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Simultaneous synergist, antagonistic and additive interactions between multiple local stressors all degrade algal turf communities on coral reefs

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Handling Editor: Kathy Van Alstyne

Abstract

1. Ecological communities are subjected to multiple anthropogenic stressors at both global and local scales that are increasing in number and magnitude. Stressors can interact in complex ways and are classified as additive, synergistic or antagonistic; the nature of the interaction is key to predicting changes and understanding community resilience. Coral reefs are among the most impacted communities and have shifted from coral- to algal-dominated states, and overfishing, nutrient enrichment and sedimentation are local stressors that often co-occur and may support degraded algal states. Short algal turfs are abundant benthic space holders on healthy reefs that may be pushed by local stressors to long algal turfs, a more degraded state that may prevent recovery to coral dominance.
2. We conducted a fully crossed three-factor field experiment on short algal turf communities manipulating herbivory pressure (+/-cages), nutrients (+/-fertilizer) and sediments (natural accumulation/removal). We applied stressors for 16 days, removed them and monitored turf height during and after manipulations.
3. We found that significant pair-wise interactions between all stressors pushed the community towards a degraded state with longer algal turfs. All three types of interactions (additive, synergistic and antagonistic) were common and occurred in equal frequency, suggesting more investigations into all types are needed to accurately predict community responses to multiple stressors. For example, when herbivores were present, nutrients and sediments interacted additively, while in the absence of herbivores, nutrients and sediments interacted synergistically. All interactions broke down following termination of experimental manipulations and all effects were undetectable after 49 days, indicating that this reef may be resilient, at least when stressors are applied on a short time-scale.
4. *Synthesis.* Because management of local stressors is often more tractable than global stressors, local management has been proposed as a means to offset global stressors. However, ecological communities often experience multiple local stressors simultaneously, and interactions between stressors, including synergisms and antagonisms, may be the source of nonlinear shifts in communities or “ecological surprises.” The majority of interactions in our study were both strong and nonlinear, and we suggest that, if pervasive across systems, nonlinear interactions may drive the recent global increase in “ecological surprises.”

KEYWORDS

antagonism, coral reefs, herbivory, interactions, multiple stressors, nutrients, resilience, sediment, synergism, turf

1 | INTRODUCTION

Mitigating climate change is challenging because it requires concerted global action while local stressors can often be directly controlled; thus, management of local stressors has been proposed as a means to offset the negative effects of global stressors (Brown, Saunders, Possingham, & Richardson, 2013; Hughes et al., 2007). A stressor is a change in an environmental or biotic variable that causes a negative response in the population or community (Underwood, 1989; Vinebrooke et al., 2004). While stressors such as increased sea surface temperature and ocean acidification require management at a global scale, stressors such as resource exploitation and reduction in water quality can be managed locally. For example, protected areas in which local anthropogenic stressors are directly managed through changes in land use and resource exploitation have been successful in improving the health of freshwater (Saunders, Meeuwig, & Vincent, 2002), marine (Halpern & Warner, 2002) and terrestrial (Gray et al., 2016) communities. Similarly, local management of water quality can improve habitat quality, diversity and ecosystem services (Saunders et al., 2002; Smith, Kimmerer, Laws, Brock, & Walsh, 1981; Stimson, Larned, & Conklin, 2001). Some recent work suggests that successful management of local stressors may enhance the resilience of communities to global stressors such as climate change. For example, herbivorous fishes conferred resilience to coral reefs following bleaching, indicating intact herbivore communities could help offset the effects of increased temperature on reefs (Hughes et al., 2007). Additionally, a modelling approach indicated that local management of water quality offset the negative effects of increased temperature on seagrasses (Brown et al., 2013). However, there is still a gap in our understanding of how to manage local stressors, as local stressors frequently interact with each other in complex and unexpected ways (Côté, Darling, & Brown, 2016; Crain, Kroeker, & Halpern, 2008; Darling & Côté, 2008).

Ecological communities often experience multiple local stressors simultaneously, and interactions among these stressors can differentially drive community response, making net effects challenging to predict (Côté et al., 2016; Crain et al., 2008; Darling & Côté, 2008). Stressors can interact in an additive, synergistic or antagonistic manner (Figure 1). Interactions are additive when their combined effect is the sum of each independently, synergistic when the combined effect is greater than the sum of each independently, and antagonistic when the combined effect is less than the sum of each independently. Thus, empirically quantifying types of interactions between multiple local stressors on ecological communities, particularly in already impacted systems, will clarify their regulatory roles and help guide management strategies (Côté et al., 2016).

Stressor interactions may govern resilience of a community to disturbance. There are many definitions of resilience (e.g. Côté &

Darling, 2010; Folke et al., 2004; Grimm & Wissel, 1997; Holling, 1973; Ives & Carpenter, 2007; Pimm, 1991); here, we divide resilience into two components, resistance and recovery (e.g. Côté & Darling, 2010). Resistance refers to the ability of a community to stay essentially unchanged, or bounded within natural variability, in the face of disturbances or changes in environmental conditions (i.e. stressors). Recovery refers to the capacity of a system to return to the initial state after a disturbance or change in environmental condition. For additive interactions, effects of mitigation should be relatively predictable. In contrast, since antagonistic interactions between stressors result in dampened effects (Côté et al., 2016), these types of interactions may increase community resistance (Figure 1). However, since antagonistic interactions reduce or mask independent main effects, management that acts on only one of the interacting stressors may increase net community impacts rather than promote recovery. Further, synergistic interactions that enhance stressor effects (reviewed in Côté et al., 2016) may erode community resistance by amplifying the independent negative effects of each stressor, creating “ecological surprises” (Figure 1; Folke et al., 2004). For synergistic interactions, management

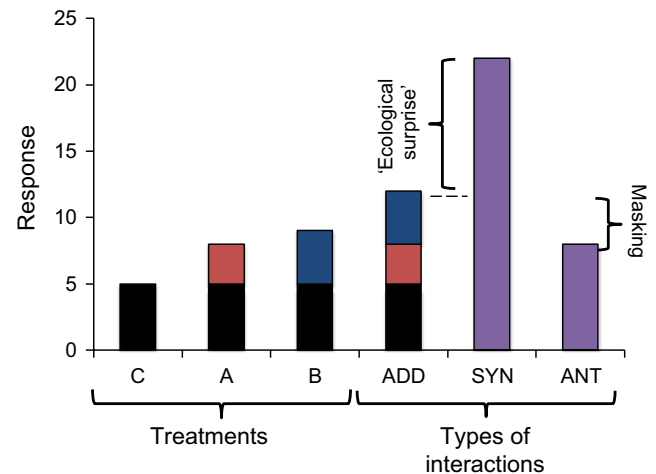


FIGURE 1 Conceptual diagram of interaction types. Treatments are control (C), and hypothetical treatments A and B. The effect of treatment A is the change in response due to A above the baseline effect of the control ($A - C$), shown in red. Similarly, the effect of treatment B is the change in response due to B above the baseline effect of the control ($B - C$), shown in blue. An interaction is additive (ADD) if response to the application of both treatment A and B is the sum of the effects of both treatments above baseline ($\text{response} = (A + B) - C$). The dashed black line shows this additive prediction. The interaction is synergistic (SYN) if the response is greater than the sum of the effects of both treatments ($\text{response} > (A + B) - C$) and is antagonistic (ANT) if less than the sum of the effects of both treatments ($\text{response} < (A + B) - C$), both depicted in purple [Colour figure can be viewed at wileyonlinelibrary.com]

of only one stressor may accelerate recovery because mitigating one stressor will dramatically reduce the net effect on the community. Thus, how multiple stressors interact may strongly affect the resilience of a community to those stressors.

It is key to study interactions among stressors because they may be the source of nonlinear changes in community structure including “ecological surprises” such as phase shifts. For example, when Caribbean reefs shifted from coral to macroalgal dominance in the 1980s, researchers postulated chronic overharvesting of key fish herbivores eroded the resilience of the coral community, making it susceptible to the effects of other stressors—two hurricanes and a devastating herbivorous urchin disease (Hughes, 1994). In Australia, ocean warming and mass bleaching in 1998 combined with experimental reductions in herbivore abundance facilitated macroalgal dominance over coral (Hughes et al., 2007). In the Florida Everglades, gradual increases in soil phosphorus levels due to agricultural development set the stage for phase shifts from sawgrass to cattail-dominated marshes when combined with another stressor—either fire, drought, or freeze (Gunderson, 2001). In savannahs, open grassy communities shifted to densely wooded communities when increased grazing by commercial livestock was combined with fire suppression (Folke et al., 2004). Thus, while a community may be resilient to a single stressor, interactions between multiple stressors may result in “ecological surprises,” motivating research on stressor interactions.

Coral reefs are among the most impacted communities globally, and multiple local anthropogenic stressors have been related to a shift from coral to a more degraded macroalgal-dominated community state, including overfishing, nutrient enrichment and sedimentation (Bellwood, Hughes, Folke, & Nyström, 2004; Halpern et al., 2008). Overfishing is common on reefs exposed to humans, and removal of herbivorous fishes weakens the top-down control necessary for maintaining coral dominance, increasing algal abundance (Hughes et al., 2007; Jackson et al., 2001; Lewis, 1986). Additionally, changes in nutrient availability may favour macroalgae and drive changes in benthic community structure (De'ath & Fabricius, 2008; Lapointe, 1997). Finally, human activities can mobilize terrestrial sediments and increase inputs into the ocean, decreasing coral cover (Fabricius, 2005) and opening space for algae. While the effects of overfishing, nutrient enrichment and sedimentation on corals have been well documented, less work has addressed their combined effects on algal communities (but see Muthukrishnan & Fong, 2014 for three-factor; Clausing et al., 2014; Goatley & Bellwood, 2012; Goatley, Bonaldo, Fox, & Bellwood, 2016 for two-factor of sediments and herbivory).

Algal turfs are highly productive benthic space holders on reefs (Adey & Goertemiller, 1987) and may be a state that can transition to either healthy coral or degraded macroalgal dominance depending on environmental stress (Muthukrishnan, Lloyd-Smith, & Fong, 2016). Thus, understanding processes that control these transitions may deepen our understanding of breakpoints in reef community resilience (Bellwood et al., 2004; Goatley et al., 2016). Healthy algal turfs that are heavily cropped and relatively sediment free are a natural component of coral reef communities, can be dominant space holders after disturbance (Adam et al., 2011; Bruno, Precht, Vroom, & Aronson, 2014;

Goatley & Bellwood, 2011; Vermeij et al., 2010; Vroom, 2010), and can facilitate coral recruitment (Birrell, McCook, & Willis, 2005). However, when stress from overfishing releases them from herbivore control, turfs can grow longer, and even transition into macroalgae (Hughes et al., 2007; Lewis, 1986) that inhibit coral recruitment (Fong & Paul, 2011). Nutrient enrichment is generally seen as a stressor to healthy coral reef communities, facilitating shifts from coral to macroalgal dominance (Burkpile & Hay, 2006; De'ath & Fabricius, 2008; Smith, Hunter, & Smith, 2010). For example, as primary producers, algal turfs respond positively to the stressor of nutrient enrichment (Vermeij et al., 2010), becoming longer, trapping more sediment (Bellwood & Fulton, 2008), and possibly creating transitions to macroalgal dominance that are more stable than shorter algal turfs. Sediment-laden turfs may experience reduced herbivory (Bellwood & Fulton, 2008; Goatley & Bellwood, 2012) and can inhibit coral recruitment (Birrell et al., 2005). Thus, small changes in turf height may dictate ecological function and be an early indicator of a shift in community function (Goatley et al., 2016). Consequently, algal turfs are important benthic space holders that may respond strongly to alterations to and interactions between stressors that reduce herbivory, increase nutrients and promote sediment accumulation, modulating shifts to macroalgal dominance.

In this study, we ask how interactions among three key local stressors may negatively affect resilience of coral reefs by positively affecting the height of the turf algal community, a transition state after natural disturbance on reefs. Specifically, we assess the nature of the interactions (additive, synergistic, antagonistic) among stressors on algal turfs and determine whether these alterations have the potential to enhance turf growth and thus erode the resilience of the coral reef community to disturbance.

2 | MATERIALS AND METHODS

To assess the main and interactive effects of herbivory, nutrient availability, and sediment accumulation, we conducted a full factorial field experiment on natural turf communities in Moorea, French Polynesia. Moorean reefs have been characterized as resilient, returning to coral dominance following multiple disturbances (Adjeroud et al., 2009). In 2008, there was a shift in community composition as corals declined due to an outbreak of a voracious coral predator, the Crown-of-Thorns sea star (*Acanthaster planci*); however, closely cropped turf maintained benthic cover at c. 40%, as opposed to transitioning to macroalgae (Adam et al., 2011), highlighting the potential for resilience of this community. Our study site was a turf-dominated patch reef system on the fringing reef on the west side of Cook's Bay along Moorea's north shore. Turf at this site comprised upright filaments (no “rhizomes” or horizontal growth) and on average was 1.4 ± 0.1 mm long with 1.3 ± 0.1 mm of sediment. The water was c. 1 m deep and tidal amplitude in this system is negligible (Hench, Leichter, & Monismith, 2008).

We conducted a fully crossed three-factor field experiment where we controlled access to herbivores (+H/-H), nutrient availability (+N/-N) and sediment accumulation (+S/-S), where -H, +N and +S

were the stressed level of each factor. We caged to simulate overfishing by limiting access to herbivores, added slow release fertilizer to apply nutrient stress and removed sediment to reduce sediment stress (see below for method details). We decided to remove sediment and allow accumulation as a stress in this site because the natural turfs started with >1 mm of sediment, a moderate load for fringing reefs within the northern bays of Moorea (Clausing et al., 2014), but a relatively high load for other reefs of this island, possibly due to a weaker flow regime in the protected bay (C. Gaynus, P. Fong, unpubl. data). Previous research shows that sedimentation rate is inversely related to water flow, and water flow decreases with distance from the forereef and distance from freshwater outflows along the fringing reef in Moorea (Gowan, Tootell, & Carpenter, 2014). Our site was on the fringing reef far from the forereef, but not close to any major freshwater outflow sources. Thus, we decided to remove sediment and allow accumulation as a stress in this site because the natural turf started with >1 mm of sediment, a moderate load for fringing reefs within the northern bays of Moorea (Clausing et al., 2014), but a relatively high load for other reefs on the island (C. Gaynus, P. Fong, unpubl. data). We had a total of eight treatments we replicated eight times ($n = 64$). We applied stressors for 16 days and then removed them, monitoring turf during and after termination of our manipulations. Experimental plots were $15 \times 15 \text{ cm}^2$ areas of 100% natural turf on dead coral heads and were randomly assigned to one of the eight treatments. Plots were at least 1 m apart to minimize any spillover effects of nutrient treatment. Manipulations began 1 May 2014 and ended 16 May 2014. Each plot was sampled on 1 May, 4 May, 8 May and 16 May during experimental manipulations, and 19 May and 6 July in 2014, 3 and 51 days after treatments ceased, respectively. On each sampling date, we measured both turf height and sediment depth to the nearest 0.5 mm. For each measurement, we used a wire mesh "comb" with teeth heights in 1-mm gradations (see Figure S1 for details). We laid this comb on the substrate at 10 random points within each plot to measure turf height and sediment depth, which were averaged to obtain a mean turf height and sediment depth for each plot. Treatments where sediment was cleared only had a turf measurement taken.

We used cages to control access to herbivores. Cages were constructed from a metal mesh material that enclosed the naturally occurring turf communities; they were $15 \times 15 \text{ cm}$ squares that were 5 cm tall with $1 \times 1 \text{ cm}^2$ openings, similar to those used in other studies to exclude herbivores (e.g. Clausing et al., 2014; Fong & Fong, 2014). These cages included a 5-cm "skirt" nailed flush to the benthos to limit accessibility to mobile invertebrates. Cage lids were made of the same mesh and attached with cable ties, so they could be removed during measurements. To control for cage effects, treatments with access to herbivores had the $15 \times 15 \times 5 \text{ cm}$ cage walls, but no lid (e.g. Clausing et al., 2014). Similar cages have been used in other studies of turf with no measurable change in flow or herbivorous fish visitation (see Clausing et al., 2014, supplemental data).

To create +/- sediment treatments, we manually removed sediment from all plots. We then allowed sediment to accumulate on +S plots while continuing removal on -S plots. This contrasts studies where sediments were experimentally added (e.g. Clausing et al., 2014; Gil,

Goldenberg, Bach, Mills, & Claudet, 2016; Goatley & Bellwood, 2013; Muthukrishnan & Fong, 2014). We choose to let sediment accumulate rather than add sediment because initial sediments depths were >1 and 2 mm additions were found to have negative effects in a previous study (Clausing et al., 2014). Further, we sought to evaluate any positive feedbacks between turf growth and sediment accumulation. Because turf is fragile, we removed sediment in the -S treatments every 4 days by waving our hands over the plots to generate current and remove as much sediment as possible.

To create +/- nutrient treatments, we left unenriched (-N) treatments in ambient seawater and used Osmocote slow release fertilizer to provide extra nutrients to enriched plots (Fong & Fong, 2014). Fifteen grams of fertilizer was bundled in nylon and attached to the cage skirt to enrich the + nutrient plots. Unenriched plots had empty nylons to control for any flow effects of the treatment. One dose of Osmocote was used for the entire 16-day period.

We ended treatments 25 May 2014 after measuring turf height and sediment depth. We ended herbivore exclusion treatments by removing the lid of the cage. In all plots, the $15 \times 15 \text{ cm}$ square cage wall remained to mark the bounds for continued measurement. We ended the sediment treatment by terminating all manual sediment clearing and allowing natural sediments to accumulate on all plots. We ended nutrient treatments by removing the Osmocote and empty bags.

To analyse the time series data on turf height, we conducted a three-factor repeated measures (RM) ANOVA, after testing if data met assumptions of parametric statistics. We followed up our RM-ANOVA with three-factor ANOVAs for each day (similar to Goatley & Bellwood, 2013). To determine how sediment depth varied with treatments, we conducted a two-factor RM-ANOVA for treatments where we allowed sediment accumulation and follow-up two-factor ANOVAs for dates during manipulations and three-factor ANOVAs for dates following manipulations. We did not conduct a three-factor RM-ANOVA during manipulations because we did not measure sediment depth in treatments where sediment was removed.

To evaluate the nature (additive, synergistic or antagonistic) of the three significant pair-wise interactions that arose by day 16, we compared the observed responses to pairs of stressors to an additive model (shown conceptually in Figure 1). The effect of a single stressor was calculated by subtracting the mean response of the "control" treatment from the mean response of the stressed treatment (single red and blue bars in Figure 1). For each pair of stressors, the "control" was the non-stressed condition, and we calculated these for both levels of the third factor. To generate a distribution of expected outcomes for the combined effect of the stressor pair, we selected random pairs of replicates for both single stressors, calculated the effect size of each stressor individually, and then summed the pair of stressors (i.e. red + blue bars); this allowed us to generate an expected distribution with variance. We then compared this generated expected distribution assuming an additive effect to the empirical data for replicates with both stressors using two-sample *t* tests. An interaction was additive if the combined effects were not statistically different from the expected sum of the independent effects (in Figure 1 diagram, red + blue bars). A significant *p*-value for the two-sample *t* test indicated the

	1	4	8	16	19	65
(a) ANOVAs on turf height						
Whole model	0.6952	0.5037	<0.0001	<0.0001	<0.0001	0.2909
H			<0.0001	<0.0001	0.0004	
S			<0.0001	<0.0001	<0.0001	
H × S			0.62	<0.0001	0.2886	
N			<0.0001	<0.0001	<0.0001	
H × N			<0.0001	<0.0001	0.976	
N × S			0.6794	0.014	0.0595	
H × N × S			0.967	0.0664	0.1867	
(b) ANOVAs on sediment height						
Whole model	0.5639	0.4741	<0.0001	<0.0001	<0.0001	0.7295
H			0.1000	0.0036	0.0003	
S			-	-	<0.0001	
H × S			-	-	0.1096	
N			0.0020	<0.001	0.0043	
H × N			0.5926	0.0044	0.5734	
N × S			-	-	0.0003	
H × N × S			-	-	0.6998	

TABLE 1 Results of ANOVAs on turf and sediment height 1 day through 65 days after the experiment began

observed data differed from the expected and the direction of this difference dictated whether the interaction was synergistic or antagonistic. Synergistic interactions were when combined effects were > additive effects, while antagonistic interactions were when combined effects were < additive. Additionally, synergistic and antagonistic interactions are identified as statistical interactions in ANOVA, signifying a nonlinearity, or dependence of the effect of one stressor on the other. In contrast, additive interactions are not statistically significant as effects of each stressor are independent and linear. We did not use a statistical approach to assess family wide error because available analyses (such as a sequential Bonferroni) are excessively conservative for field ecology (Moran, 2003).

To assess the relationship between sediment depth and turf height, we conducted a linear regression on turf height and sediment depth before (1 May), during (4 May, 8 May, 16 May for +S treatments) and after manipulations were terminated (19 May, 6 July for both S treatments).

All statistical analyses were conducted with JMP 12.

3 | RESULTS

3.1 | Treatment effects on turf height

Overall, pair-wise interactions between all stressors were significant and developed over time (three-factor RM-ANOVA, see interactions with time, Table S1a, Figure 1a,b).

Interaction effects were not immediately apparent, with no differences in turf height due to manipulations during the first 4 days of treatment (three-factor ANOVAs Table 1a, Figure 2a,b). Turf height

averaged across all treatments and across day 1 and day 4 of the experiment was $1.43 \text{ mm} \pm \text{SE } 0.05$ (grand mean, $N = 128$). On day 8, there was a main effect of sediments and an interactive effect of nutrients and herbivory on turf height. After 8 days, accumulation of sediments had a positive effect on turf height regardless of nutrients or herbivory. In contrast, the positive effect of nutrients that occurred after 8 days was stronger when turf was protected from herbivores with cages.

By day 16, all two-way interactions were significant (Figure 2a,b; Table 1a). Paired contrasts between experimental results and expected values calculated for additive effects revealed an equal distribution of additive, synergistic and antagonistic interaction types (Table 2). In treatments with herbivore access (Figure 2c, +H), the difference between turf heights due to nutrients was c. 1 mm increase in turf height irrespective of sediment treatments (Figure 2c, red); similarly, the positive effect of sediment accumulation was c. 1.5 mm irrespective of nutrient treatment (Figure 2c, blue). Thus, in the presence of herbivores, the effects of nutrients and sediments were **additive** (Figure 2c, red + blue). In contrast, in the absence of herbivores (Figure 2d, -H), the interaction between nutrients (Figure 2d, red) and sediments (Figure 2d, blue) was **synergistic**—the effect of both treatments in combination was greater than simply the sum of the two stressors in isolation (Figure 2d, purple > red + blue). In the absence of sediment (Figure 2e, -S), the removal of herbivores alone increased turf height by c. 0.7 mm (Figure 2e, red), while the addition of nutrients alone increased turf by c. 1 mm (Figure 2e, blue); however, the combined effect was c. 1.3 times less than the addition of effects (Figure 2e, purple < red + blue); thus, the interaction between nutrients and herbivores was **antagonistic**. In contrast,

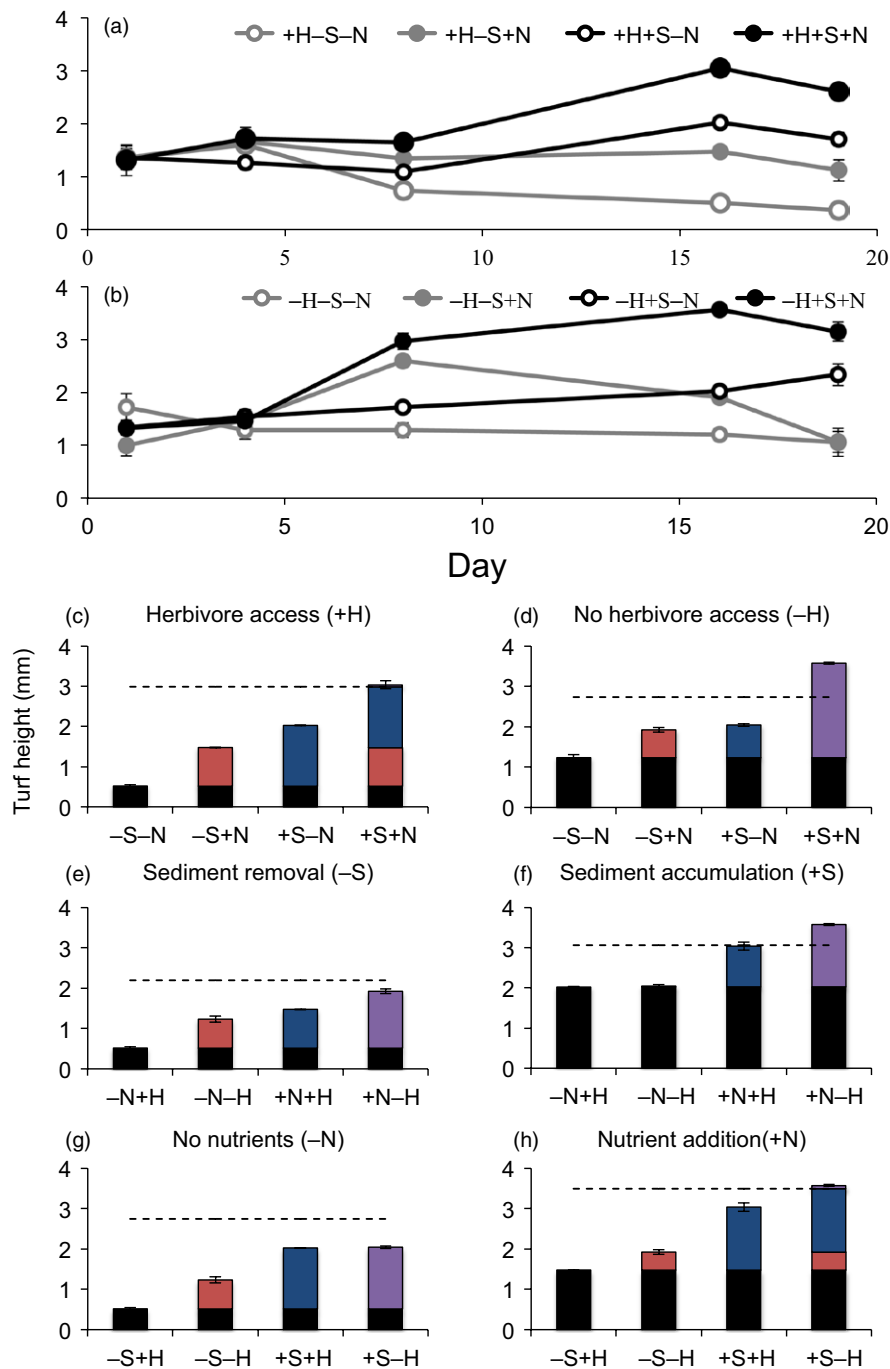


FIGURE 2 (a, b) Mean turf height \pm SE over time where (a) contains all treatments where herbivores had access (+H), while (b) contains treatments without herbivore access (-H). Black lines indicate treatments with sediment accumulation (+S), while grey lines indicate experimental sediment removal (-S). Open circles (o) indicate treatments without nutrient enrichment (-N), while closed circles (●) indicate treatments that were experimentally enriched (+N). Points without visible error bars have small enough error to be masked by the symbol. (c, d) Mean turf height \pm SE for pair-wise interaction types for nutrients and sediments (c) with and (d) without herbivores. (e, f) Mean turf height \pm SE for pair-wise interaction types for nutrients and herbivores (e) without and (d) with sediments. (g, h) Mean turf height \pm SE for pair-wise interaction types for sediments and herbivores (g) with and (f) without nutrients. For each pair, graphs in the left column are the unstressed treatment (+H, -S, -N), while graphs on the right are the stressed treatment (-H, +S, +N). In all graphs, the column on the left (black) is the baseline/control. Red bars indicate the effect of the first stressor above control, while blue bars indicate the effect of the second stressor above control. The dashed black line on all graphs indicates the predicted response to the combination of both stressors in the additive model. When the interaction type between the two stressors were additive, we stacked the effects of each treatment (red and blue) atop the control (black). When the interaction type between the two stressors were either synergistic or antagonistic, the treatment subjected to both stressors is shown in purple [Colour figure can be viewed at wileyonlinelibrary.com]

3rd stressor	Observed vs predicted effects for interaction pair	t test	Interaction type
+ Herbivores	Sediment and nutrients	0.642974	Additive
- Herbivores	Sediment and nutrients	0.000128	Synergistic
- Sediment	Herbivores and nutrients	0.023247	Antagonistic
+ Sediment	Herbivores and nutrients	<0.00001	Synergistic
- Nutrients	Herbivores and sediments	0.002347	Antagonistic
+ Nutrients	Herbivores and sediments	0.219403	Additive

Bold values are significant ($p < .05$).

when sediments were allowed to accumulate (Figure 2f, -S), there was no effect of herbivore reduction alone (Figure 2f, red [-N-H]); rather, nutrients alone increased turf height (Figure 2f, blue), and this nutrient effect was larger when herbivores were also removed (Figure 2f, purple > red + blue). Because, in the presence of sediment, herbivory was only important when plots were enriched, the interaction between herbivory and nutrients is best characterized as **synergistic**. In the absence of nutrients (Figure 2g, -N), exclusion of herbivores alone doubled turf height (Figure 2g, red), while accumulation of sediment alone quadrupled turf height (Figure 2g, blue); thus, the interaction between sediments and herbivory in the absence of nutrients was **antagonistic** as the net effect was less than the addition of combined effects (Figure 2g, purple < red + blue). In contrast, when turf was enriched (Figure 2h, +N), the exclusion of herbivores resulted in c. 0.5 mm increase in turf height (Figure 2h, red) irrespective of sediment treatment; similarly, the addition of sediment resulted in c. 1.6 mm increase in turf height (Figure 2h, blue) irrespective of herbivore access. Hence, the interaction between sediment and herbivory was **additive** when plots were enriched (Figure 2f, +S-H = red + blue).

Turf algae were reduced in height in most treatments 3 days after experimental treatments ceased (day 19, Figure 2a,b); cages and nutrients removed, sediments allowed to accumulate in all plots. However, while the interactions disappeared, significant main effects of all three treatments emerged (day 19 Table 1a). Overall, turf was longer in plots previously protected from herbivores, and shorter in plots where sediment had only accumulated for 3 days (all -S treatments). Although the nutrient effect remained positive, it also diminished in all treatments, especially those where sediments previously were removed, causing a nearly significant persistence of the N by S interaction.

Forty-nine days after treatments ceased, there were no remaining effects of any of the experimental treatments (Figure S2, Table 1a). Although turfs appeared to be longer where they had been caged and where sediment treatments had been allowed to accumulate, these trends were not significant.

3.2 | Treatment effects on sediment accumulation (+S treatments only)

There were interactive effects of herbivory and nutrients on sediment accumulation that varied over time, evidenced by a three-way interaction within the repeated measure of time (Table S2, Figure 3).

TABLE 2 Results of two-sample t tests comparing predicted vs observed combined effects

As for turf height, treatment effects did not emerge during the first 4 days of the experiment. After 8 days, nutrients positively affected sediment accumulation, increasing accumulation c. 1 mm over unenriched plots regardless of herbivory (Table 1b). By day 16, there was a significant nutrient \times herbivory interaction on sediment accumulation. In this comparison, the "control" is +H+S-N, as all treatments had sediment accumulation, and we only analysed +S treatments as sediment heights for -S were zero. Adding nutrients alone (+H+S+N) resulted in c. 0.74-mm increase in sediment depth, while herbivore exclusion alone (-H+S-N) increased sediment depth by c. 0.60 mm. Nutrients and cages interacted **additively** such that nutrient addition and herbivore exclusion (-H+S+N) increased sediment depth 1.3 mm above baseline for a total of 2.8 mm (compared to a predicted 2.9 mm for an additive interaction).

Three days after treatments ceased, a significant main effect of caging on sediment accumulation still remained (Table 1b, Figure 3, day 19), as sediment depths were more than double the thickness in plots where herbivores had previously been excluded (+C). There was also an interaction between nutrients and sediments, as plots that were previously subject to both treatments also accumulated a thicker layer of sediment. By day 65 (49 days after treatments ceased), no treatment effects remained and sediment depths were 1.62 mm \pm SE 0.08 ($N = 64$, +S treatments only).

3.3 | Turf height and sediment accumulation

Prior to initiation of experimental treatments, there was a positive linear relationship between the turf height and sediment depth ($y = 0.86x + 0.17$, $R^2 = .75$, $p < .0001$, data not shown). On day 1, there was no relationship as all plots were cleared of sediments to initiate the experiment (Figure 3). By day 8, enough sediment had naturally accumulated on +S treatments for the positive relationship to re-establish and remain through day 16. Three days after treatments ended (day 19), there was still a difference between +/- sediment plots. The difference due to experimental treatments was lost by day 65.

4 | DISCUSSION

Overall, our results indicated that interactions between multiple local stressors intensify negative community-level effects and thus may

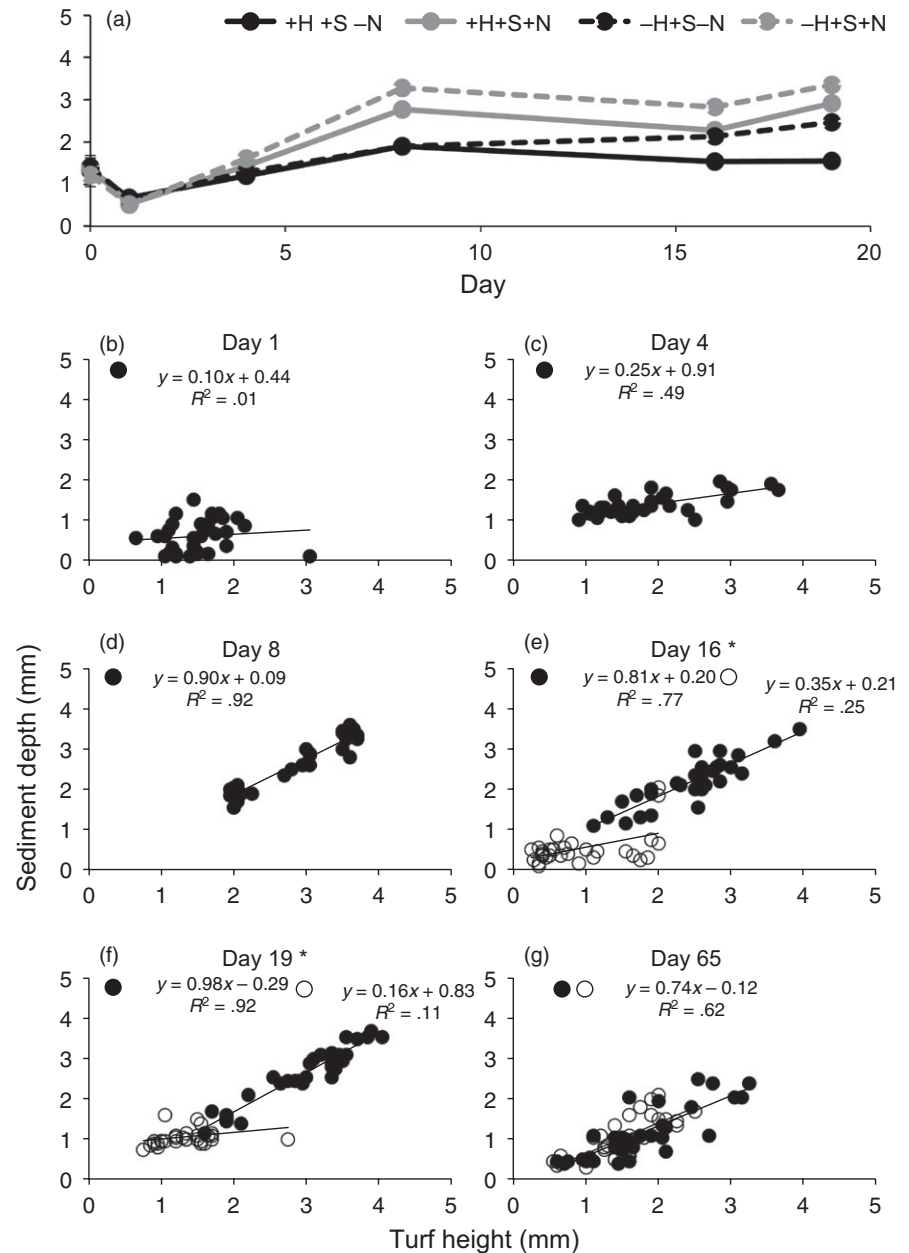


FIGURE 3 (a) Mean sediment depth \pm SE over time for the +S treatments. All treatments had sediment accumulation (+S). Solid lines (—) indicate herbivore access, while dashed lines (---) indicate herbivore exclusion. Black lines indicate treatments without nutrients, while grey lines indicate treatments with nutrient additions. (b–g) Relationships between turf height (x-axis) and sediment depth (y-axis) on the six different sample dates. Closed circles (●) are for treatments where sediment was allowed to accumulate (+S), while open circles (○) are treatments where sediment was removed; these depths were measured only on days 16, 19 and 65 after removal treatments ended and sediment was allowed to accumulate. (*) indicates regressions with a $p < .05$

erode community resilience. In every case, the effect of each pair-wise interaction resulted in longer turf, a state on coral reefs considered to be degraded, and each interaction pair was intensified (antagonistic to additive, additive to synergistic and antagonistic to synergistic) in the presence of the third stressor. This finding corroborated a meta-analysis by Crain et al. (2008) examining 48 studies that considered the impact of a third stressor on pair-wise interactions and found the addition of the third stressor both changed interaction effects two out of three times and doubled the frequency of synergistic interactions. The general pattern that stressor interactions intensify negative effects suggests ecological resilience may be easily and unpredictably eroded when communities are subject to multiple stressors. Further, the background of global climate change often interacts with and intensifies negative effects of local stressors (e.g. Ban, Graham, & Connolly, 2014; Brook, Sodhi, & Bradshaw, 2008; Brown et al., 2013;

Hughes et al., 2007). That negative community effects generally intensify with each additional stressor is an important finding as the number of potential two-way interactions increases exponentially as the number of stressors increases. One study estimated that coastal communities are subjected to more than 100 two-way interactions and subsequently thousands of higher order interactions (Côté et al., 2016). Thus, interactions between multiple stressors should be a key focus of future research, particularly in light of intensifying local stressors coupled with global climate change.

Our results also suggest that both presence of, and variance in, the type of interactions among stressors may be extremely common; thus, understanding the frequency of the different types of interactions is crucial to predicting community responses to multiple stressors. However, there is considerable uncertainty about the overall frequency of different interaction types between stressors (Côté et al.,

2016; Crain et al., 2008; Darling & Côté, 2008). A recent meta-analysis reported dramatic increases over the last 40 years in all three type of interactions, but that synergisms were increasing at double the rate of additive and antagonistic interactions (Côté et al., 2016). Yet, it remains unclear whether the frequency of interactions, particularly synergisms, in natural communities has truly risen with increasing human impacts, or if this pattern is simply due to increased research attention and publication bias. We found an even split among the three interaction types: two additive, two antagonistic and two synergistic. Thus, we found stressors commonly interacted and in a variety of ways, and suggest the generality of these interactions among multiple stressors warrants continued and focused investigation on all interaction types.

The majority of interactions among multiple stressors in our study were both strong and nonlinear, and we suggest that if this pattern is pervasive across systems, it may explain the recent prevalence of “ecological surprises” or phase shifts (Folke et al., 2004). In this scenario, if application of a single stressor cryptically erodes a communities’ resistance to secondary stressors, addition of subsequent stressors may result in rapid and dramatic community shifts with little or no warning (Folke et al., 2004). In our study, the turf community tolerated a single stressor and maintained a relatively healthy short state, but in the context of a secondary stressor grew longer, moving towards a degraded state. Researchers have suggested nonlinear interactions between multiple stressors drive phase shifts in a diverse set of communities, including coral reefs (Hughes, 1994; Hughes et al., 2007), marshes (Gunderson, 2001) and savannahs (Folke et al., 2004). Interactions among multiple stressors and the positive feedback loops they generate often accelerate extinction events (Brook et al., 2008). Thus, we suggest single stressors erode the resistance of a community to change, and interactions with additional stressors produce strong nonlinear interactions to drive “ecological surprises” such as phase shifts. Given the expected increase in both local and global stressors, we suggest interactions between stressors must be studied in the context of “ecological surprises.”

A positive feedback between sediment and algal turf, enhanced by an interaction between increased nutrients and reduced herbivory, resulted in the development of long sediment-laden turfs, which have been posited to be an alternative and stable community state in degraded reefs (Goatley et al., 2016). In our un-manipulated turf communities, sediment depth was linearly related to turf height. Further, with the added stressors of nutrient addition and herbivore removal, longer turfs grew, which then accumulated more sediment. This may push the transitional, short, productive algal turf (SPATs sensu Goatley et al., 2016) community towards longer, sediment-laden algal turfs (LSATs sensu Goatley et al., 2016), and provide a feedback loop stabilizing this state, preventing recovery to coral dominance (Birrell et al., 2005; Cinquin & Demongeot, 2002; Folke et al., 2004; Goatley et al., 2016; Schröder, Persson, & De Roos, 2005). Other researchers have found positive feedbacks stabilizing the degraded turf state and potentially stunting recovery to coral. For example, on Australian reefs, the presence of sediment reduced herbivory by up to 90%, promoting turf growth (Bellwood & Fulton, 2008; Goatley et al., 2016). We also found sediment re-accumulated rapidly, suggesting the feedback between sediment and turf is

maintained by high sedimentation rates; this result re-enforces research on turfs on the Great Barrier Reef that also found rapid sediment re-accumulation (Bellwood & Fulton, 2008). However, in our experiment, sediment increased turf height irrespective of herbivory treatment, indicating facilitation via some other process; we suggest that this may be due to nutrients provided by the sediments, which may be up to 8% organic matter (Clausing, Bittick, Fong, & Fong, 2016). Thus, our evidence indicates a positive feedback loop where sediment accumulates on turf, turf increases in height, resulting in further retention of sediment from the water column. Thus, studying positive feedbacks within the algal turf community is important to predicting stability of community shifts in coral reefs.

We hypothesize that the rapid recovery to a healthy short turf community following termination of our treatments was due to the breakdown of interactions that intensified each other and promoted turf growth and sediment accumulation. Given the general pattern in our experiment that stressor interactions (1) are common, (2) tend to intensify effects and (3) negatively impact communities, we posit that mitigation of a single stressor may have greater than expected positive impacts on targeted communities by dissolving interactions. However, we caution that if stressors interact antagonistically, management efforts may have the unintended consequence of strengthening the effect of the remaining stressor. Thus, we suggest interactions between multiple local stressors be fully explored to inform management decisions, particularly in light of global change that cannot be managed on a local scale.

ACKNOWLEDGEMENTS

We thank the staff at the Gump station for assistance and support. We thank the UCLA Ecology and Evolutionary Biology Department and the Office of Instructional Development for funding to S.J.B. and P.F. We declare no conflicts of interest.

AUTHORS’ CONTRIBUTIONS

C.R.F. conceptualized the project, conducted field work, analysed the data and wrote the MS; P.F. and S.J.B. contributed to experimental design, field work and editing.

DATA ACCESSIBILITY

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.2k80f> (Fong, Bittick, & Fong, 2017).

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How to cite this article: Fong CR, Bittick SJ, Fong P. Simultaneous synergist, antagonistic and additive interactions between multiple local stressors all degrade algal turf communities on coral reefs. *J Ecol.* 2018;106:1390–1400. <https://doi.org/10.1111/1365-2745.12914>