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Ocean acidification increases the impact of typhoons on algal communities

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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 pCO₂
- 9 •
- 10 Acidification-driven community changes were maintained by typhoon
11 disturbance
- 12 •
- 13 Turf-dominated communities displayed low resistance to 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 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.

1 INTRODUCTION

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

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

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

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

Ocean acidification, a global ‘press’ disturbance shifting carbonate chemistry conditions as increased atmospheric CO₂ is drawn down by the ocean, is projected to simplify coastal ecosystems due to losses in habitat, structural complexity, and biodiversity (Kroeker et al. 2011, Vizzini et al. 2017, Agostini et al. 2018). This ecosystem reorganisation arises due to the unequal impact that ocean acidification has on marine organisms (Connell et al. 2018), acting as both a resource for some primary producers (Koch et al. 2013, Cornwall et al. 2017), and a physiological stressor for other organisms, such as marine calcifiers (Harvey et al. 2018, Agostini et al. 2021b). By promoting the loss of certain functional groups and restructuring community composition, ocean acidification might reduce the ability of marine communities to absorb disturbances and remain unchanged, reducing their stability (Folke et al. 2004).

To capture the complexity of natural systems and investigate the long-term consequences of ocean acidification at the community-level, an increasing number of studies have used marine CO₂ seeps as natural analogues of future conditions (Hall-Spencer et al. 2008, Milazzo et al. 2014, Agostini et al. 2018, Connell et al. 2018, Foo et al. 2018). Some coastal volcanoes cause CO₂ to bubble through the seabed, creating localised gradients of acidification. These offer insights into the long-term consequences of ocean acidification on ecosystems by utilising communities that are naturally assembled, complex, and shaped by species interactions (Hall-Spencer and Harvey 2019). Studies at CO₂ seeps show that ocean acidification increases the

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

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

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

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

2 MATERIALS AND METHODS

2.1 Study site and environmental context

Algal community assessments were carried out in three locations along a $p\text{CO}_2$ gradient around Shikine Island, Japan (34°19'9" N, 139° 12'18" E) from September 2016 to December 2019. These three locations were 1) a reference $p\text{CO}_2$ area outside the influence of the CO_2 seep, 2)

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

2.2 Experimental design and analysis

2.2.1 Data collection

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

(8.5 mm width, 70 mm length) at each of the three locations ('350 μatm ', '500 μatm ' and '900 μatm '). Quadrats within these locations were deployed haphazardly over a *ca.* 400 m² area with at least 3 m between them, fixed to upward-facing substrata. As algae were the focus of this study, random stratified sampling was used to prevent the inclusion of coral within quadrats. Individual quadrats at each location were photographed (Tough TG-5, Olympus, Japan) monthly (with four exceptions when poor conditions prevented access) a total of 36 times over a period of three years (September 2016 – December 2019) for community assessment.

2.2.2 Community Analysis

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

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

2.2.3 *Algal community stability*

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

2.3 *Statistical Analysis*

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

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

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

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

3 RESULTS

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

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

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

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

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

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at the 500 μatm and 900 μatm locations did not significantly differ, suggesting (given composition did not remain constant) that they respond to environmental change in similar ways (Figure 3 PERMANOVA results).

3.2 *Effects of ocean acidification on community stability*

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

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

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

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

4 DISCUSSION

Whilst other environmental factors also influence community assembly, composition, and dynamics, global research at CO₂ seeps has consistently demonstrated clear ecosystem shifts towards simplified communities at sites with elevated $p\text{CO}_2$ levels (Johnson et al. 2012, Enochs et al. 2015, Sunday et al. 2017, Connell et al. 2018, Foo et al. 2018, Cattano et al. 2020, Harvey et al. 2021b, 2021a, Agostini et al. 2021a). These acidified communities not only have reduced ecological and structural complexity (Figure 1; Figure 4), but also lower biodiversity, raising concerns about a potential loss of ecosystem services (Hall-Spencer and Harvey 2019). Most studies investigating the ecological effects of ocean acidification have not taken seasonality into account, leaving community dynamics between seasons largely unknown (but see Godbold and Solan 2013, Baggini et al. 2014, Cattano et al. 2020, Harvey et al. 2021b). Here, we found that algal community structure consistently differed between locations with different $p\text{CO}_2$ levels (Figure 3; Figure S2), and this persisted across seasons despite profound physical disturbance from typhoons, a seasonal environmental stress which maintained the differences. In general, increased levels of $p\text{CO}_2$ caused consistent reductions in macrophyte cover (Figure 2), leaving communities dominated by turf algae, characterised by low functional diversity and structural complexity (Harvey et al. 2021b, 2021a, Agostini et al. 2021a). Conversely, reference communities featured greater algal diversity, with more extensive cover of macrophytes and calcareous algae.

Community differences between elevated $p\text{CO}_2$ and reference locations were seen year-round, however they became more pronounced during key periods of seasonal environmental change: (1) the spring algal bloom, and (2) the autumn peak typhoon season. During spring, algal biomass peaked, and the elevated and high $p\text{CO}_2$ communities became dominated by thick mats of turf algae (Harvey et al. 2019) (Figure 2). Reference communities did not become turf-dominated, but instead burgeoned with canopy-forming species (e.g. *Asparagopsis taxiformis*,

Gelidium elegans, *Sarcodia ceylanica*. The lack of turf is likely due to several factors, including the year-round persistence of macrophytes (lack of empty space), removal by physical abrasion from fleshy macroalgal thalli (Cheroske et al. 2000), shifts in top-down control (Cattano et al. 2020), and the lack of CO₂ enrichment to boost their competitive ability (Connell et al. 2018). Autumn typhoons removed the turf algal mats, exposing bare rock; a profound reset of the ecosystem state (Figures 1 and 2). Typhoon disturbance caused less change in the composition, coverage, and structural complexity of communities at reference pCO₂ levels (Figures 4 and 5). Algal persistence as low-biomass ‘new growth’ through the winter following typhoon disturbance meant that reference community structure was more stable between seasons and did not differ between the winter (after typhoon disturbance) and the following spring. It is important to note that our method of calculating structural complexity was limited in that only the functional group and not the size or biomass of the algae was considered. For example, whilst both winter and summer communities were dominated by macrophytes under ambient conditions (receiving similar scores for structural complexity), they differed markedly; summer communities had high biomass and 3-D structure, whereas winter communities had high coverage of the same functional groups, but lower biomass providing less habitat and structure.

Short periods of intense physical disturbance interacted with the effects of long-term acidification on community composition exposure to alter their dynamics. Acidified assemblages were less resistant (reduction of algal coverage and structural complexity) to disturbance from typhoons during seasonal periods of high storm frequency and strength with more pronounced losses at higher pCO₂ levels (Figures 2, 4, and 5). Community composition and associated life-histories, traits, and physiological susceptibilities underpinned these differences in community resistance. Complex macroalgal habitats can buffer the influence of climate change (Krause-Jensen et al. 2018), such as mitigating storm surge intensity due to

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

Differences were also observed in the recovery of algal communities following disturbance due to acidification-driven shifts in succession trajectories. Despite experiencing a greater initial impact, assemblages found under elevated $p\text{CO}_2$ rapidly recovered to levels of algal coverage near to those seen pre-disturbance. Enrichment of CO_2 promotes the already fast and opportunistic growth of turf algae, leading to rapid turf expansion during springtime community succession following the ecosystem reset of acidified sites by the typhoon season (Connell et al. 2018, Ferreira et al. 2021). Whilst turf coverage did not fully recover within 6-months following typhoons, the non-turf occupied space remained bare and macroalgal communities did not recover in their place (Figure 2). Previous studies have shown that turf removal can promote the recovery of macroalgal canopies (Gorman and Connell 2009), however here turf-dominance was consistently regained at the acidified sites. Due to the proximity of our sites and the scale of typhoons, our study lacked a ‘disturbance-free’ acidified treatment. Despite this, previous studies suggest that even in the absence of disturbance, due to turf-mediated reinforcing feedback loops (sediment trapping, alteration of substrate chemistry, physicochemical environment change, and recruitment inhibition) the development of macroalgal assemblages will not eventually replace established turf communities under acidified conditions (Harvey et al. 2021a). As the acidified communities were less complex than those at reference locations before typhoon disturbance, their recovery only had a low baseline to reach (Figure 4). This structurally-devoid community represents an alternate stable

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

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

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

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

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

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

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COMPETING INTERESTS

The authors declare no conflicts of interest.

DATA AVAILABILITY

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

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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 , $n = 10,818$), 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 μatm , $n = 47$) are measured values. All other values were calculated using the carbonate chemistry system analysis program CO2SYS: Seawater $p\text{CO}_2$, dissolved inorganic carbon (DIC), bicarbonate (HCO_3^-), carbonate (CO_3^{2-}), carbon dioxide (CO_2), saturation states for calcite (Ω_calcite), and aragonite ($\Omega_\text{aragonite}$). Values are presented as mean, with standard deviation below. NOTE: Carbonate chemistry data are sourced from Agostini et al. 2018, 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

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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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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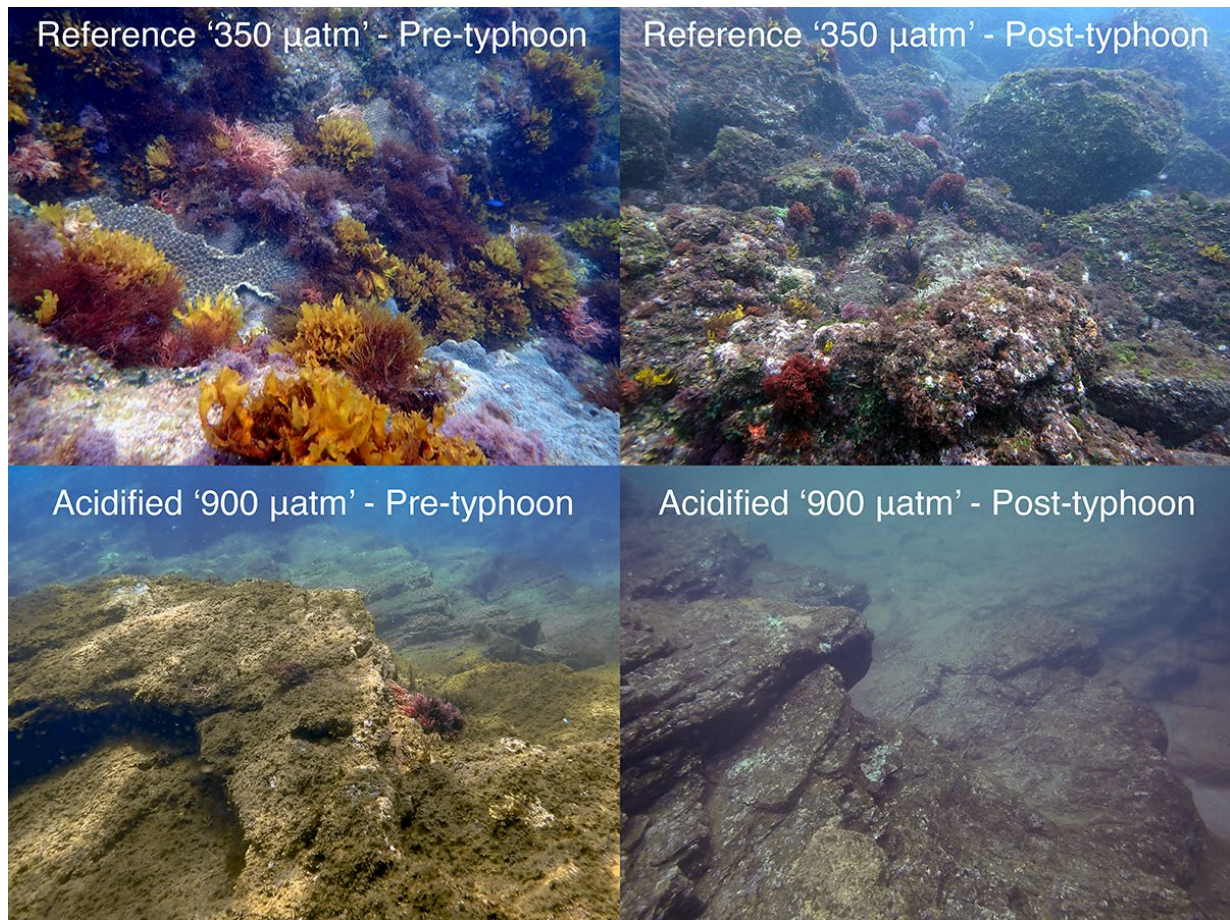


Figure 1. Examples of seascapes found at Reference '350 μatm ' and acidified '900 μatm ' $p\text{CO}_2$ locations before typhoon disturbance (pre-typhoon) and after (post-typhoon).

OA reduces resistance, but not resilience of algal communities

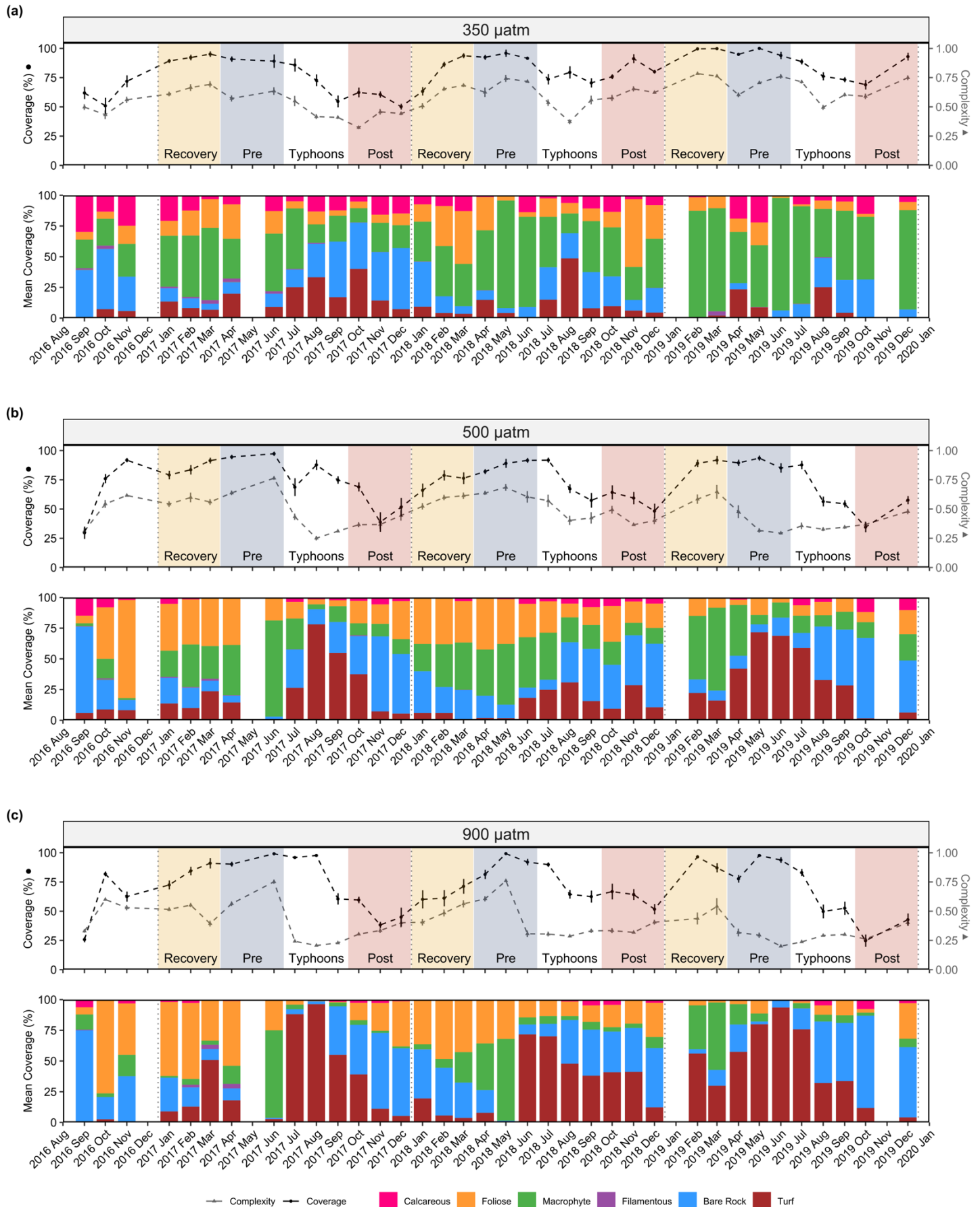


Figure 2. Average percentage cover (Black); complexity (Grey); and mean coverage (by functional group) of algal communities across each sampling month over a three-year sampling period at (a) 350 $\mu\text{atm CO}_2$; (b) 500 $\mu\text{atm CO}_2$; and (c) 900 $\mu\text{atm CO}_2$. Pre-typhoon periods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

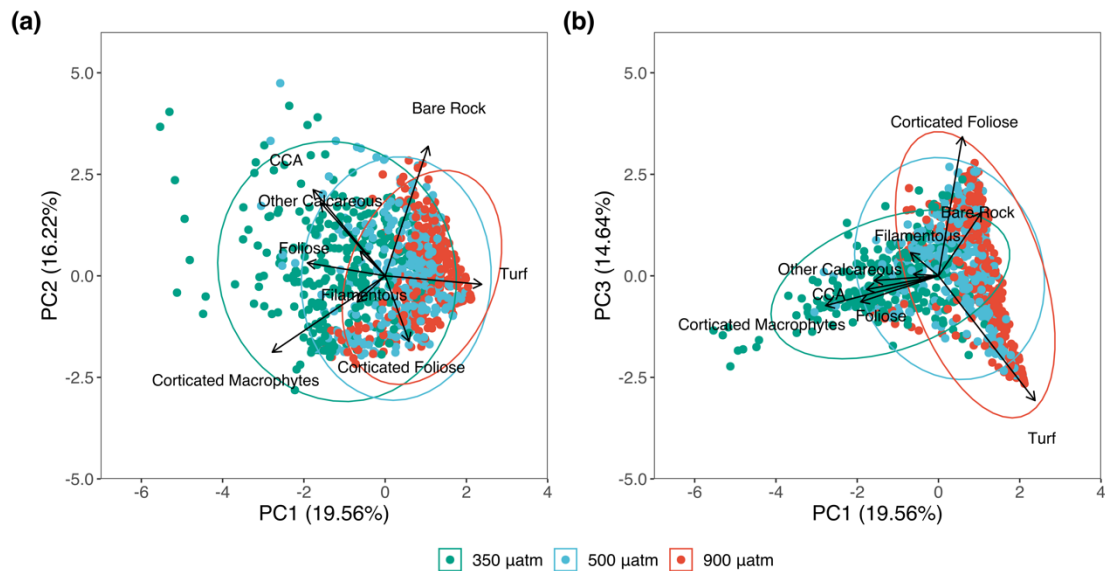


Figure 3. Community composition of algal functional groups between the three locations, 350 $\mu\text{atm CO}_2$ (Green), 500 $\mu\text{atm CO}_2$ (Blue) and 900 $\mu\text{atm CO}_2$ (Red), as assessed by principal component analysis for (a) PC1 vs. PC2 and (b) PC1 vs. PC3. See Figure S2 for comparisons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

OA reduces resistance, but not resilience of algal communities

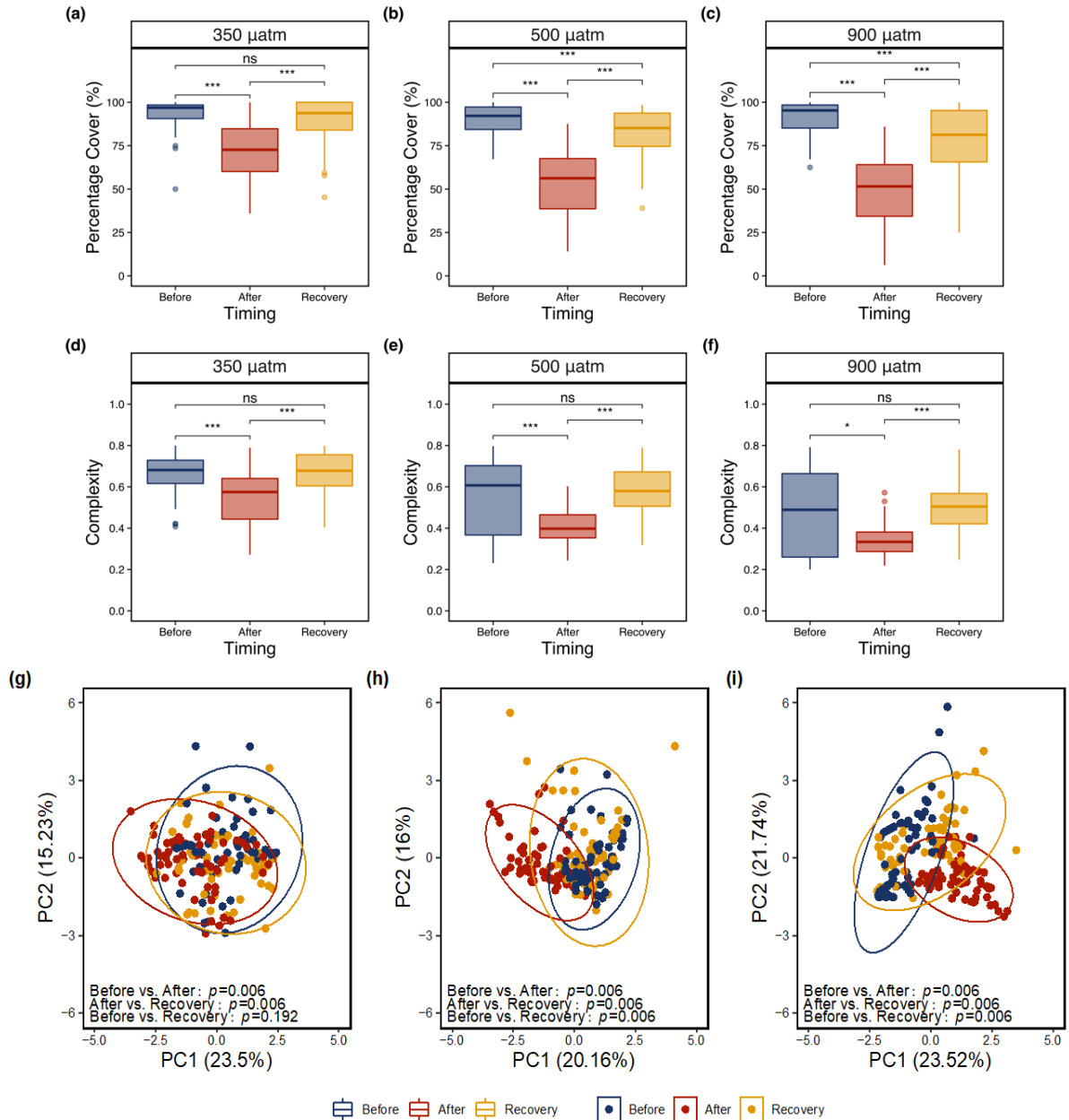
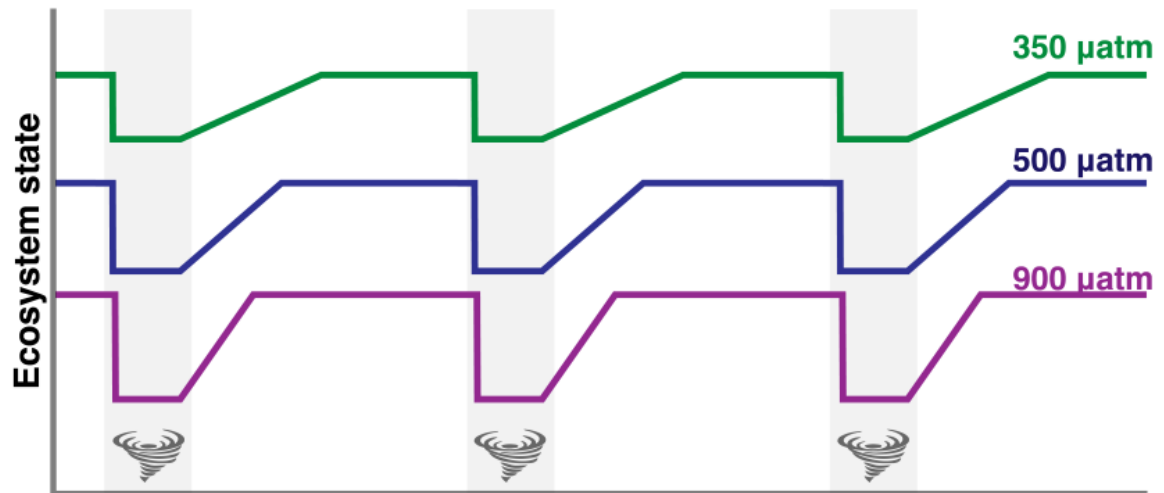
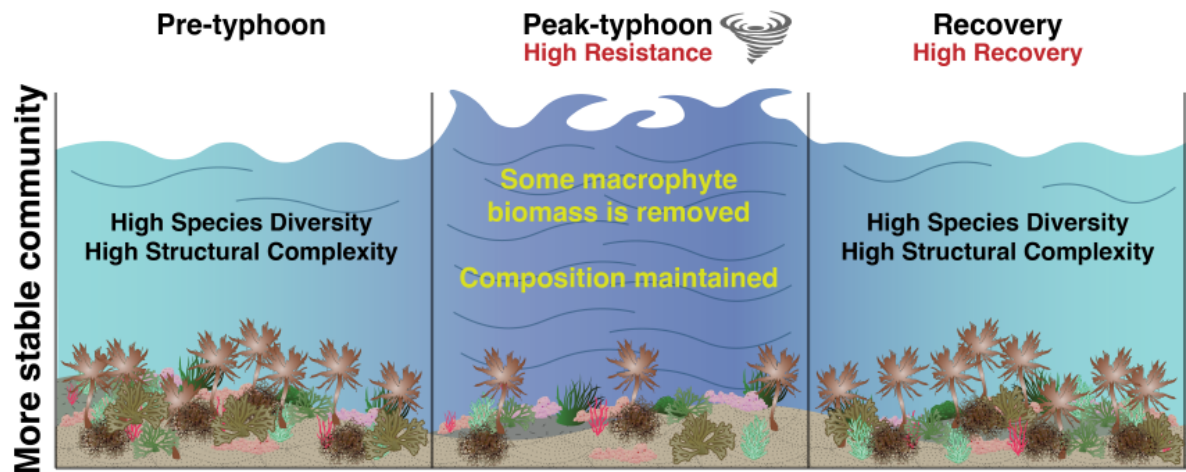


Figure 4. Percentage cover (a-c), complexity (d-f) and composition (g-i) of communities ‘Before’ (Blue) and ‘After’ the typhoon season peak (Red), and the subsequent ‘Recovery’ period (Orange). The 350 μ atm location is shown on the left (a,d,g), the 500 μ atm location in the center (b,e,h), and the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



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

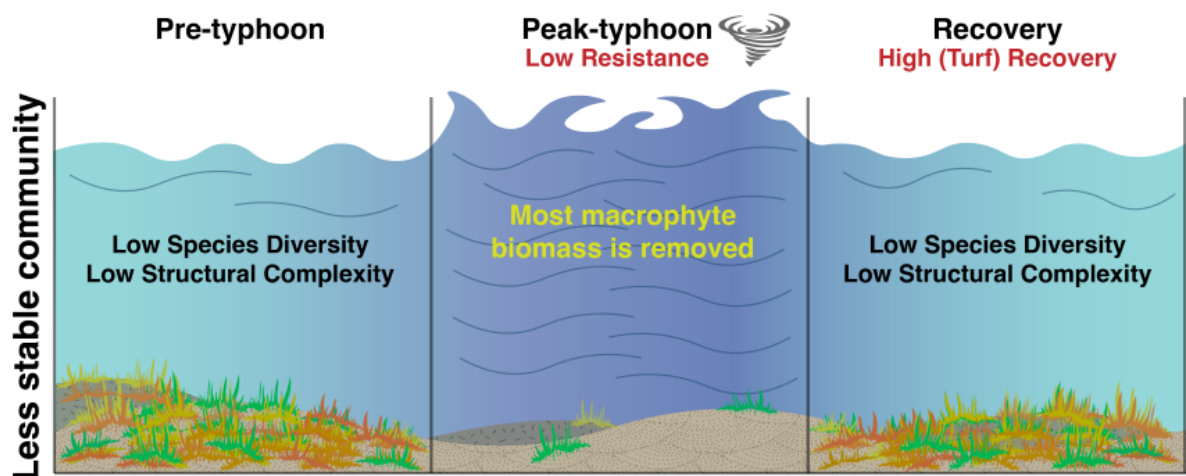


Figure 5. Schematic summary of the differences in community stability between Present-day (350 μatm = Green) and future (900 μatm = Red) CO_2 conditions in response to physical disturbance from typhoons. The ecosystem state of present-day communities is higher than those under future $p\text{CO}_2$ conditions due to persistent press disturbance from ocean acidification (leading to community compositional changes, lower functional diversity, and structural complexity). Through time, ecosystem state fluctuates with seasonal and environmental change (temperature, nutrients, disturbance), with larger fluctuations for acidified communities. Periods of intense ‘pulse’ disturbance from seasonal factors such as typhoons have significant effects on ecosystem state. Differences in the functional traits and life-history strategies of the species forming present-day (macroalgal-dominated) and future (turf-dominated) communities lead to reductions in ecosystem stability. Macroalgal assemblages are resistant to disturbance from typhoons, maintaining a more consistent composition between seasons and recovering to pre-disturbance baselines following physical disturbance. Turf-dominated communities display low resistance to typhoons, which almost entirely removes the algal community, reducing the benthos to bare substrate. Turf resilience, promoted by boosted primary production and growth under elevated $p\text{CO}_2$ conditions, meant that the empty space created was later recolonised by turf algae. In the absence of physical disturbance feedback mechanisms maintain turf-dominance and inhibit macroalgal recruitment (see Harvey et al. 2021). Regular disturbance stabilised this pattern, locking the community into an early successional stage.