Complex interactions among stressors evolve over time to drive shifts from short turfs to macroalgae on tropical reefs

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Abstract. Multiple stressors acting simultaneously on ecological communities are the new normal state. Stressor number and strength will increase with rising anthropogenic activity, making it critical to understand both stressor effects and interactions. Stressor temporal regimes vary in intensity, frequency, and duration, ranging from press to pulse. While stressors with different temporal regimes likely have divergent effects, this remains mostly unexplored, though there is some evidence communities are more resistant to pulse than press stressors. Coral reefs are among the most impacted marine communities, and degradation from coral to algal dominance has been attributed to increases in both local and global stressors. Overfishing, nutrient pollution, and increased sedimentation are all local stressors that have been implicated in shift dynamics. Nutrients and sediments are anthropogenically derived stressors to reefs that can have press and pulse temporal regimes. We conducted a 6-month fully crossed factorial field experiment on algal turf communities in Moorea, French Polynesia, manipulating access by herbivores, enrichment regime, and sedimentation regime and tracked changes in benthic community composition. We found complex interactions among stressors and stressor regimes drove a series of transitions from healthy, short algal turf communities to degraded, long algal turfs, and ultimately to macroalgal-dominated communities. While herbivory controlled final community composition after 6 months, 2- and 3-way interactions among nutrient and sediment temporal stressor regimes over time drove transition dynamics, and matching of stressor temporal regimes accelerated shifts. Some stressors cryptically eroded the resilience of the community, which was only evident when the strong ecological processes that masked these effects were disrupted. Our research highlights the need to consider temporal stressor regime as well as stressor interactions, particularly in light of predicted increases in both local and global stressors and alterations to stressor temporal regimes. Our understanding of the impacts of local stressor temporal regimes is in its infancy. Here, we provide a novel demonstration that the effects of stressor temporal regime varied and multiple stressors interacted to exhibit complex, emergent interaction effects, demonstrating the need to explicitly contrast stressor temporal regimes under multiple conditions to understand how communities will respond to future challenges.

Key words: coral reefs; herbivory; interactions; macroalgae; multiple stressors; nutrients; press; pulse; regime shifts; sediments.

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INTRODUCTION

Multiple stressors acting simultaneously have become the new normal state for ecological communities and are only projected to increase with rising anthropogenic activity, making it critical to understand how multiple stressors act and interact to drive changes in communities
Here, we define a stressor as any natural or anthropogenic pressure or factor that exceeds its natural range and causes a quantifiable change, either positive or negative, to a biological response (similar to Sanderson et al. 2002, Vinebrook et al. 2004, Halpern et al. 2007, Crain et al. 2008, Côté et al. 2016). Historically, stressor interactions have been evaluated in a pairwise framework and are classified as additive, synergistic, or antagonistic (Folt et al. 1999, Darling and Côté 2008, Crain et al. 2008, Côté et al. 2016; but see Piggott et al. 2015 for additional interaction types). Some researchers have suggested some interactions, particularly synergies, may result in ecological surprises—unpredictable non-linear changes in populations, communities, and ecosystems (e.g., Paine et al. 1998, Christensen et al. 2006, Piggott et al. 2015, Fong and Fong 2018). Therefore, interaction type has important ramifications for predicting and managing future scenarios. Crucially, this classification scheme is only useful for understanding pairwise interactions with only two levels, yet ecological communities are usually threatened by more stressors. While some recent research has expanded these classifications beyond a pairwise framework, factors are still constrained to two levels (e.g., Tekin et al. 2018). Therefore, researchers need to evaluate multiple stressors and the potential for higher-order interactions to understand how to expand this conceptual framework, and if expansion is necessary.

Variability in the temporal pattern of a stressor regime adds another layer of complexity to understanding ecological interactions because the framework for classifying interactions has only been developed for cases where each of two factors has two levels. However, stressors can occur along a gradient of intensity, frequency, and duration—ranging from press to pulse—and while stressors with different regimes likely have divergent outcomes, this remains mostly unknown. We build on the conceptual frameworks developed for perturbation dynamics (Bender et al. 1984), disturbance ecology (Sousa 1979, Connell 1997), and resource subsidies (Yang et al. 2008, Fong and Fong 2018, Fong et al. 2020), to differentiate press vs. pulsed stressor regimes. We characterized press stressor regimes as lower intensity, higher frequency, and longer duration and pulse stressor regimes as higher intensity, lower frequency, and shorter duration. This is similar to the schema used to characterize perturbations as pulse or press (Bender et al. 1984), disturbance regimes as episodic (pulse) or chronic (press; e.g., Sousa 1979, Connell 1997), and resource subsidies as pulse or interpulse (press; Yang et al. 2008). Press and pulse stressors represent the extremes and stressor regimes can range along these axes of intensity, frequency, and duration.

Experimental research directly contrasting stressor regimes indicates different temporal stressor regimes have disparate impacts on populations and communities (e.g., Hewitt and Norkko 2007, Molinos and Donohue 2011, Murphy et al. 2012, Hanley et al. 2017, Fong and Fong 2018). Additionally, there is some indirect evidence that press vs. pulse stressors may differ in their impacts. Long-term monitoring data of coral reefs indicate chronic disturbances (press stressors) degrade communities and stunts recovery while episodic disturbance (pulse stressors) induces short-term shifts from which communities can readily recover (Connell 1997), though this may depend on the pulse frequency (Hughes et al. 2019). Thus, the interaction between press and pulse stressors may be particularly potent if press stressors erode community resilience, priming these communities to shift to different states when faced with a pulse stressor, necessitating direct assessment in multiple stressor research.

While stressors occur on both the local and global scale, management of local stressors may be more tractable than enacting global policy change. Direct management of local anthropogenic stressors through the establishment of protected areas has had some success in terrestrial (Gray et al. 2016), freshwater (Saunders et al. 2002), and marine (Halpern and Warner 2002) ecosystems. Additionally, management of local stressors has been proposed as a means of offsetting global change, with some empirical research supporting this assertion (Hughes et al. 2007a, b, 2017, Brown et al. 2013). However, because we still lack a general framework for predicting the effects of multiple stressors and their interactions, exploring the consequences of these local, manageable stressors is valuable, particularly in light of projected continued global change.
Coral reefs are among the most impacted marine communities, and degradation from coral to algal dominance has been attributed to increases in both local and global stressors (Hughes 1994; Scheffer et al. 2001; Bellwood et al. 2004; Halpern et al. 2007, 2008; Hughes et al. 2007a, b, 2017). While shifts to macroalgae after a disturbance that removes coral are considered negative (Bellwood et al. 2004), shifts to closely cropped, highly productive algal turfs may represent natural transition states and are an abundant component of healthy reefs, particularly following disturbance (Bellwood et al. 2006, Mumby 2009, Vroom 2011). Short productive algal turfs are abundant, highly productive components of coral reef communities, and are the preferred resource for many herbivores (Adey and Goertemiller 1987, Vroom et al. 2006, Vroom 2011, Tebbett and Bellwood 2020). Thus, short algal turfs are comprised of heavily grazed, closely cropped algal filaments. Short algal turfs have the highest productivity of any reef space holder and mediate transitions from coral to macroalgal community dominance (Adey and Goertemiller 1987, Bellwood et al. 2004, Vroom et al. 2006, Muthukrishnan et al. 2016).

Short algal turfs dominate in early successional recovery toward coral dominance as juvenile corals can recruit to short, sediment-free algal turfs (Connell 1997, Birrell et al. 2005, Adam et al. 2011). Strong herbivory, low nutrient availability, and low sedimentation all maintain short-cropped turfs, at least over the short term (Fong et al. 2018). However, if these controlling forces are altered, turfs may transition to poor quality longer turfs that accumulate deep layers of sediments and have reduced productivity (Fong et al. 2018, Tebbett and Bellwood 2020). These long turfs may inhibit recovery because they experience reduced grazing and inhibit coral settlement, and some research suggests long, sediment laden turf may be an early indicator of community degradation (Birrell et al. 2005, Goatley et al. 2016). Further, long turfs are less productive and are thus provide less food chain support, a crucial service in this system (Tebbett and Bellwood 2020). Over the longer term, long turfs may transition to mature, fleshy macroalgal communities via growth of cropped thalli or successful recruitment and growth of macroalgal propagules (Lewis 1986, Bellwood et al. 2004, Birrell et al. 2005, Smith et al. 2010, Goatley et al. 2016, Fong et al. 2018). Short-term experimental work has demonstrated that press stressors of decreased herbivory, increased nutrients, and increased sediment interact simultaneously to shift short algal turfs to longer turfs (Fong et al. 2018). However, it remains unknown how temporal stressor regime may impact turf communities and regulate potential shifts to macroalgae over longer time scales and with pulse regimes.

Nutrients and sediments can enter coral reef communities in both press and pulse temporal regimes. Thus, contrasting these temporal regimes and understanding interactions among these stressors and herbivory on transitional algal turfs are not only of significant theoretical interest, but also critical to reef conservation. Temporal nutrient regimes can change from press to pulse, and transitions may be mediated by human activities. For example, extreme rainfall events associated with climate change can transport nutrients from land to sea, producing a short-duration, low-frequency, and high-magnitude elevation in nutrient concentrations, i.e., a pulse temporal stressor regime (Clausing and Fong 2016, Fong and Fong 2018). In Moorea, Fong et al. (2020) documented extreme rainfall events that elevated nitrogen concentrations by over 100-fold over baseline. Nutrient inputs can also have a press temporal stressor regime, where they are transported into reef communities more steadily over a longer duration with high frequency and low magnitude, such as via run-off due to coastal development, leaking septic tanks, and sewage outfalls (Smith et al. 1981, Dollar and Atkinson 1992, Fabricius 2005).

Sediment inputs can also vary from press to pulse events that may be mediated by human impacts. Rain-driven terrestrial run-off from storms and wind-driven resuspension of benthic sediments can provide episodic increases in sediment for a short duration with low frequency and high magnitude, generating a pulse temporal stressor regime (Larcombe et al. 1995, McCulloch et al. 2003, Goatley et al. 2016). In contrast, urban development and deforestation can consistently increase sedimentation for a longer duration with high frequency and low magnitude, resulting in a more press temporal stressor regime (McCulloch et al. 2003, Maina et al. 2013). Thus, coastal coral reefs can be threatened by
both press and pulse nutrients and sediments temporal stressor regimes in addition to overfishing (Bellwood et al. 2004).

Our objective is to determine how reduced herbivory interacts with press vs. pulse nutrient and sediment temporal stressor regimes to drive changes to naturally occurring coral reef algal turfs using a manipulative field approach.

**METHODS**

**Study site**

We conducted this study in Moorea, one of the Society Islands in French Polynesia. This is a high volcanic island that formed 1.5–2 Ma and is typical of the islands in the South Pacific (Neall and Trewick 2008). The island has a barrier reef 0.5–1.5 km offshore with a series of passes that allow oceanic flushing (Leichter et al. 2013). Moorea experiences a warm, wet season from November to April and a cooler, drier season between May and October.

Moorea has two large bays on the northern shore likely formed by river basins that filled during sea level rise in the Holocene (Fig. 1). These bays are 20–30 m deep and rimmed by fringing reefs. Both bays are close to oceanic passes and regularly flushed. During large storm events, to balance the increased water transport into the lagoon, these reef passes may transport surface waters out of the lagoon, onto the fore reef and offshore (Leichter et al. 2013).

Some coral reefs may more readily recover from coral loss, displaying high resilience; given the catastrophic loss of reefs globally, research focusing on these reefs may be particularly useful. Moorean reefs are highly resilient, twice returning to high coral cover within a decade of disturbance (Adjeroud et al. 2009, Edmunds et al. 2019). On the fringing reef, researchers have found variable but no long-term trends in coral cover or herbivorous fish abundance between 1983 and 2014, during which the island experienced four hurricanes and two crown of thorns outbreaks (Galzin et al. 2016). In 2008, there was a shift in community composition where corals declined and macroalgal abundance increased; however, algal turf abundances remained stable at ~40% benthic cover (Adam et al. 2011, Schmitt et al. 2019). While coral cover has generally recovered on the forereef, recent evidence suggests the lagoon has been less resilient and appears to be characterized by macroalgal vs. turf alternative stable states (Schmitt et al. 2019).

We worked on a fringing reef in the lagoon in the northwestern corner of the mouth of Cook’s Bay along the north shore (17°28′52.86″ S, 149°49′04.88″ W). This is a fringing reef behind the reef crest and is thus protected from high waves. Further, this reef is within a marine protected area where fishing is banned. This reef is characterized by live coral heads and dead coral heads covered in short turfs and some macroalgae interspersed with sand patches. Our site was approximately 1 m deep, and reefs in Moorea have negligible tidal amplitude (Hench et al. 2008).

We chose this site because it is dominated by closely cropped, short algal turfs with little sediment, our community of interest. This short turf dominance underscores the potential of this site to recover. At this site, we measured initial turf heights at an average of 1.68 ± 0.03 (SE) mm while sediment depth averaged 0.67 ± 0.04 (SE) mm. This is shorter than the proximal Gump Reef (17°29′24.28″ S, 149°49′32.96″ W), where turf height was 2.68 ± 0.15 (SE) mm as well Melissa’s Red Bouy (17°28′52.86″ S, 149°49′04.88″ W), the navigational marker in the back reef on the northeast side of the bay, where turf height was 2.14 ± 0.22 (SE) mm (Gaynus 2019).
Experimental design
We conducted a full factorial field experiment on natural algal turf communities manipulating access by herbivores, and nutrient and sediment temporal regimes. All of our experimental manipulations were conducted against the natural background variation of herbivory, nutrient availability, and sedimentation rate. Our overall approach (details below) was to manipulate herbivores in two levels, access and no access, while nutrients and sediments had three levels: ambient, press, and pulse additions. We marked off experimental plots that were $15 \times 15$ cm$^2$ areas of 100% natural algal turfs on dead coral heads. At the start of our experiment, turf was short (see above) and sediment depth averaged $0.67 \pm 0.04$ mm (SE). Plots were assigned randomly to 1 of 18 treatments. Each treatment was replicated 10 times for a total of 180 experimental units. To minimize any spillover effects of nutrient and sediment treatments, plots were separated by at least 1 m. The entire experiment spanned a $25 \times 50$ m span of reef.

To simulate the effects of overfishing, we limited access to herbivores by fully caging half the plots to exclude herbivorous fishes. Cages were constructed from metal mesh with $1 \times 1$ cm openings (as in Fong et al. 2018). Cages were $15 \times 15$ cm square enclosures that were 15 cm tall and enclosed our natural algal turf communities. Cage lids were of the same material and attached to the top so that cage lids could be lifted and replaced to measure the benthic community. Cages included a 5-cm skirt used to nail the cage flush to the benthos and limit access to invertebrate grazers. To control for cage effects, plots that herbivores could access also had the $15 \times 15$ cm enclosures with the 5-cm mesh skirt used to nail the cage to the benthos; however, these cages were only 5 cm tall and without a lid. Similar cages and cage controls have been used on algal turf communities with no measurable change in flow or herbivorous fish visitation (Clausing et al. 2014). Cages were scrubbed and repaired monthly.

To create ambient, press, and pulse nutrient treatments, we left ambient treatments unmanipulated seawater and used Osmocote slow release fertilizer to provide added nutrients for both press and pulse nutrient treatment plots (Fong and Fong 2014, Fong et al. 2018). This slow release fertilizer is comprised of 19:6 nitrogen: phosphorus. For our press nutrient treatments, 50 g of fertilizer was bundled in nylon mesh, encased in caging material, and attached to the skirt of the cage. We chose this amount of fertilizer based on Gil et al. (2016), where 50 g of Osmocote resulted in intermediate nutrient concentrations where coral growth was maximal. Press nutrient bags were changed every month to maintain elevated nutrient treatment concentrations (as in Smith et al. 2010). It is important to note that enrichment levels using this method decrease through time, so treatments may have been more akin to a series of ramped pulses as opposed to an absolutely stable press treatment. For our pulse treatments, 300 g of fertilizer was applied to plots in a similar fashion, but in a single pulse of enrichment, bags were removed from plots after 1 month. Un-enriched plots had empty nylon bags to control for any flow effects of the treatment.

To create ambient, press, and pulse sediment treatments, we left ambient treatments unmanipulated and added sediment from the site to the press and pulse treatment plots (Goatley and Bellwood 2013, Clausing et al. 2014, Muthukrishnan and Fong 2014, Gil et al. 2016). For our press treatments, we added a 50 mL volume of sediment collected and applied immediately in the field every month for the duration of the experiment. To compare these treatments to other studies, we took three replicate samples of 50 mL and 300 mL and dried the sediment to a constant dry weight. Our 50 mL treatments added 56.2 ± 2.3 (SE) g, or an average of 8.2 ± 0.3 (SE) mg·cm$^{-1}$·d$^{-1}$, while our 300 mL treatments added 290 ± 6.1 (SE) g, or an average of 43.0 ± 0.9 (SE) mg·cm$^{-1}$·d$^{-1}$. These treatments were chosen because they fall within the range of other impacted reefs (see Gil et al. 2016 for a summary table). For our pulse treatment, we added 300 mL of sediment in the first month of the experiment only. Sediment was measured volumetrically in the field and applied in an even layer on the plot. Sediment was collected directly from the benthos adjacent to the plot to model resuspension.

Our experiment was conducted over a 6-month period, beginning on 28 April 2017 and ended on 28 October 2017.
Changes in benthic community

Every month, we surveyed the benthic community in our plots and identified all algae to the lowest taxonomic unit possible in the field, hereafter called community members. Plots were surveyed with a 10 x 10 cm 25-point intercept quadrat. We identified the benthic community member under each intercept and used these data to estimate percent cover. If sediment covered the intercept, we gently removed it with a pencil tip and then replaced it after we identified the underlying benthos. There were three groups we were unable to identify to species in the field and were thus grouped by functional form. Short algal turf was defined as turf <1 cm, long algal turf was defined as turf >1 cm, and crustose coralline algae were classified as a functional form group (Fong et al. 2018, but see Littler and Littler 1980 who define short turf as <2 cm, and Burklepile and Hay 2010 who define turf as <0.5 cm). Recent research indicates productivity drops off asymptotically as turf height increases, where productivity seems minimal after 1 cm heights are reached, highlighting the significantly differing functions of short and long algal turfs (Tebbett and Bellwood 2020).

Analysis

To understand how our treatments impacted final community structure, we analyzed benthic community composition at the end of the experiment with a multivariate 3-factor permutational MANOVA in R using the adonis function in the vegan package (permutations = 9999).

We also analyzed the effects of our treatments over time on each benthic community member comprising an average of at least 5% of the benthos. These data did not meet the assumptions of parametric statistics; thus, we conducted permutational ANOVAs using the avoperm function in the permuco package in R. We chose this analysis because it makes no assumptions about the underlying distributions of the data. These analyses were constructed with our four factors (herbivory, nutrients, sediments, and time) as fixed categorical independent variables (permutations = 5000). Our dependent response variables were percent covers for each community member.

To understand how our treatments impacted general patterns of change in community structure over time, we used an ordination approach to visualize changes in the community over time. We visualized trajectories of each treatment by plotting changes in community composition in multivariate space using non-metric multidimensional scaling (nMDS). Our time points included monthly sampling over the 6 months of manipulation. Tropical macroalgae are very diverse, and some species were extreme outliers that were found in only a handful of plots; to reduce this noise, we only included community members present in >1% of surveys across all time periods in this visualization. We used the metaMDS function, projecting into two dimensions and using Euclidean distances. We used the envfit function to find the centroids for each treatment at each time point, which we used to plot community trajectories over time. We then used the ordiplot function to generate the loading vectors for each community member. All of these functions are from the vegan package (Oksanen et al. 2015) in the R programming language (R Core Team 2014).

RESULTS

At the end of the experimental disturbance, only caging had a significant effect on final community composition (Table 1). However, interactions among herbivory, nutrients, and sediments determined the rate of transitions and changes in abundances of individual dominant (>5%) community members (Table 2). Plots that shifted to macroalgae were dominated by Padina boryana and Lobophora variegata, though P. boryana was overall more abundant.

Loss of short turf

Short algal turfs experienced a complex 4-way interaction between all factors and time (Table 2, Fig. 2). Thus, all treatment combinations resulted in unique trajectories of change and this benthic functional group showed the most varied response to our experiment. While all plots started at 100% short algal turf cover by design, after 6 months, short algal turf abundance ranged from 0% to 100%.

When herbivores were excluded, communities rapidly shifted away from short algal turfs, and by the end of the experiment, all plots with herbivores excluded had less than 25% short algal turf cover (Fig. 2a–c). Overall, loss of short turfs
began in the first month for most treatments and accelerated through the fourth month before generally leveling off below ~25%. However, nutrient and sediment treatments interacted in complex ways over time resulting in different rates of change which were most pronounced in the first four months (Fig. 2a–c). Overall, interactions between nutrients and sediments determined the speed of loss of short turfs within caged treatments, though after 5 months of manipulation, all treatment combinations had less than 25% short turf.

When nutrients were available at ambient levels, treatments with ambient sediment additions lost short turf the most rapidly while both press and pulse sediment additions slowed short turf loss to a similar degree (Fig. 1a). However, after 3 months of manipulation (July), this difference had disappeared, and sediment addition no longer impacted short turf abundance. In the last 3 months of manipulation, short turf abundance had stabilized at below 25% in caged, ambient nutrient treatments across all sediment treatments.

When nutrients were supplied with press availability, loss of short turf was even across all sediment addition levels and comparable to the loss in the caged ambient nutrient + ambient sediment treatment (Fig. 1b). In August, ambient sediment treatments regained some short turf, though by the end of manipulation, all sediment treatments had comparable short turf abundance. In the last 2 months of manipulation, short turf abundance had stabilized at below 25%, though treatments with pulse sediment additions had markedly lower short turf abundance. In fact, treatments with pulse sediment additions had transitioned completely away from short algal turfs in the last 2 months of manipulation.

When nutrients were supplied with pulse availability, sediment treatment appeared to have no impact on loss of short turf. Short turfs steadily declined in abundance across all

| Factor | df | F-Ratio | P   |
|--------|----|---------|-----|
| C      | 2  | 149.655 | 0.0001 |
| N      | 2  | 0.4463  | 0.7961 |
| S      | 1  | 1.722   | 0.1277 |
| C × N  | 4  | 0.830   | 0.5128 |
| C × S  | 2  | 1.322   | 0.2536 |
| N × S  | 2  | 0.994   | 0.4355 |
| C × N × S | 4 | 0.597   | 0.8175 |

Bold indicates significant values.

Table 1. Results of final community 3-factor permutational MANOVA on benthic composition in response to our cage (C), nutrient (N), and sediment (S) treatments at the end of the experiment, conducted in R using the adonis function (n = 9999).

| Factor | Short algal turf | Long algal turf | Padina boryana | Lobophora variegata |
|--------|-----------------|-----------------|----------------|---------------------|
| C      |                 |                 |                |                     |
| N      |                 |                 |                |                     |
| S      |                 |                 |                |                     |
| C × N  | 1180.768        | 0.0002          | 77.79          | 0.0858              |
| C × N  | 33.285          | 0.5412          | 13.69          | 0.7334              |
| C × N  | 53.435          | 0.3740          | 46.88          | 0.3852              |
| C × N  | 99.283          | 0.1528          | 31.29          | 0.5298              |
| C × N  | 2.647           | 0.9492          | 32.96          | 0.5100              |
| C × N  | 68.456          | 0.6370          | 116.63         | 0.3196              |
| C × N  | 168.478         | 0.1826          | 97.91          | 0.4120              |
| T      | 27464.03        | 0.0002          | 2138.73        | 0.0002              |
| T × C  | 18214.21        | 0.0002          | 1701.52        | 0.0002              |
| T × N  | 26.046          | 0.6092          | 57.52          | 0.3152              |
| T × S  | 120.178         | 0.1126          | 176.31         | 0.0314              |
| T × C  | 207.924         | 0.0194          | 123.13         | 0.0794              |
| T × S  | 5.651           | 0.9022          | 126.27         | 0.0828              |
| T × C  | 189.764         | 0.1404          | 200.98         | 0.0930              |
| T × S  | 279.252         | 0.0336          | 110.26         | 0.3532              |

Note: Factors included cage (C), nutrient (N), sediment (S), and time (T) as well as all possible interactions. Bold indicates significant values.
sediment treatments for the first 4 months (Fig. 1c). Like with the press nutrient treatments, short turfs stabilized across all sediment treatments with abundance below 25% for the last 3 months of manipulation.

When herbivores had access, the benthic community generally remained dominated by short algal turf, though the majority of treatments experienced some loss in short turfs (Fig. 2d–f). When herbivores had access, only when no nutrients were added, and sediments were pulse did plots remain 100% short algal turfs (Fig. 2d). In all other treatment combinations, short algal turfs decreased. However, the pattern varied across treatment combinations.

When temporal stressor regime aligned, we observed the greatest loss in short turf abundance. The unique combination of pulse nutrients + pulse sediment resulted in the lowest abundance of short algal turfs at 62 ± 16.5 (SE) percent cover in the final sampling period (Fig. 2f). Similarly, the unique combination of press nutrients + pulse sediment resulted in the second lowest abundance of uncaged short turfs at 75.2 ± 13.4 (SE) percent (Fig. 2e). In comparison, the other seven uncaged treatments had an average of 95.8 ± 1.1 (SE) percent in October and were thus still predominantly short turf. Finally, when uncaged and under ambient nutrient availability, plots with ambient sediment lost the most turf, though loss was minimal with a final short turf abundance of 94.4 ± 2.9 (SE) percent (Fig. 2d).

**Transitions to long turf**

Long algal turfs developed over time both in response to both reduction in herbivory and addition of sediment, evidenced by significant time × cage and time × sediment interactions (Table 2, Fig. 3). In contrast, nutrient treatments did not drive transitions to long algal turf. Rather, both herbivore removal and sediment additions acted independently over time to increase cover of long turf.

When herbivores were excluded, long algal turfs increased in abundance over time and at the end of the experiment was >10× more abundant in caged plots. This effect did not depend on nutrient, or sediment treatment. Long turfs developed rapidly and were evident in most treatment combinations after 1 month, though development was highly variable. Over 6 months, long algal turfs increased from 0 to 27.1 ± 4.6 (SE) percent across all caged plots (Fig. 2a–c).

In contrast, long algal turfs only increased 0 to 2.3 ± 1.5 (SE) percent across all uncaged plots (Fig. 2d–f). In addition, cover of long turfs was
only measurable at the end of the experiment in plots open to herbivores in when nutrient and sediment temporal stress regimes matched, with long turfs developing only in press nutrients when sediments were press and pulse nutrients when sediments were pulse.

Sediment treatment also drove development of long algal turf, independent of herbivore or nutrient treatment. While less long turfs developed in uncaged plots, the patterns of development were similar in caged and uncaged plots. Overall, the least amount of long algal turfs developed when no sediment was applied (9.5 ± 3.5 [SE] percent across all caging and nutrient treatments). However, this pattern varied over time, where early on, long turfs developed the most in ambient nutrient, caged treatments. Overall, press sediment addition increased long turfs more than pulse, by ~45% vs. ~30% cover of long turf, respectively.

Transitions to macroalgae: Padina boryana

Padina boryana increased in cover over time across all caged treatments (Fig. 4a–c). In contrast to long turf, P. boryana took over a month to develop within cages. However, by the end of the 6-month experiment, P. boryana was the most abundant species of macroalgae, and the most abundant space holder, covering an average of 53.1 ± 5.1 (SE) percent of the benthos across all sediment and nutrient treatments. Padina boryana never developed substantial cover in plots exposed to herbivores. Overall, the development of P. boryana cover was influenced by a significant time × cage × sediment interaction (Table 2).

When herbivores were excluded, P. boryana increasingly dominated the benthos over time, though this dominance depended on sediment treatment. Padina boryana abundance was highly variable across nutrient addition treatment, and while it appears pulse nutrients stunted P. boryana development, this was not statistically significant. Within cages, ambient sediment treatments showed the most rapid development of P. boryana; both press and pulse sediment additions slowed development in the first few months.

After 4 months of manipulation, differences in P. boryana were most evident across sediment treatments with the most development in ambient, then press, then pulse treatments. When sediments treatment was ambient, P. boryana abundance was highest at 46.0 ± 7.1 (SE) percent of the benthos across nutrient treatments (Fig. 4a–c). When sediments were added in a

Fig. 3. Changes in percent cover of the long algal turf over the 6-month experiment. Points are means ± SE.
press treatment, *P. boryana* comprised 32.4 ± 6.8 (SE) percent of the benthos across nutrient treatments (Fig. 4a–c). When sediments were added in as a pulse treatment, the least amount of *P. boryana* developed at 22.6 ± 5.5 (SE) percent of the benthos across nutrient treatments.

However, at the end of 6 months, the difference between ambient and pulse sediment addition treatments had dissipated. By the end of the experiment, *P. boryana* was equally high in ambient and pulse sediment treatments at approximately 60% of the benthos, which was roughly 50% higher than in press sediment treatments.

In contrast to sediment and herbivory treatments, nutrient treatments did not affect cover of *P. boryana*, which grew equally well across all nutrient subsidy regimes.

*Padina boryana* was a negligible community member when herbivores had access to plots, never exceeding 4% cover (Fig. 4d–f).

### Transitions to macroalgae: Lobophora variegata

Overall, *Lobophora variegata* dominated far less of the benthic cover than other dominant community members, never achieving cover greater than 25%. *Lobophora variegata* experienced significant time × cage × nutrient and time × sediment interactions (Table 2, Fig. 5). *Lobophora variegata* developed both inside and outside of cages; thus, herbivory alone was unable to control this species when complemented with other stressors. By the end of the manipulation, more *L. variegata* developed in more treatments with herbivore access, comprising 4.7 ± 2.1 (SE) percent of the benthos within cages and 7.0 ± 2.3 (SE) percent of the benthos in uncaged treatments (Fig. 5d–f).

Herbivory and nutrients interacted over time to drive *L. variegata* abundance. Overall, the effect of nutrients depended on herbivory treatment. After 6 months of manipulation, when nutrients were ambient, *L. variegata* was more abundant when protected from herbivores across sediment treatments, though abundance varied substantially over time (Fig. 5a, d). In contrast, under press temporal nutrient subsidy regimes, more *L. variegata* developed in plots exposed to natural herbivory across sediment treatments (Fig. 5b, e). Finally, when pulse nutrients were supplied, across sediment treatments, herbivory treatment did not influence patterns of *L. variegata* abundance (Fig. 5c, f).

*Lobophora variegata* also experienced a significant time × sediment interaction and a moderately significant time × cage × sediment interaction. Overall, both pressed and pulsed
sediment treatments increased _L. variegata_ abundance. However, matching of temporal stressor regime appeared to result in greater final abundances of _L. variegata_. When sediments were applied as a press addition, the presence of pressed nutrients drove highest final abundance of _L. variegata_, irrespective of cage treatment (Fig. 5b, e). Similarly, when sediments were supplied as a pulsed addition, pulse nutrients drove the highest overall abundance of _L. variegata_ across cage treatments (Fig. 5c, f).

**nMDS visualization**

Visualization of the data with an nMDS helps summarize and synthesize individual overall patterns of changes in community composition (Fig. 6). All plots began with 100% short turfs by design, which is where all trajectories begin (Fig. 6). The loading plot from the nMDS shows how directional changes in space relate to different community members, where vectors show direction and length indicates strength (Fig. 6). Dominant community members were short turf, long turf, _Padina boryana_, and _Lobophora variegata_. While <5% of the benthos, community members included _Chladophora patentiramea_, CCA, _Dictyota bartyrensia_, _Dictyota fragilis_, _Halimeda spp._, _Syrupdia filamentos_, and _Turbinaria ornate_.

When caged, all plots shifted away from dominance by short turfs (Fig. 6a–c). Overall, the greatest change in benthic community structure occurred over the first four time points. When nutrients were ambient, press sediment treatments diverged substantially around the 4-month mark, though this divergence resolved by the end of manipulations, and all treatments were relatively tightly clustered. When nutrients were supplied in press additions, trajectories in the first month were similar across sediment treatments. Afterward, treatments continued to shift, with the greatest differences between press and pulse sediments. Overall, press treatments developed more long turfs while pulse treatments developed more _P. boryana_, evident from both the loading plot (Fig. 6) and the patterns of individual community members (Figs. 3b and 4c). When nutrients were in supplied as pulses, the ambient sediment treatment had the most direct and even trajectory, mostly toward _P. boryana_, evident in the loading plot and pattern of _P. boryana_ development (Fig. 4c). In contrast, the pulse nutrient + pulse sediment treatment experienced the most change in community composition.

When uncaged, most plots did not change substantially from short turf. However, the nMDS
Fig. 6. nMDS plots for our nine caged treatments over time. Ambient sediments are shown in panels (a) and (d), press in (b) and (e), and pulse in (c) and (f). Ambient sediment is shown in blue, press in yellow, and pulse in red. Ambient sediments are shown as solid lines, press in short dashes, and pulse in long dashes. Treatments all start at the same point (100% short algal turf), and time points are connected by lines. The final time point is larger than the other points with an arrow pointing to the final state for clarity. The nMDS loading plot with dominant community members has been imbedded within the figure, with vectors indicating loading and direction.

visualization highlights the role of stressor matching in driving changes in community composition. For example, the combination of pulse nutrients + pulse sediments resulted in the greatest change from short turfs (Fig. 6f) followed by the combination of press nutrients + press sediments (Fig. 6e).

DISCUSSION

We found complex interactions among multiple stressors drove a series of transitions from healthy, short algal turf communities to degraded, long algal turfs, and ultimately to macroalgal-dominated communities. While
herbivory controlled final community composition, 2-and 3-way interactions among nutrient and sediment temporal stressor regimes over time drove transition dynamics, and matching of stressor temporal regimes accelerated shifts. We found some stressors cryptically eroded the resilience of the turf community, which was only evident when the strong ecological processes that masked these effects were disrupted. Thus, our research highlights the need to consider temporal stressor regime as well as stressor interactions, particularly in light of predicted increases in both local and global stressors and alterations to stressor temporal regimes.

Complex interactions among multiple stressors drove transitions to degraded communities

Our results provide strong motivation to focus more research on complex, non-linear, higher-order interactions to further our understanding of what drives shifts from healthy to degraded communities. We show that a 4-way interaction, among three local stressors that developed over time, initiated transitions away from short, healthy algal turfs to longer turfs, an unhealthy community state. Because increases in both local and global stressors are predicted for the future (Halpern et al. 2008, Hughes et al. 2017), our research demonstrates the need to expand our assessment of multiple stressors to include more factors. Most studies on multiple stressors have focused on pairwise interactions (Crain et al. 2008), and we suggest three drivers of this pattern. First, the framework for classifying non-linear interactions typically relies on a 2-factor design and is typically constrained to two levels per factor; this is because increasing numbers of stressors makes assessment of emergent properties incredibly complex (Crain et al. 2008, but see Tekin et al. 2018). Second, the addition of a third stressor increases the number of treatments required for a fully factorial design, presenting a logistical challenge. Finally, interpretation of these complex, interactive results can be extremely challenging, even in well-studied systems (Armitage and Fong 2004).

However, our results support other research that demonstrated the application of a third stressor often changes the type and even direction of interactions, which underscores the need to expand multiple stressor research to more than pairwise interactions (Crain et al. 2008, Fong et al. 2018). For example, in a meta-analysis of anthropogenic stressors, Crain et al. (2008) found when a third stressor was applied to an interaction pair, the interaction pair changed classification 64% of the time. This is supported by our recent research on turfs, where the presence of a third stressor always changed the classification of a pairwise stressor (Fong et al. 2018). Human impacts have only accelerated, and most communities are threatened by multiple stressors (Halpern et al. 2007, Ban et al. 2014, Halpern et al. 2007). Thus, while challenging, it is important to continue to address multiple stressors simultaneously in ecological research because studying stressors in isolation or in pairs limits predictions to natural communities that are typically subjected to more stressors.

Time-series data may be particularly crucial for understanding and interpreting experiments with multiple stressors because stressors may vary in strength and take effect on different time scales. While herbivore exclusion was the only factor driving final benthic community composition, complex interactions among stressors and time drove the rate of change of species and functional groups of algae over the course of the manipulation. All four of the dominant community members had at least one interaction between a stressor and time, and crucially, short turfs experienced a 4-way interaction among all stressors and time. Thus, complex interactions among our three stressors and time dictated the rate and trajectory of shifts away from short turf. Other experiments manipulating three stressors on benthic communities on coral reefs consistently have found multiple complex non-linear interactions among stressors that often develop on different time scales; for example, herbivory typically has the most rapid effects while nutrient and sediment effects take more time to develop (Muthukrishnan and Fong 2014, Fong et al. 2018). Our study indicates time-series data may help reveal complex interactions among stressors that develop over time to drive transition dynamics.

While herbivory had the greatest influence on transitions, we provide field evidence that nutrients and sediment may facilitate slow transitions from turfs to macroalgae, even in the presence of herbivores. The unique matching of nutrient and
sediment temporal stressor regimes, pulse nutrients + pulse sediments and press nutrients + press sediments, both eroded the resistance of short algal turf communities. Similar to our results, Muthukrishnan and Fong (2014) found the combination of nutrients and sediments could drive shifts away from coral dominance over time, even with full herbivore pressure. This shift may occur with ambient herbivory pressure because sediment can suppress herbivory on both turfs and macroalgae, paralleling the effects of overfishing (Bellwood and Fulton 2008, Goatley and Bellwood 2012, Clausing et al. 2014, 2016, Fong et al. 2018). Further, sediment also can have positive effects on both turfs and macroalgae independent of suppressing herbivory, possibly by supplying additional, sediment-associated nutrients (Clausing et al. 2016, Fong et al. 2018). Thus, while herbivory is a well-established driving process on reefs (Bellwood et al. 2004, Hughes et al. 2007, Muthukrishnan and Fong 2014), nutrients and sediments are also important drivers of coral reef communities and can drive shifts away from a healthy, short algal turf-dominated community state.

**Stressor temporal regime drove transition dynamics and matches between stressor temporal regime accelerated transitions**

Temporal stressor regimes resulted in different trajectories and speeds of shifts in community composition. Our research dovetails with the framework used to compare the magnitude, frequency, and/or duration of perturbations (pulse/press), disturbances (episodic/chronic), and subsidies (pulse/interpulse; pulse/press) and comparisons and integration with this body of research may be useful for understanding the impact of stressor temporal regimes on communities. We found divergent trajectories and speeds of shifts in community states in pressed vs. pulsed stressor treatments. This does not line up with some research on perturbation and disturbance ecology. For example, research in the perturbation literature suggests populations and communities can recover following pulse perturbations while press perturbations fundamentally shift communities and populations (Bender et al. 1984). Similarly, some research suggests communities recover more readily from episodic than chronic disturbances (Connell 1997). However, we did not find recovery, rather complex interactive dynamics over time. Our research does line up with studies on pulse-interpulse dynamics, which show pulsed subsidies can have long-lasting effects on populations and communities (Ostfeld and Keesing 2000, Lundsten et al. 2010). We suggest this is because our subsidies, particularly nutrients, are a resource and do not cause mortality, a key characteristic of both perturbation and disturbance dynamics. Thus, we suggest temporal regime be fully and explicitly incorporated in research on stressors, particularly to recovering communities.

Press and pulse stressor temporal regimes had divergent effects on our community members that were likely driven by their individual traits. Our finding that community members responded differently to stressor temporal regime is similar to previous research that found different species won under press vs. pulse nutrient additions (Fong and Fong 2018). These differences are likely trait based and the result of trade-offs, which aligns with other research on variation in tolerance to perturbations, disturbances, and stressors. Our findings support previous research demonstrating some community members are more tolerant of low-frequency, high-magnitude stressors while others are more tolerant of high-frequency, low-magnitude stressors (Vinebrooke et al. 2004, Grime and Pierce 2012, Fong and Fong 2018). This trade-off is a logical expansion of the persistor/opportunistic, disturbance tolerant/sensitive, and stress tolerant/intolerant strategies commonly found in ecological communities (Stearns 1976, Littler and Littler 1980, Tilman 1990, Steebeck and Dethier 1994, Vinebrooke et al. 2004, Grime and Pierce 2012, Fong and Fong 2018). For example, *P. boryana* is more of an opportunistic species and was less able to tolerate press sediment additions than pulse sediment additions. In contrast, *L. varegensia* may be more of a persistor species; pulse nutrient + pulse sediment treatments shifted uncaged plots toward this species, suggesting *L. varegensia* can tolerate and even capitalize on pulse disturbance events. Thus, our finding of species-specific, divergent, and persistent effects of stressor temporal regime indicates frequency, magnitude, and intensity of stressors should be incorporated into future research.
Matching of stressor temporal regime accelerated transitions from healthy to degraded communities. That matching of stressors affects transition rates is important because it may commonly occur in many ecosystems. We found the unique combinations of pulse nutrients + pulse sediments eroded the resistance of short algal turf communities even in the presence of herbivores. Similarly, the combination of press nutrients + press sediments eroded the resistance of short algal turf communities in the absence of herbivores. Matching of stressors may be common because disturbances may dictate stressor temporal regime. For example, baseline river discharge may be more likely to produce press nutrient temporal regimes that co-occur with press temporal sediment regimes (Fabricius et al. 2014). In contrast, a severe storm or hurricane event may act to generate pulse nutrient that co-occur with pulse sediment subsidies (McCulloch et al. 2003, Fabricius et al. 2014, den Haan et al. 2016, Clausing and Fong 2016). Matching of stressor regimes may be particularly important in light of species co-tolerances. If tolerance to stressor pairs is positively correlated, matching of stressors may particularly devastating to sensitive species and beneficial to tolerant species (Vinebrooke et al. 2004). We suggest that naturally, stressor temporal regimes often co-occur, and species may have adapted different tolerances and are able to capitalize on the co-occurrence of pulse vs. press stressors. Thus, alignment of stressor temporal regime may be common and may facilitate shifts in community composition.

Strong ecological processes can mask cryptic erosion of community resilience by stressors that emerge when strong processes are disrupted

Ecological masking may arise when stressors cryptically erode community resilience, and addition of a subsequent stressor drives a dramatic shift in community structure and function. We found nutrients and sediments eroded the resilience of the community, which became evident when herbivory was removed. Further, our finding that final community structure varied only with herbivore pressure paired with strong interactions between herbivory and our other stressors over time suggest strong herbivore pressure may mask the effects other stressors. In parallel to our findings, Muthukrishnan and Fong (2014) found a strong effect of time on complex interactions among nutrients, sediments, and herbivory on coral domination, although only herbivory determined final benthic community structure. Further support that strong herbivory masks the effects of other stressors is a meta-analysis which found nutrient effects on coral reefs are typically only evident when herbivory is reduced (Burkepile and Hay 2006). Consequently, increased nutrient supply and sediments appear to erode the resilience of coral reef communities and prime them to shift in composition when faced with additional stressors. Abundant research has shown herbivory is among the strongest structuring processes on reefs (Hay 1981, Lewis 1986, Bellwood et al. 2004, Hughes et al. 2007, Fong and Fong 2018). This strength may mask subtler effects and be one reason herbivory has been so readily demonstrated as a strong driver on coral reefs while evidence that nutrients and sediments drive shifts is equivocal (Szmant 2002, Bellwood et al. 2004, Hughes et al. 2007a, b, but see Adam et al. 2015). Thus, we suggest responses to additional stressors, such as nutrients and sediments, be measured in the context of interactions with each other and herbivory as well as over time.

This masking by strong processes may be a common phenomenon across communities that drive ecological surprises when subsequent stressors are applied in conjunction. For example, when Caribbean reefs shifted from coral to macroalgal dominance in the 1980s, researchers postulated a background of chronic overharvesting of key herbivorous fishes primed the community to susceptibility subsequent stressors—in this case, two hurricanes and a devastating herbivorous urchin disease (Hughes 1994). Similarly, in the Florida Everglades, gradual increases in soil phosphorus levels over time due to agricultural development eroded the resilience of the community, making it more susceptible to the effects of other stressors such as fire, drought, or freeze, resulting in phase shifts from sawgrass to cattail-dominated marshes (Gunderson 2001). Finally, in savannas, open grassy communities shifted to densely wooded communities when increased grazing by commercial livestock was combined with a history of fire suppression (Folke et al. 2004). Thus, disruption of strong
ecological processes by a single stressor may lead to increased susceptibility to other stressors, resulting in ecological surprises, motivating research on stressor interactions.

CONCLUSION

Our research highlights the need to consider stressor temporal regime as well as stressor interactions, particularly in light of predicted increases in both local and global stressors and alterations to stressor temporal regimes. Many researchers have suggested management of local stressors as a means of offsetting global climate change (Hughes et al. 2007, 2017, Brown et al. 2013). These local stressors likely commonly occur with a range of magnitudes, frequencies, and durations, yet these characteristics are often not explicitly compared and contrasted in ecological research. Thus, our understanding of the impacts of local stressor temporal regimes is in its infancy (but see Murphy et al. 2012, Hanley et al. 2017, Fong et al. 2018). Here, we provide a novel demonstration that the effects of stressor temporal regime varied and multiple stressors interacted to exhibit complex, emergent interaction effects, demonstrating the need to explicitly contrast stressor temporal regimes under multiple conditions to understand how communities will respond to future challenges.

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