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# Ocean acidification increases the impact of typhoons on algal communities

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<https://www.sciencedirect.com/science/article/abs/pii/S0048969722083735#:~:text=Whilst%20the%20persistence%20of%20macroalgal,species%20with%20low%20resistance%20but>

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## **Ocean acidification increases the impact of typhoons on algal communities**

### Highlights:

- 2 Algal community dynamics studied with three-year monthly surveys at a  
3 CO<sub>2</sub> seep
- 4 •
- 5 Acidification consistently altered community composition across all seasons
- 6 •
- 7 Structurally complex communities shifted to degraded ‘turf’ state with  
8 rising *p*CO<sub>2</sub>
- 9 •
- 10 Acidification-driven community changes were maintained by typhoon  
11 disturbance
- 12 •
- 13 Turf-dominated communities displayed low resistance to typhoons

Ocean acidification alters the stabilizing mechanisms of algal communities against typhoons

14 **ABSTRACT**

15 Long-term environmental change, sudden pulses of extreme perturbation, or a combination of  
16 both can trigger regime shifts by changing the processes and feedbacks which determine  
17 community assembly, structure, and function, altering the state of ecosystems. Our  
18 understanding of the mechanisms that stabilise against regime shifts or lock communities into  
19 altered states is limited, yet also critical to anticipating future states, preventing regime shifts,  
20 and reversing unwanted state change. Ocean acidification contributes to the restructuring and  
21 simplification of algal systems, however the mechanisms through which this occurs and  
22 whether additional drivers are involved requires further study. Using monthly surveys over  
23 three years at a shallow-water volcanic seep we examined how the composition of algal  
24 communities change both seasonally and following periods of significant physical disturbance  
25 by typhoons at three levels of ocean acidification (equivalent to means of contemporary ~350  
26 and future ~500 and 900  $\mu\text{atm } p\text{CO}_2$ ). Consistent with most temperate  $\text{CO}_2$  seeps around the  
27 world, sites exposed to acidification were increasingly monopolised by structurally simple,  
28 fast-growing turf algae, and were clearly different to structurally complex macrophyte-  
29 dominated reference sites. The distinct contemporary and acidified community states were  
30 stabilised and maintained at their respective sites by different mechanisms following seasonal  
31 typhoon disturbance. Contemporary macroalgal-dominated sites were resistant to typhoon  
32 damage, recovering to the same community composition and pre-disturbance levels of algal  
33 cover and structural complexity. In contrast, significant losses of algal biomass represented a  
34 near total ecosystem reset by typhoons for the turf-dominated communities in the elevated  
35  $p\text{CO}_2$  sites (i.e. negligible resistance). A combination of disturbance and subsequent turf, but  
36 not macrophyte, recovery maintained the same structurally devoid state between years  
37 (elevated  $\text{CO}_2$  levels promote turf growth following algal removal, inhibiting macroalgal  
38 recruitment). Thus, ocean acidification may promote shifts in algal systems towards degraded

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39 ecosystem states, and short-term disturbances which reset successional trajectories may 'lock-  
40 in' these alternative states of low structural and functional diversity.

41 **1 INTRODUCTION**

42 Long-term exposure to gradual environmental change, short periods of significant perturbation,  
43 or a combination of both, can alter the structure and functioning of biological communities  
44 (Halpern et al. 2008, Petraitis et al. 2009). Ecosystems ‘stable’ against disturbance display  
45 ‘resistance’ (withstanding change in the face of disturbance) and/or ‘recovery’ (returning to the  
46 pre-disturbance state after perturbation), maintaining the same composition, functioning, and  
47 internal regulating feedbacks (Meredith et al. 2018). When systems fail to resist or recover  
48 following disturbance, regime-shifts may occur (Duarte et al. 2009), tipping ecosystems into  
49 new, reconfigured states comprised of different sets of species and controlled by different  
50 processes (Rocha et al. 2015, Wernberg et al. 2016). Regime shifts are concerning as they can  
51 lead to the dominance of fast-growing, early successional species assemblages, leading to large  
52 losses of ecological and economic resources, such as habitat provision, and biodiversity  
53 (Hastings and Wysham 2010). Many drivers of state change have been identified (for a review,  
54 see deYoung et al. 2008), however our understanding of the mechanisms that stabilise alternate  
55 ecosystems against regime shifts or lock communities into altered states is limited, yet critical  
56 to anticipating future states and the challenge of reversing unwanted state change.

57 Changes in the intensity and duration of disturbances have further implications for their  
58 potential to transition communities to a new state and maintain regime shifts, which may  
59 enhance when multiple stressors interact and operate together (Folke et al. 2004). Both ‘press’  
60 (long-term sustained perturbation such as ocean acidification), and ‘pulse’ (short but intense  
61 periods of perturbation such as storm damage) disturbances, can push ecosystems beyond  
62 tipping points, causing regime shifts (e.g. Hughes 1994, Möllmann et al. 2009, Harvey et al.  
63 2021a) with consequences for alternate states that are both difficult to predict and prevent.  
64 Crucially, these effects could exacerbate both if ‘press’ and ‘pulse’ disturbances overlap, and

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65 if the frequency, intensity, or duration disturbances increase (Posey et al. 1996, Peterson 1996,  
66 Wang et al. 2016).

67 Community stability varies as environmental conditions and ecosystem states change,  
68 determined by the positive (self-reinforcing) feedback loops within communities arising from  
69 species interactions and physiological traits that can either resist disturbance or promote  
70 recovery after perturbation (Folke et al. 2004, Connell and Ghedini 2015, Nimmo et al. 2015).

71 Ocean acidification, a global ‘press’ disturbance shifting carbonate chemistry conditions as  
72 increased atmospheric CO<sub>2</sub> is drawn down by the ocean, is projected to simplify coastal  
73 ecosystems due to losses in habitat, structural complexity, and biodiversity (Kroeker et al.  
74 2011, Vizzini et al. 2017, Agostini et al. 2018). This ecosystem reorganisation arises due to the  
75 unequal impact that ocean acidification has on marine organisms (Connell et al. 2018), acting  
76 as both a resource for some primary producers (Koch et al. 2013, Cornwall et al. 2017), and a  
77 physiological stressor for other organisms, such as marine calcifiers (Harvey et al. 2018,  
78 Agostini et al. 2021b). By promoting the loss of certain functional groups and restructuring  
79 community composition, ocean acidification might reduce the ability of marine communities  
80 to absorb disturbances and remain unchanged, reducing their stability (Folke et al. 2004).

81 To capture the complexity of natural systems and investigate the long-term consequences of  
82 ocean acidification at the community-level, an increasing number of studies have used marine  
83 CO<sub>2</sub> seeps as natural analogues of future conditions (Hall-Spencer et al. 2008, Milazzo et al.  
84 2014, Agostini et al. 2018, Connell et al. 2018, Foo et al. 2018). Some coastal volcanoes cause  
85 CO<sub>2</sub> to bubble through the seabed, creating localised gradients of acidification. These offer  
86 insights into the long-term consequences of ocean acidification on ecosystems by utilising  
87 communities that are naturally assembled, complex, and shaped by species interactions (Hall-  
88 Spencer and Harvey 2019). Studies at CO<sub>2</sub> seeps show that ocean acidification increases the

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89 probability of regime shifts in many coastal ecosystems with the large-scale loss of complex  
90 habitat-forming species (e.g. kelp forests, corals) and more homogenous algal dominance  
91 (Enochs et al. 2015, Connell et al. 2018, Harvey et al. 2021a). The degradation of community  
92 stability is often associated with shifts to lower baselines of diversity and complexity (Allison  
93 2004, Hughes and Stachowicz 2004). Simplified communities may also be more susceptible to  
94 additional perturbation, including short-term ‘pulse’ disturbance events such as storms. As  
95 such, acidification-driven changes in species interactions, composition, and community  
96 dynamics, by indirectly altering responses to additional stressors, may promote and entrench  
97 regime-shifts, maintaining conditions which enable alternate, opportunistic assemblages to  
98 dominate.

99 Typhoons, tropical cyclones with sustained winds that exceed  $33 \text{ m s}^{-1}$  (Japan Meteorological  
100 Agency 2021), are powerful low-pressure weather systems that can be both disruptive and  
101 dangerous to marine organisms and human populations (Zhan et al. 2012). Prevalent  
102 throughout the Northern and Western Pacific, typhoons typically form in the tropics before  
103 tracking poleward (Zhan et al. 2012, Hsu et al. 2013). Typhoons are highly seasonal, peaking  
104 in frequency during late summer to early autumn, therefore likely contribute to annual variation  
105 within marine communities (which for algal assemblages remains understudied). Typhoons  
106 represent a major physical ‘pulse’ disturbance for coastal ecosystems, generating large waves  
107 that can severely damage structurally important habitats such as corals (Done 1992, Harmelin-  
108 Vivien 1994), mangroves (Diele et al. 2013), seagrasses (Wilson et al. 2020), and macroalgae  
109 (Vroom et al. 2005, Hall-Spencer and Harvey 2019, Cattano et al. 2020). Typhoons also alter  
110 the community structure and functioning of species living in association with these habitats  
111 (Gardner et al. 2005, Teixidó et al. 2013), such as fish (Cattano et al. 2020) and invertebrates  
112 (Harmelin-Vivien 1994, Diele et al. 2013) amongst seaweeds (Pocklington et al. 2018,  
113 Wernberg et al. 2020). The amount of damage caused is determined by the frequency and

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114 magnitude of typhoons (Lee et al. 2012, Hsu et al. 2013) and the stability of the marine  
115 community against physical disturbance. Rising sea surface temperatures in the western North  
116 Pacific over the past 30 years have meant that the average latitude at which typhoons reach  
117 their peak intensity has increased (Kossin et al. 2016). The impacts of strong typhoons on  
118 temperate coastal communities have and will continue to become increasingly common,  
119 exacerbated by climate heating (Webster et al. 2005, Mann and Emanuel 2006, Lee et al. 2012,  
120 Murakami et al. 2012, Zhan et al. 2012).

121 Prior to this study we observed that algal community coverage and composition varied  
122 seasonally and was greatly affected following typhoon disturbance, however this response  
123 appeared to differ between the ambient and elevated  $p\text{CO}_2$  areas of our study site (Figure 1).  
124 In this study, we test this observation and investigate algal communities along a natural  $p\text{CO}_2$   
125 gradient in Japan to assess how their composition varies with increasing  $p\text{CO}_2$ . We also  
126 investigate the seasonality of algal communities to understand patterns of compositional  
127 change and how this is altered by ocean acidification. We then examine how ocean  
128 acidification-driven changes in community structure mediates their stability (resistance and  
129 recovery) against seasonal ‘pulses’ of typhoon disturbance. By conducting the study over three  
130 years, we were able to test the responses (resistance and recovery) of algal communities to  
131 several typhoon seasons. This temporal replication provides new insights into the future impact  
132 of typhoons on acidified oceans.

## 133 2 MATERIALS AND METHODS

### 134 2.1 *Study site and environmental context*

135 Algal community assessments were carried out in three locations along a  $p\text{CO}_2$  gradient around  
136 Shikine Island, Japan (34°19'9" N, 139° 12'18" E) from September 2016 to December 2019.  
137 These three locations were 1) a reference  $p\text{CO}_2$  area outside the influence of the  $\text{CO}_2$  seep, 2)



138 a ‘near-future’ elevated  $p\text{CO}_2$  area, and 3) an ‘end-of-the-century’ elevated  $p\text{CO}_2$  area  
139 (hereafter referred to as ‘350  $\mu\text{atm}$ ’, ‘500  $\mu\text{atm}$ ’ and ‘900  $\mu\text{atm}$ ’, respectively). The acidified  
140 sites offer potential for space-for-time analyses, serving as analogues for future conditions  
141 under projections of changing ocean pH (RCP 8.5 scenario, IPCC 2013). The Shikine-jima  
142 seep site has been surveyed since 2014, and its carbonate chemistry and biology are well  
143 characterised (Agostini et al. 2015, 2018, 2021a, Harvey et al. 2018, 2019, 2021b, 2021a,  
144 Witkowski et al. 2019, Kerfahi et al. 2020, Cattano et al. 2020). Located at  $34^\circ$  north, Shikine  
145 Island is within the temperate-subtropical biogeographic boundary zone (See Figure S1). Here,  
146 the coastal communities on rocky reef habitats are dominated by large stands of macroalgae  
147 (Harvey et al. 2021b). The  $p\text{CO}_2$  conditions are temporally stable over the long-term, while  
148 still following natural diurnal and seasonal variation, and are not confounded by differences in  
149 temperature, salinity, dissolved oxygen, total alkalinity, nutrients or depth relative to reference  
150 sites (Agostini et al. 2015, 2018, Harvey et al. 2019, 2021b, Agostini et al. 2021a). The ‘350  
151  $\mu\text{atm}$ ’ location had a mean  $\text{pH}_T$  of  $8.137 \pm 0.056$  (SD), the ‘500  $\mu\text{atm}$ ’ location area had a mean  
152  $\text{pH}_T$  of  $7.983 \pm 0.119$  (SD), and the ‘900  $\mu\text{atm}$ ’ location had a mean  $\text{pH}_T$  of  $7.781 \pm 0.105$  (SD).  
153 The mean carbonate chemistry of the three locations is presented in Table 1. A full description  
154 of the locations is provided in the supplementary material (Figure S1). The area of Shikine  
155 Island, is exposed to frequent and significant disturbance from tropical cyclones (including  
156 typhoons), which peak in frequency during the late summer and early autumn (August-  
157 September) (Yumoto and Matsuura 2001). For specific information regarding typhoon  
158 characteristics and dates during the study period, see Table S1.

## 159 **2.2 Experimental design and analysis**

### 160 **2.2.1 Data collection**

161 To determine how ocean acidification influences the composition and structure of algal  
162 communities over time, eight permanent quadrats (50 x 50 cm) were marked using anchor bolts

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163 (8.5 mm width, 70 mm length) at each of the three locations ('350  $\mu\text{atm}$ ', '500  $\mu\text{atm}$ ' and '900  
164  $\mu\text{atm}$ '). Quadrats within these locations were deployed haphazardly over a *ca.* 400 m<sup>2</sup> area with  
165 at least 3 m between them, fixed to upward-facing substrata. As algae were the focus of this  
166 study, random stratified sampling was used to prevent the inclusion of coral within quadrats.  
167 Individual quadrats at each location were photographed (Tough TG-5, Olympus, Japan)  
168 monthly (with four exceptions when poor conditions prevented access) a total of 36 times over  
169 a period of three years (September 2016 – December 2019) for community assessment.

### 170 2.2.2 *Community Analysis*

171 Following methods used by Harvey *et al.* (2021b), algal community composition was assessed  
172 using the ImageJ Fiji processing package. An 8 x 8 grid of points ( $n = 64$ ) was superimposed  
173 onto each of the photoquadrats, before the abundance of the algal functional group under each  
174 point was identified and recorded. Functional groups were assigned following descriptions  
175 provided by Steneck and Dethier (1994), sorting algal groups based on their morphology,  
176 thallus size and complexity: filamentous algae, foliose algae, corticated foliose algae,  
177 corticated macrophytes, turf algae, microalgae, leathery macrophytes, articulated calcareous  
178 algae, and crustose coralline algae (CCA). For a list of the dominant species and associated  
179 functional groups at each location, refer to the supplementary material (Table S2). The  
180 complexity of the algal community within each quadrat was also determined following Steneck  
181 and Dethier (1994), whereby ranks (0-5) assigned to the biogenic habitat complexity provided  
182 by each functional group were combined with their relative abundance within each of the  
183 communities that they occurred. The total structural complexity was calculated using the  
184 following ranking categories: other = 0 (ie. macroinvertebrates), bare rock = 0, microalgae = 1,  
185 turf = 1, filamentous algae = 2, foliose algae = 3, CCA = 3, corticated foliose algae = 3.5,  
186 articulated calcareous algae = 4, corticated macrophytes = 4, and leathery macrophytes = 5. To  
187 calculate overall community complexity, the complexity value associated with the group

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188 represented under each superimposed point were summed (for example, for a community  
189 consisting entirely of filamentous algae:  $64 \times 2 = 128$ ). Complexity values were then  
190 standardised between 0 and 1 (dividing total quadrat score by the maximum potential score of  
191 320).

### 192 2.2.3 *Algal community stability*

193 Changes in community percentage cover and complexity were assessed between different  
194 stages of the typhoon season hereby referred to as ‘Before’, ‘After’, and ‘Recovery’  
195 respectively. For all  $p\text{CO}_2$  levels, communities possessed their highest level of algal coverage  
196 and structural complexity during the ‘Before’ period (April-June) prior to the peak typhoon  
197 season, facilitated by summer growth and low-levels of disturbance. The ‘After’ period  
198 (October-December) refers to the months following the peak typhoon season when typhoons  
199 had reduced communities to low levels of algal cover and structural complexity. A ‘Recovery’  
200 period (January-March) coincided with the start of the spring algal bloom, during which the  
201 algae began to grow following disturbance.

### 202 2.3 *Statistical Analysis*

203 Statistical analyses were conducted using R (version 4.04; R Core Team, 2021), with the  
204 ‘vegan’ (Oksanen et al., 2019) and ‘lme4’ (Bates et al. 2015) packages. The ‘ggplot2’  
205 (Wickham, 2016) and ‘ggpubr’ (Kassambara, 2019) packages were used for figure production.  
206 For each of the analyses performed, the package and specific function used in R are listed  
207 below as ‘package::function’.

208 Differences in community composition (based on the relative percentage cover of different  
209 functional groups) between locations (three levels: (‘350  $\mu\text{atm}$ ’, ‘500  $\mu\text{atm}$ ’ and ‘900  $\mu\text{atm}$ ’)  
210 were visualised using principal component analysis (PCA; ggord::biplot). The significance of  
211 these differences were then determined using one-way and post-hoc pairwise permutational

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212 analysis of variance (PERMANOVA) comparisons based on Bray–Curtis dissimilarity  
213 (vegan::vegdist and vegan::adonis).

214 To test for differences in the responses of both the percentage cover and structural complexity  
215 of algal communities exposed to different levels of typhoon disturbance and  $p\text{CO}_2$ , general  
216 linear mixed effect models (GLMM) were made, with ‘Timing’ (three levels: ‘Before’, ‘After’,  
217 and ‘Recovery’) and ‘Location’ (three levels: (‘350  $\mu\text{atm}$ ’, ‘500  $\mu\text{atm}$ ’ and ‘900  $\mu\text{atm}$ ’) as fixed  
218 factors, and ‘Quadrat’, ‘Month’, and ‘Year’ as nested random effects (lme4::lmer and  
219 emmeans::pairwise). The typhoon period itself was excluded from these analyses as changes  
220 in community composition is confounded by the exact timing, strength, and number of storms  
221 in relation to sampling, reducing the accuracy of interannual comparisons. The same models  
222 were also used to test how differences in algal functional group abundance at different times  
223 (relative to the peak typhoon season) explained these patterns of community percentage cover  
224 and complexity change. By assessing how communities respond following typhoon  
225 disturbance, we could assess whether mechanisms of resistance (low immediate impact of  
226 disturbance), resilience (rapid return to pre-disturbance states), or both were controlling  
227 community dynamics.

228

## 229 **3 RESULTS**

### 230 ***3.1 Community differences between $p\text{CO}_2$ conditions and seasons***

231 For all three locations (‘350  $\mu\text{atm}$ ’, ‘500  $\mu\text{atm}$ ’ and ‘900  $\mu\text{atm}$ ’), the percentage cover and  
232 community composition of the algal communities showed clear patterns within and between  
233 years (Figure 2). High algal coverage was observed during the ‘pre-typhoon’ spring and  
234 summer months (around April to June), whereas the occurrence of bare rock increased in the

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235 autumn to winter months (around September to December) following the typhoon season when  
236 physical disturbance was greatest (Figure 2).

237 Overall community composition was clearly separated by 'Location', associated with changes  
238 in  $p\text{CO}_2$  (PERMANOVA: Location,  $F_{2, 858} = 63.61$ ,  $p < 0.001$ ; Figure 3; Table 2). Community  
239 composition at the 350  $\mu\text{atm}$  location showed clear and consistent differences to both the 500  
240  $\mu\text{atm}$  and 900  $\mu\text{atm}$  locations (Figure 3; Table S3 PERMANOVA *post-hoc*: all  $p < 0.01$ ).  
241 Communities in the 350  $\mu\text{atm}$  location had higher structural complexity, with greater coverage  
242 of corticated macrophytes, foliose algae, and crustose coralline algae, compared to the turf and  
243 bare rock dominated acidified sites (Figure 2). Communities within each  $p\text{CO}_2$  conditions  
244 varied and responded similarly between seasons, however differences were consistently  
245 maintained between  $p\text{CO}_2$  conditions (Figure 2). At the 350  $\mu\text{atm}$  location, the spring and  
246 summer months had extensive growth of species such as *Asparagopsis taxiformis* and *Gelidium*  
247 *elegans* (Figure 2; Table S2). Although typhoons removed significant algal biomass (Figure 1)  
248 macroalgal persistence through the typhoon season, emerging as 'new growth' in winter,  
249 formed the basis of the summer community composition, maintaining a more consistent  
250 structure between seasons (Figure 2; Table S2).

251 At both the 500  $\mu\text{atm}$  and 900  $\mu\text{atm}$  locations, community composition was more variable  
252 (Figures 4 (g-i) and S2). The highly productive spring and summer months saw the rapid  
253 growth of thick turf algal mats, compared to mix of corticated foliose alga (*Zonaria* sp.) and  
254 bare rock present during the autumn and winter months due to the impacts of typhoon  
255 disturbance – ie. the physical removal of turf (Figures 1 and S2). Despite significant differences  
256 between the 500  $\mu\text{atm}$  and 900  $\mu\text{atm}$  locations (Table S3), their community composition had a  
257 higher degree of overlap due to the similarities in their functional groups (structurally simpler  
258 turf algae and corticated foliose algae). For 9 of the 12 months, the composition of communities

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259 at the 500  $\mu\text{atm}$  and 900  $\mu\text{atm}$  locations did not significantly differ, suggesting (given  
260 composition did not remain constant) that they respond to environmental change in similar  
261 ways (Figure 3 PERMANOVA results).

### 262 **3.2 Effects of ocean acidification on community stability**

263 Algal communities under different  $p\text{CO}_2$  conditions responded to typhoon disturbance  
264 differently (Figures 1 and 2). The percentage cover (%) of algal communities was significantly  
265 impacted by ‘Timing’, but not  $p\text{CO}_2$  condition (‘Location’), with a significant interactive effect  
266 demonstrating changes in the response of the community over time (Type III ANOVA:  
267 Timing\*Location,  $X^2 = 46.58$ ,  $p = < 0.001$ ; Table 3 and Figure 4a-c). Algal percentage cover  
268 (%  $\pm$  SD) ‘Before’ ( $93.48 \pm 8.21$ ,  $90.33 \pm 8.58$ , and  $91.27 \pm 9.85$ ) and ‘After’ ( $72.75 \pm 16.50$ ,  
269  $52.93 \pm 19.45$ , and  $49.15 \pm 19.39$ ) typhoons differed significantly at each location (‘350  $\mu\text{atm}$ ’,  
270 ‘500  $\mu\text{atm}$ ’ and ‘900  $\mu\text{atm}$ ’) (Figure 4a-c). The algal coverage of ‘Before’ and ‘Recovery’  
271 ( $89.92 \pm 12.41$ ,  $82.01 \pm 13.76$ , and  $78.00 \pm 18.81$ ) communities (growing in the months  
272 following typhoons) also significantly differed for acidified communities, but not under  
273 reference  $p\text{CO}_2$  conditions (Table S4). The coverage of reference communities remained more  
274 stable over time due to resistance to physical disturbance and algal recovery. Although  
275 typhoons had a lasting effect on the coverage of acidified communities, these faced far more  
276 significant reductions in algal coverage due to typhoon disturbance yet still rapidly recovered,  
277 returning to near pre-disturbance conditions (Figure 4a-c; Table S4).

278 The structural complexity of algal communities was also significantly impacted by both  
279 ‘Timing’ (ANOVA:  $X^2 = 33.30$ ,  $p = < 0.001$ ) and ‘Location’ (ANOVA:  $X^2 = 77.88$ ,  $p = < 0.001$ ;  
280 Table 3 and Figure 4d-f). Structural complexity was significantly reduced in the ‘After’  
281 communities when compared to the ‘Before’ and ‘Recovery’ communities either side of the  
282 peak typhoon season (Figure 4d-f). The structural complexity of these communities did not

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283 significantly differ, indicating a return to pre-disturbance levels within the 6 months following  
284 the typhoon season. Unlike percentage cover, which started at similar levels for each of the  
285 communities prior to disturbance, the mean structural complexity ( $\pm$  SD) of the algal  
286 communities in the pre-typhoon season ('Before') was significantly higher for the Reference  
287  $p\text{CO}_2$  communities ('350  $\mu\text{atm}$ ' =  $0.670 \pm 0.095$ ; '500  $\mu\text{atm}$ ' =  $0.552 \pm 0.182$ ; '900  $\mu\text{atm}$ ' =  
288  $0.471 \pm 0.215$ ; PERMANOVA *post-hoc*: all  $p < 0.001$ ). Despite displaying similar losses in  
289 structural complexity 'After' typhoon disturbance ( $0.552 \pm 0.139$ ,  $0.411 \pm 0.093$ , and  
290  $0.345 \pm 0.076$ ) and a subsequent 'Recovery' of complexity to pre-disturbance levels at each  
291 location ( $0.670 \pm 0.097$ ,  $0.584 \pm 0.101$ , and  $0.487 \pm 0.119$ ), the communities exposed to  
292 increased  $p\text{CO}_2$  remained less complex than the communities found at the reference location  
293 (Figure 4d-f; Table 3, Figure 5; PERMANOVA *post-hoc*: all  $p < 0.001$ ). As they began at low  
294 levels of structural complexity, the increased  $p\text{CO}_2$  communities possessed both less structure  
295 to lose following disturbance, but also lower baselines to subsequently recover to.

296 Acidification-driven changes in community composition, and differences in the response of  
297 individual algal functional groups to typhoon disturbance explained these changes in  
298 community percentage cover and structural complexity (Figure 4g-i; Figure S3; Figure S4).  
299 Typhoons had a large impact on algal community composition, which differed significantly  
300 between all timing pairs, apart from the 'Before' and 'Recovery' communities at '350  $\mu\text{atm}$ '  
301 (Figure 4; Figure S4 PERMANOVA results). Calcareous and filamentous algae did not  
302 significantly change in abundance between  $p\text{CO}_2$  conditions or timings (remaining at low  
303 frequency), whereas fleshy macrophytes had reduced abundance following disturbance at  
304 every location. Bare rock and turf algae, which increased in abundance following typhoon  
305 disturbance, also had a stronger association with typhoon seasonality, underpinning the main  
306 differences between the 'After' communities and those of the 'Before' and 'Recovery' timings  
307 for each location (Figure S4).

308 **4 DISCUSSION**

309 Whilst other environmental factors also influence community assembly, composition, and  
310 dynamics, global research at CO<sub>2</sub> seeps has consistently demonstrated clear ecosystem shifts  
311 towards simplified communities at sites with elevated *p*CO<sub>2</sub> levels (Johnson et al. 2012, Enochs  
312 et al. 2015, Sunday et al. 2017, Connell et al. 2018, Foo et al. 2018, Cattano et al. 2020, Harvey  
313 et al. 2021b, 2021a, Agostini et al. 2021a). These acidified communities not only have reduced  
314 ecological and structural complexity (Figure 1; Figure 4), but also lower biodiversity, raising  
315 concerns about a potential loss of ecosystem services (Hall-Spencer and Harvey 2019). Most  
316 studies investigating the ecological effects of ocean acidification have not taken seasonality  
317 into account, leaving community dynamics between seasons largely unknown (but see Godbold  
318 and Solan 2013, Baggini et al. 2014, Cattano et al. 2020, Harvey et al. 2021b). Here, we found  
319 that algal community structure consistently differed between locations with different *p*CO<sub>2</sub>  
320 levels (Figure 3; Figure S2), and this persisted across seasons despite profound physical  
321 disturbance from typhoons, a seasonal environmental stress which maintained the differences.  
322 In general, increased levels of *p*CO<sub>2</sub> caused consistent reductions in macrophyte cover (Figure  
323 2), leaving communities dominated by turf algae, characterised by low functional diversity and  
324 structural complexity (Harvey et al. 2021b, 2021a, Agostini et al. 2021a). Conversely,  
325 reference communities featured greater algal diversity, with more extensive cover of  
326 macrophytes and calcareous algae.

327 Community differences between elevated *p*CO<sub>2</sub> and reference locations were seen year-round,  
328 however they became more pronounced during key periods of seasonal environmental change:  
329 (1) the spring algal bloom, and (2) the autumn peak typhoon season. During spring, algal  
330 biomass peaked, and the elevated and high *p*CO<sub>2</sub> communities became dominated by thick  
331 mats of turf algae (Harvey et al. 2019) (Figure 2). Reference communities did not become turf-  
332 dominated, but instead burgeoned with canopy-forming species (e.g. *Asparagopsis taxiformis*,



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333 *Gelidium elegans*, *Sarcodia ceylanica*. The lack of turf is likely due to several factors,  
334 including the year-round persistence of macrophytes (lack of empty space), removal by  
335 physical abrasion from fleshy macroalgal thalli (Cheroske et al. 2000), shifts in top-down  
336 control (Cattano et al. 2020), and the lack of CO<sub>2</sub> enrichment to boost their competitive ability  
337 (Connell et al. 2018). Autumn typhoons removed the turf algal mats, exposing bare rock; a  
338 profound reset of the ecosystem state (Figures 1 and 2). Typhoon disturbance caused less  
339 change in the composition, coverage, and structural complexity of communities at reference  
340 *p*CO<sub>2</sub> levels (Figures 4 and 5). Algal persistence as low-biomass ‘new growth’ through the  
341 winter following typhoon disturbance meant that reference community structure was more  
342 stable between seasons and did not differ between the winter (after typhoon disturbance) and  
343 the following spring. It is important to note that our method of calculating structural complexity  
344 was limited in that only the functional group and not the size or biomass of the algae was  
345 considered. For example, whilst both winter and summer communities were dominated by  
346 macrophytes under ambient conditions (receiving similar scores for structural complexity),  
347 they differed markedly; summer communities had high biomass and 3-D structure, whereas  
348 winter communities had high coverage of the same functional groups, but lower biomass  
349 providing less habitat and structure.

350 Short periods of intense physical disturbance interacted with the effects of long-term  
351 acidification on community composition exposure to alter their dynamics. Acidified  
352 assemblages were less resistant (reduction of algal coverage and structural complexity) to  
353 disturbance from typhoons during seasonal periods of high storm frequency and strength with  
354 more pronounced losses at higher *p*CO<sub>2</sub> levels (Figures 2, 4, and 5). Community composition  
355 and associated life-histories, traits, and physiological susceptibilities underpinned these  
356 differences in community resistance. Complex macroalgal habitats can buffer the influence of  
357 climate change (Krause-Jensen et al. 2018), such as mitigating storm surge intensity due to

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358 their capacity to attenuate water flow (Rosman et al. 2007) resisting change until disturbances  
359 of a greater magnitude are experienced (Schowalter 2006, Levin and Möllmann 2015). The  
360 weaker attachment strength and low complexity of the algal groups associated with acidified  
361 conditions, such as turfs (Peterson 1996, Harvey et al. 2021a), leaves acidified communities  
362 more susceptible to removal by physical disturbance (Wada et al. 2021), representing low  
363 levels of resistance (Figures 4 and 5).

364 Differences were also observed in the recovery of algal communities following disturbance  
365 due to acidification-driven shifts in succession trajectories. Despite experiencing a greater  
366 initial impact, assemblages found under elevated  $p\text{CO}_2$  rapidly recovered to levels of algal  
367 coverage near to those seen pre-disturbance. Enrichment of  $\text{CO}_2$  promotes the already fast and  
368 opportunistic growth of turf algae, leading to rapid turf expansion during springtime  
369 community succession following the ecosystem reset of acidified sites by the typhoon season  
370 (Connell et al. 2018, Ferreira et al. 2021). Whilst turf coverage did not fully recover within 6-  
371 months following typhoons, the non-turf occupied space remained bare and macroalgal  
372 communities did not recover in their place (Figure 2). Previous studies have shown that turf  
373 removal can promote the recovery of macroalgal canopies (Gorman and Connell 2009),  
374 however here turf-dominance was consistently regained at the acidified sites. Due to the  
375 proximity of our sites and the scale of typhoons, our study lacked a ‘disturbance-free’ acidified  
376 treatment. Despite this, previous studies suggest that even in the absence of disturbance, due  
377 to turf-mediated reinforcing feedback loops (sediment trapping, alteration of substrate  
378 chemistry, physicochemical environment change, and recruitment inhibition) the development  
379 of macroalgal assemblages will not eventually replace established turf communities under  
380 acidified conditions (Harvey et al. 2021a). As the acidified communities were less complex  
381 than those at reference locations before typhoon disturbance, their recovery only had a low  
382 baseline to reach (Figure 4). This structurally-devoid community represents an alternate stable

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383 state maintained by a combination of ‘boosted’ turf growth , the turf-mediated inhibition of  
384 slower-growing, structurally complex macrophytes (Ghedini and Connell 2017b) , and regular  
385 ‘resetting’ of succession by physical disturbance under elevated  $p\text{CO}_2$  conditions (Gorman and  
386 Connell 2009, Harvey et al. 2021b).

387 Similar to patterns seen in systems enriched with nutrients (Worm et al. 1999, Gorman et al.  
388 2009) shifts in dominance towards fast-growing *r*-selected species have increasingly been  
389 documented under acidified conditions (Connell and Russell 2010, Harvey et al. 2019, Agostini  
390 et al. 2021a, Harvey et al. 2021a), whereby opportunistic species rapidly monopolise primary  
391 space, replacing algal canopies (Airoldi 2003, Gorman and Connell 2009). Under reference  
392 conditions grazing (top-down control) and competition (bottom-up effects) rapidly exclude turf  
393 algae, preventing such a regime shift (Kéfi et al. 2016). Concern is growing that rising  $p\text{CO}_2$   
394 will threaten the feedbacks that stop turfs from monopolising space, and additional coincidental  
395 biotic and abiotic change may further reinforce the competitive advantages turf gain over  
396 slower growing, typically dominant groups (such as macroalgae; Hughes 1994, Connell and  
397 Russell 2010, Ghedini and Connell 2017a), making state transitions within algal systems more  
398 likely (Ghedini et al. 2015, Harvey et al. 2021a).

399 The strength and likelihood of typhoons in temperate latitudes is being enhanced by global  
400 warming (Webster et al. 2005, Mann and Emanuel 2006, Lee et al. 2012, Murakami et al. 2012,  
401 2012, Zhan et al. 2012, Wang et al. 2022). The competitive edge of turf algae over macroalgal  
402 canopy formers are limited to their early life-history stages (O’Brien and Scheibling 2018) and  
403 is therefore weak under stable conditions. Reductions in recovery time between typhoons and  
404 extension of the typhoon season alters the competitive balance of algal communities however,  
405 particularly those exposed to other stressors such as ocean acidification (Kroeker et al. 2013,  
406 Pessarrodona et al. 2021). Although communities with extensive foundation species coverage

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407 display resistance to turf-system regime shifts (Falkenberg et al. 2012), if sufficiently high-  
408 levels of disturbance were to remove slower-growing macroalgal canopies, their recovery and  
409 recruitment could be inhibited in favour of *r*-selected turf algae (O'Brien and Scheibling 2018,  
410 Harvey et al. 2021b). Facilitated by rapid recruitment and fast rates of growth, turf algae might  
411 monopolize the space created by stronger typhoons, during the shortened periods occurring  
412 between disturbance events, and following the end of the typhoon season, helping to further  
413 drive regime shifts from macroalgal to turf-dominated communities (Pessarrodona et al. 2021).

414 Our findings reveal that the globally observed tendency for complex ecosystem states to be  
415 replaced by simple ecosystem states due to human impacts is likely to become entrenched by  
416 ocean acidification. Algal communities differed in their composition with increasing  $p\text{CO}_2$  and  
417 this was maintained across the year, with the largest changes coinciding with associated  
418 environmental change (nutrient rich spring algal blooms and stormy typhoon seasons).  
419 Between years, the same ecosystem states were maintained within each respective  $p\text{CO}_2$   
420 condition. Our findings suggest that the acidification-driven changes in algal community  
421 structure (with different life-histories and traits altering the mechanism of response to  
422 disturbance by typhoons) have significant implications for the maintenance and stability of the  
423 different ecosystem states observed between locations (Figure 5). Over three annual cycles of  
424 near total ecosystem reset by typhoons following extensive algal removal (i.e. negligible  
425 resistance), communities in acidified conditions rapidly returned to the same state (i.e. high  
426 recovery). This comprised of dominance by highly productive, opportunistic algal turfs which  
427 provide little structural complexity but cover the substrate and inhibit macroalgal recruitment.  
428 Whilst the persistence of contemporary, macroalgal-dominated communities relies on both  
429 initial resistance to and subsequent recovery from typhoons, the combination of ocean  
430 acidification and typhoons increases the probability of ecosystem shifts to simpler states  
431 dominated by fast-growing 'weedy' species with low resistance but fast recovery that 'locks-

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432 in' the new ecosystem state (Harvey et al. 2021a). The anticipated increase in typhoon  
433 intensity, frequency, and duration would further reinforce this low complexity state, reducing  
434 the time for algal recovery and keeping the community in an early successional stage.  
435 Crucially, such shifts that reduce ecosystem complexity in the marine realm can also reduce  
436 ecosystem productivity and associated species diversity. Future work should examine how  
437 reductions of community stability against disturbance might change ecosystem capacity to  
438 maintain original functionality following perturbation.

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449

450 **COMPETING INTERESTS**

451 The authors declare no conflicts of interest.

452

453 **DATA AVAILABILITY**

454 [Upon acceptance] Raw data used to create Figs 2-4 and Tables 2-3 will be supplied and stored  
455 in the Pangaea repository (<http://pangaea.de>).

456

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699 **Table 1. Summary of the carbonate chemistry for the 350  $\mu\text{atm}$  and 900  $\mu\text{atm}$  locations. The  $\text{pH}_T$  (350  $\mu\text{atm}$ ,  $n = 1964$ ; 500  $\mu\text{atm}$ ,  $n = 1760$ ; 900  $\mu\text{atm}$ ,**  
700  **$n = 10,818$ ), salinity (350  $\mu\text{atm}$ ,  $n = 1964$ ; 500  $\mu\text{atm}$ ,  $n = 1760$ ; 900  $\mu\text{atm}$ ,  $n = 10,818$ ), and total alkalinity ( $A_T$ ; 350  $\mu\text{atm}$ ,  $n = 56$ ; 500  $\mu\text{atm}$ ,  $n = 10$ ; 900**  
701  **$\mu\text{atm}$ ,  $n = 47$ ) are measured values. All other values were calculated using the carbonate chemistry system analysis program CO2SYS: Seawater  $p\text{CO}_2$ ,**  
702 **dissolved inorganic carbon (DIC), bicarbonate ( $\text{HCO}_3^-$ ), carbonate ( $\text{CO}_3^{2-}$ ), carbon dioxide ( $\text{CO}_2$ ), saturation states for calcite ( $\Omega_{\text{calcite}}$ ), and aragonite**  
703 **( $\Omega_{\text{aragonite}}$ ). Values are presented as mean, with standard deviation below. NOTE: Carbonate chemistry data are sourced from Agostini et al. 2018,**  
704 **Harvey et al. 2019, and Harvey, Kon, et al., 2021.**

Location	$\text{pH}_T$	Salinity (psu)	$A_T$ ( $\mu\text{mol kg}^{-1}$ )	$p\text{CO}_2$ ( $\mu\text{atm}$ )	DIC ( $\mu\text{mol kg}^{-1}$ )	$\text{HCO}_3^-$ ( $\mu\text{mol kg}^{-1}$ )	$\text{CO}_3^{2-}$ ( $\mu\text{mol kg}^{-1}$ )	$\Omega_{\text{calcite}}$	$\Omega_{\text{aragonite}}$
'350 $\mu\text{atm}$ '	8.137	34.504	2264.29	316.057	1962.694	1740.629	211.979	5.087	3.301
	0.056	0.427	15.34	47.466	34.376	55.084	22.221	0.534	0.348
'500 $\mu\text{atm}$ '	7.990	34.17	2264.35	471.30	2031.16	1852.31	163.71	3.94	2.56
	0.086	0.44	16.62	117.01	40.16	60.59	24.88	0.59	0.39
'900 $\mu\text{atm}$ '	7.788	34.351	2268.33	841.148	2125.785	1984.889	115.150	2.771	1.805
	0.106	0.484	19.45	291.762	39.381	52.510	21.308	0.512	0.336

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**Table 2. PERMANOVA summary for the effects of  $p\text{CO}_2$  ('350  $\mu\text{atm}$ ' vs. '500  $\mu\text{atm}$ ' vs. '900  $\mu\text{atm}$ ') on algal community composition. For p-values, \*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$ .**

<b>Term</b>	<b><i>df</i></b>	<b>Sum Sq.</b>	<b>Mean Sq.</b>	<b><i>F</i></b>	<b><i>p</i></b>
$p\text{CO}_2$	2	21.96	10.98	63.13	0.001 ***
Residuals	858	148.1	0.173		
Total	860	170.0			

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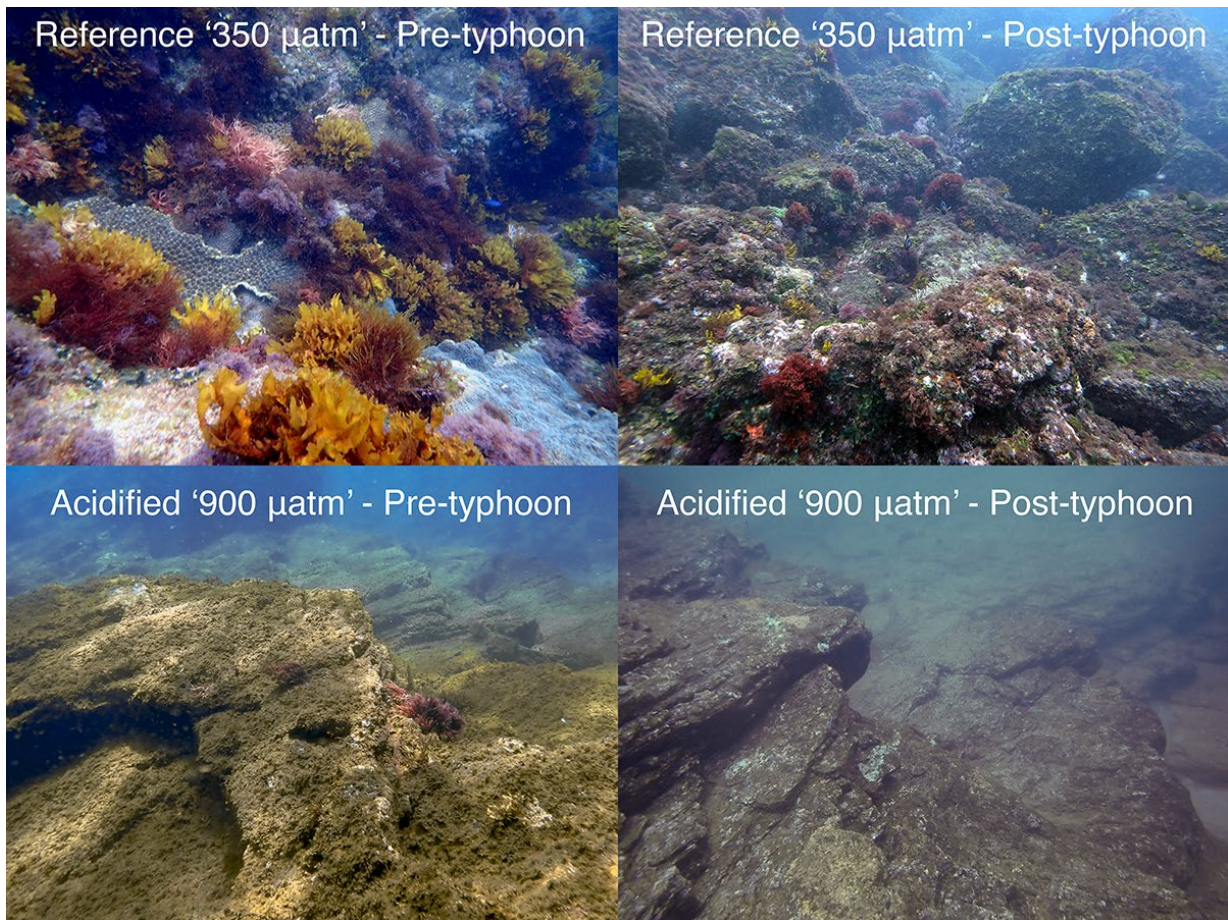
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**Table 3. Type III Wald chi-square Analysis of Deviance summary for the effect of timing ('Before' vs. 'After' vs. 'Recovery') and  $p\text{CO}_2$  condition ('350  $\mu\text{atm}$ ' vs. '500  $\mu\text{atm}$ ' vs. '900  $\mu\text{atm}$ ') on algal community (a) percentage cover (%) and (b) complexity. For  $p$ -values, \*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$ .**

<b>a) Cover (%)</b>	<b>Term</b>	<b><math>X^2</math></b>	<b><math>df</math></b>	<b><math>p</math></b>
	Intercept	1875	1	< 0.001 ***
	Timing	73.43	2	< 0.001 ***
	$p\text{CO}_2$	1.208	2	0.547
	Timing x $p\text{CO}_2$	46.58	4	< 0.001 ***
<b>b) Complexity</b>	<b>Term</b>	<b><math>X^2</math></b>	<b><math>df</math></b>	<b><math>p</math></b>
	Intercept	1539	1	< 0.001 ***
	Timing	33.30	2	< 0.001 ***
	$p\text{CO}_2$	77.88	2	< 0.001 ***
	Timing x $p\text{CO}_2$	3.193	4	0.5261

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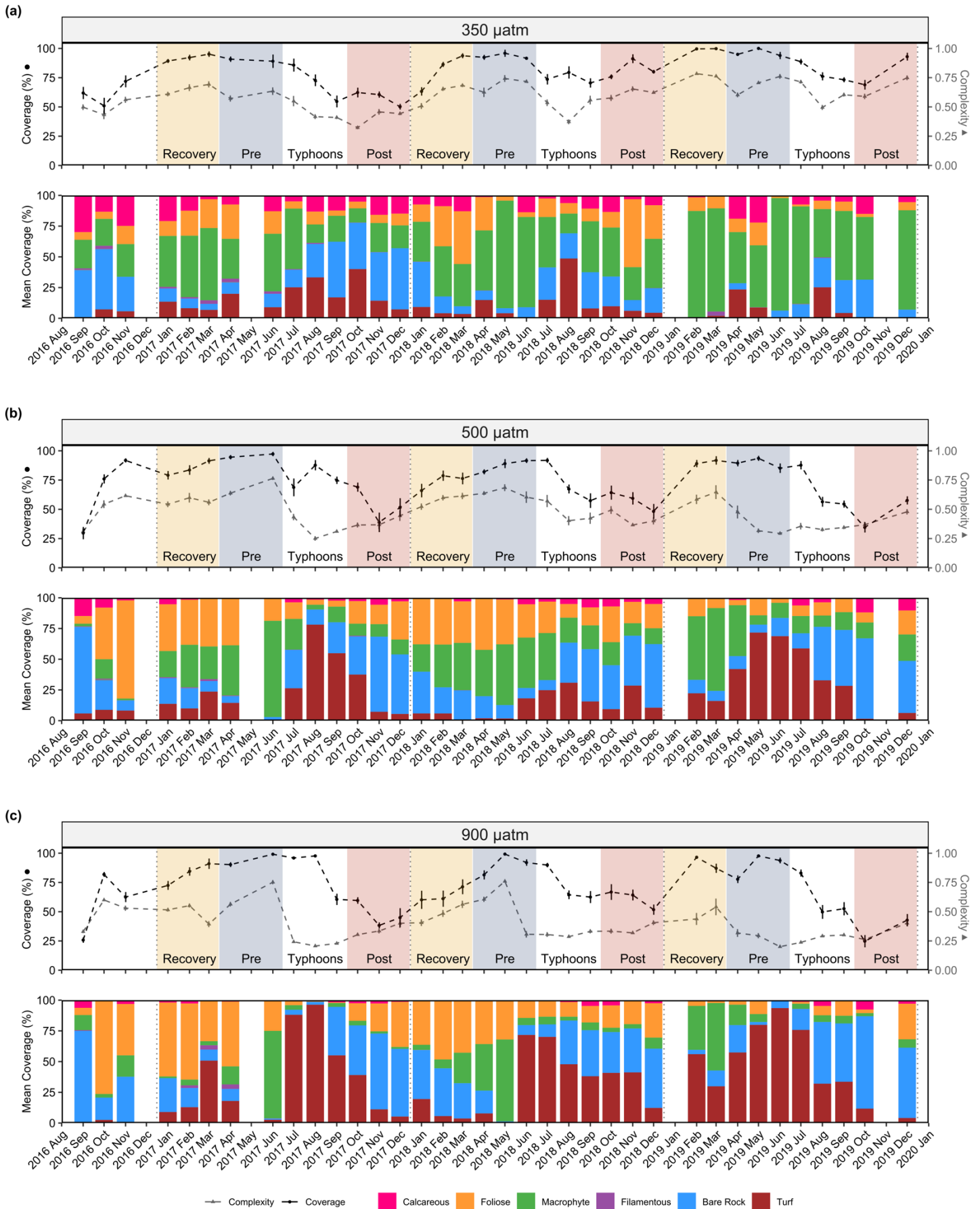


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712 **Figure 1.** Examples of seascapes found at Reference '350 μatm' and acidified '900 μatm'  $p\text{CO}_2$

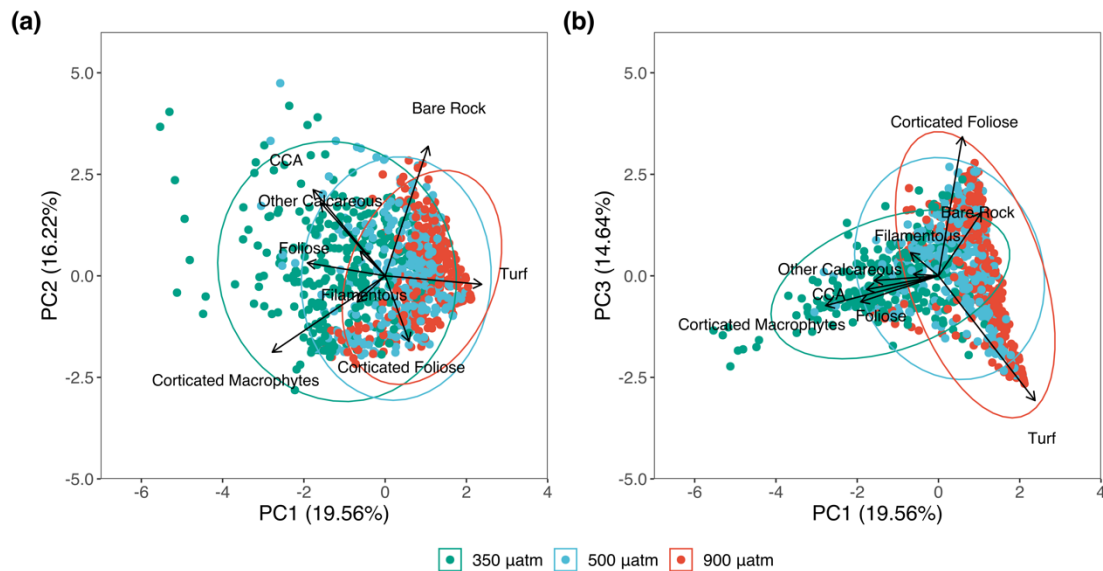
713 locations before typhoon disturbance (pre-typhoon) and after (post-typhoon).

# OA reduces resistance, but not resilience of algal communities



715 **Figure 2.** Average percentage cover (Black); complexity (Grey); and mean coverage (by  
 716 functional group) of algal communities across each sampling month over a three-year sampling  
 717 period at (a) 350  $\mu\text{atm CO}_2$ ; (b) 500  $\mu\text{atm CO}_2$ ; and (c) 900  $\mu\text{atm CO}_2$ . Pre-typhoon periods  
 718 (“Pre”; April to June; blue), post-typhoon periods (“Post”; October to December; red), and  
 719 recovery periods (“Recovery”; January to March; yellow) are indicated on the figure. Typhoon  
 720 periods (July to September) are marked as “Typhoons”. Dotted vertical lines denote the start  
 721 of each new year (2017-2020).

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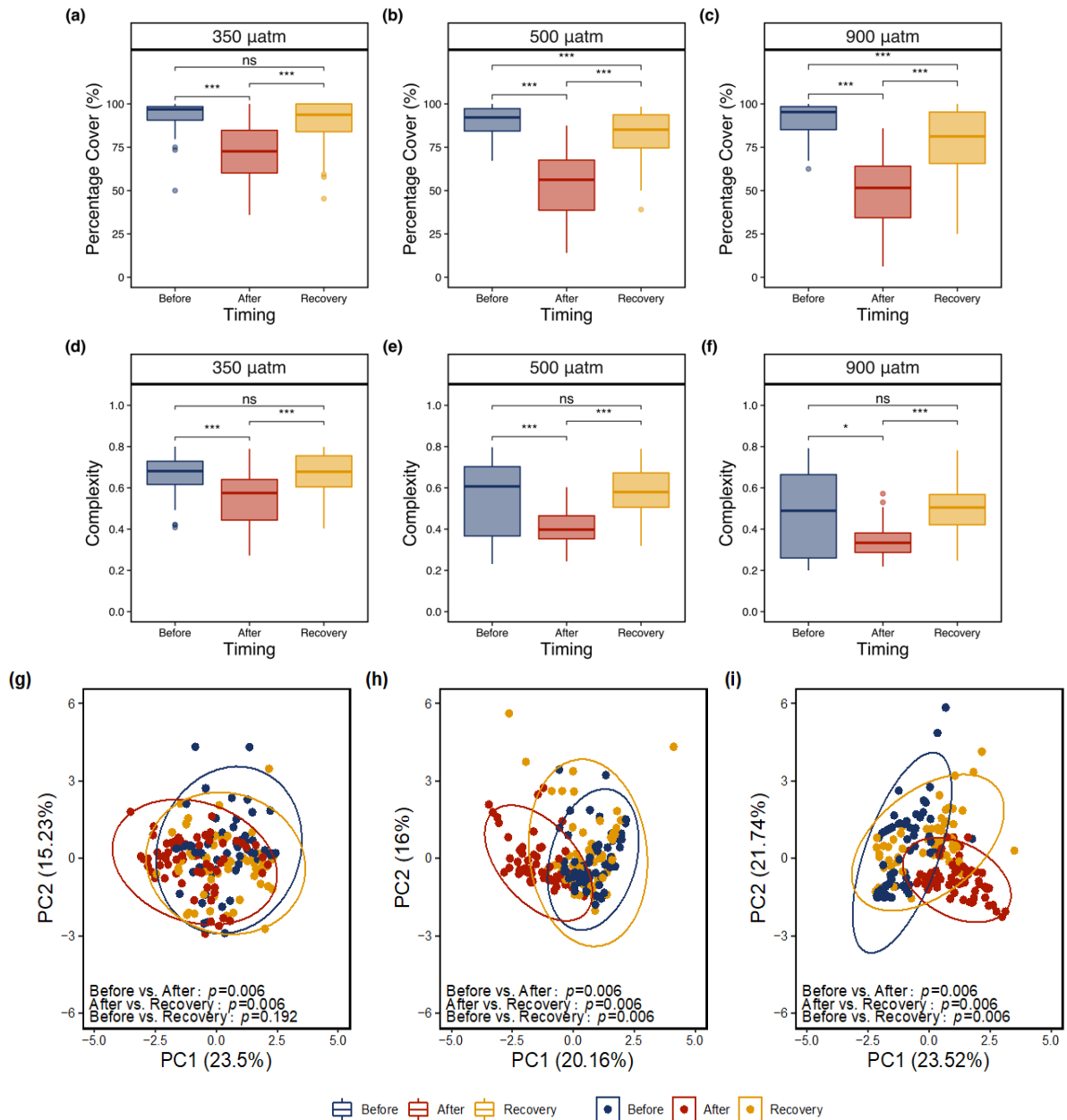


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724 **Figure 3.** Community composition of algal functional groups between the three locations, 350  
 725  $\mu\text{atm CO}_2$  (Green), 500  $\mu\text{atm CO}_2$  (Blue) and 900  $\mu\text{atm CO}_2$  (Red), as assessed by principal  
 726 component analysis for (a) PC1 vs. PC2 and (b) PC1 vs. PC3. See Figure S2 for comparisons  
 727 of the locations at each month.

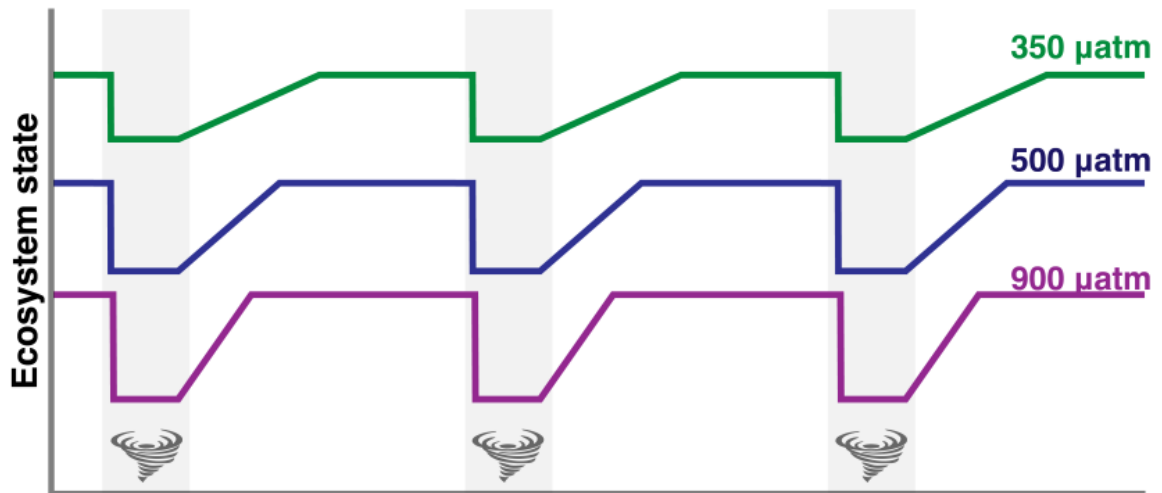
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## OA reduces resistance, but not resilience of algal communities

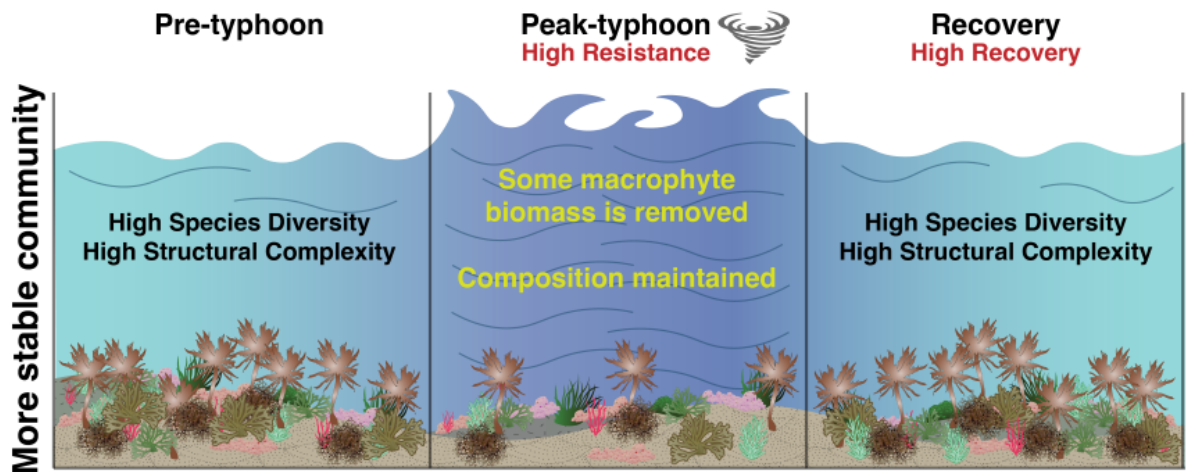


**Figure 4.** Percentage cover (a-c), complexity (d-f) and composition (g-i) of communities ‘Before’ (Blue) and ‘After’ the typhoon season peak (Red), and the subsequent ‘Recovery’ period (Orange). The 350  $\mu\text{atm}$  location is shown on the left (a,d,g), the 500  $\mu\text{atm}$  location in the center (b,e,h), and the 900  $\mu\text{atm}$  location on the right (c,f,i). NOTES: Pairwise comparisons within Panels a-f are carried out by Type III ANOVA following GLMM (ns,  $p > 0.05$ ; \*  $p < 0.05$ ; \*\*  $p < 0.01$ ; \*\*\*  $p < 0.001$ ) with the individuals points in a-f indicating outliers. To see the Panels a-f separated by year, see Figure S3, and for more detailed statistics, see Table S4 and S5.

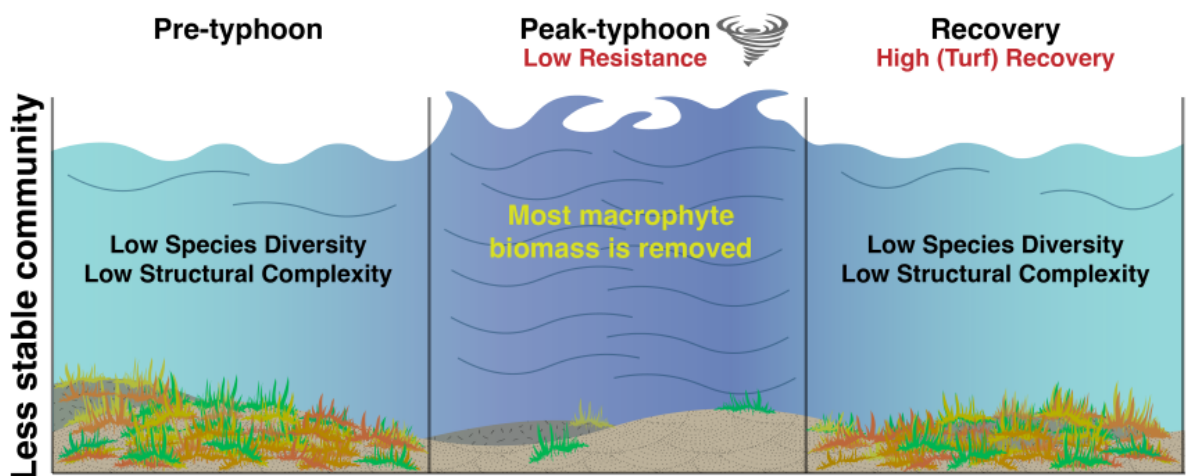
(a)



(b) Present-day Conditions (350  $\mu\text{atm}$ )



(c) Future Conditions (500  $\mu\text{atm}$ , 900  $\mu\text{atm}$ )



730 **Figure 5.** Schematic summary of the differences in community stability between Present-day  
731 (350  $\mu\text{atm}$  = Green) and future (900  $\mu\text{atm}$  = Red)  $\text{CO}_2$  conditions in response to physical  
732 disturbance from typhoons. The ecosystem state of present-day communities is higher than  
733 those under future  $p\text{CO}_2$  conditions due to persistent press disturbance from ocean acidification  
734 (leading to community compositional changes, lower functional diversity, and structural  
735 complexity). Through time, ecosystem state fluctuates with seasonal and environmental change  
736 (temperature, nutrients, disturbance), with larger fluctuations for acidified communities.  
737 Periods of intense ‘pulse’ disturbance from seasonal factors such as typhoons have significant  
738 effects on ecosystem state. Differences in the functional traits and life-history strategies of the  
739 species forming present-day (macroalgal-dominated) and future (turf-dominated) communities  
740 lead to reductions in ecosystem stability. Macroalgal assemblages are resistant to disturbance  
741 from typhoons, maintaining a more consistent composition between seasons and recovering to  
742 pre-disturbance baselines following physical disturbance. Turf-dominated communities  
743 display low resistance to typhoons, which almost entirely removes the algal community,  
744 reducing the benthos to bare substrate. Turf resilience, promoted by boosted primary  
745 production and growth under elevated  $p\text{CO}_2$  conditions, meant that the empty space created  
746 was later recolonised by turf algae. In the absence of physical disturbance feedback  
747 mechanisms maintain turf-dominance and inhibit macroalgal recruitment (see Harvey et al.  
748 2021). Regular disturbance stabilised this pattern, locking the community into an early  
749 successional stage.