 indicators of disturbance (see Supplementary Methods, Fig. S2). For visualization purposes, and  
to contrast reefs exposed to local disturbance extremes, we also classified each site as one of five  
562 distinct disturbance levels (very low, low, medium, high, and very high) based upon clear  
breakpoints in our continuous disturbance metric (Fig. 1A, table S1) (57, 80). These terms should

564 be regarded as being relative to other levels of disturbance around the atoll, rather than absolute  
levels of human disturbance.

566 In addition to local human disturbance, we also quantified site-specific oceanographic  
parameters to assess their influence on benthic community composition around the atoll (detailed  
568 in Supplementary Methods). We extracted remotely-sensed data for maximum net primary  
productivity and wave energy from the open-source data product Marine Socio-Environmental  
570 Covariates (MSEC (83)) and defined site exposure (i.e., windward versus leeward) based on the  
dominant wind direction (southeasterly (84)).

572

### Field methods

574 To examine how heat stress interacts with chronic local human disturbance, we conducted  
benthic surveys at nineteen forereef sites on the atoll during nine expeditions between 2013 and  
576 2017: four prior to the onset of thermal stress (July 2013, August 2014, January and May 2015),  
three during the El Niño-induced heat stress (July and November 2015, March/April 2016), and  
578 two after the event (November 2016, July 2017). The surveyed reefs at each site are all at 10–12  
m depth on sloping, fringing reefs, with no back reef or significant reef crest formations, and  
580 adjacent sites are all more than 1 km apart (with one exception) (85). On average, we surveyed  
10.4 ± 4.9 sites per expedition, for a total of 94 surveys (table S7); logistical and weather  
582 constraints associated with working in such a remote location prevented surveying all sites in  
each time point (table S7).

584 To survey sites, we photographed the benthos underneath a 1 m<sup>2</sup> gridded quadrat (mean =  
28.1 ± 4.1 quadrats per site) at randomly selected positions adjacent to a sixty meter transect that  
586 had been placed along the 10–12 m isobath (n = 2,637 photos total; table S7). Photographs were

taken with a Canon Powershot digital camera (G15 and G16 models with an Ikelite housing and  
588 wide-angle lens dome) that was white-balanced at depth on each dive. We analyzed all benthic  
photos using CoralNet, an open-source online software for benthic image analysis (86), by  
590 projecting 100 random points onto each image and manually identifying the substrate beneath  
each point (n = 259,359 total) from our custom label set (n = 103 identification tags), which  
592 consisted of coral (table S6) and non-coral animals, algae, bacteria, and abiotic substrates, such  
as sand and sediment. Recognizing that some corals cannot be definitively identified to the  
594 species level by morphology alone, we have identified some corals to the genus level only. For  
each coral taxon, we confirmed that the morphotype was consistent across all sites. We also  
596 included separate labels for bleaching and non-bleaching coral tissue (e.g., ‘bleaching *Porites*’,  
‘*Porites*’), thus allowing us to determine the proportion of points per site in each expedition that  
598 were bleaching for each coral taxon. We quantified each site’s benthic community composition  
in each surveyed time point by dividing the total number of points for each substrate type by the  
600 total number of annotated points from all quadrats (detailed in Supplementary Methods).

Additionally, we tagged and photographed 834 individual coral colonies from seven  
602 species at thirteen of our nineteen monitoring sites (Fig. 1A) and tracked their fate over the  
course of the El Niño event. We selected three common corals as our focal species (*Porites*  
604 *lobata*, *Pocillopora grandis*, *Montipora aequituberculata*) because they were found at all sites  
and include different life history strategies, with the first classified as being a ‘stress-tolerant’  
606 coral, a group that is defined by slow growing, massive species and the capacity to tolerate  
chronically stressful and variable environments, and the latter two considered to be ‘competitive’  
608 corals, a group typified by large, branching and plating species with fast growth and the capacity  
to dominate communities (19, 87–89) (table S6). We aimed to tag twelve colonies of each of

610 these three species per site. We also tagged up to six colonies per site of each of four less  
common species (*Favites pentagona*, *Dipsastraea* spp. (primarily *D. matthaii*), *Platygyra*  
612 *ryukyuensis*, *Hydnophora microconos*), each of which has a stress-tolerant life history strategy  
(88) (table S6). Tagged coral colonies were located along the same transects as the benthic  
614 photoquadrats. Colonies were first tagged and photographed during the August 2014 expedition,  
prior to the onset of heat stress. For each coral, we photographed the entire colony parallel to the  
616 colony surface with a ruler next to it for scale; macro shots were taken of the colony surface to  
aid in identification where necessary. In each subsequent expedition (except November 2015),  
618 we re-photographed each colony that could be relocated and also tagged and photographed  
additional colonies.

620 We assigned each coral colony a bleaching status for each time point in which it was  
photographed using the following visual criteria: 1) no bleaching or paling; 2) some light  
622 bleaching but less than 5 cm across the largest patch and less than 50% of colony pale; 3)  
bleaching in patches >5 cm or more than 50% of colony pale; 4) severe or complete bleaching  
624 (>80%) or the entire colony pale. For binomial treatments of bleaching, we considered categories  
1 and 2 to be “healthy” and categories 3 and 4 to be “bleached”. Thus, colonies were assigned to  
626 “bleached” if they had at least one patch of their surface that was bleached and greater than 5 cm  
across or if more than 50% of the surface of the coral was faded.

628 In total, we were able to determine the survivorship status of 474 of the tagged colonies  
(average of  $n = 36.5$  colonies per site; range = 9 to 56; Table S7); the remaining colonies could  
630 not be relocated after the heatwave. Corals were recorded as surviving the heatwave if they were  
found alive at any time point following the event, and as not surviving it if they were found dead  
632 upon first inspection post-heatwave. This occurred at the end of the heatwave (March/April

2016) for most colonies, and in the two subsequent expeditions for corals located at sites that we  
634 had either been unable to fully sample (i.e., one dive instead of two to three to search for all  
corals) or sample at all (due to unfavorable weather conditions or logistical constraints) in  
636 March/April 2016.

### 638 **Temperature and thermal stress**

We quantified temperature on Kiritimati during the 2015–2016 El Niño event using both  
640 remotely sensed data extracted from NOAA’s Coral Temp product (42), as well as high precision  
*in situ* temperature loggers (Sea-Bird Scientific SBE 56;  $\pm 0.001^\circ\text{C}$  precision). *In situ* loggers  
642 were deployed at sites around the atoll (minimum of one logger deployed per disturbance level;  $n$   
= 17 sites, including  $n = 12$  of the sites surveyed in this manuscript) between 2011 and 2016, all  
644 at  $\sim 10$  m depth (range 8–12 m) on the forereef (fig. S1). For both data sources, we quantified  
temperature for all available sites around the atoll as in Claar et al. (90) and averaged across sites  
646 to produce a measure of island-wide temperature.

To assess the potential influence of baseline temperatures on coral communities around  
648 the atoll prior to the 2015–2016 El Niño, we also extracted the maximum monthly mean  
temperature (91) for each site from NOAA Coral Reef Watch’s (CRW) monthly mean sea  
650 surface temperature climatology, which are produced at a 5-km spatial resolution  
(<ftp://ftp.star.nesdis.noaa.gov/pub/sod/mecb/crw/data/5km/v3.1/climatology/nc/>).

652 We quantified thermal stress on Kiritimati during the 2015–2016 El Niño as degree  
heating weeks (DHW;  $^\circ\text{C}$ -weeks), the metric most commonly employed to assess coral bleaching  
654 risk. Corals are sensitive to temperatures more than  $1^\circ\text{C}$  above their long-term maximum  
monthly mean (MMM) sea surface temperature (SST), known as the bleaching threshold. DHW

656 is a measure of accumulated thermal stress, which is defined as the rolling sum of temperatures  
above the bleaching threshold during the preceding twelve weeks (92, 93). Significant coral  
658 bleaching is expected to occur once cumulative thermal stress has exceeded 4 °C-weeks (NOAA  
CRW Bleaching Alert Level 1), with widespread bleaching and some mortality typically  
660 expected at > 8 °C-weeks (NOAA CRW Bleaching Alert Level 2) (43).

DHW values for Kiritimati were extracted from the U.S. NOAA CRW's 5-km DHW  
662 product (NOAA CRW Daily Global 5-km Satellite Coral Bleaching Heat Stress Degree Heating  
Week Version 3.1) (93) for January 2011–December 2016 (90), for each of the nineteen study  
664 sites, and used to calculate an island-wide mean (Table S3). Comparisons of these satellite-  
derived thermal stress values to *in situ* estimates in a previous study (90) yielded consistent  
666 results. Herein, we present the satellite-derived DHW data and analyses employing these data for  
comparability with other coral bleaching studies. Additionally, to compare the thermal stress  
668 experienced on Kiritimati during this heatwave to earlier events, we extracted DHW values (as  
above) from 1985 to 2018 (Fig. S4).

670

### Statistical analyses

672 Analyses were conducted in R 4.0.4. interfaced with Rstudio 1.4.1106.

We fit a series of generalized linear mixed-effects models (GLMMs) with the benthic  
674 community composition data, in which the overall proportion of hard coral cover (i.e., the  
response variable) was modelled with a beta error distribution and a logit link, using the  
676 *glmmTMB* package (94). First, to examine influences on coral cover prior to the 2015–2016 El  
Niño, we modelled overall hard coral cover as a function of chronic local disturbance  
678 (continuous) and three environmental variables: maximum net primary productivity (NPP; mg C

m<sup>-2</sup> day<sup>-1</sup>), sea surface temperature, and site exposure (windward vs. sheltered). Second, to assess  
680 the influence of prolonged heat stress on coral communities, and if chronic local human  
disturbance modulates heat stress impacts, we modelled overall hard coral cover as a function of  
682 heatwave period (before vs. after), maximum heat stress experienced during the El Niño (i.e.,  
maximum site-level DHW), chronic local disturbance, and a two-way interaction between  
684 heatwave period and disturbance. Third, we examined if the impact of the heatwave on coral  
cover was modulated by the pre-El Niño coral community composition. To do so, we defined a  
686 ‘dominant coral life history’ covariate for each site by classifying each coral species according to  
its life history strategy (following (88), table S6), then classifying each site as ‘stress-tolerant  
688 dominated’ (if > 60% of the corals at that site had this life history strategy), ‘competitive  
dominated’ (if > 60% of the corals at that site had this life history strategy), or ‘mixed’ (if there  
690 was no dominant life history type). We included this covariate as a fixed effect in a model of  
overall hard coral cover, with a two-way interaction between it and heatwave period (before vs.  
692 after); maximum site-level DHW was also included as a fixed effect. Fourth, to directly quantify  
the impacts of heat stress on corals with distinct life history types, we fit separate models for the  
694 cover of stress-tolerant corals and the cover of competitive corals. In these models, coral cover  
was modelled as a function of heatwave period, chronic local disturbance (including the two-way  
696 interaction with heatwave period), and maximum site-level DHW. We fit two different versions  
of these life history models: one where the cover of each life history type was calculated as the  
698 proportion of overall benthic cover and one where it was calculated as the proportion of total  
hard coral cover. In all models, continuous explanatory variables were standardized using the  
700 ‘rescale’ function in the *arm* package, and site was included as a random effect to account for the  
non-independence of data collected at the same site over time. Expedition was also included as a



702 random effect in all models (with site and expedition modelled as crossed random effects),  
except for the competitive coral cover model, as its inclusion in this model led to convergence  
704 issues. To test the sensitivity of the competitive model to this change, we ran all the other models  
without expedition as well and found that this did not result in any significant changes to the  
706 model results. See Supplementary Methods for additional details.

We also employed a multivariate approach to examine differences in hard coral  
708 community composition across the disturbance gradient, both before and after the heatwave, by  
conducting multivariate ordinations and statistical analyses using the *vegan* package (95). A site-  
710 by-species matrix was created for the entire hard coral community using measures of percent  
cover. We performed multivariate ordinations (principal coordinates analysis; PCoA) using the  
712 ‘betadisper’ function to visualize differences in the coral communities amongst the three most  
disparate (very low, medium, very high) levels of local human disturbance and across heat stress  
714 periods. We then tested for significant differences in coral community structure using  
permutational multivariate analysis of variance tests (PERMANOVA; ‘adonis’ function) with  
716 999 permutations and Bray–Curtis distances. Heat stress, human disturbance, and their  
interaction were included as fixed effects, while site was incorporated as a blocking factor using  
718 the strata term in ‘adonis’.

We used our longitudinal tagged coral dataset to directly examine the impact of  
720 prolonged heat stress on the survival of individual coral colonies. In all cases, coral survival was  
modelled using generalized linear models (GLMs), with a binomial distribution and logit link, in  
722 the *stats* package. We modelled the survival of stress-tolerant and competitive corals separately,  
with coral species, chronic local disturbance, maximum site-level DHW, maximum net primary  
724 productivity, and site exposure (windward vs. sheltered) included as fixed effects in each model,

plus a two-way interaction between coral species and local disturbance. We present the results of  
726 these models, and visualizations of these models without species included (to show the  
relationship between coral survival of each life history strategy and disturbance; Fig. 5, B, and  
728 C), as well as an overall model (all species, with a species-by-disturbance interaction, to show  
the relationship between survival of all seven coral species with disturbance; Fig. 5F). To  
730 visualize the overall pattern, we also modelled and displayed all corals together without life  
history or species in the model (Fig. 5A), but with the other covariates. All continuous  
732 explanatory variables were standardized using the ‘rescale’ function in the *arm* package. For  
each of these model subsets (e.g. overall model, stress-tolerant model, competitive model, etc.),  
734 we ran models with all possible combinations of variables. We then used AIC to determine the  
top model for each model subset. In all cases, the model with disturbance (and the two-way life  
736 history or species interactions, where included) but without any of the environmental variables  
had the lowest AIC. Additionally, in all cases, for the models within 4  $\Delta$ AIC of the model with  
738 the lowest AIC, disturbance (and the two-way life history or species interactions, where  
included) was significant, but other variables were not. We initially also included ‘site’ as a  
740 random effect, but in all cases this worsened the model fit.

Finally, to assess if bleaching is an accurate metric of heatwave outcomes for corals, we  
742 a) used the benthic photoquadrat data to test if the extent of bleaching at a site early in the  
heatwave (July 2015) was a predictor of the final overall coral cover loss at each site, and b) used  
744 the tagged coral colony data to test if corals that exhibited bleaching early in the heatwave had  
lower survival through the event. First, using the photoquadrat data, we calculated the proportion  
746 of hard corals that were bleached in July 2015 at each site ( $n = 13$  sites, as not all sites were  
surveyed in July 2015; fig. S7) as well as the loss of coral cover. The proportion of coral cover

748 lost at each site was calculated by averaging coral cover values across field seasons within each  
heatwave period, then using the following formula:

750 (1) Loss of coral cover = 
$$\frac{\text{Mean coral cover 'before'} - \text{Mean coral cover 'after'}}{\text{Mean coral cover 'before'}}$$

We modelled the loss of coral cover as a function of three continuous variables—proportion of  
752 bleached corals, local disturbance, and maximum heat stress (°C-weeks)—using GLMMs with a  
beta error distribution and logit link. Separate models were fit for the overall hard coral  
754 community and for both competitive and stress-tolerant corals. Next, using the tagged coral  
colony data, we modelled coral survival using GLMs with a binomial distribution and a logit  
756 link. Bleaching status, coral species, disturbance, and exposure were included as fixed effects,  
along with a two-way interaction between coral species and bleaching status. We first treated  
758 bleaching as a binary state (as detailed above and reported in the results) and tested the  
sensitivity of our results to this assumption by also modelling the four different bleaching  
760 categories (see Supplementary Materials). We conducted all of these models both for the overall  
tagged coral dataset, and then for the stress-tolerant and competitive coral species separately.  
762 Bleaching results did not differ across any of these different model forms.

764

766 **References**

- 768 1. T. L. Frölicher, E. M. Fischer, N. Gruber, Marine heatwaves under global warming. *Nature*.  
560, 360–364 (2018).
- 770 2. IPCC, “IPCC Special Report on the Ocean and Cryosphere in a Changing Climate” (2019).
- 772 3. E. C. J. Oliver, M. T. Burrows, M. G. Donat, A. Sen Gupta, L. V. Alexander, S. E. Perkins-  
Kirkpatrick, J. A. Benthuyesen, A. J. Hobday, N. J. Holbrook, P. J. Moore, M. S. Thomsen, T.  
774 Wernberg, D. A. Smale, Projected marine heatwaves in the 21st century and the potential for  
ecological impact. *Front. Mar. Sci.* **6**, 734 (2019).
- 776 4. B. E. Brown, Coral bleaching: causes and consequences. *Coral Reefs*. **16**, S129–S138  
(1997).
- 778 5. A. C. Baker, P. W. Glynn, B. Riegl, Climate change and coral reef bleaching: an ecological  
assessment of long-term impacts, recovery trends and future outlook. *Estuar. Coast. Shelf  
Sci.* **80**, 435–471 (2008).
- 780 6. T. P. Hughes, Climate change, human Impacts, and the resilience of coral reefs. *Science*.  
**301**, 929–933 (2003).
- 782 7. S. D. Donner, W. J. Skirving, C. M. Little, M. Oppenheimer, O. Hoegh-Guldberg, Global  
assessment of coral bleaching and required rates of adaptation under climate change. *Global  
784 Change Biol.* **11**, 2251–2265 (2005).
- 786 8. O. Hoegh-Guldberg, P. J. Mumby, A. J. Hooten, R. S. Steneck, P. Greenfield, E. Gomez, C.  
D. Harvell, P. F. Sale, A. J. Edwards, K. Caldeira, N. Knowlton, C. M. Eakin, R. Iglesias-  
Prieto, N. Muthiga, R. H. Bradbury, A. Dubi, M. E. Hatziolos, Coral reefs under rapid  
788 climate change and ocean acidification. *Science*. **318**, 1737–1742 (2007).
- 790 9. E. C. J. Oliver, M. G. Donat, M. T. Burrows, P. J. Moore, D. A. Smale, L. V. Alexander, J.  
A. Benthuyesen, M. Feng, A. Sen Gupta, A. J. Hobday, N. J. Holbrook, S. E. Perkins-  
Kirkpatrick, H. A. Scannell, S. C. Straub, T. Wernberg, Longer and more frequent marine  
792 heatwaves over the past century. *Nat Commun.* **9**, 1324 (2018).
- 794 10. S. F. Heron, J. A. Maynard, R. van Hooidonk, C. M. Eakin, Warming trends and bleaching  
stress of the world’s coral reefs 1985–2012. *Sci Rep.* **6**, 38402 (2016).
- 796 11. C. M. Eakin, H. P. A. Sweatman, R. E. Brainard, The 2014–2017 global-scale coral  
bleaching event: insights and impacts. *Coral Reefs*. **38**, 539–545 (2019).
- 798 12. R. van Hooidonk, J. Maynard, J. Tanelander, J. Gove, G. Ahmadi, L. Raymundo, G.  
Williams, S. F. Heron, S. Planes, Local-scale projections of coral reef futures and  
implications of the Paris Agreement. *Sci Rep.* **6**, 39666 (2016).
- 800 13. L. Burke, K. Reytar, M. Spalding, A. Perry, “Reefs at risk revisited” (World Resources  
Institute, 2011), pp. 1–130.

- 802 14. C. M. Crain, K. Kroeker, B. S. Halpern, Interactive and cumulative effects of multiple  
human stressors in marine systems. *Ecol. Lett.* **11**, 1304–1315 (2008).
- 804 15. M. Ateweberhan, D. A. Feary, S. Keshavmurthy, A. Chen, M. H. Schleyer, C. R. C.  
806 Sheppard, Climate change impacts on coral reefs: synergies with local effects, possibilities  
for acclimation, and management implications. *Mar. Pollut. Bull.* **74**, 526–539 (2013).
- 808 16. J. E. Carilli, R. D. Norris, B. A. Black, S. M. Walsh, M. McField, Local stressors reduce  
coral resilience to bleaching. *PLoS ONE*. **4**, e6324 (2009).
- 810 17. J. E. Carilli, R. D. Norris, B. Black, S. M. Walsh, M. McField, Century-scale records of coral  
growth rates indicate that local stressors reduce coral thermal tolerance threshold. *Glob  
Change Biol.* **16**, 1247–1257 (2010).
- 812 18. J. F. Bruno, I. M. Côté, L. T. Toth, Climate change, coral loss, and the curious case of the  
814 parrotfish paradigm: why don't marine protected areas improve reef resilience? *Ann. Rev.  
Mar. Sci.* **11**, 307–334 (2019).
- 816 19. E. S. Darling, T. R. McClanahan, I. M. Côté, Life histories predict coral community  
disassembly under multiple stressors. *Glob Change Biol.* **19**, 1930–1940 (2012).
- 818 20. T. P. Hughes, J. T. Kerry, M. Álvarez-Noriega, J. G. Álvarez-Romero, K. D. Anderson, A.  
H. Baird, R. C. Babcock, M. Beger, D. R. Bellwood, R. Berkelmans, T. C. Bridge, I. R.  
820 Butler, M. Byrne, N. E. Cantin, S. Comeau, S. R. Connolly, G. S. Cumming, S. J. Dalton, G.  
Diaz-Pulido, C. M. Eakin, W. F. Figueira, J. P. Gilmour, H. B. Harrison, S. F. Heron, A. S.  
822 Hoey, J.-P. A. Hobbs, M. O. Hoogenboom, E. V. Kennedy, C. Kuo, J. M. Lough, R. J. Lowe,  
G. Liu, M. T. McCulloch, H. A. Malcolm, M. J. McWilliam, J. M. Pandolfi, R. J. Pears, M.  
824 S. Pratchett, V. Schoepf, T. Simpson, W. J. Skirving, B. Sommer, G. Torda, D. R.  
Wachenfeld, B. L. Willis, S. K. Wilson, Global warming and recurrent mass bleaching of  
corals. *Nature*. **543**, 373–377 (2017).
- 826 21. J. M. Pandolfi, Global trajectories of the long-term decline of coral reef ecosystems. *Science*.  
**301**, 955–958 (2003).
- 828 22. T. P. Hughes, M. L. Barnes, D. R. Bellwood, J. E. Cinner, G. S. Cumming, J. B. C. Jackson,  
830 J. Kleypas, I. A. van de Leemput, J. M. Lough, T. H. Morrison, S. R. Palumbi, E. H. van  
Nes, M. Scheffer, Coral reefs in the Anthropocene. *Nature*. **546**, 82–90 (2017).
- 832 23. K. E. Carpenter, M. Abrar, G. Aeby, R. B. Aronson, S. Banks, A. Bruckner, A. Chiriboga, J.  
Cortes, J. C. Delbeek, L. DeVantier, G. J. Edgar, A. J. Edwards, D. Fenner, H. M. Guzman,  
834 B. W. Hoeksema, G. Hodgson, O. Johan, W. Y. Licuanan, S. R. Livingstone, E. R. Lovell, J.  
A. Moore, D. O. Obura, D. Ochavillo, B. A. Polidoro, W. F. Precht, M. C. Quibilan, C.  
836 Reboton, Z. T. Richards, A. D. Rogers, J. Sanciangco, A. Sheppard, C. Sheppard, J. Smith,  
S. Stuart, E. Turak, J. E. N. Veron, C. Wallace, E. Weil, E. Wood, One-third of reef-building  
838 corals face elevated extinction risk from climate change and local impacts. *Science*. **321**,  
560–563 (2008).

- 840 24. C. P. Nadeau, M. C. Urban, J. R. Bridle, Climates past, present, and yet-to-come shape  
climate change vulnerabilities. *Trends Ecol. Evol.* **32**, 786–800 (2017).
- 842 25. D. J. Suggett, D. J. Smith, Coral bleaching patterns are the outcome of complex biological  
and environmental networking. *Glob Change Biol.* **26**, 68–79 (2019).
- 844 26. O. Hoegh-Guldberg, Climate change, coral bleaching and the future of the world’s coral  
reefs. *Mar. Freshwater Res.* **50**, 839–866 (1999).
- 846 27. H. M. Putnam, K. L. Barott, T. D. Ainsworth, R. D. Gates, The vulnerability and resilience  
of reef-building corals. *Current Biology.* **27**, R528–R540 (2017).
- 848 28. H. M. Putnam, M. Stat, X. Pochon, R. D. Gates, Endosymbiotic flexibility associates with  
environmental sensitivity in scleractinian corals. *Proc. R. Soc. B.* **279**, 4352–4361 (2012).
- 850 29. R. Cunning, A. C. Baker, Excess algal symbionts increase the susceptibility of reef corals to  
bleaching. *Nature Clim Change.* **3**, 259–262 (2013).
- 852 30. D. J. Suggett, M. E. Warner, W. Leggat, Symbiotic dinoflagellate functional diversity  
mediates coral survival under ecological crisis. *Trends Ecol. Evol.* **32**, 735–745 (2017).
- 854 31. G. B. Dixon, S. W. Davies, G. A. Aglyamova, E. Meyer, Genomic determinants of coral heat  
tolerance across latitudes. *Science.* **348**, 1460–1462 (2015).
- 856 32. S. R. Palumbi, D. J. Barshis, N. Traylor-Knowles, R. A. Bay, Mechanisms of reef coral  
resistance to future climate change. *Science.* **344**, 895 (2014).
- 858 33. Y. Loya, K. Sakai, K. Yamazato, Y. Nakano, H. Sambali, R. van Woesik, Coral bleaching:  
the winners and the losers. *Ecol. Lett.* **4**, 122–131 (2001).
34. Y. Baskin, Winners and losers in a changing world. *BioScience.* **48**, 788–792 (1998).
- 860 35. R. D. Vinebrooke, K. L. Cottingham, J. Norberg, Marten Scheffer, S. I. Dodson, S. C.  
Maberly, U. Sommer, Impacts of multiple stressors on biodiversity and ecosystem  
862 functioning: the role of species co-tolerance. *Oikos.* **104**, 451–457 (2004).
- 864 36. P. A. Keddy, Assembly and response rules: two goals for predictive community ecology.  
*Journal of Vegetation Science.* **3**, 157–164 (1992).
- 866 37. S. I. Passy, M. Bottin, J. Soininen, H. Hillebrand, Environmental filtering and taxonomic  
relatedness underlie the species richness–evenness relationship. *Hydrobiologia.* **787**, 243–  
253 (2017).
- 868 38. A. G. Grottoli, M. E. Warner, S. J. Levas, M. D. Aschaffenburg, V. Schoepf, M. McGinley,  
J. Baumann, Y. Matsui, The cumulative impact of annual coral bleaching can turn some  
870 coral species winners into losers. *Glob Change Biol.* **20**, 3823–3833 (2014).

- 872 39. I. M. Côté, E. S. Darling, C. J. Brown, Interactions among ecosystem stressors and their  
importance in conservation. *Proc. R. Soc. B.* **283**, 20152592 (2016).
- 874 40. D. C. Claar, J. K. Baum, Timing matters: survey timing during extended heat stress can  
influence perceptions of coral susceptibility to bleaching. *Coral Reefs.* **38**, 559–565 (2019).
- 876 41. M. G. Gleason, Effects of disturbance on coral communities: bleaching in Moorea, French  
Polynesia. *Coral Reefs.* **12**, 193–201 (1993).
- 878 42. E. Maturi, A. Harris, J. Mittaz, J. Sapper, G. Wick, X. Zhu, P. Dash, P. Koner, A new high-  
resolution sea surface temperature blended analysis. *Bull. Am. Meteorol. Soc.* **98**, 1015–1026  
(2017).
- 880 43. G. Liu, S. Heron, C. Eakin, F. Muller-Karger, M. Vega-Rodriguez, L. Guild, J. De La Cour,  
882 E. Geiger, W. Skirving, T. Burgess, A. Strong, A. Harris, E. Maturi, A. Ignatov, J. Sapper, J.  
Li, S. Lynds, Reef-scale thermal stress monitoring of coral ecosystems: new 5-km global  
products from NOAA Coral Reef Watch. *Remote Sensing.* **6**, 11579–11606 (2014).
- 884 44. M. D. Fox, A. L. Carter, C. B. Edwards, Y. Takeshita, M. D. Johnson, V. Petrovic, C. G.  
886 Amir, E. Sala, S. A. Sandin, J. E. Smith, Limited coral mortality following acute thermal  
stress and widespread bleaching on Palmyra Atoll, central Pacific. *Coral Reefs.* **38**, 701–712  
(2019).
- 888 45. B. Vargas-Ángel, B. Huntington, R. E. Brainard, R. Venegas, T. Oliver, H. Barkley, A.  
890 Cohen, El Niño-associated catastrophic coral mortality at Jarvis Island, central Equatorial  
Pacific. *Coral Reefs.* **38**, 731–741 (2019).
- 892 46. H. C. Barkley, A. L. Cohen, N. R. Mollica, R. E. Brainard, H. E. Rivera, T. M. DeCarlo, G.  
P. Lohmann, E. J. Drenkard, A. E. Alpert, C. W. Young, B. Vargas-Ángel, K. C. Lino, T. A.  
894 Oliver, K. R. Pietro, V. H. Luu, Repeat bleaching of a central Pacific coral reef over the past  
six decades (1960–2016). *Commun Biol.* **1**, 177 (2018).
- 896 47. E. A. Dinsdale, O. Pantos, S. Smriga, R. A. Edwards, F. Angly, L. Wegley, M. Hatay, D.  
Hall, E. Brown, M. Haynes, L. Krause, E. Sala, S. A. Sandin, R. V. Thurber, B. L. Willis, F.  
898 Azam, N. Knowlton, F. Rohwer, Microbial ecology of four coral atolls in the Northern Line  
Islands. *PLoS ONE.* **3**, e1584 (2008).
- 900 48. J. M. McDevitt-Irwin, M. Garren, R. McMinds, R. Vega Thurber, J. K. Baum, Variable  
interaction outcomes of local disturbance and El Niño-induced heat stress on coral  
microbiome alpha and beta diversity. *Coral Reefs.* **38**, 331–345 (2019).
- 902 49. M. Garren, L. Raymundo, J. Guest, C. D. Harvell, F. Azam, Resilience of coral-associated  
bacterial communities exposed to fish farm effluent. *PLoS ONE.* **4**, e7319 (2009).
- 904 50. C. Roder, T. Bayer, M. Aranda, M. Kruse, C. R. Voolstra, Microbiome structure of the  
906 fungid coral *C. tenactis echinata* aligns with environmental differences. *Mol Ecol.* **24**,  
3501–3511 (2015).

51. J. R. Zaneveld, D. E. Burkepile, A. A. Shantz, C. E. Pritchard, R. McMinds, J. P. Payet, R. Welsh, A. M. S. Correa, N. P. Lemoine, S. Rosales, C. Fuchs, J. A. Maynard, R. V. Thurber, Overfishing and nutrient pollution interact with temperature to disrupt coral reefs down to microbial scales. *Nat Commun.* **7**, 11833 (2016).
52. D. C. Claar, J. M. McDevitt-Irwin, M. Garren, R. Vega Thurber, R. D. Gates, J. K. Baum, Increased diversity and concordant shifts in community structure of coral-associated Symbiodiniaceae and bacteria subjected to chronic human disturbance. *Mol Ecol.* **29**, 2477–2491 (2020).
53. S. Roitman, T. López-Londoño, F. Joseph Pollock, K. B. Ritchie, C. T. Galindo-Martínez, K. Gómez-Campo, L. A. González-Guerrero, V. Pizarro, M. López-Victoria, R. Iglesias-Prieto, M. Medina, Surviving marginalized reefs: assessing the implications of the microbiome on coral physiology and survivorship. *Coral Reefs.* **39**, 795–807 (2020).
54. M. Stat, R. D. Gates, Clade D *Symbiodinium* in scleractinian corals: a “nugget” of hope, a selfish opportunist, an ominous sign, or all of the above? *J. Mar. Biol.* **2011**, 1–9 (2011).
55. T. F. Cooper, R. Berkelmans, K. E. Ulstrup, S. Weeks, B. Radford, A. M. Jones, J. Doyle, M. Canto, R. A. O’Leary, M. J. H. van Oppen, Environmental factors controlling the distribution of *Symbiodinium* harboured by the coral *Acropora millepora* on the Great Barrier Reef. *PLoS ONE.* **6**, e25536 (2011).
56. E. V. Kennedy, L. Tonk, N. L. Foster, I. Chollett, J.-C. Ortiz, S. Dove, O. Hoegh-Guldberg, P. J. Mumby, J. R. Stevens, *Symbiodinium* biogeography tracks environmental patterns rather than host genetics in a key Caribbean reef-builder, *Orbicella annularis*. *Proc. R. Soc. B.* **283**, 20161938 (2016).
57. D. C. Claar, S. Starko, K. L. Tietjen, H. E. Epstein, R. Cunning, K. M. Cobb, A. C. Baker, R. D. Gates, J. K. Baum, Dynamic symbioses reveal pathways to coral survival through prolonged heatwaves. *Nat Commun.* **11**, 6097 (2020).
58. M. K. Donovan, T. C. Adam, A. A. Shantz, K. E. Speare, K. S. Munsterman, M. M. Rice, R. J. Schmitt, S. J. Holbrook, D. E. Burkepile, Nitrogen pollution interacts with heat stress to increase coral bleaching across the seascape. *Proc. Natl. Acad. Sci. U.S.A.* **117**, 5351–5357 (2020).
59. I. M. Côté, E. S. Darling, Rethinking ecosystem resilience in the face of climate change. *PLoS Biol.* **8**, e1000438 (2010).
60. A. E. Bates, R. S. C. Cooke, M. I. Duncan, G. J. Edgar, J. F. Bruno, L. Benedetti-Cecchi, I. M. Côté, J. S. Lefcheck, M. J. Costello, N. Barrett, T. J. Bird, P. B. Fenberg, R. D. Stuart-Smith, Climate resilience in marine protected areas and the ‘Protection Paradox.’ *Biological Conservation.* **236**, 305–314 (2019).
61. S. E. Cannon, E. Aram, T. Beiateuea, A. Kiareti, M. Peter, S. D. Donner, Coral reefs in the Gilbert Islands of Kiribati: resistance, resilience, and recovery after more than a decade of multiple stressors. *PLoS ONE.* **16**, e0255304 (2021).



- 946 62. E. V. Kennedy, J. Vercelloni, B. P. Neal, Ambariyanto, D. E. P. Bryant, A. Ganase, P.  
Gartrell, K. Brown, C. J. S. Kim, M. Hudatwi, A. Hadi, A. Prabowo, P. Prihatinningsih, S.  
948 Haryanta, K. Markey, S. Green, P. Dalton, S. Lopez-Marcano, A. Rodriguez-Ramirez, M.  
Gonzalez-Rivero, O. Hoegh-Guldberg, Coral reef community changes in Karimunjawa  
950 National Park, Indonesia: assessing the efficacy of management in the face of local and  
global stressors. *JMSE*. **8**, 760 (2020).
- 952 63. J. H. Baumann, L. Z. Zhao, A. C. Stier, J. F. Bruno, Remoteness does not enhance coral reef  
resilience. *Glob Change Biol*. **28**, 417–428 (2021).
- 954 64. O. Hoegh-Guldberg, E. V. Kennedy, H. L. Beyer, C. McClennen, H. P. Possingham,  
Securing a long-term future for coral reefs. *Trends Ecol. Evol.* **33**, 936–944 (2018).
- 956 65. H. L. Beyer, E. V. Kennedy, M. Beger, C. A. Chen, J. E. Cinner, E. S. Darling, C. M. Eakin,  
R. D. Gates, S. F. Heron, N. Knowlton, D. O. Obura, S. R. Palumbi, H. P. Possingham, M.  
Puotinen, R. K. Runtig, W. J. Skirving, M. Spalding, K. A. Wilson, S. Wood, J. E. Veron,  
958 O. Hoegh-Guldberg, Risk-sensitive planning for conserving coral reefs under rapid climate  
change. *Conservation Lett.* **11** (2018), doi:10.1111/conl.12587.
- 960 66. A. Baird, P. Marshall, Mortality, growth and reproduction in scleractinian corals following  
bleaching on the Great Barrier Reef. *Mar. Ecol. Prog. Ser.* **237**, 133–141 (2002).
- 962 67. Masson-Delmotte, V., “IPCC, 2021: Climate Change 2021: The Physical Science Basis.  
Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental  
964 Panel on Climate Change [(eds.)]. Cambridge University Press. In Press. , V., P. Zhai, A.  
Pirani, S.L. Connors, C. Péan, S. Berger, N. Caud, Y. Chen, L. Goldfarb, M.I. Gomis, M.  
966 Huang, K. Leitzell, E. Lonnoy, J.B.R. Matthews, T.K. Maycock, T. Waterfield, O. Yelekçi,  
R. Yu, and B. Zhou.”
- 968 68. T. P. Hughes, K. D. Anderson, S. R. Connolly, S. F. Heron, J. T. Kerry, J. M. Lough, A. H.  
Baird, J. K. Baum, M. L. Berumen, T. C. Bridge, D. C. Claar, C. M. Eakin, J. P. Gilmour, N.  
970 A. J. Graham, H. Harrison, J.-P. A. Hobbs, A. S. Hoey, M. Hoogenboom, R. J. Lowe, M. T.  
McCulloch, J. M. Pandolfi, M. Pratchett, V. Schoepf, G. Torda, S. K. Wilson, Spatial and  
972 temporal patterns of mass bleaching of corals in the Anthropocene. *Science*. **359**, 80–83  
(2018).
- 974 69. N. A. J. Graham, K. L. Nash, J. T. Kool, Coral reef recovery dynamics in a changing world.  
*Coral Reefs*. **30**, 283–294 (2011).
- 976 70. J. P. Gilmour, L. D. Smith, A. J. Heyward, A. H. Baird, M. S. Pratchett, Recovery of an  
isolated coral reef system following severe disturbance. *Science*. **340**, 69–71 (2013).
- 978 71. C. Sheppard, A. Harris, A. Sheppard, Archipelago-wide coral recovery patterns since 1998 in  
the Chagos Archipelago, central Indian Ocean. *Mar. Ecol. Prog. Ser.* **362**, 109–117 (2008).
- 980 72. C. Pisapia, D. Burn, R. Yoosuf, A. Najeeb, K. D. Anderson, M. S. Pratchett, Coral recovery  
in the central Maldives archipelago since the last major mass-bleaching, in 1998. *Sci Rep*. **6**,  
982 34720 (2016).

- 984 73. N. A. J. Graham, S. Jennings, M. A. MacNeil, D. Mouillot, S. K. Wilson, Predicting climate-  
driven regime shifts versus rebound potential in coral reefs. *Nature*. **518**, 94–97 (2015).
- 986 74. J. P. W. Robinson, S. K. Wilson, N. A. J. Graham, Abiotic and biotic controls on coral  
recovery 16 years after mass bleaching. *Coral Reefs*. **38**, 1255–1265 (2019).
- 988 75. S. K. Wilson, J. P. W. Robinson, K. Chong-Seng, J. Robinson, N. A. J. Graham, Boom and  
bust of keystone structure on coral reefs. *Coral Reefs*. **38**, 625–635 (2019).
- 990 76. IPCC, “Summary for Policymakers. In: Global Warming of 1.5°C. An IPCC special report  
on the impacts of global warming of 1.5°C above pre-industrial levels and related global  
992 greenhouse gas emission pathways, in the context of strengthening the global response to the  
threat of climate change, sustainable development, and efforts to eradicate poverty [Masson-  
Delmotte, V., P. Zhai, H.-O. Pörtner, D. Roberts, J. Skea, P.R. Shukla, A. Pirani, W.  
994 Moufouma-Okia, C. Péan, R. Pidcock, S. Connors, J.B.R. Matthews, Y. Chen, X. Zhou, M.I.  
Gomis, E. Lonnoy, T. Maycock, M. Tignor, and T. Waterfield (eds.)]. World Meteorological  
996 Organization, Geneva, Switzerland, 32 pp.” (2018).
77. K. E. Trenberth, The definition of El Niño. *Bull. Am. Meteorol. Soc.* **78**, 7 (1997).
- 998 78. S. L. Wear, R. V. Thurber, Sewage pollution: mitigation is key for coral reef stewardship.  
*Ann. N.Y. Acad. Sci.* **1355**, 15–30 (2015).
- 1000 79. K. E. Fabricius, Effects of terrestrial runoff on the ecology of corals and coral reefs: review  
and synthesis. *Mar. Pollut. Bull.* **50**, 125–146 (2005).
- 1002 80. J. M. T. Magel, S. A. Dimoff, J. K. Baum, Direct and indirect effects of climate change-  
amplified pulse heat stress events on coral reef fish communities. *Ecol Appl.* **30** (2020),  
1004 doi:10.1002/eap.2124.
81. National Statistics Office, “2015 Population and Housing Census” (Ministry of Finance,  
1006 Bairiki, Tarawa, 2016), p. 197.
- 1008 82. M. S. Watson, D. C. Claar, J. K. Baum, Subsistence in isolation: fishing dependence and  
perceptions of change on Kiritimati, the world’s largest atoll. *Ocean & Coastal  
Management*. **123**, 1–8 (2016).
- 1010 83. L. A. Yeager, P. Marchand, D. A. Gill, J. K. Baum, J. M. McPherson, Marine Socio-  
Environmental Covariates: queryable global layers of environmental and anthropogenic  
1012 variables for marine ecosystem studies. *Ecology*. **98**, 1976–1976 (2017).
- 1014 84. C. Bosserelle, S. Reddy, D. Lai, “WACOP wave climate reports. Kiribati, Kiritimati”  
(Secretariat of the Pacific Community, 2015), pp. 1–15.
- 1016 85. S. M. Walsh, Ecosystem-scale effects of nutrients and fishing on coral reefs. *J. Mar. Biol.*  
**2011**, 1–13 (2011).

- 1018 86. O. Beijbom, P. J. Edmunds, C. Roelfsema, J. Smith, D. I. Kline, B. P. Neal, M. J. Dunlap, V.  
Moriarty, T.-Y. Fan, C.-J. Tan, S. Chan, T. Treibitz, A. Gamst, B. G. Mitchell, D. Kriegman,  
1020 Towards automated annotation of benthic survey images: variability of human experts and  
operational modes of automation. *PLoS ONE*. **10**, e0130312 (2015).
- 1022 87. P. G. Rachello-Dolmen, D. F. R. Cleary, Relating coral species traits to environmental  
conditions in the Jakarta Bay/Pulau Seribu reef system, Indonesia. *Estuar. Coast. Shelf Sci.*  
**73**, 816–826 (2007).
- 1024 88. J. S. Madin, M. O. Hoogenboom, S. R. Connolly, E. S. Darling, D. S. Falster, D. Huang, S.  
A. Keith, T. Mizerek, J. M. Pandolfi, H. M. Putnam, A. H. Baird, A trait-based approach to  
1026 advance coral reef science. *Trends Ecol. Evol.* **31**, 419–428 (2016).
- 1028 89. J. B. C. Jackson, T. P. Hughes, Adaptive strategies of coral-reef invertebrates: coral-reef  
environments that are regularly disturbed by storms and by predation often favor the very  
1030 organisms most susceptible to damage by these processes. *American Scientist*. **73**, 265–274  
(1985).
- 1032 90. D. C. Claar, K. M. Cobb, J. K. Baum, In situ and remotely sensed temperature comparisons  
on a Central Pacific atoll. *Coral Reefs*. **38**, 1343–1349 (2019).
- 1034 91. A. E. Strong, C. S. Barrientos, C. Duda, J. Sapper, Improved satellite techniques for  
monitoring coral reef bleaching. *Proceedings 8th International Coral Reef Symposium*. **2**,  
1495–1498 (1997).
- 1036 92. G. Liu, A. E. Strong, W. Skirving, L. F. Arzayus, Overview of NOAA Coral Reef Watch  
Program’s near-real-time satellite global coral bleaching monitoring activities. *Proceedings*  
1038 *of the 10th International Coral Reef Symposium*. **12**, 1783–1793 (2006).
- 1040 93. NOAA, NOAA Coral Reef Watch Daily Global 5-km Satellite Coral Bleaching Sea Surface  
Temperature Product v3.1 (2013), (available at  
<https://coralreefwatch.noaa.gov/product/5km/>).
- 1042 94. M. E. Brooks, K. Kristensen, K. J. van Benthem, A. Magnusson, C. Berg W., A. Nielsen, H.  
Skaug J., M. Mächler, B. Bolker M., glmmTMB balances speed and flexibility among  
1044 packages for zero-inflated generalized linear mixed modeling. *The R Journal*. **9**, 378 (2017).
- 1046 95. J. Oksanen, *Vegan: an introduction to ordination* (2019; [http://cran.r-project.org/  
web/packages/vegan/vignettes/introvegan](http://cran.r-project.org/web/packages/vegan/vignettes/introvegan)).
- 1048 96. S. J. Dollar, Wave stress and coral community structure in Hawaii. *Coral Reefs*. **1**, 71–81  
(1982).
- 1050 97. I. D. Williams, J. K. Baum, A. Heenan, K. M. Hanson, M. O. Nadon, R. E. Brainard, Human,  
Oceanographic and Habitat Drivers of Central and Western Pacific Coral Reef Fish  
Assemblages. *PLoS ONE*. **10**, e0120516 (2015).

- 1052 98. G. J. Williams, J. E. Smith, E. J. Conklin, J. M. Gove, E. Sala, S. A. Sandin, Benthic  
1054 communities at two remote Pacific coral reefs: effects of reef habitat, depth, and wave  
energy gradients on spatial patterns. *PeerJ*. **1**, e81 (2013).
- 1056 99. J. P. W. Robinson, I. D. Williams, L. A. Yeager, J. M. McPherson, J. Clark, T. A. Oliver, J.  
1058 K. Baum, Environmental conditions and herbivore biomass determine coral reef benthic  
community composition: implications for quantitative baselines. *Coral Reefs*. **37**, 1157–1168  
(2018).

1060

## Acknowledgements

1062 We gratefully acknowledge our collaborators and friends on Kiritimati who facilitated this  
1064 research, R. Bebe, P. Tofinga, T. Kirata, T. Alefaio, V. Hnanguie, F. Tiata, J. Teem, and L.  
1066 Teem; L. Szostek, M. Watson, S. McNally, K. Cox, T. Stovel, J. Mortimer, J. Burns, K. Bruce  
for help collecting the field data; N. O'Brien, L. Szostek, R. Hansen, E. Giannantonio and A.  
Kozachuk for assistance with benthic image processing.

1068

### **Funding:**

National Science Foundation (NSF) RAPID grant OCE-1446402 (JKB, KMC)  
1070 Rufford Maurice Laing Foundation (JKB)  
Natural Sciences and Engineering Research Council of Canada (NSERC) Discovery  
1072 Grant (JKB)  
Natural Sciences and Engineering Research Council of Canada (NSERC) EWR Steacie  
1074 Memorial Fellowship (JKB)  
Canadian Foundation for Innovation (CFI) Leaders Opportunity Fund (JKB)  
1076 British Columbia Knowledge Development Fund (JKB)  
University of Victoria (JKB, DCC)  
1078 University of Victoria Centre for Asia-Pacific Initiatives (JKB, DCC)  
David and Lucile Packard Foundation (JKB)  
1080 The Pew Charitable Trusts, Pew Fellowship in Marine Conservation (JKB)  
Natural Sciences and Engineering Research Council of Canada (NSERC) Vanier Canada  
1082 Graduate Scholarship (DCC)  
Natural Sciences and Engineering Research Council of Canada Canada (NSERC)  
1084 Graduate Scholarships (JMTM, DM)  
National Oceanic and Atmospheric Administration (NOAA) Climate and Global Change  
1086 Postdoctoral Fellowship Program, administered by UCAR's Cooperative Programs for  
the Advancement of Earth System Science (CPAESS) award NA18NWS4620043B  
1088 (DCC)  
American Academy of Underwater Sciences (DCC)  
1090 International Society for Reef Studies (DCC)  
National Geographic Young Explorers Grant ((DCC)  
1092 Women Divers Hall of Fame (DCC)  
Sea-Bird Electronics equipment grant (DCC)  
1094 Divers Alert Network (DCC).

- 1096        **Author Contributions:**  
                  Conceptualization: JKB
- 1098        Data collection: JKB, DCC, KLT, JMI, KMC, DGM  
                  Data processing: DGM
- 1100        Data analysis: KLT, JMTM, DCC, JKB  
                  Writing—original draft: JKB
- 1102        Writing—review & editing: JKB, DCC, KLT, JMTM, DGM, KMC, JMI
- 1104        **Competing Interests:** Authors declare that they have no competing interests.
- 1106        **Data and materials availability:** Data reported in this paper are provided on Zenodo;  
                  code to reproduce the analyses and figures is provided on GitHub  
1108        [<https://github.com/baumlab> with repository made public upon after acceptance].