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Bolstered physical defences under nutrient-enriched conditions may facilitate a secondary foundational algal species in the South Pacific

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Summary

1. Humans have a long history of changing species' ranges and habitat distributions, making studies of the ecological processes that may facilitate these changes of key importance, particularly in cases where a primary foundation species is replaced by another, less desirable species.

2. We investigated the impact of nutrients and herbivory on *Turbinaria ornata*, a secondary foundational macroalga that depends on and likely competes with coral, the primary foundational community. *T. ornata* is also rapidly expanding in range and habitat across the South Pacific. We conducted (i) a mesocosm experiment assessing relative nutrient limitation, (ii) a field experiment comparing importance of nutrients (+/−) and herbivory (+/−) to biomass accumulation, and (iii) an herbivory assay and toughness test comparing enriched and ambient thalli to assess changes to anti-herbivory defences.

3. We found no evidence of growth being nutrient limited in *T. ornata*; rather than stimulating growth, nutrient addition deterred herbivores. However, when physical toughness was removed, enriched algae were preferred, with consumption rates 25-fold those of unenriched algae. Additionally, enriched thalli were tougher than ambient thalli, suggesting physical defences were bolstered by nutrient enrichment.

4. *Synthesis.* We found a unique interaction where nutrients inhibit herbivory and facilitate *Turbinaria ornata* biomass accumulation. While concern is often placed on degradation of foundation species via anthropogenic change, instead here we show that anthropogenic change can facilitate secondary foundation species. This facilitation may allow a secondary foundation species to better compete with primary foundation species.

Key-words: anti-herbivory defences, aquatic plant ecology, coral reefs, human impacts, secondary foundation species, top-down and bottom-up control, *Turbinaria ornata*

Introduction

Human alterations of major ecological processes have resulted in world-wide changes in species' geographic ranges as well as their distribution among habitats (e.g. Ellison *et al.* 2005; temperate and tropical forests; Orth *et al.* 2006; seagrass beds; Rohr, Mahan & Kim 2009; hemlock groves; Veldman & Putz 2011; Amazon basin grasslands and forests; Saintilan *et al.* 2014; mangroves and saltmarsh plants). While human impacts usually result in overall loss of foundation species (Ellison *et al.* 2005; Orth *et al.* 2006), in some cases, humans may facilitate a switch from one dominant foundation species to a secondary, often less desirable, foundation species (Rohr, Mahan & Kim 2009; Veldman & Putz 2011; Saintilan *et al.* 2014). While all foundation species, by definition, support community structure, species composition and ecosystem functioning (see Ellison *et al.* 2005 for a review), secondary foundation species are dependent on primary foundation species for space or habitat stabilization such as moss epiphytes to their oak hosts (Angelini & Silliman 2014) or mussels in a cordgrass habitat (Altieri, Silliman & Bertness 2007). As humans impact the physical and abiotic environment, there can be consequences to interactions between primary and secondary foundation species that will have cascading effects to the communities they support (see Angelini *et al.* 2011). Because shifts between foundational species have large impacts on their dependent communities' structure and functioning, studies of the

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*Correspondence author. E-mail: sbittick@ucla.edu ecological processes that may facilitate these changes are of key importance.

Anthropogenic changes to major ecological controlling forces, such as nutrient limitation and its interaction with herbivory, are known to impact the composition and abundance of primary producers in many ecosystems (e.g. grasslands in Tilman & Downing 1996; terrestrial and aquatic systems in Hillebrand *et al.* 2007). Overall, increased nutrients have been found to stimulate herbivory on coral reefs (Boyer *et al.* 2004; Chan *et al.* 2012), in saltmarshes (He & Silliman 2015) and on rocky reefs (Gruner *et al.* 2008). Further, theory predicts enrichment will translate directly to increased primary productivity and more diverse food webs (e.g. Oksanen *et al.* 1981; with concurrent high consumption in Worm *et al.* 2002; but see Rosenzweig 1971 for a discussion of the paradox of enrichment). As for many primary producers, coral reef macroalgae are thought to be controlled by interactions between top-down and bottom-up forces. Although there is high spatial and temporal variability in algal response to nutrient addition, many tropical macroalgae experience opportunistic growth when exposed to inputs of nitrogen and phosphorous (e.g. Fong *et al.* 2003), as these nutrients tend to be limiting in tropical systems (for a review, see Fong & Paul 2011). Macroalgae is also strongly controlled by high herbivory on coral reefs, though overfishing can result in a decrease in herbivory pressure (Hughes *et al.* 2010; Fong & Paul 2011). Further, a meta-analysis found that nutrients only increased algal abundance in the absence of herbivores (Burkepile & Hay 2006). Subsequent studies follow similar trends but vary across time, space and species (e.g. Smith, Hunter & Smith 2010). Both empirical studies and theoretical predictions suggest that interactions between nutrients and herbivory should increase both primary productivity and consumption by herbivores. However, what is unknown is whether these predictions hold true for secondary foundation species when humans manipulate top-down and bottom-up controls.

Macroalgae have increased on reefs over the last 40 years (e.g. Bellwood *et al.* 2004) and can (i) compete directly with coral for space and light, as well as (ii) inhibit recruitment of juvenile corals (see Fong & Paul 2011 for a review; also Box & Mumby 2007). Typically, these macroalgae are opportunistic species that respond quickly to nutrients and are highly palatable (Littler & Littler 1980). In contrast, *Turbinaria ornata* is a secondary foundational brown macroalga (see methods for rationale) that has been increasing in range and habitat usage within its range in the South Pacific over the last 35 years. Prior to 1980, *T. ornata* was confined to the Austral and Society islands but by 1990 appeared on the northern and southern Tuamotu islands (Martinez *et al.* 2006). While it is still unclear what processes are driving this expansion (Stiger & Payri 2005), possible explanations include changes in top-down and bottom-up processes and their interactions. Only a handful of studies have examined the effect of nutrients and herbivory on *T. ornata,* and results from these studies have been mixed. For example, one study on the Great Barrier Reef showed that inshore *T. ornata* did not respond to nutrients by increasing biomass but did store nutrients in their tissues (Schaffelke 1999). A study from Tahiti found *T. ornata* had greater concentrations of phenols, the aromatic molecules responsible for chemical defence, in an area with high nutrient input (Stiger, Deslandes & Payri 2004). This contrasts with *Fucus distichus*, a closely related brown alga, that had no or a negative relationship between nutrient availability and phenol content (Yates & Peckol 1993; Koivikko *et al.* 2005); rather, herbivory induced chemical defences in this alga (Koivikko *et al.* 2005). Finally, Chan *et al.* (2012) found a congener, *T. turbinata,* became more palatable in response to nutrient input in the Caribbean. Thus, a range of interactions between nutrients and herbivory have been found in closely related algae. It is important to further our understanding of these complex interactions as human-induced alterations of these controlling top-down and bottom-up processes will only intensify in the future.

We evaluated the role of anthropogenic alterations of nutrients and herbivory in promoting the persistence of *T. ornata* on coral reefs of the South Pacific. Specifically, we asked (i) Does *T. ornata* grow in response to nutrients? (bottom-up control), (ii) Does herbivory control *T. ornata* biomass? (top-down control), and (iii) Is there any interaction between nutrients and herbivory that may lead to the persistence of *T. ornata*?

Materials and methods

STUDY SPECIES

Turbinaria ornata forms dense aggregations ($\bar{x} = 267.2 \pm 17.1$ SEM thalli per m^2, $n = 80$) on hard reef substrates formerly dominated by corals and has been observed to facilitate other species by providing habitat structure, refuge, or both to other macroalgae (Bittick *et al.* 2010), juvenile fish (J.D. Harvey, S.J. Bittick, T.M. Johnson, T.A. Fryman, R.J. Clausing, C.R. Fong & P.M. Fong, in prep) and invertebrates (S.K. Briley, unpubl. data). By supporting a high density of epiphytes, *T. ornata* also provides trophic support to herbivores (S.J. Bittick, S. Scoma, R.J. Clausing, C.R. Fong & P. Fong in prep). Because *T. ornata* facilitates a diverse community but depends on corals to form the hard substrate for attachment, it can be considered a secondary foundation species.

Turbinaria ornata belongs to the thick-leathery functional form group that is predicted to be slower growing and less responsive to nutrients compared to other types of more opportunistic macroalgae (Littler & Littler 1980). Previous studies showed that *T. ornata* has high morphological plasticity where flow increases tensile (breaking) strength (Stewart 2006a). Reproductive *T. ornata* thalli detach seasonally through natural senescence and as a result of high wave energy. This results in formation of rafts that may facilitate dispersal, though the direct effect on dispersal has not been studied (Stewart 2006b). *Turbinaria ornata* also contains chemical (Deslandes, Payri & Stiger 1997; Stiger, Deslandes & Payri 2004) and mechanical (physical toughness; Payri, N'Yeurt & Orempüller 2004) defences to deter herbivores, though in Australia *T. ornata* was found to be highly palatable (Mantyka & Bellwood 2007).

STUDY SITES

To evaluate whether our results showed the same overall pattern across space and time, all experiments were repeated for two different patch reef sites; however, logistical constraints prohibited running the experiments simultaneously. Our two sites were Gump Reef (17°29′17.25″S, 149°49′32.26″W) situated at the mouth of Cook's Bay and Sailing School (17°28′59.81″S, 149°50′45.70″W) located at the mouth of Opunohu Bay. We expected higher ambient nutrients at Gump Reef due to a larger human population, more agricultural development, and greater mean riverine input in Cook's Bay (Letourneur *et al.* 2013). This expectation was evaluated by analysing tissue nitrogen and phosphorous for *T. ornata* thalli collected from the two sites because *T. ornata* store nutrients in its tissues (Schaffelke 1999). Tissue nutrient concentrations (% nitrogen and phosphorous) confirmed lower nutrient levels at Sailing School (see Appendix S1, in Supporting Information). Additionally, a follow-up study determined herbivore abundance to be much lower at Gump than Sailing School (J.L. Bergman, B.N. Dang, M. Tabatabaee, M.M. McGowan, C.R. Fong, S.J. Bittick & P. Fong, unpubl. data).

EXPERIMENTAL APPROACHES

To determine whether *T. ornata* growth was nutrient limited, we conducted a two-factor bioassay varying the supply of nitrogen (+/− N) and phosphorous (+/− P) in a fully crossed factorial design. Forty small *T. ornata* (5–10 cm tall) thalli were collected from two sites, Gump Reef on 25 April 2012 and Sailing School Reef on 6 May 2012. All (−) treatments used ambient sea water from the respective site. For enriched (+) treatments, nitrate ($NaNO_3$) and phosphate (NaH_2PO_4) were added to ambient sea water from each site to achieve concentrations 20 μM N and 2 μM P above ambient as in Fong *et al.* (2003). Each thallus was spun in a salad spinner for 1 min, wet weighed ($\bar{x}$ = 3.45 g ± 0.12 SEM) and randomly assigned to one of the four treatments with 10 replicates. Eight hundred mL of the appropriate treatment sea water (−N−P, +N−P, −N+P, +N+P) and a *T. ornata* thallus were put into each of 40 1000 mL plastic cups. The cups were set haphazardly in a flow through water-table for temperature regulation. After 5 days, thalli were reweighed, and growth was calculated as per cent change from initial biomass. Data from both sites met the assumptions of normality and homogeneity of variance and were analysed by a two-factor ANOVA using the statistical software JMP version 11.

An *in situ* two factor, fully crossed experiment varying nutrient addition (+/− N) and access to herbivores (+/− H) was repeated at Gump (25–30 April 2012) and Sailing School (9–14 May 2012) reefs to determine whether *T. ornata* biomass was controlled by bottom-up and/or top-down processes or their interaction. Herbivore access was limited by exclusion cages (six sided; $10 \times 10 \times 15$ cm^3 L × W × H) constructed from hardware cloth with 1 cm openings. Light restriction by caging material was < 10%, and there was no measured restriction to flow in similar cages used at the same site (Clausing *et al.* 2014). Thalli open to herbivores were attached to square (10 × 10 cm) bases of the same hardware cloth. Forty *T. ornata* thalli were collected from Gump and Sailing School reefs and wet weighed ($\bar{x}$ = 6.26 g ± 0.25 SEM). Individual thalli were assigned to four treatments: ambient nutrients and uncaged (−N+H), ambient nutrients and caged (−N−H), nutrient enriched and uncaged (+N+H) and nutrient enriched and caged (+N−H). Nutrient enrichment was achieved by placing 20 g of slow-release fertilizer (Osmocote 19N:6P:12K) in a mesh bag attached either to a cage bottom or open platform. Ten replicates of each treatment were deployed at both sites by randomly attaching the cage or open platform to hard substrate. After 6 days, all experimental units were collected, and the final wet weight and height of each thallus were recorded. Data from both sites were non-normal and heteroscedastic, and these issues were not resolved by common transformations. We used a two-factor univariate variation of permutational multivariate analysis of variance (PERMANOVA) in PRIMER-e v6. This technique has been found to be robust against violations of normality and heterogeneity of variance (McArdle & Anderson 2001; McNatty, Abbott & Lester 2009; Anderson & Walsh 2013). Similarity matrices were constructed using Euclidean distances, which is appropriate for biomass change data where values can be zero or negative (Norkko *et al.* 2013). The model was run on untransformed data for 999 permutations to obtain *P*-values.

A one-factor experiment was conducted to determine whether nutrient-enriched thalli deter herbivores due to increases in chemical defence. Dried nutrient-enriched and ambient thalli from the Gump Reef *in situ* experiment were ground into as fine a powder as possible to remove the influence of any physical defence. The ground material was added to trays of hot agar solution and poured over window screen mesh as thinly as possible. This method was adapted from a technique used by Hay, Kappel & Fenical (1994). No algae were added to a third tray resulting in a control treatment of only agar. Ten experimental units (~5 cm × 7 cm) were cut from each of the three trays and set out in a blocked pattern on Gump Reef on 23 May 2012. Photographs were taken of each plate before and after 3 days in the field. Initial and final surface areas were estimated using ImageJ software. Herbivory was calculated as per cent change in area. Data met the assumptions of parametric statistics and were analysed in JMP using a one-factor blocked ANOVA.

To evaluate whether physical defences were impacted by nutrients, an enrichment experiment was conducted, and then a penetrometer used to determine the relative toughness of nutrient-enriched and ambient *T. ornata* thalli. Twenty *T. ornata* thalli were collected from Gump Reef on 20 April 2013 assigned to nutrient-enriched (as described for field experiment) or ambient treatments and placed back on Gump Reef. Thalli were collected 6 days later, and a blade selected from the most apical (newest algal growth) ring was placed on a platform under an insect-dissecting pin with a small plastic cup attached. Incremental weight was then added to the cup until the pin just pierced the *T. ornata* blade. This method was adapted from Duffy & Hay (1991). The weight was recorded as the mass required to penetrate the thallus, and differences between means for ambient and enriched thalli were determined by a *t*-test in JMP.

Results

Although patterns of growth varied between Sailing School and Gump Reef, there were no significant increases in growth in response to either nitrogen or phosphorous addition. For both sites, growth ranged from < 1 to 6% over the 5-day experiment (Figure 1).

At Sailing School, there was a significant interaction between nutrients and herbivory on per cent change in algal biomass (PERMANOVA, NutrXHerb interaction $P = 0.027$), where herbivores only consumed algae under ambient nutrient conditions (Table 1; Figure 2a). The pattern was the same at Gump Reef (Figure 2b), but the interaction was not significant ($P = 0.107$). While both sites had greatest herbivory rates when nutrients were ambient and herbivores allowed access, net loss in this treatment (−N+H) was nearly threefold greater at Gump compared to Sailing School. When nutrients were added, consumption by herbivores was greatly reduced, resulting in only small losses in biomass at Gump Reef, and increased biomass at Sailing School, presumably due to growth exceeding herbivory in this treatment. When caged,

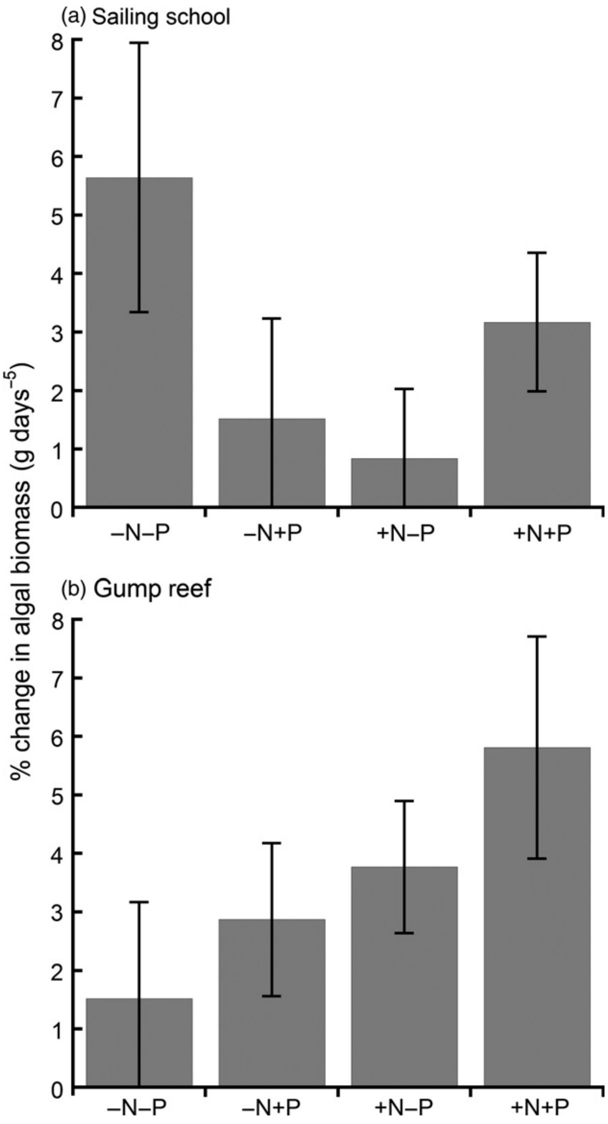


Fig. 1. Results of a two-factor nutrient addition, +/− nitrogen (N) and +/− phosphorous (P), mesocosm experiment at Sailing School reef (a) and Gump reef (b). Bars show mean per cent change (± SEM) of algal biomass.

algae at Sailing School grew an average of 10–15% while those at Gump Reef either did not change or showed small losses. Similarity in the magnitude of the caging by nutrient interaction between the two sites (net difference of 25–30% change in biomass between −N+H treatments and all others) indicated that the difference between sites was driven by higher growth at Sailing School than Gump as opposed to different herbivory rates.

In contrast to the field manipulation, when physical defences were removed, herbivores preferentially grazed on agar containing nutrient-enriched thalli (Figure 3a). Only the agar plates containing thalli enriched by fertilizer showed significant loss in surface area by herbivory (blocked ANOVA, P-value = 0.0021). The agar containing algal thalli grown under ambient nutrients and those with no *T. ornata* thalli were not significantly different from each other, and their mean per cent change was near zero.

Table 1. Results from the permutational analysis (PERMANOVA) of differences in *T. ornata* biomass change for the *in situ* two-factor (Nutrients and Herbivory) experiments conducted at Gump and Sailing School reefs.

PERMANOVA	df	SS	MS	Pseudo-F	P(perm)
Sailing School					
Nutrients (Nutr)	1	529.62	529.62	1.9731	0.179
Herbivory (Herb)	1	1752.4	1752.4	6.5285	**0.018**
Nutr × Herb	1	1508.4	1508.4	5.6193	**0.027**
Res	33	8858	268.42		
Total	36	12947			
Gump					
Nutrients (Nutr)	1	1016.3	1016.3	2.2475	0.165
Herbivory (Herb)	1	1878.8	1878.8	4.1547	0.053
Nutr × Herb	1	1331.5	1331.5	2.9444	0.107
Res	35	15827	452.21		
Total	38	19842			

Bold numbers represent significant P-values (<0.05).

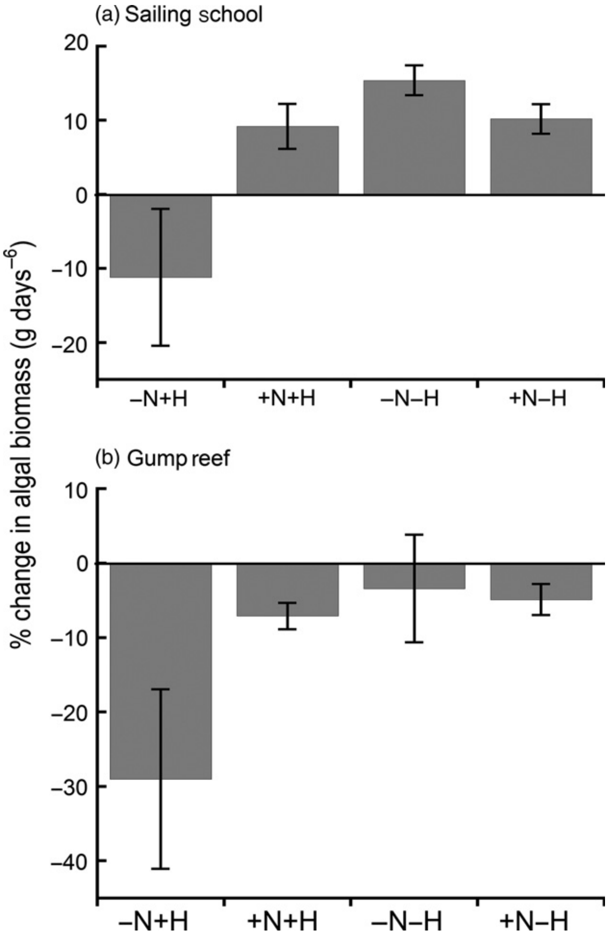
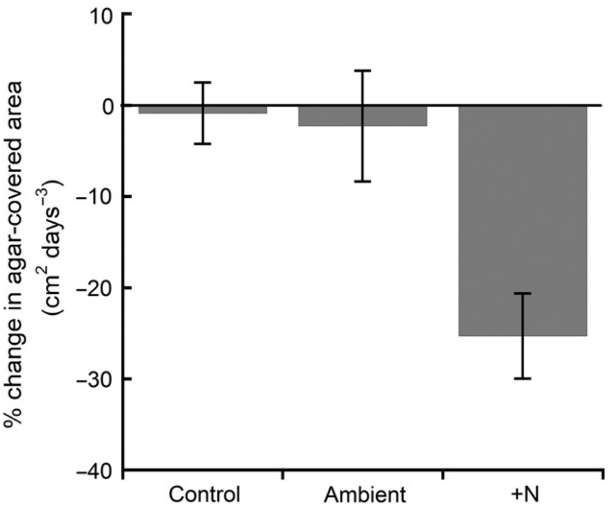


Fig. 2. Results of a two-factor *in situ* experiment manipulating nutrients (+/− N) and herbivory (+/− H) repeated at two sites – Sailing School (a) and Gump (b). Bars are mean per cent change (+/− SEM) of algal biomass.

There was a significant effect of nutrient enrichment on the toughness of *T. ornata* thalli (t-test, P-value = 0.0002; Figure 3b). There was nearly a 30% increase in the weight


(a) Agar

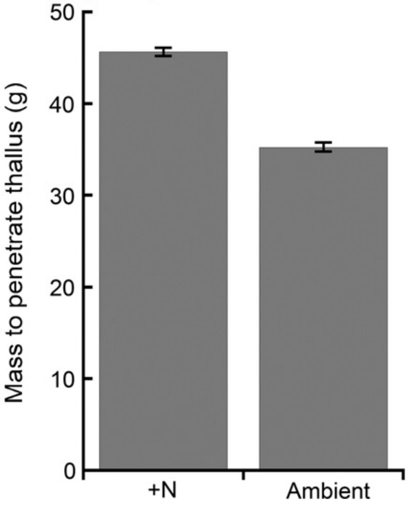

(b) Toughness

Fig. 3. (a) Palatability study of ground nutrient enriched (+N) and ambient *T. ornata* placed in agar shows that enriched thalli are consumed preferentially (ANOVA, $P = 0.0021$), and thus, there is not a chemical deterrent associated with increased nutrient load. (b) Confirmation that *T. ornata* thalli are protected from herbivory by nutrients through a strengthening of physical defences, or thalli toughness (*t*-test, $P = 0.0002$).

needed to pierce the thalli of nutrient-enriched compared to ambient *T. ornata* thalli.

Discussion

We found a unique interaction whereby enhanced physical defences with nutrient enrichment released *T. ornata* from herbivore control, which may allow expansion of *T. ornata* to habitats where it is usually controlled by high herbivory. This is a novel finding because, in this case, reduction in herbivory is the indirect result of nutrient enrichment, not the direct result of overfishing, as is commonly found in other reef systems (e.g. Hughes *et al.* 2010). The finding that nutrients decrease herbivory contrasts to previous empirical work and theoretical predictions that enrichment will, if anything, stimulate herbivory and trophic complexity (see Oksanen *et al.* 1981; Hillebrand *et al.* 2007; marine examples in Gruner *et al.* 2008; He & Silliman 2015). Additionally, most other studies examining interactions of nutrients and herbivory on coral reef algae have found herbivory to be more important, and that nutrients are only important in the absence of herbivores (see Burkepile & Hay 2006 for a meta-analysis).

Our results suggest that human impacts that alleviate nutrient limitation, and thereby reduce herbivory, may facilitate *T. ornata*'s expansion of its range and habitat usage. This expands upon previous evidence that biotic and abiotic interactions have strong effects on communities supported by foundation species (Ellison *et al.* 2005) by suggesting strong interactions are also important for a secondary foundation species that may be replacing a primary foundation species. Human alterations of abiotic factors have been found to change the outcome of interspecific interactions, specifically competition, across ecosystem types (Briggs *et al.* 2005; Veldman & Putz 2011; Saintilan *et al.* 2014). Mangroves, for example, have expanded into saltmarshes in areas where climate change has resulted in warmer winter temperatures (Saintilan *et al.* 2014). Competitive outcomes between mangroves and saltmarsh graminoids are mediated by environmental conditions, and mangroves are predicted to be competitively dominant when winter temperatures are higher and droughts more frequent (Osland *et al.* 2013; Saintilan *et al.* 2014). Similarly, the reduction of the abiotic controlling force of fire on grassland prairies allowed shrubs to recruit, become competitively dominant, and replace previously dominant C4 grasses (Briggs *et al.* 2005). Once large stands established, more frequent fire regimes did not necessarily reverse the shift because the large and persistent shrubs also protected fire-sensitive recruits and species. Changes to nutrient availability have also resulted in shifts in species dominance in each of these ecosystems (for a review see Smith, Tilman & Nekola 1999). Although the drivers occur at different scales, human-induced change of abiotic forces (winter temperature, fire frequency and nutrient levels) has caused each of these foundation species to be released from biotic controls (competition and herbivory) that previously restricted their distribution. This caused large community and ecosystem shifts for saltmarsh, grassland and forest systems, and we predict this is true for reef systems where *T. ornata* is expanding and potentially competing with coral as well. Our study adds to a growing body of literature that suggests human alterations of key abiotic forces, such as nutrient limitation, can cause shifts in foundation species by changing the strength and even direction of interspecific interactions (e.g. Briggs *et al.* 2005; Veldman & Putz 2011; Osland *et al.* 2013; Saintilan *et al.* 2014).

The bolstering of *T. ornata*'s physical defences in response to increased nutrients is a unique finding, as previous work on the effects of nutrients on defences has either considered chemical defences or cases where physical defences decline. Some studies have found enhanced phenols may serve as chemical defences in *T. ornata* (Stiger, Deslandes & Payri 2004) and temperate brown macroalgae (Yates & Peckol

1993; Koivikko *et al.* 2005) in response to nutrients, but increased phenols in brown algae may not always result in decreased herbivory pressure (for a review, see Targett & Arnold 1998). A physical anti-herbivore response to nutrients appears to be novel except in calcifying forms of algae. Calcium carbonate ($CaCO_3$) mineralization has been shown to decrease in response to elevated levels of phosphates in several species of calcifying algae presumably making them more susceptible to herbivory (e.g. *Halimeda* in Demes, Bell & Dawes 2009). However, the direction of the nutrient effect is opposite; nutrients stimulated defences in *T. ornata*, but reduced them in calcifying algae. In terrestrial systems, resource allocation and carbon nutrient balance theories predict that nutrient-rich environments will yield plants with decreased physical defences, such as sclerophylly or leaf hardening, although a meta-analysis of 50 studies did not find conclusive results (Endara & Coley 2011). Previous studies of physical toughness as a defence in non-calcifying macroalgae have usually focused on herbivory by amphipods and found differences based on algal species (e.g. Duffy & Hay 1991) and tissue type (e.g. Taylor, Sotka & Hay 2002), but have not been linked to nutrient regimes. Rather, nutrients have been found to increase the palatability of *T. turbinata,* a Caribbean congener (Chan *et al.* 2012). However, it is unknown whether this has any relation to a change in defences, though when physical defences were removed, we found enriched *T. ornata* became more palatable as well. It is likely that increased toughness has additional population-level effects other than deterrence of herbivores, such as increased breaking strength that may reduce dispersal via thalli detachment and rafting. Clearly, more research is needed to explore the full implications of this finding. However, our results demonstrated *T. ornata's* distribution and abundance may be controlled, at least in part, by a unique interaction between top-down and bottom-up processes that facilitate *T. ornata* populations by increasing physical defences in contrast to the potential decreases in calcifying algae and in terrestrial systems.

Turbinaria ornata does not have an opportunistic life-history strategy like other algae that typically dominate in response to nutrient enrichment in marine and estuarine ecosystems in general (for a review, see Fong 2008) and coral reefs in particular (e.g. Folke *et al.* 2004). Rather, our results support *T. ornata's* designation as a species with a ‘persistor’ life-history strategy (Littler & Littler 1980), as it did not respond directly to nutrient input by increasing growth. In comparison, some species of opportunistic macroalgae can increase growth by 20% or more in just 3 days when subjected to nutrient enrichment (Fong *et al.* 2003). Overall, *T. ornata* grows relatively slowly, like many other foundation species (e.g. Ellison *et al.* 2005). In contrast to our results, where nutrients facilitated a secondary foundational species, in systems dominated by slower growing foundation species, nutrient enrichment often causes replacement by rapidly growing opportunists. In seagrass beds, for example, nutrient run-off causes increased micro- and macroalgal growth and subsequent seagrass loss (Orth *et al.* 2006). Similarly, higher nutrients on coral reefs can cause phytoplankton blooms or corals can be overgrown by opportunistic macroalgae (Hughes *et al.* 2010; Fong & Paul 2011). However, there are several terrestrial examples where slow growing, long-lived foundation species such as hardwood forest trees (Rohr, Mahan & Kim 2009), grassland shrubs (Briggs *et al.* 2005) and mangroves (Saintilan *et al.* 2014) are the replacement species. Our study adds a novel aquatic example to these terrestrial cases and replacement by a persistent secondary foundation species may be of greater concern than by more temporary, ephemeral algal species.

Although the global decline of foundation species is well documented (Ellison *et al.* 2005), much work is still needed to understand the potentially complex drivers of change. In many systems, a suite of human impacts has changed the range and habitat boundaries of foundation species by releasing them from limiting ecological forces (Briggs *et al.* 2005; Rohr, Mahan & Kim 2009; Veldman & Putz 2011; Saintilan *et al.* 2014). In some cases, expansions into new geographic regions and local habitats have occurred at the expense of an original foundation species. While it is unknown whether *T. ornata* directly replaces other foundation species in the system (such as corals), as with mangroves and saltmarsh plants, recruits of both occupy the same substrate. Further, as a secondary foundation species dependent on the hard substrate afforded by calcium carbonate deposition by corals, we expect a shift from a coral to *T. ornata* dominated reef to result in an overall decline in reef resilience. Further, a recent study suggested that *T. ornata* recruits may negatively affect coral recruits (Brandl, Hoey & Bellwood 2014). As human impacts are becoming more pervasive, it is essential not only to understand the numerous systems in which foundation species are degraded but also to evaluate drivers in cases where secondary foundation species are expanding at the expense of the original foundation community.

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Data accessibility

Data deposited in the Dryad repository: http://datadryad.org/resource/doi:10.5061/dryad.s5pb0 (Bittick, Clausing, Fong & Fong 2016).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Tissue nutrient data from *T. ornata* collected at Sailing School and Gump Reefs.

Figure S1. Percent tissue nitrogen at Sailing School vs. Gump Reef.

Figure S2. Percent tissue phosphorous at Sailing School vs. Gump Reef.