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Published in:

Science of the Total Environment

DOI:

[10.1016/j.scitotenv.2022.161269](https://doi.org/10.1016/j.scitotenv.2022.161269)

Publication date:

2023

Link:

[Link to publication in PEARL](#)

Citation for published version (APA):

Hudson, C. J., Agostini, S., Wada, S., Hall-Spencer, J. M., Connell, S. D., & Harvey, B. P. (2023). Ocean acidification increases the impact of typhoons on algal communities. *Science of the Total Environment*, 865(0). <https://doi.org/10.1016/j.scitotenv.2022.161269>

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This is the author's pre-proof manuscript. The final published version of this work (the version of record) is published by Elsevier in *Science of the Total Environment*. The manuscript was made available online on the 30 December 2022 at

<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 CO₂ 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*CO₂
- 9 •
- 10 Acidification-driven community changes were maintained by typhoon
11 disturbance
- 12 •
- 13 Turf-dominated communities displayed low resistance to typhoons

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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 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 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 CO₂ 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 CO₂ 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 CO₂ 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 CO₂ 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 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 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 μatm ’, ‘500 μatm ’ and ‘900 μatm ’, 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° 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 μatm ’ location had a mean pH_T of 8.137 ± 0.056 (SD), the ‘500 μatm ’ location area had a mean
152 pH_T of 7.983 ± 0.119 (SD), and the ‘900 μatm ’ location had a mean pH_T of 7.781 ± 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 μatm ', '500 μatm ' and '900
164 μatm '). Quadrats within these locations were deployed haphazardly over a *ca.* 400 m² 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 μatm ’, ‘500 μatm ’ and ‘900 μatm ’)
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 μatm ’, ‘500 μatm ’ and ‘900 μatm ’) 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 μatm ’, ‘500 μatm ’ and ‘900 μatm ’), 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 μatm location showed clear and consistent differences to both the 500
240 μatm and 900 μatm locations (Figure 3; Table S3 PERMANOVA *post-hoc*: all $p < 0.01$).
241 Communities in the 350 μatm 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 μatm 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 μatm and 900 μatm 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 μatm and 900 μatm 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 μatm and 900 μatm 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 ± 8.21 , 90.33 ± 8.58 , and 91.27 ± 9.85) and ‘After’ (72.75 ± 16.50 ,
269 52.93 ± 19.45 , and 49.15 ± 19.39) typhoons differed significantly at each location (‘350 μatm ’,
270 ‘500 μatm ’ and ‘900 μatm ’) (Figure 4a-c). The algal coverage of ‘Before’ and ‘Recovery’
271 (89.92 ± 12.41 , 82.01 ± 13.76 , and 78.00 ± 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 μatm ' = 0.670 ± 0.095 ; '500 μatm ' = 0.552 ± 0.182 ; '900 μatm ' =
288 0.471 ± 0.215 ; PERMANOVA *post-hoc*: all $p < 0.001$). Despite displaying similar losses in
289 structural complexity 'After' typhoon disturbance (0.552 ± 0.139 , 0.411 ± 0.093 , and
290 0.345 ± 0.076) and a subsequent 'Recovery' of complexity to pre-disturbance levels at each
291 location (0.670 ± 0.097 , 0.584 ± 0.101 , and 0.487 ± 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 μatm '
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 CO₂ seeps has consistently demonstrated clear ecosystem shifts
311 towards simplified communities at sites with elevated *p*CO₂ 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*CO₂
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*CO₂ 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*CO₂ 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*CO₂ 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 CO₂ 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*CO₂ 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*CO₂ 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 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.

439 **ACKNOWLEDGEMENTS**

440 We thank the technical staff at 'Shimoda Marine Research Center, University of Tsukuba' for
441 their assistance aboard RV *Tsukuba II* and at our study site, and the Japan Fisheries agencies
442 of Nijima/Shikine Island (Tokyo prefecture) for their support. This project was supported by
443 the 'International Education and Research Laboratory Program', University of Tsukuba. This
444 work was also supported by JSPS KAKENHI Grant Number 17K17622, and we acknowledge
445 funding support from the Ministry of Environment, Government of Japan (Suishinhi: 4RF-
446 1701). This project contributes towards the International CO₂ Natural Analogues (ICONA)
447 Network and the national committees of the Scientific Committee on Oceanic Research
448 (SCOR) Changing Oceans Biological Systems project (OCE-1840868).

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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Ocean acidification alters the stabilizing mechanisms of algal communities against typhoons

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699 **Table 1. Summary of the carbonate chemistry for the 350 μatm and 900 μatm locations. The pH_T (350 μatm , $n = 1964$; 500 μatm , $n = 1760$; 900 μatm ,**
700 **$n = 10,818$), salinity (350 μatm , $n = 1964$; 500 μatm , $n = 1760$; 900 μatm , $n = 10,818$), and total alkalinity (A_T ; 350 μatm , $n = 56$; 500 μatm , $n = 10$; 900**
701 **μatm , $n = 47$) 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 (HCO_3^-), carbonate (CO_3^{2-}), carbon dioxide (CO_2), saturation states for calcite (Ω_{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 | pH_T | Salinity (psu) | A_T ($\mu\text{mol kg}^{-1}$) | $p\text{CO}_2$ (μatm) | DIC ($\mu\text{mol kg}^{-1}$) | HCO_3^- ($\mu\text{mol kg}^{-1}$) | CO_3^{2-} ($\mu\text{mol kg}^{-1}$) | Ω_{calcite} | $\Omega_{\text{aragonite}}$ |
|------------------------|---------------|-------------------|--------------------------------------|---------------------------------------|------------------------------------|---|---|---------------------------|-----------------------------|
| '350 μatm ' | 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 μatm ' | 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 μatm ' | 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 μatm ' vs. '500 μatm ' vs. '900 μatm ') on algal community composition. For p-values, * $p < 0.05$, ** $p < 0.01$, * $p < 0.001$.**

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

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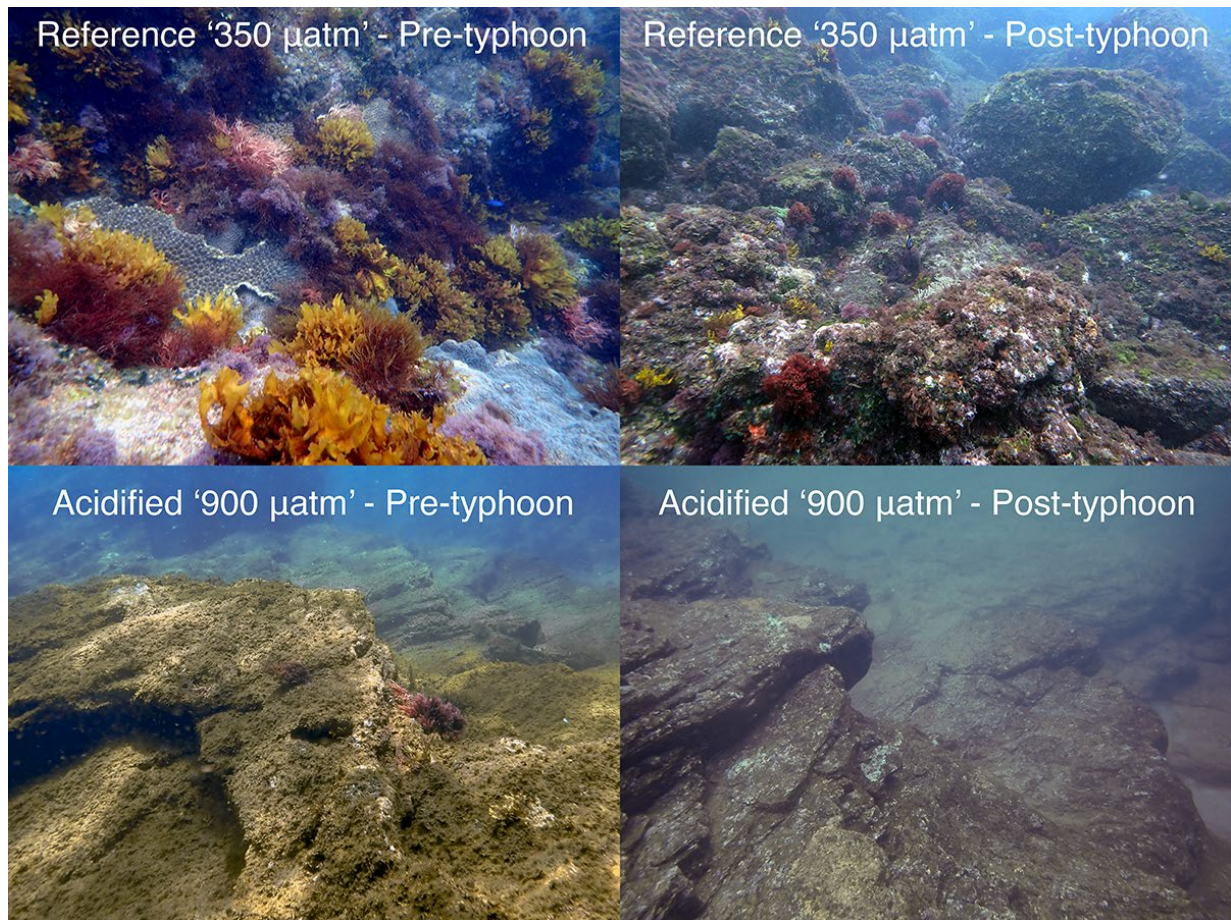
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Table 3. Type III Wald chi-square Analysis of Deviance summary for the effect of timing ('Before' vs. 'After' vs. 'Recovery') and $p\text{CO}_2$ condition ('350 μatm ' vs. '500 μatm ' vs. '900 μatm ') on algal community (a) percentage cover (%) and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

| a) Cover (%) | Term | X^2 | df | p |
|----------------------|-------------------------|-------------------------|------------------------|-----------------------|
| | 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) Complexity | Term | X^2 | df | p |
| | 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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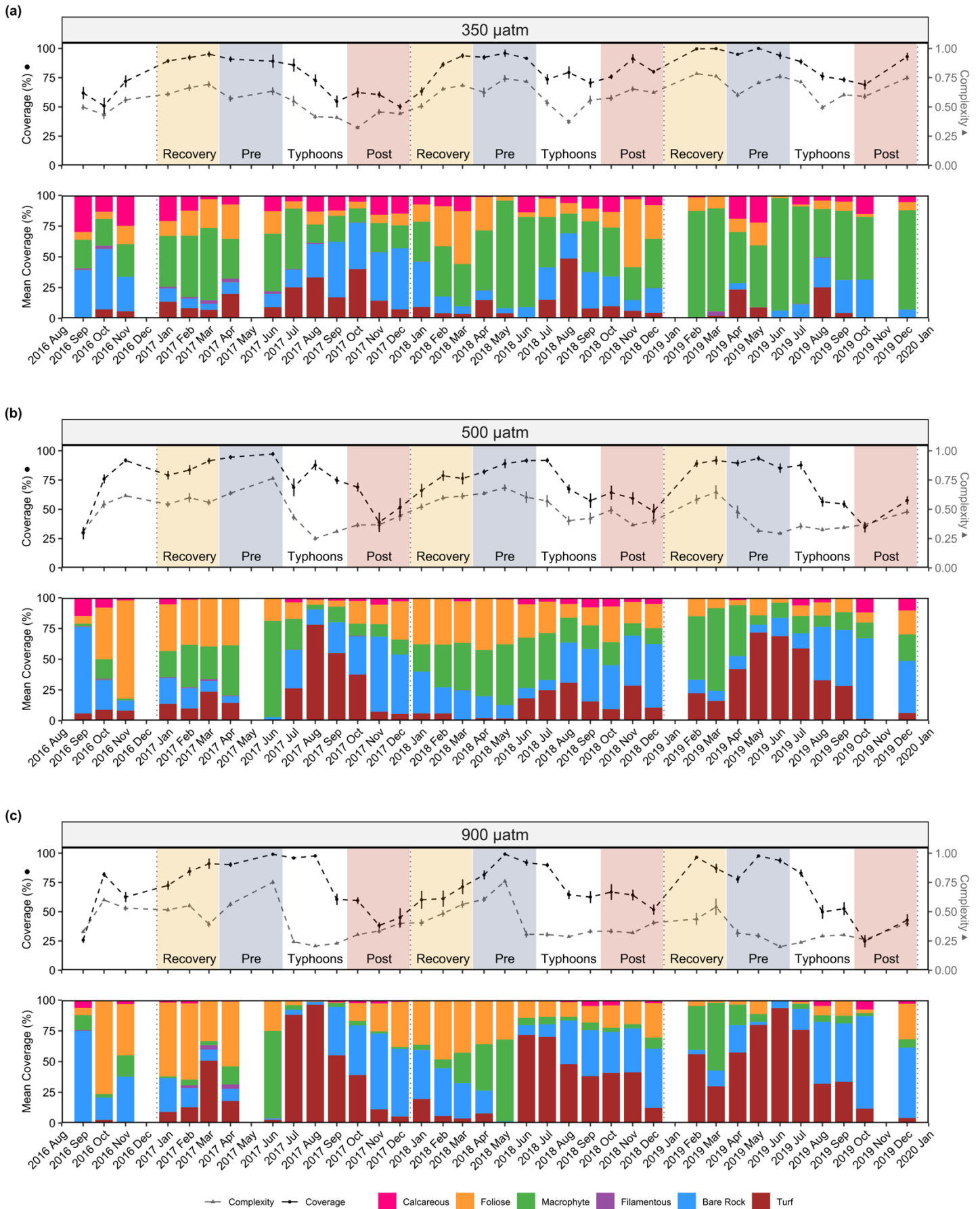


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712 **Figure 1.** Examples of seascapes found at Reference '350 μatm' and acidified '900 μatm' $p\text{CO}_2$

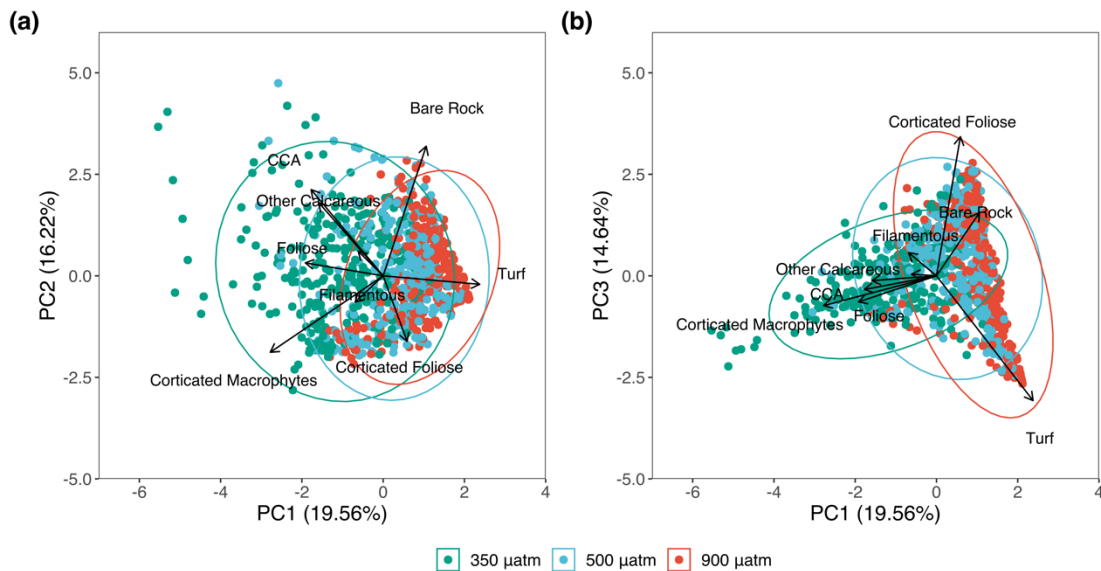
713 locations before typhoon disturbance (pre-typhoon) and after (post-typhoon).

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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723

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

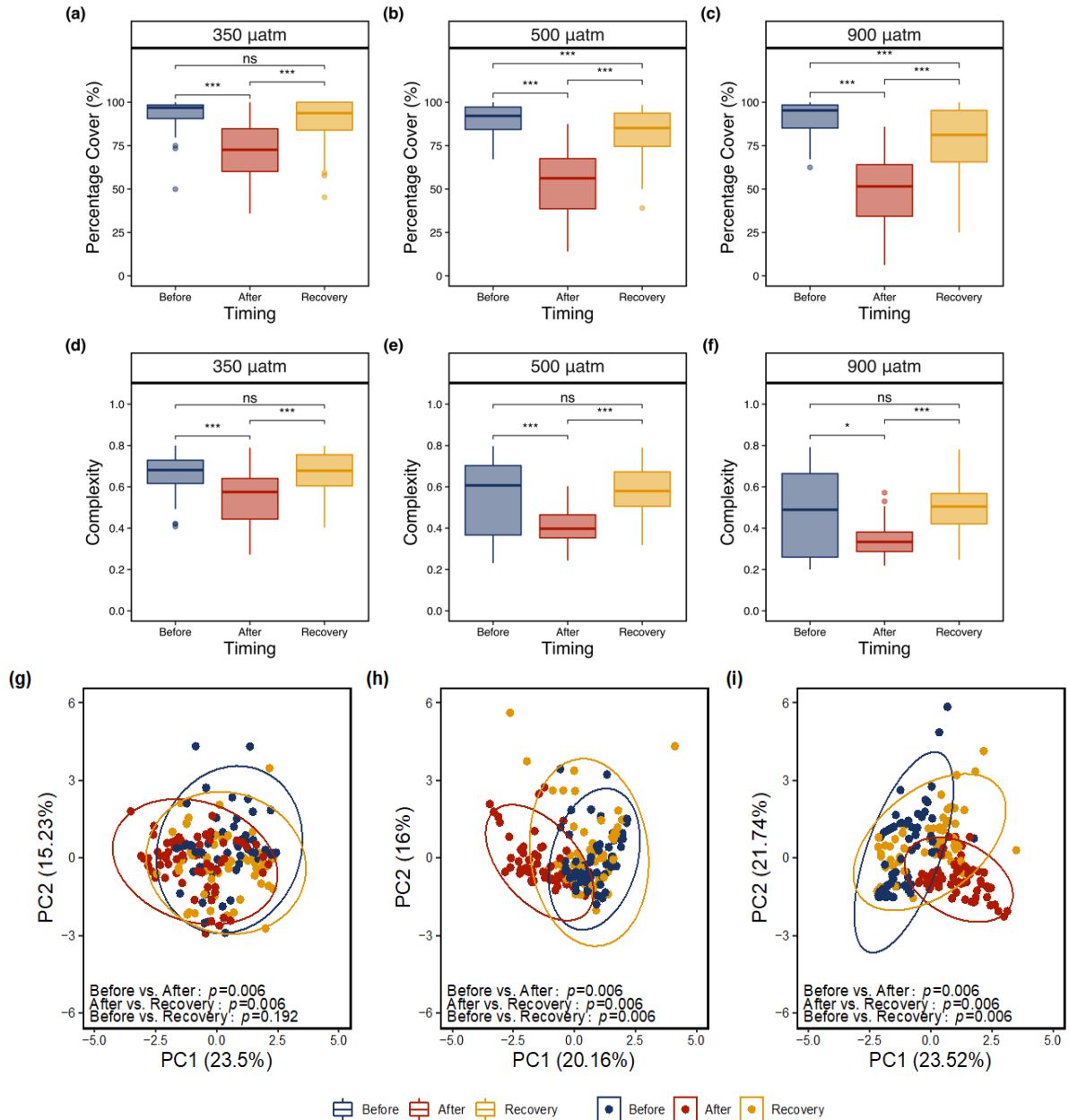
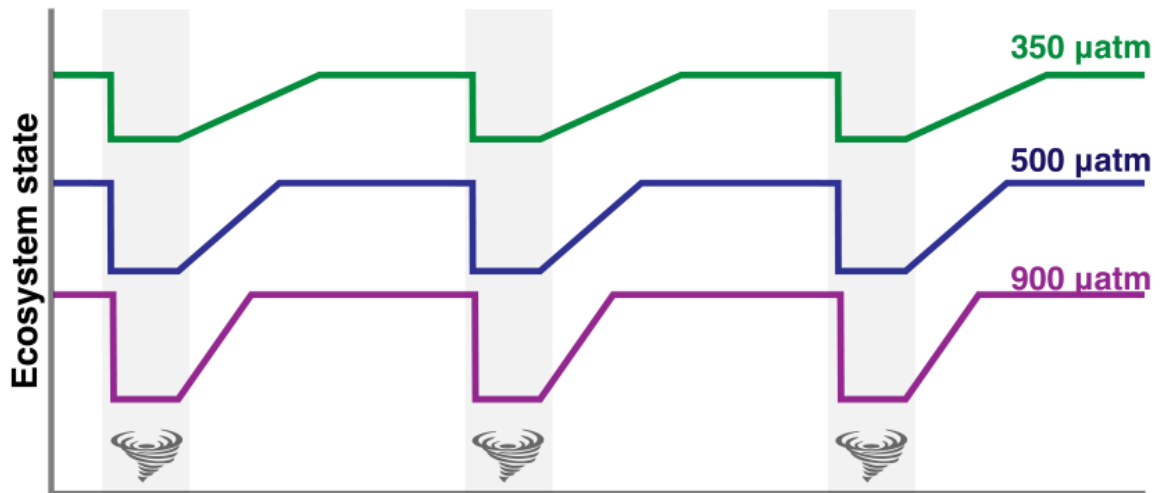
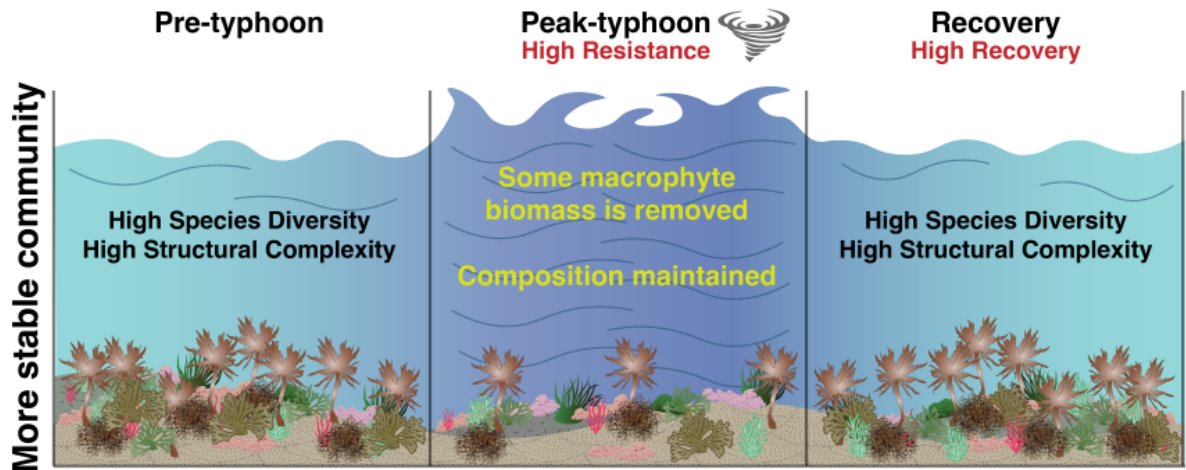


Figure 4. Percentage cover (a-c), complexity (d-f) and composition (g-i) of communities ‘Before’ (Blue) and ‘After’ the typhoon season peak (Red), and the subsequent ‘Recovery’ period (Orange). The 350 μatm location is shown on the left (a,d,g), the 500 μatm location in the center (b,e,h), and the 900 μatm 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.

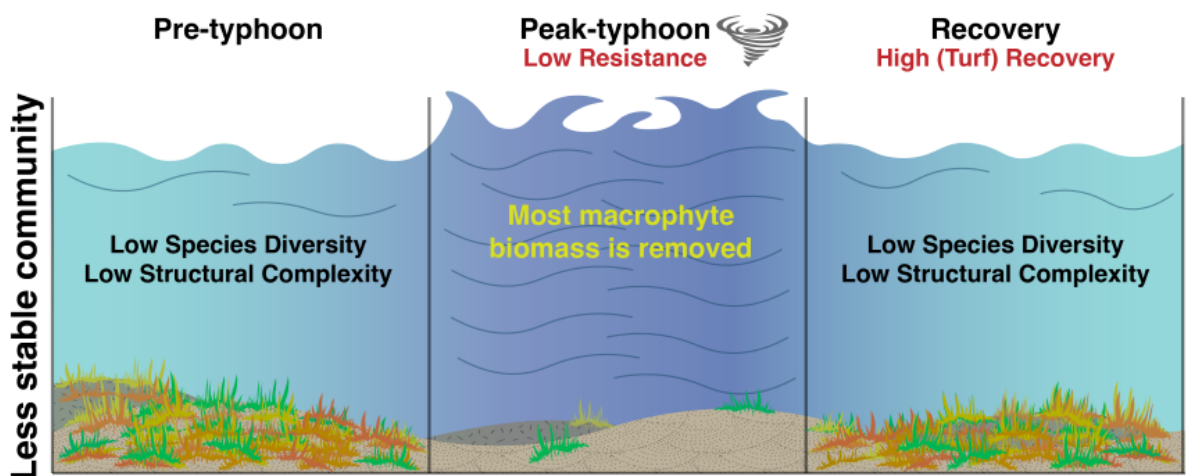
(a)



(b) Present-day Conditions (350 μatm)



(c) Future Conditions (500 μatm, 900 μatm)



730 **Figure 5.** Schematic summary of the differences in community stability between Present-day
731 (350 μatm = Green) and future (900 μatm = Red) 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.