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An integrated empirical and modeling approach to evaluate determinants of community structure and alternate stable states dynamics on tropical reefs

Author
Muthukrishnan, Ranjan

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An integrated empirical and modeling approach to evaluate determinants of community structure and alternate stable states dynamics on tropical reefs

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by

Ranjan Muthukrishnan

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ABSTRACT OF THE DISSERTATION

An integrated empirical and modeling approach to evaluate determinants of community structure and alternate stable states dynamics on tropical reefs

by

Ranjan Muthukrishnan
Doctor of Philosophy in Biology
University of California, Los Angeles, 2013
Professor Peggy Marie Fong, Chair

Coral reefs have seen precipitous declines across the globe that are generally associated with transitions to reefs dominated by algae. Understanding the causes and dynamics of these transitions is of critical importance for the implementation of effective management strategies to protect reefs that remain healthy and to recover degraded reefs. To address these issues I evaluated the potential resilience of coral reefs at Isla Contadora, Panamá in the Easter Tropical Pacific (ETP), to different anthropogenic stresses with an integrated approach using empirical and modeling methods. Direct community response to stressors was investigated with experimental manipulations of herbivore abundance, nutrient supply and sediment loading. These experiments showed that any of the three stressors could push reefs toward algal dominance but that the effects of particular stressors were variable and highly dependent on the environmental context in which they were applied. In addition, I identified that herbivory rates and nutrient availability, two critical controls of community structure, vary in response to the local abundance of coral and algae. Because both processes are stronger in the community state they support they act as positive feedbacks pushing reefs toward divergent community states and producing patchy spatial patterning. Using these empirical results I developed a spatially explicit simulation model that incorporated and tested if the environmental conditions measured in the ETP supported alternative stable states (ASS). ASS theory is a dominant conceptual framework for understanding processes that support resilience of ecological communities in the face of anthropogenic disturbance, and, by combining empirical and modeling methods, I propose a rapid and non-destructive method to evaluate ASS in fragile habitats. Using the model I demonstrated that the presence of positive feedback are essential for ASS and the strength of those feedbacks is the critical factor that separates systems with phase shifts and ASS. With data from Isla Contadora I was also able to identify the particular conditions under which ETP reefs should display ASS and demonstrated that the reefs at Isla Contadora exist within that range suggesting they exist as ASS.

The dissertation of Ranjan Muthukrishnan is approved.

Paul Henry Barber

James O. Lloyd-Smith

Mary E. Power

Peggy Marie Fong, Committee Chair

University of California, Los Angeles

2013

To the boys of Manhappening: Jason, Julian, Ravi, Josh, Matt, Kelly, Aman, Idan and Aravind. Thanks for making a weird, awkward kid from Kansas feel comfortable enough to keep being weird and exploring and trying to understand the world because it turns out that's most of what it takes to be a scientist.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

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Adventure Awaits

VITA

2003	B.A. in Integrative Biology University of California, Berkeley
2002-2006	Research Assistant University of California, Berkeley
2005	Lab Technician, Division of Gene Expression and Regulation The Wistar Institute, Philadelphia Pennsylvania
2006	Lab/Field Technician, Dept. of Biology University of Pennsylvania
2006	Field Research Assistant, Dept. of Biology Villanova University
2007	Research Assistant, School of Natural Resources University of Nebraska, Lincoln
2007	UCLA Foundation Fellow University of California, Los Angeles
2008-2009	UCLA Graduate Research Mentorship Fellow University of California, Los Angeles
2008-2009	Teaching Assistant UCLA Department of Ecology and Evolutionary Biology University of California, Los Angeles
2008-2013	National Science Foundation Graduate Research Fellow University of California, Los Angeles
2012-2013	UCLA Dissertation Year Fellow University of California, Los Angeles

PRESENTATIONS

Muthukrishnan, R. 2012. Catastrophic community shifts in tropical reef ecosystems: External stresses and internal feedbacks. Invited seminar CSU Fullerton Dept. of Biological Science.

Muthukrishnan, R. 2012. Determinants of community structure in tropical reef ecosystems: External stresses and internal feedbacks. Invited seminar UC San Diego/San Diego State University Coral Club.

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* Denotes first author was an undergraduate

CHAPTER 1:

Benthic community structure and stabilizing mechanisms provide support for alternative stable state theory in a tropical reef ecosystem

Abstract

Substantial recent attention has been placed on the idea that dramatic community shifts may represent shifts between alternative stable states (ASS), though robust evidence is still lacking. We tested both an underlying assumption of and predictions from this theory to evaluate whether shifts from coral-dominated to algal-dominated tropical reefs represent alternative stable states on two reefs around Isla Contadora, Republic of Panamá. Theory predicts that ASS systems display a bimodal distribution of community states within the same environment because of feedback processes that push the systems away from intermediate states. Surveys of benthic community structure showed that community states were distributed in patches either dominated by coral or by algae, while intermediate assemblages were rare. We compared the strength of two feedback mechanisms in algal- and coral-dominated states, facilitation of algal growth and herbivory, and found higher rates of algal growth in the algal-dominated community and higher rates of herbivory in the coral-dominated community. In combination, these mechanisms appear to stabilize these alternate states by supporting algal proliferation in the algal-dominated state and suppressing algal expansion in the coral-dominated state. The presence of stabilizing mechanisms for both the coral- and algal-dominated community states and the distribution of communities with distinct boundaries provides the first direct empirical support for the presence of ASS on tropical reefs.

Keywords: Alternative stable states, feedbacks, coral reefs, herbivory, facilitation

Introduction

Recent dramatic and catastrophic community shifts in systems as diverse as coral reefs (Hughes 1994), deserts (Foley *et al.* 2003), forests (Odion *et al.* 2010) and rocky intertidal shores (Petraitis *et al.* 2009) are widely attributed to disturbance-mediated shifts between alternative stable states (ASS). Because these disturbances can be natural or the result of a plethora of human impacts, ASS theory has taken on renewed importance for conservation and restoration (Suding *et al.* 2004). A fundamental aspect of ASS theory is that for a given ecosystem, there is a range of environmental conditions (between a and b in Fig. 1-1) where multiple community types can arise and be stable, but large disturbances can initiate shifts between states (Beisner *et al.* 2003; Scheffer & Carpenter 2003). Once a sufficiently strong disturbance pushes the community past the unstable equilibrium (dashed line in Fig. 1-1), feedback mechanisms continue to push the system toward and then stabilize the new state (Fong & Paul 2011). As a result, any attempt to understand or manage these ecosystems that fails to consider internal feedback mechanisms will be incomplete and likely ineffective (Zedler 2000). Through field surveys and experiments, we demonstrated that both the structure of and variation in strength of ecological processes between coral- and algal-dominated communities support the hypothesis that they exist as alternative stable states.

Despite the recent widespread application of ASS theory to explain rapid community change in diverse systems, empirical evidence supporting the theory is limited (Schroder *et al.* 2005; Dudgeon *et al.* 2010) and generally follows three lines of evidence. In ASS systems, theory predicts stability to small disturbances in community state, but rapid and catastrophic changes when perturbations cross a threshold (Scheffer & Carpenter 2003); thus, one approach to test for ASS is to experimentally perturb communities and evaluate recovery from or stability of the new state (Petraitis & Dudgeon 1999; Chase 2003). However, such tests can be practically challenging and in threatened ecosystems they are ethically questionable. A second approach based on this prediction is to observe community transitions in long-term monitoring or paleo-ecological studies; ASS will produce transitions that occur as sudden jumps separated by long periods of relative stasis (Foley *et al.* 2003). Analogously, a spatial pattern of sharp boundaries between community states that share the same environmental conditions is also considered strong evidence for ASS and can be recognized by bimodal patterns in the frequency distribution of community composition (Wilson & Agnew 1992; Scheffer & Carpenter 2003). A third line of support is to identify mechanisms that drive the rapid divergence between states, and maintain the system in the alternate state by inhibiting reverse transitions (Wilson & Agnew 1992; Scheffer & Carpenter 2003). Such mechanisms push the system toward a particular state, but because they increase in magnitude in the new community state relative to the original, they limit recovery and are self-reinforcing (Fig. 1-1). Here, we use the last two approaches, searching for sharp spatial transitions in community composition and quantifying stabilizing mechanisms, to assess the presence of alternative stable states in a coral reef ecosystem. While we acknowledge that these do not satisfy all the criteria proposed to rigorously evaluate ASS (Petraitis *et al.* 2009; Dudgeon *et al.* 2010), they are non-destructive and can provide compelling evidence that the necessary conditions exist (stabilizing mechanisms) and have persisted over time (sharply delineated community types).

Catastrophic and unpredicted losses of corals around the globe (Bruno & Selig 2007; Carpenter *et al.* 2008) coupled with large-scale community shifts to reefs dominated by less desirable community members, such as fleshy macroalgae or algal turfs (Hughes *et al.* 2007; Maliao *et al.* 2008), have led many researchers to suggest that algal- and coral-dominated communities represent ASS for tropical reefs (Knowlton 1992; Scheffer et al. 2001). While a system with ASS would produce exactly these types of extreme and rapid transitions, explicit tests for the presence of ASS have rarely been conducted (Dudgeon *et al.* 2010). Some work has suggested that the rate or effectiveness of herbivory increases with coral cover (Friedlander & Parrish 1998; Graham *et al.* 2006) and can be diminished by high algal abundances (Williams *et al.* 2001; Bellwood & Fulton 2008; Hoey & Bellwood 2011), which could produce a stabilizing feedback and provide a mechanism for ASS. There is also emerging indirect evidence that the accumulation of algae is facilitated by the presence of other algae, partly via associational defenses (Hay 1986; Fong *et al.* 2006; Bittick *et al.* 2010), but potentially also from increased N processing and retention in algal patches through internal release of dissolved organic nitrogen (Fong et al. 2004). However, direct comparisons of any of these mechanisms across community states in a single system, which would be necessary to show feedbacks and provide support for ASS, have not been done. Here we present the first field data that compare the relative strength of two stabilizing ecological processes, facilitation of nutrient availability and herbivory, between two community states on tropical reefs. By evaluating the boundaries between community states and comparing rates of herbivory, algal growth, and nutrient limitation across community states, we are able to identify feedbacks and their effects, providing explicit tests of assumptions of and predictions from ASS theory.

The eastern tropical Pacific (ETP) offers an ideal setting to evaluate ASS dynamics in a coral reef ecosystem because of its repeated disturbance from El Niño/Southern Oscillation (ENSO) events and the observed pattern of patches dominated by coral or algae in relatively close spatial proximity (Glynn & Mate 1997). The ETP is regularly subjected to high temperature excursions during ENSO events and the Gulf of Panamá also experiences seasonal upwelling of cold water (Glynn & Mate 1997), both of which provide disturbances that may initiate transitions between alternate states. While previous ENSO events have led to severe coral mortality, rapid recovery has also been recorded, though the extent has been patchy and variable (Glynn & Fong 2006; Guzman & Cortés 2007). In addition, while coral reefs are generally high diversity ecosystems, reefs of the ETP are relatively species poor (Glynn & Mate 1997), which makes experimental studies more tractable. Furthermore, reefs of the ETP are excellent for studies of basic community dynamics due to relatively intact herbivore communities and generally low human impacts (Glynn 2004).

To test the hypothesis that tropical reefs exist as alternative stable states, we evaluated the spatial distribution of coral and algae, and the strengths of two potential stabilizing mechanisms, herbivory and algal nutrient facilitation, across community states. The sharp boundaries between algal-dominated and coral-dominated communities in an ASS system are expected to produce a bimodal distribution in percent cover of coral and algae in surveys of benthic cover (Scheffer & Carpenter 2003). Further, ASS requires self-reinforcing feedbacks and we predict that the presence of live coral increases herbivory rates such that higher levels of herbivory will be seen in the coral-dominated than the algal-dominated community. Conversely, we hypothesize that a second feedback mechanism, facilitation of nutrient availability by algae and subsequent alleviation of nutrient limitation, will produce higher rates of algal growth in the algal-dominated relative to the coral-dominated community.

Materials and Methods

To evaluate whether ETP reefs exist as alternative stable states, we used field surveys to determine if benthic community composition patterns are bimodal and field bioassays to determine if differences in algal growth or consumption between states act as stabilizing mechanisms for coral- and algal-dominated states. All surveys and assays were conducted on reefs surrounding Isla Contadora, Republic of Panamá, approximately 65 kilometers southeast of Panamá City in the Pacific Ocean. Studies were conducted on two reefs: Larga Reef, which is within an embayment on the eastern side of the island, and Suecas Reef along the more exposed southern side of the island. The reef framework is dominated by nearly continuous stands of the branching corals *Pocillopora damicornis* and *P. elegans*, while colonies of a few species of massive corals are also present in lower abundances (Glynn & Mate 1997). Algae in the system are generally encrusting or turf forms that cover dead coral skeletons and coral rubble, or low-relief macroalgae that is usually found in the interstices between coral or rubble where it is relatively inaccessible to herbivores. The reefs are relatively shallow, reaching a maximum depth of only 3-4m below mean low water, and the shallowest colonies are exposed at moderate to extreme low tides (Glynn & Mate 1997).

To determine if coral and algae are distributed in distinct patches, we conducted surveys of benthic community composition at Larga and Suecas Reefs during 14-28 October 2009. Individual 1m^2 plots (n=156) were randomly selected on hard reef substratum and the percent cover of live coral and algae were estimated using a point-intercept method. Plots of this size were typically larger than individual algal or coral colonies, but far smaller than the expanse of coral framework or large algal patches, which we felt made it an appropriate scale to capture heterogeneity within patches. Benthic cover at each point was categorized as either: live coral, algae (including macroalgae, turf and crustose corraline algae), sediment or other. Percent cover was calculated for each category and histograms of benthic cover for both coral and algae were produced with cover values grouped into bins of 10% width, starting with 0-10%.

To test if there were differences in strength of top down control on reef algae between coral- and algal-dominated communities, which act as a stabilizing mechanism (Fig. 1-1 dark arrows), bioassays were used to compare herbivory rates. Assays were conducted at Suecas Reef in November 2008 and January 2009. Distinct patches that were visually evaluated to be coral-dominated (>95% live coral) or algal-dominated (>95% algae) and at the same depth were identified for this portion of the study. For the bioassay, we transplanted bundles of caged and uncaged thalli of a palatable red macroalga from the genus *Laurencia* into each community type and measured change in mass over time. Algae were collected from an adjacent reef immediately prior to the experiment, cleaned of sediment, invertebrates and epiphytes, spun in a salad spinner at a constant rate for 1 minute, then cable-tied into 3 g bundles. Half of the bundles were protected from herbivory by cylindrical cages of plastic hardware cloth (10cm diameter x 15 cm height, 1.3 cm mesh size) to control for handling losses and algal growth.

To deploy assays, ~3m lines were anchored in each community and open and caged algal bundles were attached haphazardly ~25-50 cm apart. Replication of algal bundles was 6 fold in November and 10 fold in January. After 24 hours, each bundle was collected, spun, and reweighed. In the coral-dominated state many samples were completely consumed, which produced a conservative estimate of consumption rate, but still provided relative measures between communities.

To determine herbivory rates, we adjusted for the net effect of handling losses and algal growth by calculating the average final biomass of caged samples for each state. In each treatment the change in biomass of caged samples was < 6% of initial weight and there was no significant pattern between community states (t-test, November p=0.330, January p=0.737). Herbivory rates were calculated by subtracting the final biomass of uncaged samples from the average final biomass of caged samples for the appropriate state. The data were tested for normality and homogeneity of variances and an x^2 transformation was used to meet the assumptions of parametric statistics. Herbivory rates were compared between community states and dates using a 2-factor ANOVA.

To quantify a facilitative feedback of algal abundance on algal growth, growth rates were compared between community states at both Suecas Reef and Larga Reef in December 2009. At Suecas Reef, growth assays used the same locations as the herbivory assays, and new sites were identified at Larga Reef using the same criteria. In addition, to evaluate if the facilitative effect shared the same spatial boundary as the community state, assays were deployed at 5 points along a transect that crossed between community states at Larga Reef. The transect was centered on the boundary between states and assays were placed at the boundary and 5m and 10m into each state. Algae were collected and processed as for herbivory assays, except that samples were 2 grams and all samples were placed into window screen cages (approx 15cm x 15cm; 1mm mesh size) to prevent herbivory. Cages were attached to lines (5 cages per line ~20cm apart) and anchored flush with the substrate at the appropriate position (n=10 at boundary and 5m positions at Larga Reef and n=15 at 10m positions at Larga Reef and both positions at Suecas Reef). Lines at the boundary were placed directly at the base of the transition to coral framework. Assays were deployed for 6 days then collected and reweighed and daily growth rates (as % of initial wet weight) was calculated. All data met assumptions of parametric statistics and growth rates at Larga Reef were compared using a 1-factor ANOVA followed by post hoc comparisons using Tukey's HSD. For Suecas Reef, growth rates were compared using a t-test.

Nutrient limitation was measured in the two community states at Larga Reef concurrently with the algal growth assays. An additional set of caged algae (n=15) was grown with nutrient enrichment at both 10m positions used in the growth assays. Ten grams of Osmocote slow-release fertilizer (14%N:14%P:14%K) was placed inside a diffuser made from a nylon stocking and included with the algae in the window screen cages. To limit flux of nutrients to ambient samples, enriched samples were placed a minimum distance of 2 meters away. Samples were collected and processed as in the algal growth assays and daily % growth rates calculated. The change in growth rate due to enrichment was calculated by subtracting the average growth rate of ambient samples from each enriched sample from that community state (Equation 1).

$$C_e = g_e - g_a \quad Equation\ 1$$

Where C_e is change due to enrichment, g_a represents the average growth rate (in percent change per day) from all ambient samples (n=15) and g_e is growth of individual enriched samples. These data met assumptions for parametric statistics and were compared between the coral- and algal-dominated states using a t-test.

Results

The frequency distributions of both coral and algal cover showed strongly bimodal patterns (Fig. 1-2 a-b). Coral was found in either very high abundance, with the largest number of plots between 80-90% cover, or at very low abundance, with a second peak in number of plots in the 0-10% cover. Because the majority of quadrats were either coral- or algal-dominated, algal cover had the opposite pattern and was most frequently in the 10-20% cover category but there was also a second mode in the 90-100% cover category.

Rates of herbivory were consistently higher in the coral-dominated state across both dates (Fig. 1-3). Overall herbivory rates were nearly 75% higher in the coral-dominated state compared to the algal-dominated state, which produced a significant main effect of community state ($F_{1,28}=10.828$, $p=0.0027$). There was no significant effect of date ($F_{1,28}= 0.737$, $p=0.3980$) nor was there a significant interaction between factors ($F_{1,28}=0.107$, $p=0.7461$) which indicates the difference between community states was consistent across time.

In the algal growth assay, the algal-dominated state produced significantly higher growth rates on both reefs (Fig. 1-4). At Suecas Reef algal growth rates measured in the algal-dominated state were nearly twice as high as in the coral-dominated state (t=4.637, df=28, $p<0.0001$). At Larga Reef we found the same pattern between states with a distinct shift between growth rates at the boundary. A 1-factor ANOVA identified differences in growth between positions along the gradient ($F_{4,55}=9.606$, $p=0.00006$). Post hoc comparisons showed no difference between growth within the algal-dominated community of Larga Reef, but both were higher than all other positions including the boundary. The boundary and the two coral positions grouped together with no difference between them.

Nutrient enrichment produced an increase in algal growth in the coral but not the algal-dominated community (Fig. 1-5; t = 2.758, df = 28, p = 0.0101), demonstrating nutrients were limiting only in the coral-dominated community. In the coral-dominated state, growth rates under enrichment increased more than a third from an average of 6.3% to 8.6% daily increase in biomass. Enrichment in the coral-dominated state increased growth rates to levels similar to those seen in the algal-dominated state, removing the difference seen between states under ambient conditions.

Discussion

Our experiments demonstrated that strong facilitation of algal growth within algal communities is a novel mechanism promoting stability of algal-dominated tropical reefs by ameliorating nutrient limitation. Conversely, within coral communities, strong nutrient limitation due to the absence of this facilitative effect maintains coral dominance. Facilitative mechanisms that arise from the establishment of a particular community assemblage and aid the growth and establishment of new individuals have been shown in diverse ecosystems (Callaway *et al.* 2002; Maestre *et al.* 2003) but up to the present such mechanisms have not been evaluated in tropical reefs. However in other marine systems, facilitative algae-invertebrate interactions have increased community stability by increasing nutrient cycling via excretion of nitrogenous wastes (Giannotti & McGlathery 2001) and accelerating nutrient regeneration from sediments (Fong *et al.* 1997). The incorporation of cyanobacteria in algal turfs can further increase nutrient availability through nitrogen fixation (Fong & Paul 2011). The presence of facilitation has also been sufficient to produce ASS in models of community dynamics by increasing the abundance of certain community members that are strong interactors, which drives divergence between community states (Baskett & Salomon 2010). While there has been theoretical support, this is the first empirical evidence of a facilitative mechanism stabilizing alternate states in coral reefs, and of nutrient facilitation in specific occurring on reefs.

We found that higher herbivory in coral communities and lower herbivory in algal communities is a second stabilizing mechanism driving the maintenance of both community states. While the importance of top-down processes in controlling coral reef communities has been well studied (Ogden & Lobel 1978; Burkepile & Hay 2006; Heck & Valentine 2007), no other work has explicitly compared top-down control between community states to identify feedbacks that can stabilize multiple states. The complex three-dimensional structure produced by growing coral may provide a mechanism for this feedback as herbivorous fish and sea urchins have been shown to prefer greater structure (Friedlander & Parrish 1998; Lee 2006). Increasing biomass of chemically defended algae has also been shown to inhibit herbivore activity in algal-dominated communities, despite the increase in structure some algal communities provide (Hoey & Bellwood 2011). Our herbivory assays show similar patterns with high herbivory in the coral-dominated community, and reduced herbivory in the algal-dominated community. However, in our study system three-dimensional complexity is much lower in the algal-dominated state compared to the coral-dominated state, suggesting that different mechanisms are producing similar reductions in herbivory in these different systems. If taken together these two sets of results suggest that herbivores are not simply responding to structural complexity, but are reacting to the presence of algae specifically. In addition, algae with anti-herbivore defenses are common (Paul *et al.* 2007; Paul & Ritson-Williams 2008) and the presence of these species in an algal community can reduce herbivory not only on themselves but also on the broader community by providing an associational defense (Hay 1986; Fong *et al.* 2006;

Bittick *et al.* 2010). This variation in the level of herbivory facilitates multiple states and confers resilience to each of them.

Through increased nutrient availability and habitat for herbivores, algae and coral, respectively, modify their local environment in ways that make conditions more favorable for themselves which produces abrupt shifts in community composition as previous work has predicted (Wilson & Agnew 1992). In a number of terrestrial plant communities sharp boundaries have been identified that are produced or amplified by vegetation that shifts bottom-up controls in the system (Adema *et al.* 2002; Eppinga *et al.* 2009). In contrast, the only example of a sharp boundary produced by habitat modification we were able to identify in a marine ecosystem (Konar & Estes 2003) involved the modification of a top-down control by a community dominant physically excluding a consumer. Many studies recognize that corals are often distributed in disjoint patches and that the distributions of other organisms are tightly linked to the extent of coral framework (*e.g.* Munday *et al.* 1997; Garpe & Öhman 2003). However, our work adds a mechanistic explanation for the shape of and causes for the edges of those patches, specifically that sharp boundaries result from biotic feedbacks on both sides of the boundary.

Having a working theoretical framework upon which to further our understanding of ecological processes, especially resilience, is key to developing and implementing effective conservation strategies; thus, testing the underlying assumptions necessary for and predictions from ASS theory in coral reefs is an important task. We have begun this process by presenting three separate lines of evidence that support the existence of alternative stable states in reefs of the ETP. The algal-dominated state showed facilitation of algal growth through an amelioration of nutrient limitation.

Conversely stronger top-down control through herbivory in the coral-dominated state promotes continued coral dominance. Together, these mechanisms can drive tropical reefs toward these separate community states and produce sharp spatial boundaries between them. While these types of methods cannot definitively discriminate between phase shifts and ASS (*sensu* Dudgeon *et al.* 2010; Fong & Paul 2011) or test the stability of the system, they provide strong evidence to justify future efforts. Furthermore, for fragile, endangered, or difficult to manipulate ecosystems these strategies offer the best available evidence when more destructive methods are inappropriate or conservation efforts require a timely evaluation. As such this work can serve as a model for rapid and non-invasive methods to evaluate ASS in other systems. In addition we hope that our work will spur further explicit tests of ASS theory, particularly the search for additional feedback mechanisms. Such tests will reveal much about what controls tropical reef community structure and can inspire increasingly effective strategies to help conserve them in the future.

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Figures

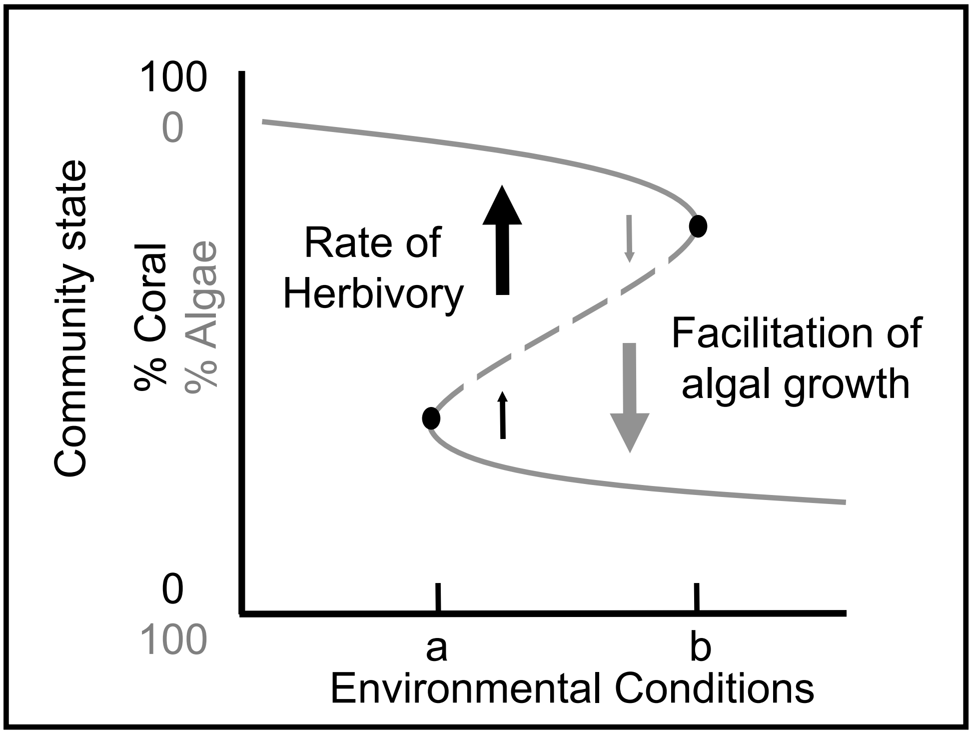

Fig. 1-1 Herbivory and algal growth can stabilize alternate states if their rates increase as the relative abundance of coral and algae increases or decreases, respectively. Size of arrows represents relative strength of process, at that particular community state.

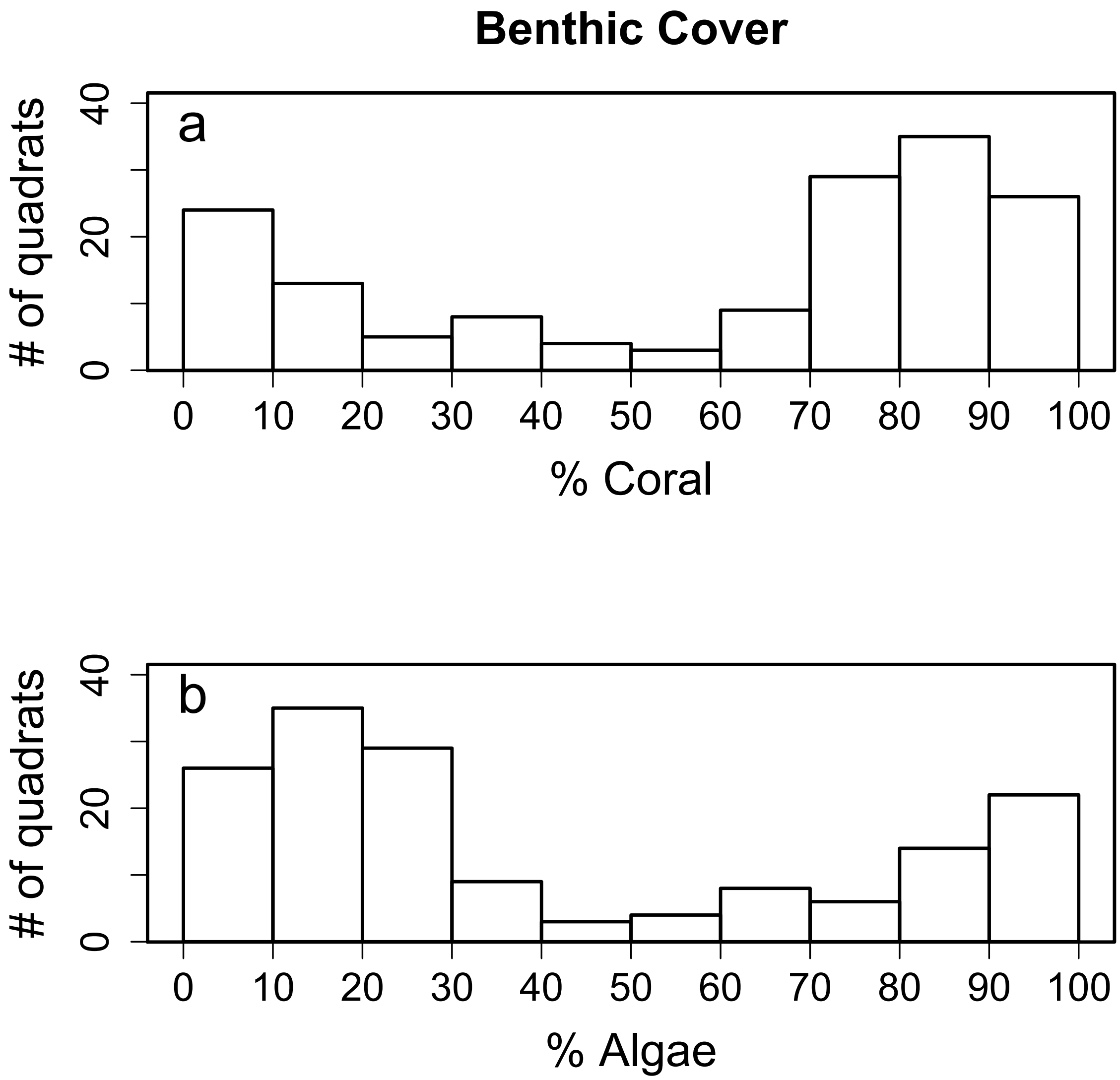

Fig. 1-2 Surveys of benthic cover showed the frequency of areas with different percent covers of coral (a) and algae (b). Histograms are binned in intervals of 10% (0-10%, >10%- 20%, etc.).

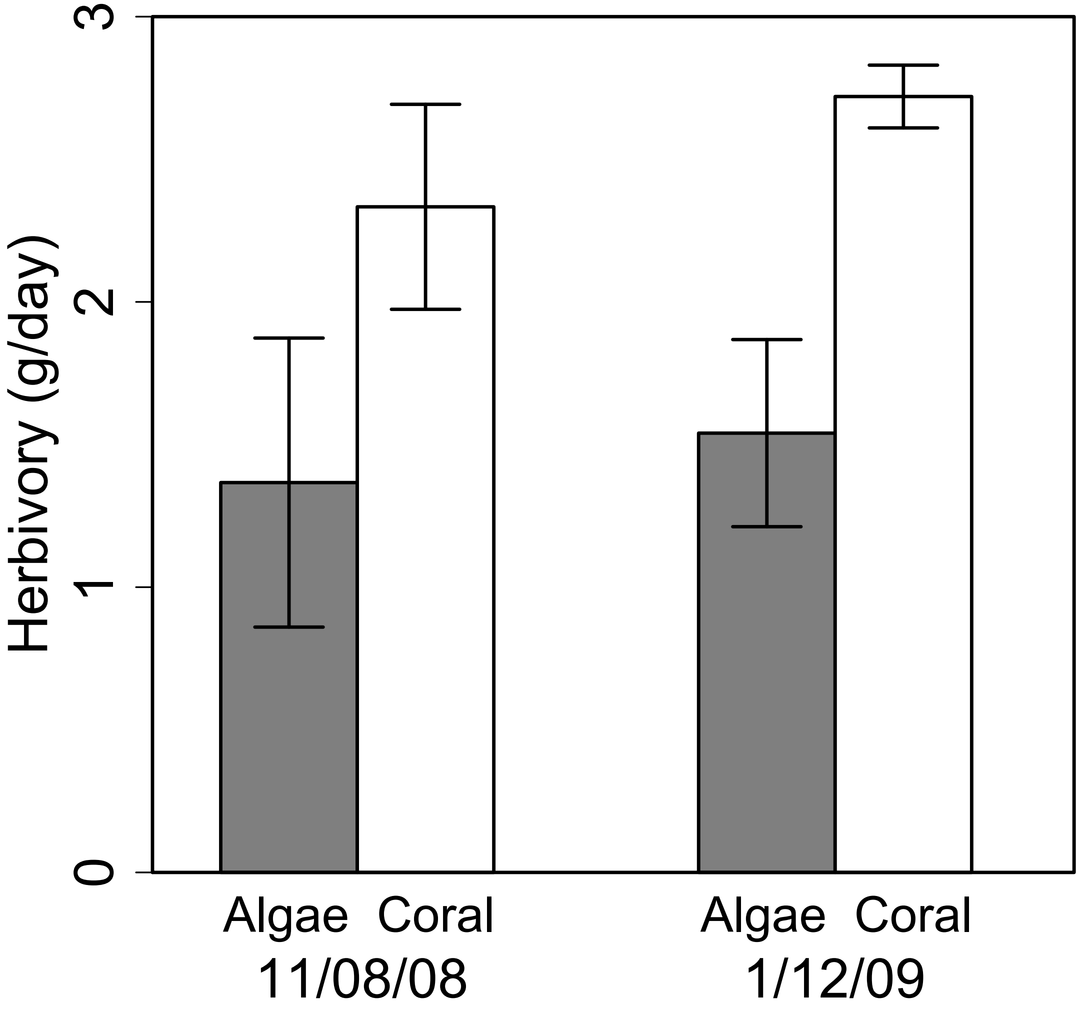

Fig. 1-3 *In situ* assays conducted on two dates compared herbivory pressure between coral-dominated and algal-dominated communities.

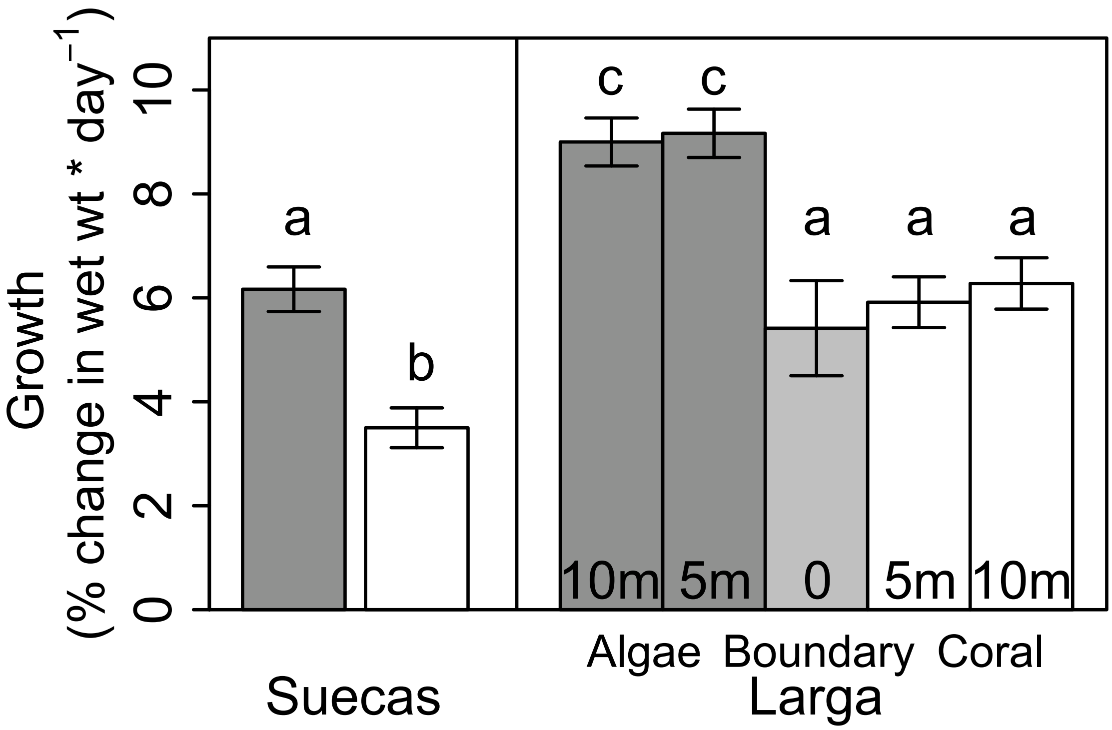

Fig. 1-4 *In situ* assays compared algal growth rates at two reefs between coral-dominated and algal-dominated communities. At Larga Reef growth rates were measured along a gradient from a coral-dominated to algal-dominated state with measurements taken at 10m and 5m into in each state and at the boundary between states.

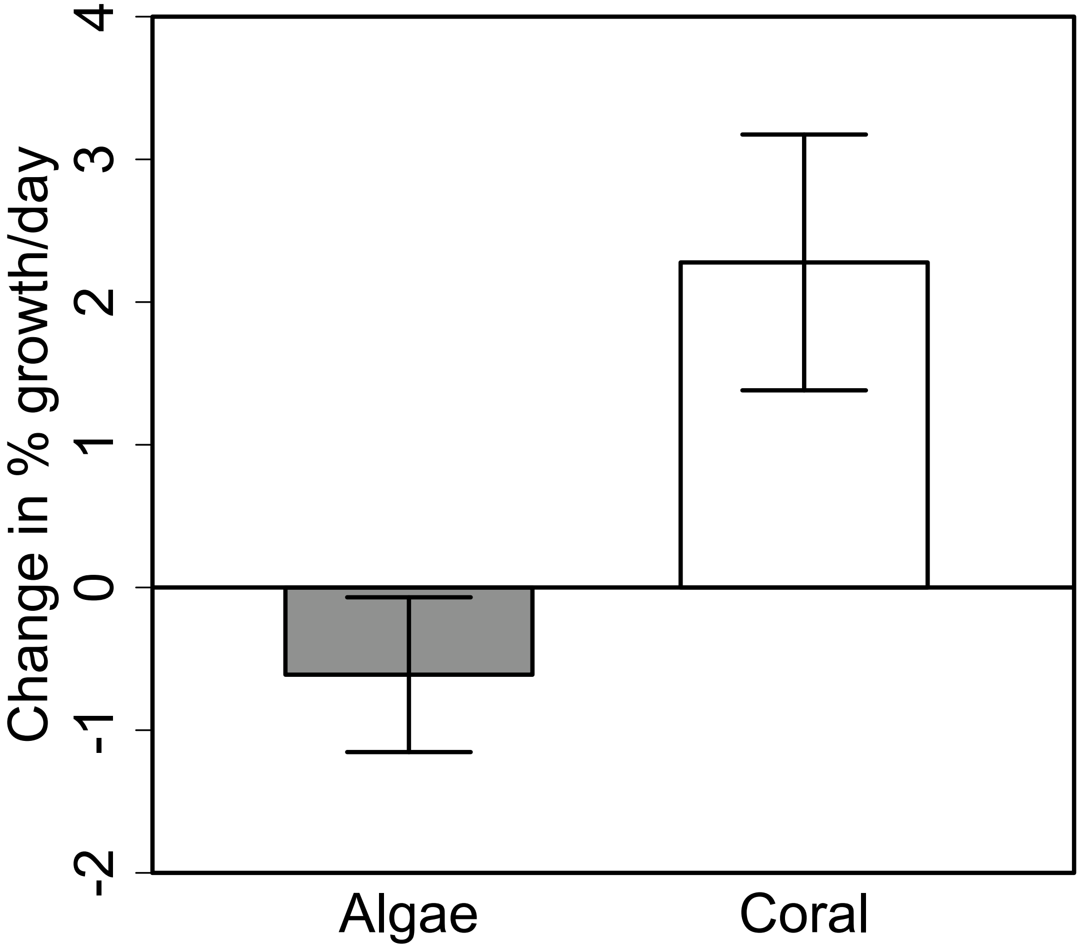

Fig. 1-5 *In situ* nutrient enrichment experiments compared the change in percent growth relative to ambient conditions between algal-dominated and coral-dominated communities at Larga Reef.

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CHAPTER 2:

Environmental context alters the relative importance of multiple stressors controlling coral and algal abundance on coral reefs

Abstract

Coral reefs across the globe are impacted by multiple natural and anthropogenic stressors that are driving coral declines, but the relative importance of different stressors and the ways they interact remain poorly understood. Because coral reefs exist in variable environments, effective prediction of community response to stressors requires understanding variability in responses across a broad range of conditions. To evaluate the role of multiple stressors in a highly variable environmental context, we experimentally manipulated three stressors (herbivore abundance, nutrient levels and sediment loading) on plots of a natural reef in the Eastern Tropical Pacific spanning both a non-upwelling and upwelling period. Monitoring of the benthic community showed complex responses with all three stressors impacting the community, but under different environmental contexts and on different community members. There was strong top-down control, largely on macroalgae, during the non-upwelling season; however, this control was lost during the upwelling season. During upwelling there was a transition to control by nutrient and sediment levels, but these controls were seen mainly on coral and turf algae as opposed to other algal types. Transitions among controlling factors and individual community-member responses indicated that each stressor had the potential to impact community structure but environmental context strongly influenced outcomes. Thus it is critical to evaluate community dynamics under a variety of conditions to understand how stressors will impact a community.

Introduction

Coral communities have been declining across the globe (Gardner et al. 2003; Pandolfi et al. 2003; Bruno and Selig 2007), often associated with a shift from reefs dominated by long-lived scleractinian corals to reefs dominated by fleshy macroalgae or algal turfs (Smith et al. 1981; Hughes 1994; Maliao et al. 2008). With a few notable, extremely remote exceptions (Knowlton and Jackson 2008; Sandin et al. 2008; Barott et al. 2010) most reefs are influenced by direct human impacts (Halpern et al. 2008; Knowlton and Jackson 2008; Hughes et al. 2010; Burke et al. 2011). Thus, understanding how reefs respond to anthropogenic stressors is critical to predict the future of those ecosystems.

Most coral reef ecosystems are also affected by multiple stressors simultaneously and under a variety of environmental contexts leading to a breadth of potential interactive consequences (Hughes and Connell 1999; Halpern et al. 2008). In other ecosystems, the most common focus of studies of multiple stressors has been on synergistic interactions that produce larger impacts than individual stressors, and potentially drive major community shifts (Paine et al. 1998; Hughes and Connell 1999; Vinebrooke et al. 2004); however, a range of interaction types from synergistic to antagonistic have been observed (Crain et al. 2008; Darling and Côté 2008; Tylianakis et al. 2008). This variability in interactions may be an indication of context dependency with responses changing under different conditions (Crain et al. 2004, 2008). Hence there is a need to evaluate the effects of multiple stressors under a range of environmental contexts in order to understand how real ecosystems will respond to continued anthropogenic influences (Agrawal et al. 2007).

Coral declines have been related to a number of anthropogenic stressors (Richmond 1993; Pandolfi et al. 2005) including overfishing, nutrient enrichment, and sedimentation. Overfishing is near ubiquitous on reefs with any level of human exposure (Jackson et al. 2001; Newman et al. 2006; Sandin et al. 2008) and has been argued to be the fundamental factor leading to community shifts to algal-dominated tropical reefs (Jackson et al. 2001). Rapid rates of herbivory on healthy coral reefs result in strong top-down control of algal biomass accumulation even with high rates of algal growth (McClanahan et al. 1996; Aronson and Precht 2000). This is a key mechanism of coral reef resilience that allows reefs to adapt to conditions that support greater algal growth and yet maintain low algal abundance (Bellwood et al. 2004). As overfishing reduces herbivore populations those controls are removed and algal biomass is able to increase, often dramatically (Hughes et al. 2007; Mumby et al. 2007; Burkepile and Hay 2009).

Increases in nutrient supplies are a second anthropogenic impact on reefs and are thought to increase the competitiveness of algae; however, experimental evidence supporting this claim is equivocal. Nutrient inputs are common in many coastal systems, including coral reefs, where terrestrial runoff brings in organic material and excess fertilizer from agricultural use (Tilman et al. 2001; Smith et al. 2003; Fabricius 2005) or in areas near human habitation where sewage is allowed to enter the system (Smith et al. 1981; Hunter and Evans 1995). Nutrient enrichment can change the competitive landscape between coral and algae in favor of algae because of their ability to respond to nutrient influxes by increasing growth rate (Bell 1992; Lapointe 1997; Kuffner and Paul 2001; McClanahan et al. 2003). This suggests that increased nutrient levels should drive reefs toward algal dominance; however, most experimental tests of the effects of increased nutrients on reef community structure have shown mixed results and have not produced the expected major shifts to algal dominance (Koop et al. 2001; Szmant 2002; Fong and Paul 2011). This disconnect could be a result of the logistical limitations of experimental work and the far more complex and dynamic context of real reefs (Fong and Paul 2011). For example, increased herbivory can compensate for nutrient-related increases in growth (Boyer et al. 2004; Fong et al. 2006; Sotka and Hay 2009; Chan et al. 2012) and the high wave energy environment of coral reefs may make it difficult for *in situ* manipulations to maintain nutrient levels reflective of large-scale anthropogenic enrichment.

A third common stressor on coral reefs is an increase in sediment loading that arises from numerous anthropogenic activities (Rogers 1990; Fabricius 2005). Sediments have been shown to reduce metabolism and tissue growth leading to reduced survival of hard coral colonies (Nugues and Roberts 2003; Fabricius 2005; Stewart et al. 2006). Nutrient-rich sediments can lead to coral mortality via microbially-mediated local hypoxia and reductions in pH (Weber et al. 2012). Sediments have also been shown to inhibit coral settlement (Birrell et al. 2005) and this can impede coral recruits from repopulating reefs after a disturbance. Sediments can benefit algae directly by reducing herbivory rates (Bellwood and Fulton 2008; Goatley and Bellwood 2012). At the same time sediments have been shown to negatively affect algae, though evidence from tropical reefs is limited. Increased sediment loads decreased recruitment, growth and survival of some types of *Sargassum* (Umar et al. 1998), decreased rates of recruitment of filamentous turfs (Kendrick 1991), and have been correlated with lower abundance of crustose corraline algae (CCA)(Fabricius and De'ath 2001). Thus, although increased sediment may be a stressor on both coral and algae, the net negative impacts on coral may be much greater, leading to the expectation that higher sediment loads favor algae (McCook 1999).

Tests of community responses to individual stressors are informative but it is also important to evaluate interactions, as multiple stressors often co-occur (Crain et al. 2008; Darling and Côté 2008). For example high sediment loads suppress herbivory by fish (Bellwood and Fulton 2008), exacerbating the effect of overharvesting of herbivores. Overharvesting can also erode the coral community's resilience to nutrient enrichment if there is no longer sufficient herbivory pressure to compensate for increased growth rates (Boyer et al. 2004). Nutrient enrichment can enhance coral diseases leading to higher mortality (Bruno et al. 2003; Voss and Richardson 2006). Anthropogenic stressors can also limit the resilience of communities such that they are unable to tolerate natural disturbances (Lessios 1988; Hughes and Connell 1999). Interactions among stressors can have a range of effects, from synergisms that strengthen both to antagonistic effects that can limit each other (Breitburg et al. 1998; Darling and Côté 2008). Thus is it important to evaluate both individual and interactive effects of stressors that may co-occur on coral reefs to have a more complete picture of their potential effects.

Because coral reefs experience significant natural environmental variability, it is important to consider how the effects of and interactions between anthropogenic stressors vary under dynamic environmental contexts. Natural environmental variability on tropical reefs can arise from processes such as seasonal changes (Brown et al. 1999; Fagoonee et al. 1999), or longer period events such as the Pacific Decadal Oscillation and El Nino Southern Oscillation (Fiedler 2002; Mantua and Hare 2002). If community responses to anthropogenic stressors shift in response to natural variability it can have significant consequences for community structure. Seasonal upwelling in the Gulf of Panamá offers an opportunity to evaluate community response to stressors on a single reef but under very different environmental regimes (Chelton et al. 2001; Pennington et al. 2006; D'Croz and O'Dea 2007). For example, upwelling provides a natural manipulation of nutrient levels, increasing nutrients up to 50-fold over the non-upwelling season (D'Croz and O'Dea 2007). However, upwelling changes the environmental context in a number of other ways including increased turbidity and salinity and lower water temperatures (D'Croz and O'Dea 2007) with the cold water significantly reducing herbivore activity (Smith 2008). These shifts can have a direct influence on some stressors (e.g. upwelled nutrients add to experimental nutrient enrichment) but environmental differences can also have an indirect influence on the effects of stressors by changing the resilience or susceptibility of community members. While upwelling may not be common on tropical reefs, it does provide an opportunity to evaluate the relative strengths of different controls of community structure under very different environmental contexts that has proved useful in other marine systems (Menge et al. 2002, 2003).

Our objective was to investigate the individual and interactive effects of multiple stressors on coral reef community composition and evaluate the potential for changing roles under different environmental contexts. We used experimental manipulations to simulate anthropogenic eutrophication, increased sediment loading, and overfishing on a reef in the Eastern Tropical Pacific (ETP) and monitored benthic community composition for ~6 months. By manipulating multiple stressors individually and in combination and by allowing the experiment to continue through both non-upwelling and upwelling seasons, we were able to consider the effect of interactions on community dynamics and evaluate responses under different environmental regimes.

Methods

Our study was conducted at Isla Contadora reef, Republic of Panamá, approximately 65 kilometers southeast of Panamá City in the Pacific Ocean. Reefs of the ETP have relatively intact herbivore communities and generally low levels of other human impacts (Glynn 2004). The study was conducted at Suecas Reef along the more exposed southern side of the island. The reef framework is dominated by nearly continuous stands of the branching corals *Pocillopora damicornis* and *P. elegans*, while colonies of a few species of massive corals are present in lower abundances (Glynn and Mate 1997). Algae on ETP reefs are generally encrusting or turf forms that cover dead coral skeletons and coral rubble, or low-relief macroalgae that are usually found in the interstices between coral or rubble where they are is relatively inaccessible to herbivores (Smith 2005; Wartian 2006). The reefs are relatively shallow, reaching a maximum depth of only 3-4m below mean low water, and the shallowest colonies are exposed at moderate to extreme low tides (Glynn and Mate 1997).

The Gulf of Panamá, where Isla Contadora is located, experiences seasonal upwelling generally between January-April (Glynn and Mate 1997). Upwelling is driven by strong winds that blow from the Caribbean across the isthmus of Panama during boreal winter, driving warmer surface waters offshore and pulling deeper water up toward the surface (Kessler 2006; Pennington et al. 2006). The deeper water is nutrient rich and during upwelling average water column NO_3^- concentrations have been shown to increase ~50 fold, PO_4^{3-} concentrations ~10 fold and *chlorophyll a* (an integrated measure of the biological response) ~6 fold over non-upwelling values (D'Croz and O'Dea 2007). In addition water temperature can drop nearly 10°C, and turbidity and salinity are shown to significantly increase during upwelling (D'Croz and O'Dea 2007; Smith 2008).

To evaluate the individual and interactive effects of three stressors, nutrient enrichment, sediment, and herbivore removal, on reef community structure we manipulated each stressor in a 3-factor fully crossed experiment. At Suecas reef 45 plots were haphazardly selected with depths 1-4m below mean low water, similar topographic complexity (1.16±0.02; mean±SE of ratio between the length of a fine-link chain allowed to conform to topography and the straight line length of the plot, following Risk 1972), and as close to complete coral cover as possible (93.9±0.6%; see supplemental material and Fig. 2-S1 for details on initial composition). Plots were placed a minimum of 2m apart to limit spillover effects from nutrient addition plots (following Wartian 2006). Plots were 1.2 x 0.7m; this allowed for 1.0 x 0.5m sampling area with a 10cm buffer to the edge of the plot. Each of the three factors was either manipulated (+ caging, + nutrients, + sediments) or left at ambient levels (- caging, - nutrients, - sediments) in a fully crossed design resulting in 8 treatments. Treatments were randomly assigned to plots with 5-fold replication. In addition, a partial cage treatment (+partial cages, -nutrients, -sediments) was included in the experiment, and handled equivalently to other treatments, to evaluate cage effects by comparison with ambient condition plots (- caging, - nutrients, - sediment).

Herbivore exclosure cages were constructed of wire fencing with 2.5 x 2.5cm mesh openings. Cages had 4 sides and a top and were 1.2 x 0.7 x 0.45m (L x W x H). The study reef was largely monospecific stands of branching coral that were roughly the same height giving the appearance of a "flat" field of coral, though with significant interstitial space between branches. To keep cages in place a narrow trench was dug around each caged plot, 1m rebar stakes were driven into 2 opposing corners and the cage was slipped around the intact plot and trenches were refilled. Trenches were

~15 cm deep so the cages extended ~30cm above the surface of the reef . To minimize confounding effects between treatments, all uncaged plots were also trenched and refilled. Cages were manually scoured to remove fouling as needed, approximately every two weeks.

Nutrient additions consisted of two 50g nylon bags of Osmocote slow-release fertilizer (19% N, 6% P, 12% K) placed in each nutrient addition plot. This method had previously been used effectively in this system (Wartian 2006) and slow-release Osmocote has been suggested as an optimal method of nutrient enrichment in tropical coral reefs (Littler et al. 2006). Nutrient bags were wrapped in window screening and attached to rebar stakes in each plot and replaced with fresh Osmocote approximately every two weeks. In uncaged plots, small (10 x 10 x 10 cm; 2.5cm mesh) cages were built around nutrient bags to prevent disturbance by fish. See supplemental material for evaluation of nutrient addition efficacy.

To mimic increased loading of resuspended local sediments, 500 mL of sediment was collected from sand flats adjacent to the reef, passed through a 2mm sieve (to remove large particles that were less likely to be resuspended and transported around the reef), and distributed over each sediment addition plot. Additions were repeated every two weeks (approx. 900g wet weight for each addition; ~80g/m^2*day). While natural rates of sediment loading can be spatially and temporally variable, this treatment was in the range (34-95g/m^2*day) of other offshore ETP reefs (Zapata et al. 2010) though received in a single dosing. However, this treatment was considerably less than rates measured at mainland sites with very high sediment loads (446 g/m^2*day; Alvarado et al. 2009).

Community composition was recorded with digital photographs using a 10 megapixel digital camera. The camera was mounted on a PVC quadrapod with a 0.5 x 0.5m quadrat attached at the bottom. Rebar stakes were placed in each plot as a guide for placement of the quadrapod, which allowed images to be taken from the same place and height for each sampling period. Images were taken before manipulations, after 12 weeks (end of the non-upwelling season), and after 24 weeks (end of upwelling season). Images were color corrected in Adobe Photoshop (Adobe Systems Inc., San Jose, CA) if necessary then analyzed using ImageJ image processing software (NIH, Bethesda, MD). Using this software we were able to identify different benthic community members and measure their size to get high resolution measures of cover of different substrates. Benthic cover was separated into 5 categories: live coral, turf algae, macroalgae, CCA, or other. Turf algae were comprised of filamentous algae and mats less than 1cm in height. Macroalgae was larger than 1cm in height with visible branching structure. The category CCA included both encrusting and upright calcareous branched forms, though encrusting algae were dominant. Other non-coral substrate, which included sponges, terrestrial organic material such as leaves, and sediment were categorized as "other". Areas where the benthos was obscured by objects in the image (rebar, flagging tape, nutrient diffusers) were identified as obscured and that space was not included in the percent cover calculations. Percent cover was calculated as the percent of non-obscured space in the plot occupied by each category. Initial variation in composition between plots was minimal (see supplemental figure 2-S1), but to account for initial variation percent cover values for each plot were converted to absolute change in percent cover during the non-upwelling season (week 12 - initial) and upwelling season (week 24 - week 12) for each plot.

To evaluate the individual and interactive effects of stressors on community composition, changes in benthic cover were analyzed independently for the different seasons using a multivariate approach with changes in % cover of coral, macroalgae, turf algae and CCA as multiple response variables. Our responses were not always normally distributed in all seasons, which in turn influenced multivariate normality, thus we analyzed the data using a non-parametric permutational 3-factor MANOVA (PERMANOVA) with the adonis function from the vegan package in the R programming language (which was used for all statistical analysis and graphing; version 2.15.1, R Development Core Team 2012). Significant multivariate analyses were followed with 3-factor permutaional ANOVAs that compared the effect of treatments on each community member (also using the adonis function). In addition we ran a separate univariate test with total algal cover (the sum of macroalgae + turf + CCA) as the response variable.

Results

Analysis of cage controls is described in supplemental materials. Overall, the cage control and ambient condition plots showed no significant differences for any response variable or time period, suggesting caging artifacts were minimal.

The multivariate community response that considers all community members simultaneously showed significantly different responses between treatments but these patterns changed between seasons. In the non-upwelling season there was a significant effect of herbivore exclosures on overall community response while a significant interaction between nutrient enrichment and sediment addition was seen during upwelling (PERMANOVA, Table 1). In addition during the upwelling season there was a nearly significant (p=0.056) main effect of nutrient enrichment on the multivariate response.

In the non-upwelling season the only experimental manipulation that had a significant influence on any member of the reef community was herbivore exclosures. The experimental simulation of overfishing drove significant decreases in coral and increases in algal cover (Table 2a, Fig. 2-1). Responses of coral and total algae were nearly mirror images, indicating that when coral was lost, it was replaced by algae. While there were losses in coral percent cover in all treatments, overall they were ~3 times greater in caged (7.2±1.1%) versus uncaged treatments (2.4±0.4%). Neither nutrient enrichment nor sediment addition had a significant effect on the cover of coral or algae.

When evaluating members of the algal community separately, we found that the increases in total algae in response to caging was largely driven by changes in macroalgal cover (Table 2a, Fig. 2-2a) which showed the same response pattern and was the only algal type that showed a significant response to any stressor. During the non-upwelling season macroalgal cover showed little change in uncaged treatments (overall average -0.2±0.4%) but showed significantly greater increases in cover in caged treatments (overall 3.9±1.0%). At the same time, macroalgal cover did not display a significant response to any other treatment. While turf algae increased substantially in all treatments (between 2.0% and 4.4%), there were no significant differences among treatments (Fig. 2-2b, Table 2a). CCA showed less change over time (between -0.4% and 1.3%) than turf algae but also had no significant differences between treatments (Fig. 2-2c, Table 2a).

During the upwelling season there continued to be overall loss of coral and gain of algal cover in all treatments except the unmanipulated (control) treatment. However, herbivore exclosures no longer had a significant effect on coral or total algal cover (Fig. 2-3, Table 2b). Rather, nutrient enrichment, which previously had no effect, significantly reduced coral cover. Losses doubled from an average of -4.2±1.0% across all ambient nutrient treatments to an average of -7.8±1.1% across all nutrient enrichment treatments. Similarly, nutrient addition increased the expansion of algal cover (from 3.9±1.1% to 7.8±1.1%) in all unenriched treatments relative to all nutrient addition treatments. There was no significant effect of sediment addition on cover of coral or total algae.

Evaluation of the algal community during upwelling showed that the only algal type that responded significantly to any treatment was turf algae (Fig. 2-4, Table 2b). Turf algae, when considered separately, responded to nutrient enrichment but in an interactive manner with sediment addition rather than as a main effect (Table 2b). Turf algal cover increased roughly equivalently in both sediment addition (8.0±1.8%) and nutrient enrichment (7.9±2.0%) treatments (averaging across both caged and uncaged plots). However, because the combination of stressors did not have a greater effect than either alone (6.9±0.9%) the effects of nutrient enrichment and sediment addition are essentially reduced in the presence of the other stressor. This reduction in effect depending on the presence of the other stressor produces the significant interaction (and the lack of significant main effect). Changes in cover of macroalgae and CCA showed no significant responses to any treatment. However, CCA responses shifted from mixed in the non-upwelling season to more overall losses during upwelling (between -1.8% and -0.1%). In addition, macroalgal cover also had generally lower responses than during the non-upwelling season but with a less consistent pattern than CCA (between 1.7% lost and 3.6% gained).

Discussion

There is a breadth of evidence that many anthropogenic stressors can drive coral declines and increases in algal abundance (Burke et al. 2011) and while each of the 3 stressors we manipulated had those effects, we found that responses to particular stressors were not consistent across seasons, stressor combinations or algal types. The presence of a particular stressor was, by itself, not a particularly effective predictor of community impacts. Rather, we found that environmental context, in the form of natural seasonal variability, had a strong influence on community response to stressors, thus the presence of stressors as well the environmental context determined outcomes. This finding aligns with the expectations of Hughes and Connell (1999) and Crain (2008) that responses to stressors can be context dependent. Top-down control, while strong in the non-upwelling season, was not a major force structuring the community under upwelling conditions. This is likely driven, at least in part, because the lower temperatures during upwelling limit herbivore activity (Smith 2008). This could also be due to lower growth rates of tropical macroalgae in cold conditions (Hwang et al. 2004) as they were the community member most affected by herbivores in the non-upwelling season. In contrast, during upwelling the reef became more susceptible to nutrient and sediment stresses producing coral declines and/or increases in algal abundance under those stressors. Proliferation of turf algae during upwelling could be a result of a shift in competitive balance in favor of algae over coral. This shift could be a result of a direct benefit to algae from extra nutrients or reduced coral competitiveness, from lower temperatures, lower light, or changes in other oceanographic conditions observed in the region during upwelling (D'Croz and O'Dea 2007) combined with the increased stress incurred from higher sediment loads (Fabricius 2005; Weber et al. 2012). Understanding the impacts of context dependency and the development of robust expectation in the face of that variability remain major ecological knowledge gaps in many systems (Agrawal et al. 2007; Crain et al. 2008), but are necessary for effective prediction of coral reef responses to anthropogenic stressors.

Our experimental results suggest reefs may have a non-linear relationship to nutrient enrichment. During the upwelling season, neither experimental nutrient enrichment nor upwelling alone was sufficiently strong to elicit a response in community composition. Only the combination of upwelled nutrients plus experimental addition resulted in a significant change in community composition. One possible explanation of this pattern is that the community only responds after it crosses a critical threshold of nutrient enrichment. Though our responses were seen largely with turf rather than macroalgae, such threshold responses could explain the disconnect between manipulative studies that have found limited evidence for nutrient effects on community structure (Koop et al. 2001; Szmant 2002; Burkepile and Hay 2006) and the apparent role of nutrients in classic examples of community shifts such as Kaneohe Bay (Smith et al. 1981). The feasible scales for manipulative experiments may simply be insufficient to reflect anthropogenic stressors such as eutrophication at appropriate scales (Carpenter 1996); thus, despite the associated challenges, natural gradients or "experiments" such as upwelling may be the best approach to evaluating certain types of large scale stressors (Menge et al. 2004). Because threshold shifts may show few early warnings and may be particularly hard to recover from, recognizing the potential for such non-linear responses is key so that conservation efforts can be taken beforehand (Scheffer et al. 2009; Suding and Hobbs 2009; Hughes et al. 2010).

In our experiment we had relatively little evidence of interactions between stressors and no indications of additive or synergistic interactions. The only interaction we identified was an antagonistic relationship between nutrient enrichment and sediment addition on the abundance of turf algae during the upwelling season. That interaction indicated a mitigating effect between the two stressors as the effect of their combination was not greater than either stressor alone. It is possible that negative effects of sediment on algae via limitation of gas exchange, reduction in light, physical abrasion, etc. (Kendrick 1991; Fabricius and De'ath 2001; Weber et al. 2012) limit the ability of turf algae to take advantage of the added nutrients. Alternatively, if sediment addition acts to increase nutrient supply due to high nutrient levels in the sediment (Weber et al. 2006), the combination of stressors may have little effect if the system already crossed the critical threshold from either of the stressors alone. The presence of antagonistic interactions between stressors has been seen in a number of systems and may actually be an indication of resilience mechanisms (Crain et al. 2008) or co-tolerance (Vinebrooke et al. 2004) that could be beneficial to coral reefs facing anthropogenic stressors. However, responses and interactions are highly variable depending on the particular stressors, the organisms involved, and environmental context (Burkepile and Hay 2006; Crain et al. 2008; Darling and Côté 2008) and broad generalizations are difficult to make. Thus a mechanistic understanding of the impacts of particular stressors remains critical to predict their interactions and ultimate community level impacts (Maltby 1999; Olden and Poff 2003; Crain et al. 2008).

We found that environmental conditions, which varied under different upwelling conditions, have a major influence on how communities respond to particular stressors. If expectations of how coral reefs will respond to stressors are based on a single environmental context, this will not effectively predict responses as conditions change, making this a critical limitation to our understanding of reef community dynamics. Thus it is important to consider responses under different conditions and combinations to better evaluate the robustness of current predictions and evaluate when and how they might break down. Such efforts may become particularly relevant in the context of global climate change (Hoegh-Guldberg et al. 2007) or chronic anthropogenic stressors (Hughes and Connell 1999; Nystrom et al. 2000) that may place reefs into a fundamentally new set of circumstances. This work offers one attempt to consider varied conditions and shows the need for environmental context to be explicitly included in efforts at understanding how communities will respond to their current and future challenges.

Tables

Table 2-1. Results of multivariate 3-factor permutational MANOVA using change in percent cover of coral, macroalgae, turf algae and CCA as multiple response variables. Analyses were done using Euclidean distances and results are based on 10,000 permutations.

A)

PERMANOVA on response in non-upwelling season

Factor	*df*	*Pseudo-F*	*P*
Caging	1	10.41	**<0.001**
Nutrients	1	0.25	0.807
Sediment	1	0.04	0.983
Caging x Nutrients	1	1.05	0.340
Caging x Sediment	1	0.36	0.711
Nutrients x Sediment	1	0.79	0.440
Caging x Nutrients x Sediment	1	0.20	0.857

B)

PERMANOVA on response in non-upwelling season

Factor	*df*	*Pseudo-F*	*P*
Caging	1	1.26	0.287
Nutrients	1	3.00	0.056
Sediment	1	1.47	0.224
Caging x Nutrients	1	0.18	0.854
Caging x Sediment	1	1.71	0.185
Nutrients x Sediment	1	3.28	**0.044**
Caging x Nutrients x Sediment	1	0.41	0.662

Table 2-2. Results of univariate 3-factor permutational ANOVAs for each of 5 response variables. Analyses were done using Euclidean distances and results are based on 10,000 permutations.

A) Non-upwelling season

		Coral		Total Algae		Macroalgae		Turf algae		CCA	
Factor	*df*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Caging	1	14.95	**<0.001**	16.23	**0.001**	13.08	**0.001**	0.10	0.757	2.08	0.157
Nutrients	1	0.40	0.536	0.20	0.664	0.12	0.730	0.18	0.665	0.25	0.621
Sediment	1	0.03	0.863	0.17	0.687	0.00	0.968	0.06	0.805	0.27	0.615
Caging x Nutrients	1	2.01	0.163	1.69	0.202	0.13	0.716	0.58	0.449	1.23	0.284
Caging x Sediment	1	0.54	0.467	0.84	0.376	0.01	0.913	0.18	0.674	1.85	0.195
Nutrients x Sediment	1	0.00	0.971	0.04	0.843	1.75	0.189	0.82	0.380	0.74	0.403
Caging x Nutrients x Sediment	1	0.03	0.867	0.10	0.756	0.35	0.568	0.28	0.604	0.22	0.642

B) Upwelling season

		Coral		Total Algae		Macroalgae		Turf algae		CCA	
Factor	*df*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Caging	1	1.18	0.283	0.75	0.394	3.26	0.082	0.37	0.543	0.22	0.641
Nutrients	1	6.06	**0.022**	6.27	**0.019**	0.76	0.390	1.88	0.179	1.49	0.237
Sediment	1	1.44	0.238	0.96	0.326	0.27	0.615	2.19	0.152	0.47	0.503
Caging x Nutrients	1	0.10	0.766	0.01	0.916	0.09	0.765	0.27	0.597	0.52	0.477
Caging x Sediment	1	3.18	0.083	3.34	0.077	2.13	0.156	0.50	0.486	0.02	0.889
Nutrients x Sediment	1	3.34	0.080	2.53	0.125	0.56	0.465	4.86	**0.038**	0.43	0.531
Caging x Nutrients x Sediment	1	0.46	0.504	0.24	0.619	1.02	0.323	0.00	0.960	1.22	0.277

Figures

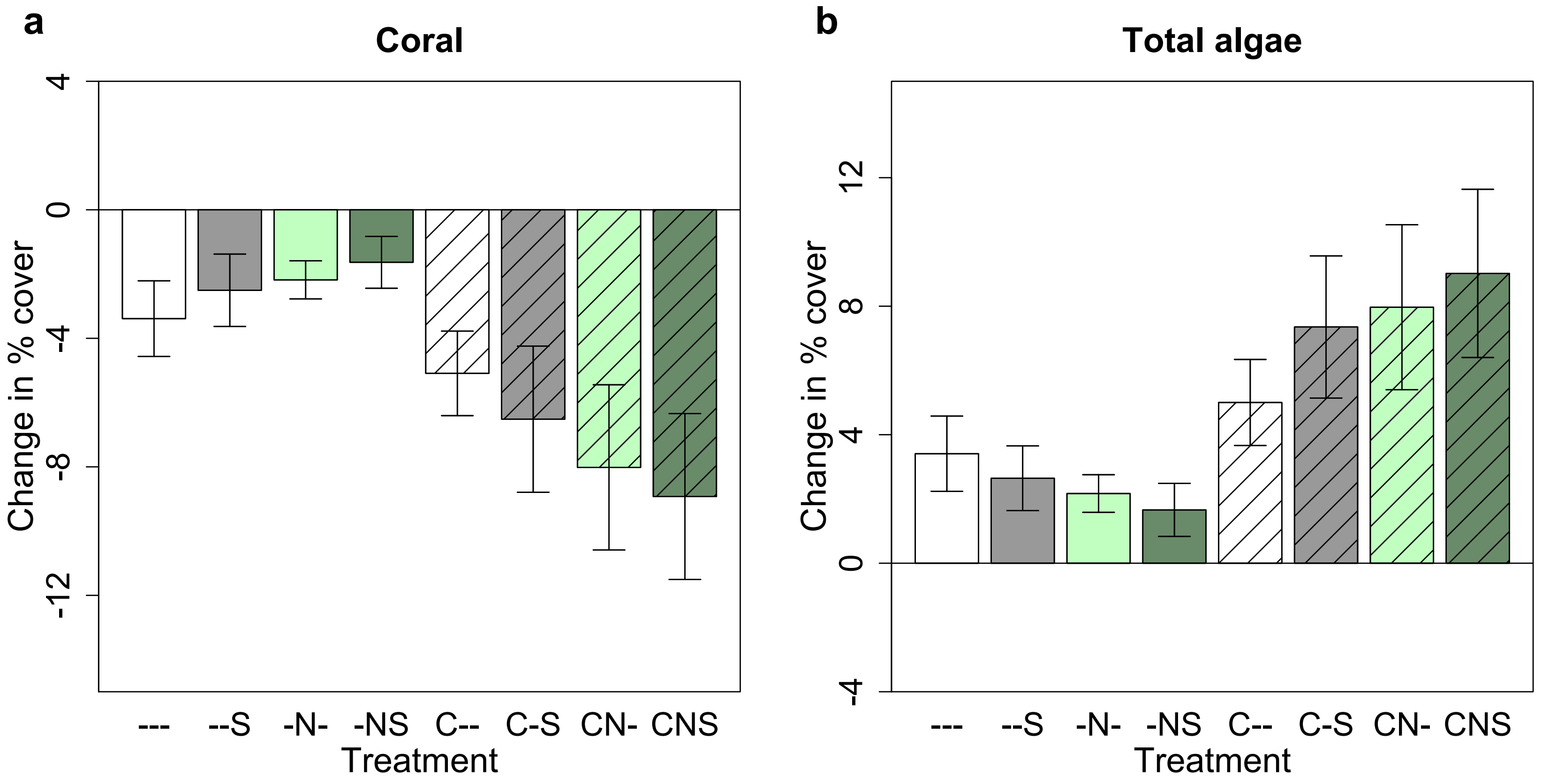

Fig. 2-1 Change in percent cover of (a) live coral and (b) total algae during the non-upwelling season. Hatched bars indicate treatments with cages (C), green bars indicate nutrient enrichment treatments (N) and shaded bars indicate sediment addition (S). Error bars show ± 1 SE.

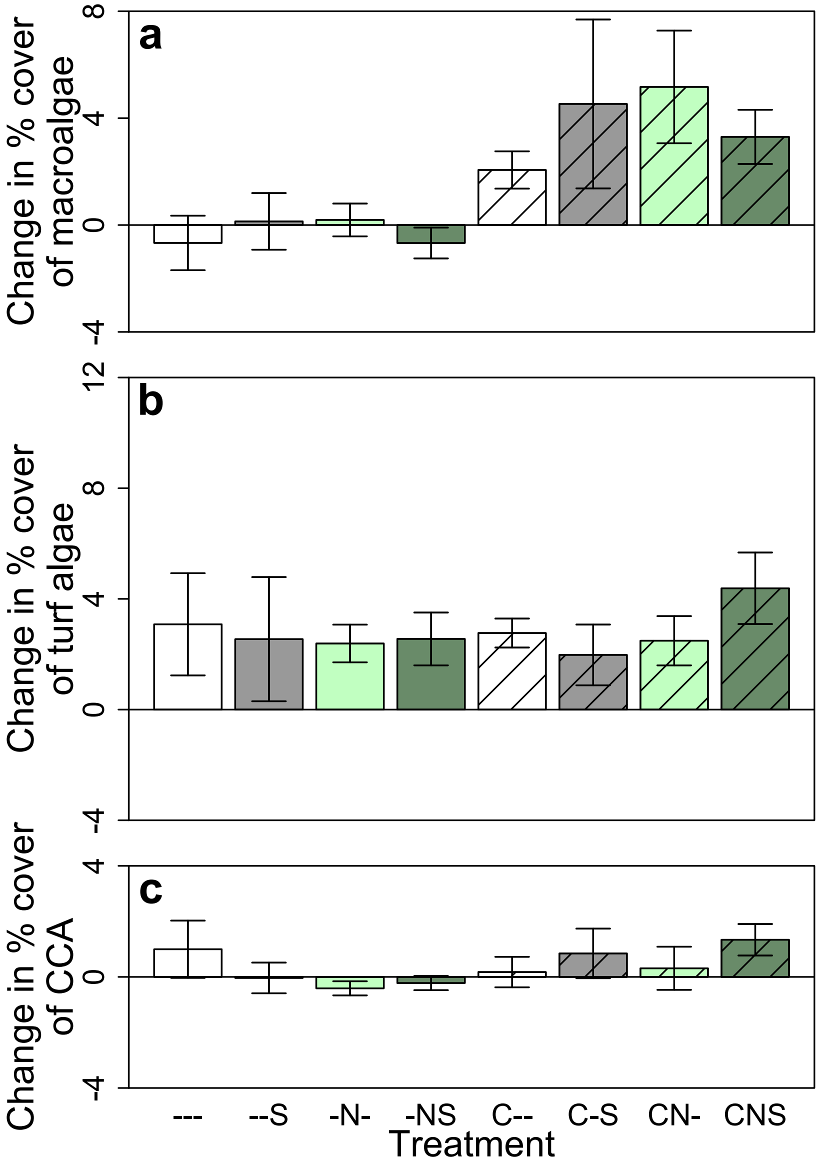

Fig. 2-2 Change in percent cover of different algae types (a) macroalgae, (b) turf algae and (c) CCA during the non-upwelling season. Bars represent the same treatments as in Fig. 2-1.

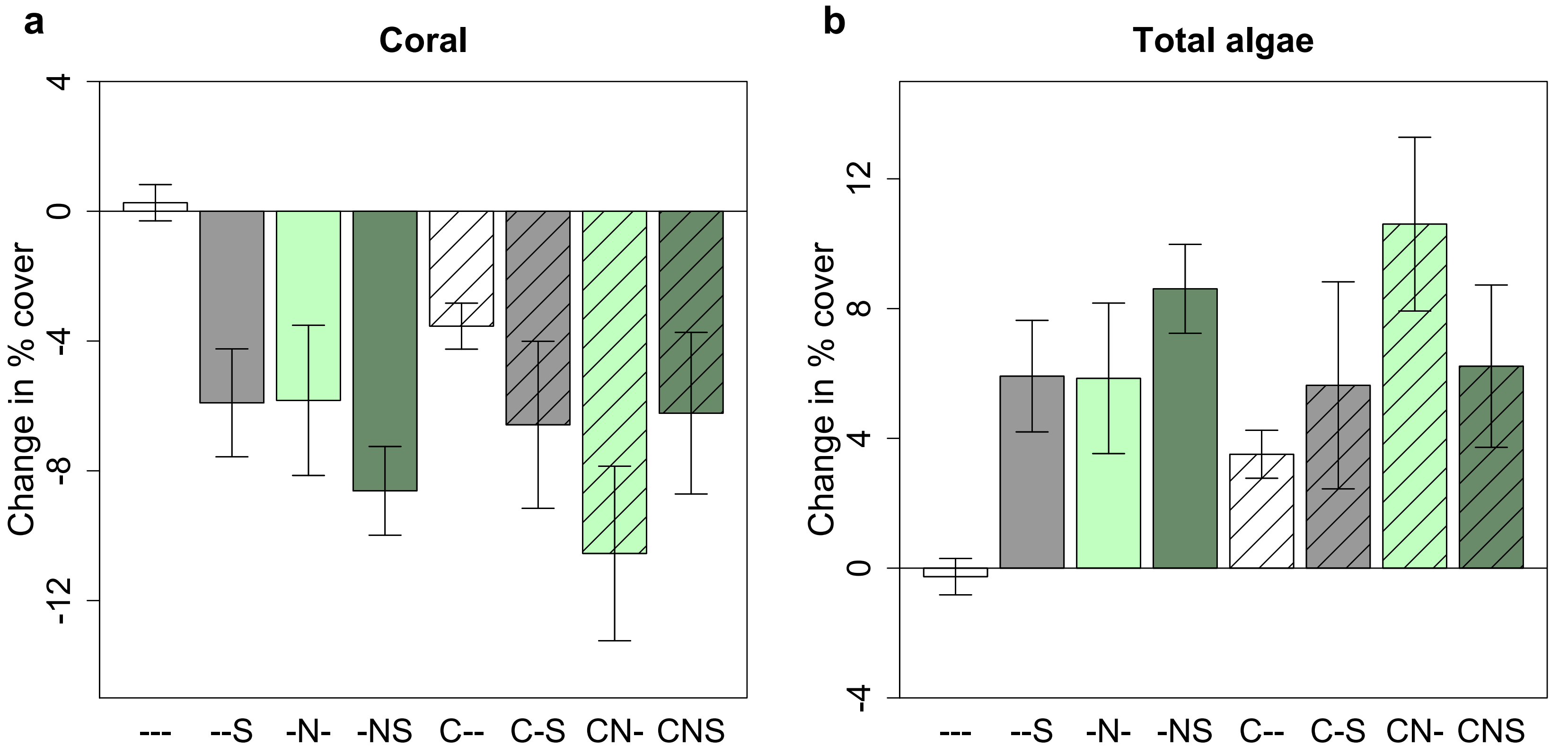

Fig. 2-3 Change in percent cover of (a) live coral and (b) total algae during the upwelling season. Bars represent the same treatments as in Fig. 2-1.

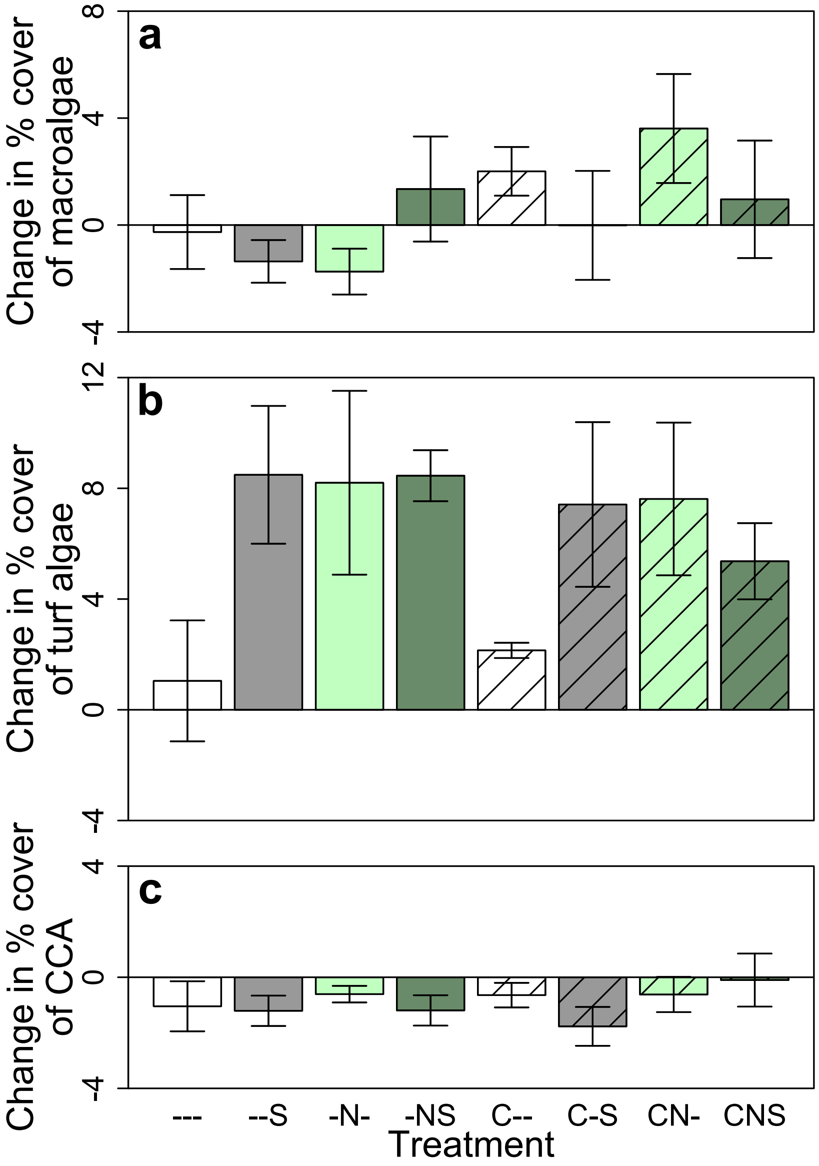

Fig. 2-4 Change in percent cover of different algae types (a) macroalgae, (b) turf algae and (c) CCA during the upwelling season. Bars represent the same treatments as in Fig. 2-1.

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Supplemental Material

Initial community structure of experimental plots

Plots were chosen to represent high coral cover areas of Suecas reef at Isla Contadora with similar community composition. Plots were heavily dominated by live coral (93.9±0.6%, mean±SE; Fig. 2-S1) with the remaining area taken up by a largely by a mixed assemblage of algae (6.3±0.7%) with other substrate making up <0.1% of the total cover. Plots were randomly assigned to treatments so initial variability reflects the natural standing variability on the reef.

Evaluation of caging effects

Partial cages for cage controls were constructed of the same material and in the same manner as the complete cages, but cage controls consisted of only the long (1.2m) sides and tops of the cage with the short (0.7m) sides left open. Cage control plots were maintained identically to the full cages and monitored with digital photographs in the same manner as all other treatments.

Caging effects were tested with a series of t-tests (Welch's two sample t-test using the t.test function from the R stats package) that compared cover categories between ambient condition plots (-caging, -nutrients, -sediment) and cage control plots (+partial cages, -nutrients, -sediment). Separate tests compared percent cover of each benthic community member (coral, macroalgae, turf algae, and CCA) between the cage control plots and the ambient condition plots for each of the three time points measured (initial, end of non-upwelling season, end of upwelling season). No significant differences were seen for any community member at any time point (Table 2-S1) so caging effects were assumed to be minimal.

Evaluation of nutrient enrichment

The effectiveness of nutrient enrichment was evaluated by collecting seawater from within and outside nutrient enrichment plots and analyzing their nutrient content (following Wartian, 2006). Samples were collected in November 2008 during the non-upwelling season. Three samples were taken at each of four nutrient enrichment plots with samples collected from directly above the nutrient diffuser and from 2m shoreward of the nutrient diffuser. Samples were collected 24 hours after deployment of nutrient diffusers and by opening empty acid-washed 125 mL Nalgene bottles within 2cm of the reef surface. Water samples were placed in a refrigerator in the dark while waiting to be processed and then filtered through a GF/C Whatman glass microfiber filter using a handpump. After filtration, samples were kept frozen until they were analyzed at the UC Davis Analytical laboratory for total N (via total combustion method). Data were analyzed using a mixed-effects model with distance (0 vs 2m) as a fixed effect and plot as a random effect (using the lme function from the nlme package in R).

Water column levels of total N were higher at the nutrient diffusers (0.39±0.07 mg/L; Fig. 2-S2) than 2m away (0.20±0.01 mg/L) with the 2m samples similar to ambient non-upwelling conditions measured in the Gulf of Panama (D'Croz & O'Dea, 2007). This difference was statistically significant (fixed effect of distance: *df*=19, *t*=3.14, *p*<.0001) indicating that our manipulations were able to raise nutrient supply in nutrient enrichment plots.

Supplementary Table

Table 2-S1. T-tests comparing percent cover of each benthic community member between ambient condition plots and cage control plots for each time point.

A) Initial time point

Community member	*df*	*T*	*P*
Coral	3.72	1.73	0.163
Macroalgae	3.10	-1.79	0.168
Turf algae	6.33	-0.51	0.626
CCA	4.49	1.38	0.232

B) End of non-upwelling

Community member	*df*	*T*	*P*
Coral	3.55	1.24	0.292
Macroalgae	3.13	-1.02	0.381
Turf algae	4.87	-0.03	0.974
CCA	4.36	-0.60	0.581

C) End of upwelling

Community member	*df*	*T*	*P*
Coral	6.37	0.02	0.986
Macroalgae	6.61	0.04	0.973
Turf algae	6.94	-0.27	0.796
CCA	3.00	-1.64	0.199

Supplementary Figures

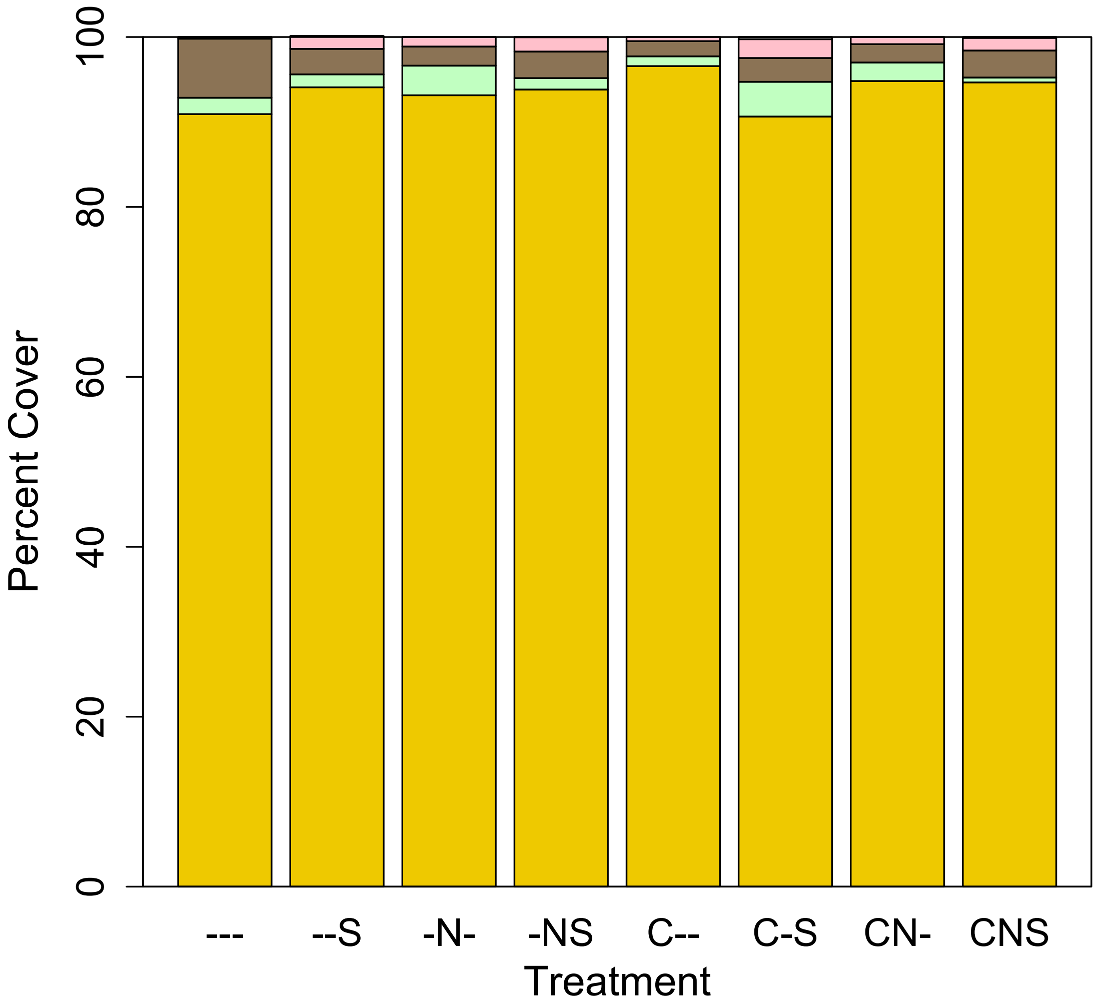

Fig. 2-S1 Percent cover of different substrate types at the initial time point across treatments. Different colors represent different substrate types: gold=coral, green=macroalgae, brown=turf algae, pink=CCA, grey=sediment.

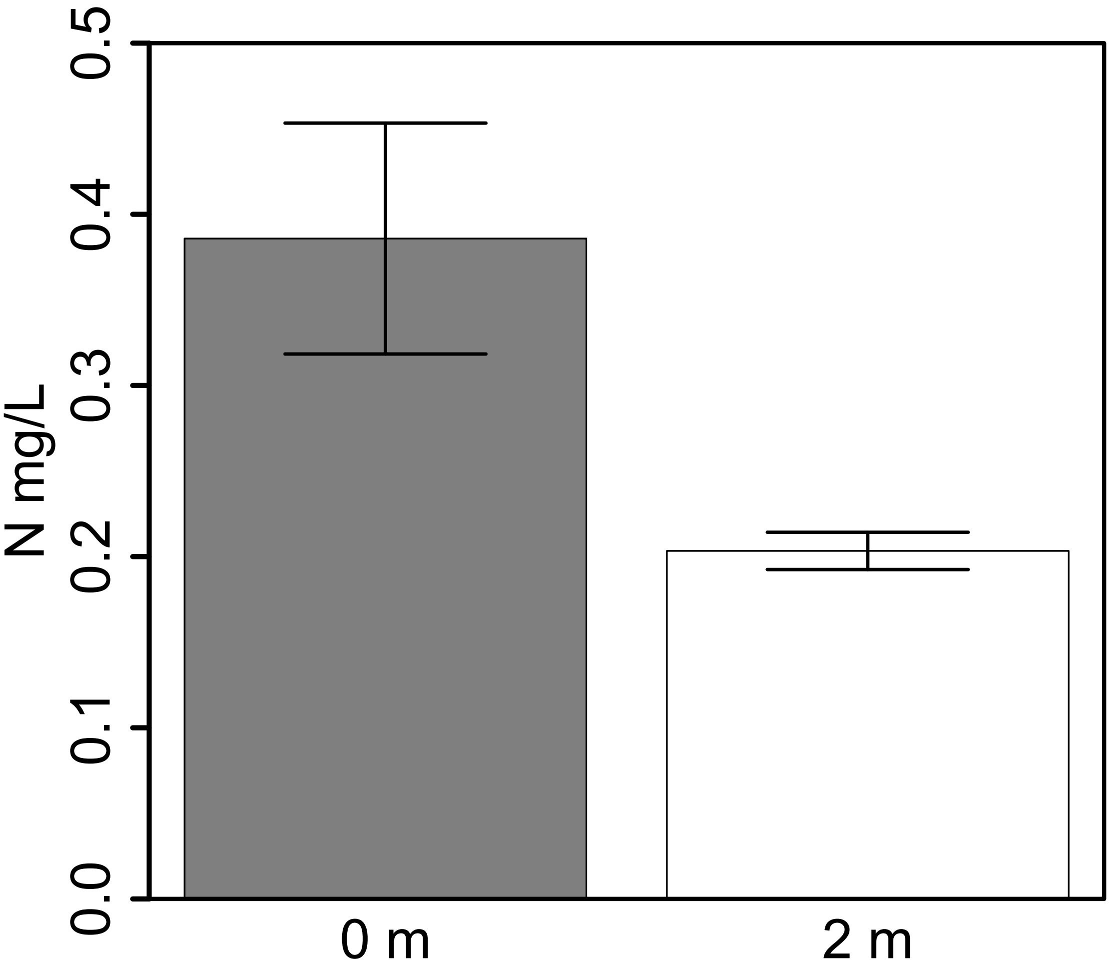

Fig. 2-S2 Nutrient levels measured from water collected within nutrient enrichment plots (0m) and outside of plots (2m).

CHAPTER 3:

Why are some reefs so resilient?

Positive feedbacks produce alternate stable states dynamics on tropical reefs

Abstract

Alternate stable states (ASS) theory is a dominant conceptual framework for understanding processes that support resilience of ecological communities in the face of anthropogenic disturbance. For decades, coral reefs have been cited as an example of ASS yet convincing empirical evaluations have been elusive. Using measurements of algal growth and consumption we identified spatially-associated positive feedback mechanisms on coral reefs and developed a simulation model of community dynamics based on those mechanisms. The model showed that positive feedbacks were central to producing hysteresis and bistability, two hallmarks of ASS, and that reefs with the conditions we measured at Isla Contadora displayed ASS dynamics in model simulations that matched field observations. This combination of empirical fieldwork and simulation modeling approaches offers a non-destructive strategy to evaluate ASS ideal for threatened ecosystems.

Main Text

Ecosystems across the globe are affected by anthropogenic influences such as pollution, resource extraction, habitat loss and global climate change, often causing dramatic shifts in community composition (Vitousek et al. 1997, Folke et al. 2004). The scale and consequences of such shifts, combined with their unexpected nature, has renewed interest in applying threshold models and alternate stable states (ASS; sensu Scheffer 2009) theory to disturbed systems in an attempt to understand and predict shifts before they occur (Scheffer et al. 2009, Suding and Hobbs 2009). However, robust and convincing methods for evaluating ASS that can be applied broadly in threatened ecosystems have not been established (Mumby et al. 2012). Two hallmarks of ASS that could be used as diagnostic criteria are bistability (the potential for either of two community states to arise and persist under the same environmental conditions) and hysteresis (different paths and environmental thresholds for forward and reverse transitions between community states) (Scheffer 2009) but these can be difficult to evaluate empirically because tests are often destructive or require unfeasibly long time scales (Suding and Hobbs 2009). Positive feedbacks are central to ASS and can be identified empirically, but have been considered an ineffective diagnostic criterion because they are a necessary but not sufficient condition for ASS (Scheffer 2009). There is a pressing need to develop new methods for evaluating ASS and discriminating ASS from phase shifts, a simpler threshold dynamic that does not exhibit bistability or hysteresis, that can be applied in threatened or fragile ecosystems (Suding and Hobbs 2009, Dudgeon et al. 2010).

Coral reefs are affected by a myriad of anthropogenic stresses which have produced global declines of coral and transitions to communities dominated by algae (Folke et al. 2004, Pandolfi et al. 2005, Mumby and Steneck 2008), and these transitions are often cited as classic examples of ASS (Scheffer et al. 2001, Folke et al. 2004). This assertion has major implications for conservation policy but remains poorly validated and contentious (Dudgeon et al. 2010, Mumby et al. 2012, Toth et al. 2012), making reefs a crucial test bed for new strategies to evaluate ASS. Because declines in coral occur in tandem with environmental changes from stresses such as eutrophication or overfishing (McCook 1999, Pandolfi et al. 2005, Mumby and Steneck 2008) rather than in stable environments, and because systematic tests to evaluate ASS are often logistically or ethically infeasible in reef systems, it has been difficult to identify whether these transitions represent phase shifts or ASS (Suding and Hobbs 2009). By using a combination of empirical and theoretical methods we demonstrate how a simple simulation model based on spatially-localized positive feedback mechanisms can be used to evaluate the presence of ASS quickly and non-destructively in a tropical reef community.

Using a series of experimental bioassays we identified two positive feedbacks important in structuring tropical reef communities: increased herbivory rates associated with higher coral cover and increased algal growth rates with high algal cover. Because both processes are stronger in the community state they support, they act as positive feedbacks (Fig. 1). Herbivory rates were nearly 2-fold higher in coral-dominated compared to algal-dominated states. Algal growth was faster and showed no nutrient limitation in the algal-dominated state, while nutrients strongly limited growth in the coral-dominated state. Differences in herbivory may be attributed to the structural complexity of coral that shelters herbivores and enhances local algal consumption (Randall 1965, Lee 2006). Nutrient limitation can be ameliorated within algal-dominated states due to efficient uptake, recycling, and nitrogen fixation increasing the local nutrient pool (Fong et al. 2004). Competition between coral and algae is influenced by environmental conditions (McCook 1999), but these feedbacks indicate that at local scales those drivers can be mediated by current community members in a self-supporting manner. As a result algal abundance is limited in the coral-dominated state by strong herbivory pressure and low nutrient availability and facilitated in the algal-dominated state by release from both of these constraints.

To explore the long-term dynamical consequences of these spatially-localized feedbacks, we incorporated them into a cellular automaton model (details in supplement). Each cell in our model represents a 10cm x 10cm patch of reef and can be occupied by live coral, turf algae, macroalgae covering live coral, or macroalgae over dead coral. Between two-week timesteps, individual cells either persist or transition to another state via growth or recruitment of coral or algae or consumption of algae by herbivores (Fig. S1). Transition probabilities for each process are calculated for every cell at each timestep based on environmental conditions. Global nutrient supply and herbivore abundance, which represent habitat degradation via eutrophication or overharvesting of herbivores, ultimately control the environment by determining the range of possible conditions. However, feedbacks within the present community can modify the local environment such that transitions are determined by both global environmental conditions and local community composition.

Using this model we tested for bistability under four scenarios: no feedbacks, nutrient feedback only, herbivory feedback only, and both feedbacks. Under each scenario we ran simulations across a range of global herbivore abundances and global nutrient supplies (Fig. 2). Simulations were initialized with the full range of abundances of coral and algae (0-100%) and the frequency of coral- or algal-dominated outcomes after ~7.5 years (200 timesteps) was quantified. In pristine environments (abundant herbivores/low nutrients) all simulations became coral-dominated, independent of initial community composition or feedback strengths, while in highly degraded environments algal domination was the only outcome. With no feedbacks, there was a sharp threshold in environmental parameters separating the algal-dominated and coral-dominated domains. This represented a phase shift where only a single community type persisted for any given environment and a narrow threshold separated environments which produced drastically different communities (Gunderson 2001). With feedbacks, a range of environments showed bistability with outcomes strongly determined by initial composition. This occurred because as coral or algae increased in abundance the local environment became more strongly controlled by their feedback modifications and each community became increasingly resilient (Shurin et al. 2004). While the herbivory feedback had a generally broader influence, the nutrient feedback did have an effect when alone; however, its influence was stronger with both feedbacks indicated by the increased region of bistability in this scenario (see Supp. Fig. 2 for a broader range of feedback parameters).

To test whether feedbacks produced hysteresis, we ran simulations that mimicked the processes of environmental degradation and remediation under the four feedback scenarios.

Simulations were initialized with a coral-dominated reef under pristine conditions and community composition was tracked while reef conditions were incrementally degraded via eutrophication or harvesting of herbivores (black lines Figs. 3, S3, S4). After the reef transitioned to algal dominance, global nutrient supply was reduced or herbivores returned until initial conditions were reestablished (red lines Figs. 3, S3, S4). All simulations showed threshold dynamics in community shifts consistent with empirical observations (e.g. Hughes 1994) and expected from a switch in the dominant competitor along the environmental gradient (Terborgh 1971). Comparison of the pathways for the forward and reverse shifts, however, shows distinct differences in the feedback scenarios. Without feedbacks, degradation and recovery followed the same pathways, reflecting phase shift dynamics. With either feedback on its own, recovery required restoration of environmental conditions beyond the forward threshold, and the presence of both feedbacks produced a wider range of hysteresis.

Our theoretical analyses demonstrated that positive feedbacks in herbivory or nutrient availability can produce ASS in model coral reef communities. To evaluate whether the model accurately reflects the dynamics of and predicts ASS for actual reefs we compared reefs of Isla Contadora, Panamá with reefs simulated using parameters estimated from field data. Bistability analysis of reefs initialized with a range of initial compositions showed multiple attractors with strong sensitivity to initial conditions, indicating that parameters estimated for these reefs place them in the regime where ASS dynamics occur (Fig. 4a). We compared community composition in field surveys of benthic cover with subsampled patches of simulated reefs (see supplement for details) and observed a bimodal distribution of coral cover, indicative of patchy spatial distributions with sharp boundaries, in both model results and empirical surveys (Fig. 4b,c). This segregation of community states is predicted from theory and has become a common indicator of ASS (Heffernan 2008, Scheffer 2009, Hirota et al. 2011). In contrast, simulations using the same environmental parameters but no positive feedbacks produced a unimodal distribution of cover indicating an unstructured community (Fig. 4d) further indicating that positive feedbacks are a central driver of reef community structure.

Our analyses have shown that positive feedbacks in herbivory or nutrient availability can produce ASS in model coral reef communities. To evaluate whether real reefs fall into the parameter regime where ASS dynamics occur, we estimated model parameters from field data collected at Isla Contadora, Panamá. Reefs simulated using these parameters showed multiple attractors with strong sensitivity to initial conditions, a clear signature of ASS (Fig. 4a). Further, to test whether the model accurately reflects the dynamics of real reefs, we compared community composition in field surveys of benthic cover with subsampled patches of simulated reefs (see supplement for details). In both model results and empirical surveys, we observed a bimodal distribution of coral cover, indicative of patchy spatial distributions with sharp boundaries (Fig. 4b,c). This segregation of community states is predicted from theory and has become a common indicator of ASS (Heffernan 2008, Scheffer 2009, Hirota et al. 2011). In contrast, simulations using the same environmental parameters but no positive feedbacks produced a unimodal distribution of cover indicating a non-patchy community structure (Fig. 4d). Thus the positive feedbacks observed at Isla Contadora (Fig. 1) are clearly influencing reef community structure, and should produce ASS.

Our combined approach of empirical measurements and simulation modeling offers a practical method to evaluate ASS in real systems where other strategies may not be appropriate. Analysis of the model shows that increasing feedback strength alone separates systems with phase shift dynamics versus ASS (a cusp bifurcation sensu Scheffer 2009). In real systems, recognition of such dynamics and prediction of the specific thresholds that produce community shifts remains a challenging problem (Scheffer et al. 2009). However, using our field-parameterized models we were able to identify the range of environmental conditions under which Eastern Tropical Pacific reefs should display ASS and show that our study reefs lie within that range. This strategy is generalizable to any system with positive feedbacks, making it broadly applicable. Recent work has identified positive feedbacks in a wide range of communities including semi-arid grasslands (Rietkerk et al. 2004), intertidal mudflats (Koppel et al. 2001), alpine plants (Callaway et al. 2002) and shallow lakes (Scheffer et al. 1993), suggesting that feedbacks may have widespread influence on community structure. In systems of conservation interest, recognition of positive feedbacks may also help identify management strategies that would be particularly effective or vulnerable to failure. For example modification of abiotic conditions to support a preferred community may be more efficiently achieved by the introduction of ecosystem engineers that create a positive feedback than by active modification, which may not persist (Byers et al. 2006, Scheffer 2009, Suding and Hobbs 2009).

The degradation of ecosystems in general and of coral reefs in particular is a global problem with numerous anthropogenic causes (Vitousek et al. 1997, Folke et al. 2004, Pandolfi et al. 2005, Mumby and Steneck 2008). The potential for nonlinear responses to such stresses complicates management of these systems, because there are few warning signals of impending community shifts and initial resilience can be misinterpreted as certain stresses having no effect (Scheffer et al. 2009, Suding and Hobbs 2009). Recognition of ASS or phase shift dynamics can help managers develop better expectations of how their systems will respond to stresses and if they are near critical threshold. Designing management practices so they foster positive feedbacks that support preferred community states can be particularly efficient strategies for recovery (Byers et al. 2006). In light of continued human impacts on natural environments there is a pressing need for the development of new methods to evaluate the resilience of ecosystems that can be employed readily and efficiently in real ecosystems (Thrush et al. 2009, Hughes et al. 2010) and this work offers one vision of such a strategy.

Figures

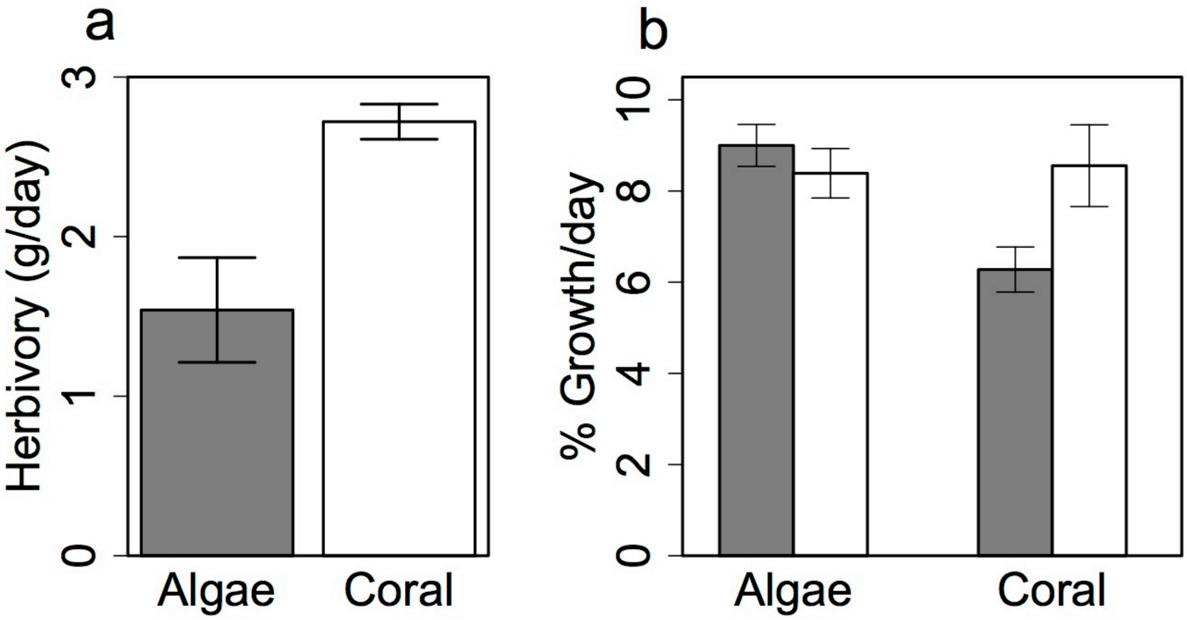

Fig. 3-1 Rates of (a) herbivory and (b) algal growth in coral-dominated and algal-dominated states at Isla Contadora, Panamá (error bars indicate ±SE). Herbivory rates differed significantly between community states (t-test, t_{11}=-3.411, p=0.005). White bars in b represent nutrient enrichment while grey bars are ambient nutrient conditions. Nutrients only stimulated growth (and therefore show nutrient limitation) in the coral-dominated state, resulting in a significant interaction (2-factor ANOVA, p for interaction = 0.024).

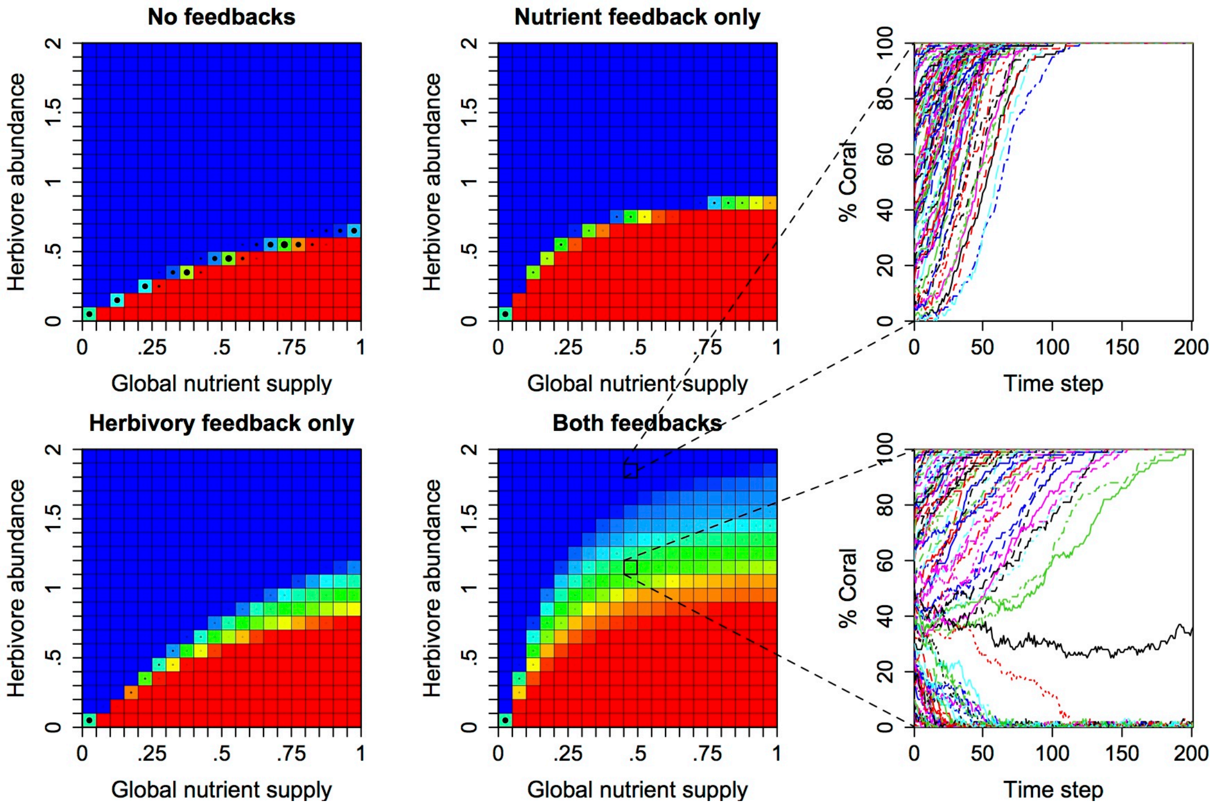

Fig. 3-2 Evaluation of bistability under a range of global environmental conditions (herbivore abundance and ambient nutrient supply).Twenty-five replicate simulations were initialized with each of 21 levels of coral cover and the frequency of coral or algal dominance measured after 200 timesteps. Simulations were run for 4 feedback scenarios: (a) no feedbacks, (b) herbivory feedback only, (c) nutrient feedback only, and (d) both feedbacks. Colors represent % of simulations that ended with more than 50% coral cover. Dark blue squares indicate conditions where all simulations ended in a coral-dominated state, red squares indicate that all simulations ended in an algal-dominated state, and intermediate colors denote where outcomes were split between states. The size of the black dot in each cell represents the proportion of runs that ended with intermediate (25%-75%) coral cover. Thus only intermediate-colored squares with small or no dots represent bistability as opposed to stochastic noise. Tracks of individual simulation runs are shown for two

parameter sets with both feedbacks that lead to (e) a coral-dominated state and (f) a bistable system (only one-fifth of runs are shown for visual clarity; see supplement for full details on model structure and all parameters used in simulations).

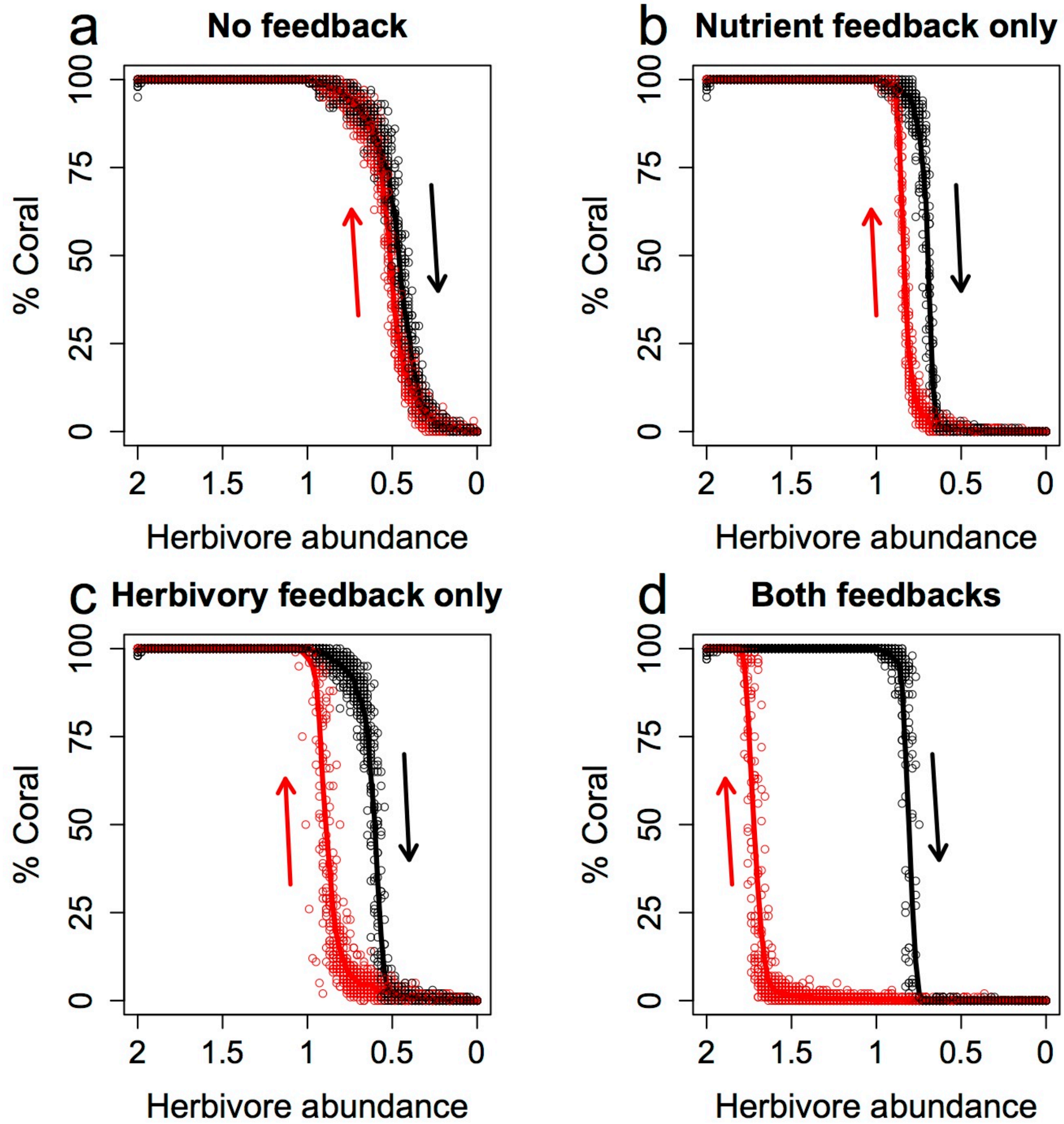

Fig. 3-3 Evaluation of hysteresis under 4 feedback scenarios: (a) no feedbacks, (b) herbivory feedback only, (c) nutrient feedback only, and (d) both feedbacks, and % coral cover was tracked through time as herbivore abundance was varied from 2 to 0 (through 30 evenly

spaced levels, changing every 20 timesteps) and back again. Black circles represent values as herbivore abundance decreases while red dots are values as conditions recover, for 25 replicate simulations. Lines show the mean value across all replicates and arrows show the direction of change during degradation and remediation.

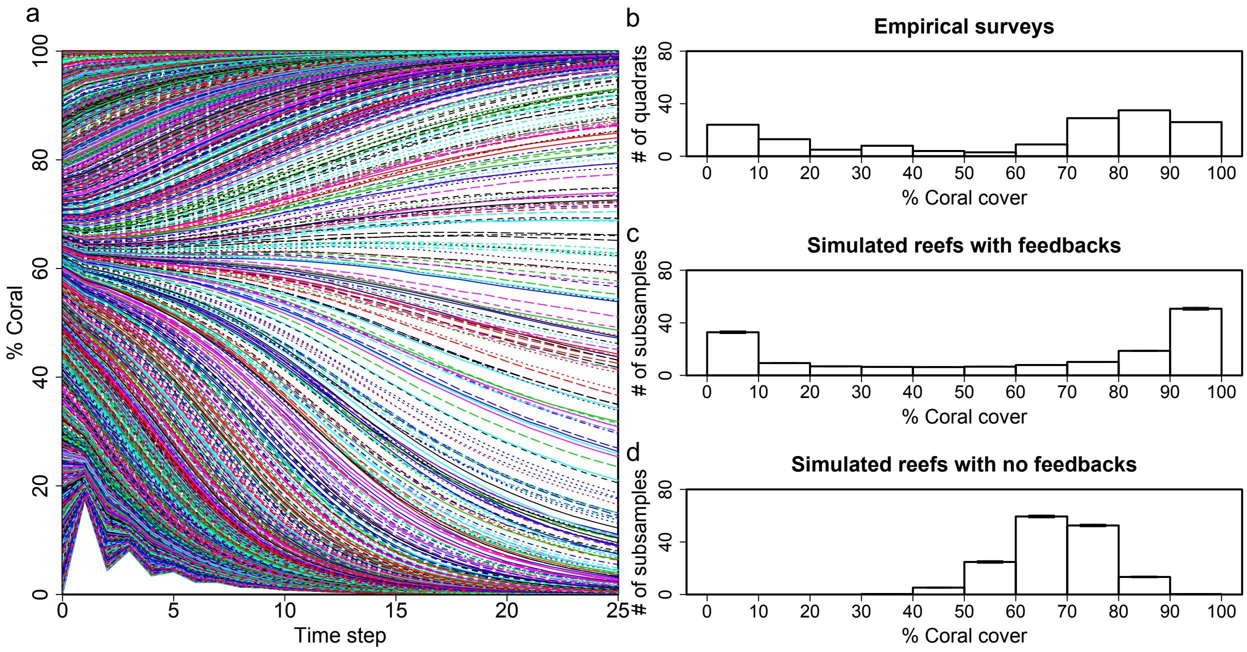

Fig. 3-4 (a) Simulations run using empirical parameters for Isla Contadora, Panamá exhibit bistability (only one-fifth of total runs shown for clarity). Spatial organization of coral and algal patches is shown by histograms of % coral cover in (b) 1m x 1m quadrats in field surveys of benthic cover at Isla Contadora, (c) subsampled 10x10 cell patches from 100 simulated reefs created with empirically-measured feedback and environmental parameters (see supplement for details on parameter estimation, error bars indicate ±SE based on the 100 replicate reefs) and (d) subsampled patches of simulated reefs with the same environmental conditions as in b, but no positive feedbacks.

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Supplemental material

Table of Contents

1. Empirical methods

2. Model structure

3. Simulations

1. Empirical Methods

1.1 Study Site

All studies were conducted on reefs surrounding Isla Contadora, Republic of Panamá, approximately 65 kilometers southeast of Panamá City in the Pacific Ocean. The reefs of the ETP offer an excellent setting to evaluate mechanisms driving community resilience because they have a long history of thermal disturbances associated with El-Niño Southern Oscillation (ENSO) and recovery has been noted to be extremely patchy, with areas dominated by coral or algae existing in close proximity (Glynn and Mate 1997). Furthermore, reefs of the ETP have relatively intact herbivore communities and generally low levels of other human impacts (Glynn 2004). The reef framework is dominated by nearly continuous stands of the branching corals *Pocillopora damicornis* and *P. elegans*, while colonies of a few species of massive corals are present in lower abundances (Glynn and Mate 1997). Algae in the system are generally encrusting or turf forms that cover dead coral skeletons and coral rubble, or low-relief macroalgae that are usually found in the interstices between coral or rubble where it is relatively inaccessible to herbivores, suggestive of significant top-down control. The reefs are relatively shallow, reaching a maximum depth of only 3-4m below mean low water, and the shallowest colonies are exposed at moderate to extreme low tides (Glynn and Mate 1997). The Gulf of Panamá, where Isla Contadora is located, also experiences seasonal upwelling generally between Jan.-April (Glynn and Mate 1997) which generally lowers temperatures and increases turbidity, salinity and nutrient levels (D'Croz and O'Dea 2007). Our studies were conducted on two reefs: Larga Reef which is within an embayment on the eastern side of the island and Suecas Reef along the more exposed southern side of the island.

1.2 Herbivory experiments

To test for a positive feedback between the strength of top-down control on reef algae and local community composition, we compared herbivory rates between coral- and algal-dominated communities under favorable conditions for consumption (high palatability and accessibility). Experiments were conducted at Suecas Reef in January 2009. Adjacent and distinct patches at the same depth that were visually evaluated to be coral-dominated (>95% live coral) or algal-dominated (>95% algae) were identified and used as treatments for the study. For the experiment, we transplanted caged and uncaged thalli of a palatable red macroalga from the genus *Laurencia* into each community type and measured change in mass over time. Algae were collected from an adjacent reef immediately prior to the experiment, cleaned of sediment, invertebrates and epiphytes, spun in a salad spinner at a constant rate for 1 minute, then cable-tied into 3 g bundles. Half of the bundles were protected from herbivory by cylindrical cages of plastic hardware cloth (10cm diameter x 15 cm height, 1.3 cm mesh size) to estimate algal growth in the absence of herbivores and control for handling losses. Experiments were deployed on ~3m long lines anchored to the substrate in each community and open and caged algal bundles were attached haphazardly ~25-50 cm apart with 10-fold replication. After 24 hours, each bundle was collected, respun, and reweighed. In the coral-dominated state many uncaged samples were completely consumed; for these we calculated a conservative estimate of consumption by assuming that consumption occurred at a fixed rate over the entire time the samples were exposed.

Handling losses and algal growth were adjusted for in the measures of herbivory using the average final biomass of caged samples for each state. In each treatment the change in biomass of caged samples was <6% of initial mass and there was no significant pattern between community states (t-test, $t_{17.8}=0.341$, $p=0.738$). Herbivory rates were calculated by subtracting the final biomass of uncaged samples from the average final biomass of caged samples for the appropriate community state (Fig. 3-1). The data were tested for assumptions of parametric statistics and while they met the assumption of normality the treatments had unequal variances. Thus herbivory rates were compared between community states using Welch's two-sample t-test, which is adapted for unequal variances, with the t.test function in the stats package for the R programming language (version 12.5.1, R Development Core Team 2012).

1.3 Algal growth experiments

To evaluate a possible positive feedback between algal growth rates and algal abundance, algal growth rates and nutrient limitation were compared between algal- and coral-dominated states at Larga Reef at the end of the non-upwelling season in December 2009. Sites at Larga Reef were chosen using the same substrate criteria used for the herbivory experiments at Suecas reef. Algae were collected and processed as for herbivory experiments, except that samples were 2 grams and all samples were placed into cages made of window screening (approx 15cm x 15cm; 1mm mesh size) to prevent herbivory. Half of the samples was enriched with ten grams of Osmocote slow-release fertilizer (14%N:14%P:14%K) placed inside a diffuser made from a nylon stocking and included with the algae in the screen cages (n=15 for each community state x nutrient treatment condition). To limit flux of nutrients to ambient samples, enriched samples were placed a minimum distance of 2 meters from ambient samples (which has been shown to be far enough from nutrient diffusers that no nutrient enrichment can be detected, Wartian 2006). The percent change in biomass of samples from both coral- and algal-dominated states grown under enriched and ambient nutrient conditions were analyzed using a 2-factor ANOVA with community state and nutrient enrichment as main effects using the lm and Anova functions from the stats and car packages respectively (Fig. 3-1).

1.4 Benthic cover surveys

To determine the spatial distribution of coral and algae, we conducted surveys of benthic community composition in October 2009 at Larga and Suecas reefs. Individual 1m^2 plots (n=156) were randomly selected on hard reef substratum and percent cover of live coral and algae were estimated using a point-intercept method. In order to reflect the dynamics of both reefs and to increase sample size we combined data from the two sites. Because the scale of measurement strongly influences the ability to detect spatial patterns, we chose 1m^2 plots in order to capture heterogeneity of patches. This follows the recommended guideline to use sampling scales relevant to the organisms being studied (Wiens 1989); in this system 1m^2 plots are typically larger than individual algal or coral colonies, but far smaller than the expanse of coral framework or algal patches. Further, several studies suggest that major processes affecting coral and algal abundance, such as growth, herbivory and direct interactions between coral and algae occur on scales smaller than 1m (reviewed in McCook et al. 2001). Within each plot a grid of lines 10cm apart from each other was placed over the substrate, and we counted the number of intersection points that had live coral directly underneath. Using those values we estimated percent cover of live coral for each plot and produced a histogram of all plots with cover values grouped into bins of 5% width, starting with 0-5% (Fig. 3-4b).

2. Model structure

2.1 Overall model design and strategy

We used a stochastic cellular automaton (CA) model written and executed using the R programming language to evaluate the dynamics of coral and algal competition for space under varying environmental conditions. The model was based on a square grid of cells (10x10 cells for all analyses, except where otherwise noted) where each cell could exist in one of 4 states that represent the major members of the benthic community: live coral (L), macroalgae covering live coral (M_1), macroalgae covering dead coral (M_2), or a mixed community of grazed algal turfs and crustose coralline algae (T). Individual cells can transition to a different state via consumption of macroalgae by herbivores, settlement of new coral recruits, lateral growth of adjacent coral, coral mortality by prolonged coverage of macroalgae, settlement of algal propagules, or lateral overgrowth of adjacent algae (Fig. 3-S1). At each timestep environmental conditions were calculated for each cell based on global conditions and properties of the local neighborhood, and these were used to produce transition probabilities for each of the six processes (Table 3-S1). We designed the model to integrate information from other empirical datasets collected in the ETP (Chapter 2, Muthukrishnan, *unpublished data*), thus timesteps represent two week time periods and individual cells represent 10cm x 10cm patches of reef. We drew on the wealth of research from the ETP to choose values for scaling factors and parameters ranges that were in line with conditions observed in the ETP (Glynn and Fong 2006, Glynn, *unpublished data*, Fong, *unpublished data*, Chapter 2).

Using the CA we simulated the dynamics of reefs under a range of environmental conditions reflecting levels of environmental degradation (via harvesting of herbivores or eutrophication) and with a variety of possible feedback conditions. These simulations allowed us to evaluate the influence of environmental conditions and feedbacks on community dynamics and in particular we searched for conditions that could produce bistability and hysteresis in reef systems as a test for alternative stable states (ASS) dynamics.

2.2 Calculation of local conditions

The global environment was determined by parameters for global nutrient supply (*n*) and herbivore abundance (*h*) but these conditions were modified by the local neighborhood via feedback processes, that then determined local nutrient supply (*N*) and herbivory pressure (*H*; all parameters and derived quantities are summarized in Table 3-S2 and Table 3-S3). Algae are able to increase local nutrient availability (Fong et al. 2004) via uptake and recycling of nutrients from the water column, which facilitates algal growth (Fig. 3-1b). Corals facilitate both higher recruitment and activity of herbivores (Fig. 3-1a), likely by creation of spatially complex habitat that provides refuges from predators (Randall 1965, Lee 2006). In real systems the strength of these feedback processes can vary depending on the biology of the species present in the community. We represent this variation with parameters for the efficiency (*e*) of algal nutrient cycling and the proportion of herbivores that have strong spatial fidelity (*f*) for coral substrate.

Both feedback processes are spatially limited and thus their effects are functions of the composition of the local neighborhood, but because they arise from separate mechanisms the local neighborhood composition is calculated separately for algae and coral. Released nutrients are very quickly taken up on reefs, so the facilitative effect of algae on nutrient levels decays with distance. Thus we calculate the nutrient facilitation neighborhood of a given cell as the weighted proportion of neighboring cells that are occupied by algae (of any type M_1, M_2, or T), with weights decreasing as the square of distance out to a maximum nutrient facilitation distance d_n. The model treats distance as a series of concentric rings out from the focal cell, and cells within a ring are equivalent whether they are vertically, horizontally or diagonally connected. Thus algal abundance (L_a) in the algal facilitation neighborhood is calculated as

$$L_a = \sum_{i=1}^{d_n} \frac{x_i}{i^2} \Bigg/ \sum_{i=1}^{d_n} \frac{1}{i^2} \qquad eq. 1$$

where x_i is the proportion of cells in the i^{th} band out from the focal cell that are occupied by any type of algae. The denominator serves to normalize the weighted mean calculation so that N_n can range from 0 to 1. In contrast to nutrient facilitation, herbivores exhibiting spatial fidelity tend to consume algae uniformly up to a fixed distance from coral refuges, rather than reducing herbivory pressure with distance from coral (Randall 1965, Ogden et al. 1973). To reflect this pattern, the coral abundance (L_c) in the coral facilitation neighborhood is calculated simply as the overall proportion of coral cells within all the rings out to the herbivory facilitation distance (d_h).

Local nutrient supply (N) is dependent on global nutrient supply (n) modified by the nutrient facilitation feedback that allows nearby algae to increase local nutrient availability via fixation and recycling. Thus n sets a base level for nutrient availability that is enriched by an amount assumed to be linearly proportional to L_a (with constant of proportionality e) according to the equation:

$$N = n\big(1 + (eL_a)\big) \quad eq. 2$$

Values for g can vary as a consequence of natural or anthropogenic nutrient loading and can take any non-negative value, with $g = 0$ representing a completely nutrient free environment where algae cannot grow at all.

Similarly, potential herbivory pressure is controlled by the overall abundance of herbivores (h), though the herbivory pressure experienced in a given cell can be reduced if herbivores are unwilling to range far from coral refuges. For the fraction f of herbivores that exhibit strong spatial fidelity, we set their consumption rate as proportional to L_c while the rest of the herbivore community is not influenced by the local neighborhood. Thus the herbivory pressure experienced in a particular cell can be described as:

$$H = h\left(1 - f + (fL_c)\right) \quad eq.3$$

2.3 Transition Processes

Six processes drive transitions between states (Fig. 3-S1; Table 3-S1). Five of these processes occur as Poisson processes with probabilities determined by local environmental conditions and community composition:

1) Consumption
2) Algal growth
3) Algal settlement
4) Coral growth
5) Coral recruitment.

The sixth process, coral mortality under new macroalgae, occurs only for cells in the M_1 state and occurs automatically if the macroalgae in that cell are not consumed in that timestep.

Consumption of macroalgae in the M_1 state returns the cell to the L state but from the M_2 state, leads to the T state because the underlying substrate has died and newly opened substrate is quickly colonized by turf algae (McCook et al. 2001). Coral recruitment and lateral overgrowth are assumed to occur only on cells in the T state (and lead to the L state) because macroalgae are more effective at directly competing with coral and inhibiting coral recruitment than mixed turf assemblages (McCook et al. 2001, Jompa and McCook 2003, Fong and Paul 2011) and CCA are an important cue for recruitment (Hadfield et al. 2001, Fong and Paul 2011). Similarly macroalgal growth or settlement on the T state leads directly to the M_2 state because there is no underlying live coral but from the L state leads to the M_1 state. Transitions to coral take precedence so transitions from the T state to the M_2 state only occur if coral growth or recruitment *do not* occur and algal growth and settlement do occur. Only macroalgae are able to take over coral cells so transitions from the L state to the T state do not occur. If none of the allowed transition processes occur a cell will persist in its current state.

In each timestep of the simulation, probabilities for each transition process are re-calculated for each cell based on current local environmental conditions. For each transition we created an expression based on the key factors that control the rate of the process, including scaling coefficients to allow rates to correspond with empirical values for ETP systems (equations 6-10). For a transition process occurring at average rate λ, we calculated the probability that a transition occurred during a single timestep using the standard exponential formulation:

$$P(Transition) = 1 - e^{-\lambda \Delta t} \quad eq.\ 4$$

where λ is expressed in units of a single timestep (e.g. the average number of algal propagules that settle in a cell in a 2 week window). For processes such as lateral growth of coral or macroalgae that can occur from any directly adjacent coral or macroalgal cell, this calculation is modified to account for the number of sources from which lateral growth can occur (i.e., the number of cells in the directly adjacent ring that are coral or macroalgae). This leads to the formulation:

$$P(Transition) = 1 - e^{-\lambda A \Delta t} \quad eq.\ 5$$

where *A* is the number of directly adjacent coral (A_c) or macroalgal (A_a) cells.

Rate expressions for each process were calculated using the local environmental variables (*H, N*), as calculated above, as well as scaling coefficients for each process (σ, see below for estimation of values). Local herbivory pressure (*H*) controls the rate of macroalgal consumption (λ_h) in a cell:

$$\lambda_h = \sigma_h H \quad eq.6.$$

Lateral growth of macroalgae (λ_a) increases as a function of local nutrient supply (*N*) but is reduced by higher herbivory pressure

$$\lambda_a = \sigma_a N(1 - H) \quad eq.7.$$

Settlement of new algal propagules (λ_p) is dependent on the supply of algal propagules (*p*), but is also controlled by *N* and *H*:

$$\lambda_p = \sigma_p p N(1 - H) \quad eq.8.$$

The recruitment rate of new coral colonies (λ_r) is based on a single empirically estimated parameter of supply of coral recruits, *r*

$$\lambda_r = \sigma_r r \quad eq.9.$$

Lateral growth of coral (λ_c) increases as a function of the abundance of coral in the local neighborhood (N_c)

$$\lambda_c = \sigma_c L_c \quad eq. 10.$$

These rates then lead to the following probabilities for each process

$$P(consumption) = 1 - e^{-\sigma_h H \Delta t} \quad eq.\ 11$$

$$P(algal\ growth) = 1 - e^{-\sigma_a N(1-H)\Delta t} \quad eq.\ 12$$

$$P(algal\ settlement) = 1 - e^{-\sigma_p p N(1-H)\Delta t} \quad eq.\ 13$$

$$P(\square oral\ growth) = 1 - e^{-\sigma_r r A_a \Delta t} \quad eq.\ 14$$

$$P(coral\ recruitment) = 1 - e^{-\sigma_c L_c \Delta t} \quad eq.\ 15$$

that are calculated independently for each cell.

2.4 Scaling coefficients

Using data from a 6 month experiment that manipulated nutrient supply and herbivore abundance and monitored benthic community composition at Isla Contadora (Chapter 2), recovery after those manipulations (Muthukrishnan, *unpublished data*) and long term (~40 years) monitoring of reefs including recovery after El niño related mortality (Glynn and Fong 2006, Glynn, *unpublished data*) and the herbivory and growth experiments as a guide for natural rates we chose values for the scaling factors σ_h, σ_a and σ_c. Values were chosen so that process rates reflective of the ETP were produced within reasonable ranges of other parameters with useful benchmarks. Under favorable conditions algal growth rates were quite rapid (Muthukrishnan Chapter 2, Fig. 3-1b) based on these data, σ_a was set such that the probability of algal lateral growth (eq. 11) was 0.9 when N=1, H=0 and A_a=8 (σ_a = 0.288). Live coral framework expanded into adjacent areas and patches recovered from disturbance readily (Glynn and Fong 2006, Muthukrishnan, *unpublished data*), though much less rapidly than algae. To approach those empirical values σ_c was set such that the probability of coral lateral growth into a cell (eq. 13) was 0.05 per timestep when both the neighborhood and directly adjacent cells are 50% coral (L_c=0.5, A_c=4; σ_c=0.257). Maximal rates of herbivory in the system were very high (Fig. 3-1a) and when herbivores are abundant they can remove macroalgae very efficiently (Muthukrishnan, *unpublished data*), thus we set σ_h such that the probability of macroalgal consumption (in eq. 10) was 0.75 when H is 1 (σ_h=1.386). Because r and p are free parameters (or directly estimated from empirical data) we used values of 1 for both σ_r and σ_p.

3 Simulations

3.1 General conditions

To create initial landscapes that ranged in coral cover for simulations in the bistability and hysteresis analyses a series of simulations were conducted starting from a randomly mixed initial community (the state of each cell was determined by a Bernoulli trial with a 50% probability for the L state and a 50% probability for the M_1 state) and run for 20 time steps as this allowed for the initial random spatial distribution to coalesce into patches that reflected the spatial structure of real ETP reefs. These simulations were run under a parameter set that was chosen because it was able to produce a range of outcomes (e=0.6, f=0.6, n=0.5, h=0.455, d_h=1, d_n=1, p=0, r=0) and simulations were repeated until for each of our 21 stating cover values (0%, 5%, 10%, ..., 100% coral) 25 separate landscapes were produced in which the % coral cover after 20 time steps exactly matched that value. The complementary algal cells were mixed between the M_1, M_2, and T states and example landscapes for each initial value can be seen in Fig. 3-S5.

Using these landscapes, each replicate run for the bistability and hysteresis analyses (see below) was initialized using a unique starting configuration but with consistent coral and algal abundances (with the exception of the 100% coral condition that cannot have any variation). Because the rates of recruitment of new coral and algal patches are substantially slower than the growth of existing patches and have only a weak effect on community dynamics, both r and p were fixed at low values (0.01 for both) for all simulations in the bistability and hysteresis analyses (all parameters and values used in simulations are summarized in Table 3-S2). Sensitivity analyses were conducted for both parameters, and showed that the qualitative conclusions did not change across multiple orders of magnitude for each parameter (Figs. S6, S7). Facilitation distances of d_n=1 and d_h=3 were used to reflect the generally tighter spatial extent of the nutrient feedback than the herbivory feedback. Sensitivity of these parameters was also tested by running analyses with the nutrient feedback distance larger than the herbivory feedback distance (d_n=3, d_h=1), both feedbacks equal and tightly constrained (d_n=1, d_h=1), and with no spatial component (by allowing the L_a and L_c to be determined as the global proportion of algae or coral respectively). These scenarios also showed no qualitative differences from the outcomes for the standard parameters (Fig. 3-S8).

3.2 Bistability tests

To test whether reefs can have multiple stable community compositions under the same environmental conditions, we ran simulations from a range of initial community compositions under constant assumptions about environmental parameters for the duration of the simulation run. We tested for bistability in those simulations by evaluating whether outcomes were split between separate attractors for coral-dominated and algal-dominated communities. To understand the controls on community dynamics, separate simulations were repeated across a range of global environmental conditions as well as different feedback strengths. Simulations were run for 20 values of herbivore abundance, *h*, ranging from 0 to 2, and of global nutrient supply, *n*, ranging from 0 to 1. The strengths of the feedback processes were also varied, with herbivore fidelity *f* ranging from none to complete (0 to 1), and nutrient facilitation *e* ranging from no additional facilitation to the potential for an 8 fold increase in nutrient supply (0 to 8). For each set of parameters (*n, h, e* and *f*), 25 replicate simulations were run from each of 21 initial starting coral abundances that ranged from no coral to 100% coral in increments of 5%, using the different landscapes created above, and allowed to run for 200 time steps. Heatmaps were produced with cells that indicate the proportion of all runs from all starting abundances that ended with greater than 50% coral for each parameter set (Figs. 2a-d, S2). The frequency of intermediate outcomes (final % coral between 25-75%) was indicated with circles of varying sizes plotted in the middle of the appropriate heatmap cell. In figure 3-2 of the main text we show results for the four main scenarios: the no feedback condition (e=0, f=0), a nutrient feedback only condition (e=2, f=0), an herbivory feedback only condition (e=0, f=0.6), and a combined feedback condition (e=2, f=0.6). These same scenarios are used in the sensitivity analyses (Figs S6-S8). The results for the full range of feedback parameters are shown in figure 3-S2 and qualitatively match the results of the focal feedback scenarios (Fig. 3-2) but show a more graded response indicating that strength of positive feedbacks determine the region of bistability, with phase shifts produced at low feedback strengths. In addition, the combination of herbivory and nutrient feedbacks expands the region of bistability further than either feedback on its own.

3.3 Hysteresis tests

To evaluate whether reefs have environmental thresholds beyond which they undergo rapid changes in community composition and if these thresholds differ depending on the direction of transition (hysteresis) we ran simulations in which community composition was monitored while environmental conditions (*h* or *n*) were degraded then restored. Twenty-five replicate simulations were run using the same feedback parameters (*e* and *f*) as in the bistability analysis (no feedback, nutrient feedback only, herbivory feedback only, and both feedbacks). All replicates started at 90% coral but with different initial landscape configurations. First, we kept *n* constant at 0.4 while *h* initially began at 2 and shifted every 20 time steps through 30 evenly spaced increments down to a value of 0. After reaching 0, it returned through the same increments back to a value of 2. The % coral cover was measured every 20 steps (just before *h* changed) and was plotted for each replicate. The average across all replicates was then plotted with bold lines (results of the main four feedback scenarios are shown in Fig. 3-3, while the results for the full range of feedback parameters are shown in Fig. 3-S3) showing that hysteresis occurs when feedbacks are present and the distance between forward and reverse thresholds expands as feedback strength increases. The combination of both feedbacks also expands the extent of hysteresis beyond the amount seen from of either feedback on its own. An analogous set of simulations was run to explore hysteresis under varying global nutrient supplies (with *n* varying from 0 to 1 and *h* held constant at 0.5; results for all conditions in Fig. 3-S4) and showed qualitatively similar results though increasing feedback strength tended to move the coral to algal threshold as well as change the distance between thresholds.

3.4 Comparison of spatial patterns between simulated and real reefs

To compare the model's behavior against that of real reefs we used empirical data from Isla Contadora and other portions of the ETP to estimate values for all parameters, which we used to create a large distribution of simulated reefs. We then compared spatial patterns between the simulated reefs and actual reefs of Isla Contadora using *in situ* benthic cover surveys (see empirical methods above) and analogous subsamples of the simulated reefs. Values for h and f were calculated using data from the herbivory assays (see above). Incorporating the measures of herbivory rates from adjacent algal and coral-dominated patches (Fig. 3-1) into eq. 3 we were able to create a system of equations from which we could determine f:

$$\lambda_{h1} = \sigma_h h\big(1 - f + (fL_{c1})\big) \quad eq. 16$$

$$\lambda_{h2} = \sigma_h h\big(1 - f + (fL_{c2})\big) \quad eq. 17$$

where λ_{h1} is the local herbivory rate in the coral-dominated state where the local coral abundance was 95%, and λ_{h2} is the local herbivory rate in the algal-dominated state which had only 5% coral cover. Our herbivory assays measured rates of algal consumption of 2.72±0.11(mean±SE) and 1.54±0.33 g/day for the coral-dominated and algal-dominated states respectively. As experimental samples had an initial weight of 3 grams, proportional consumption values were λ_{h1}=90.7%/day, λ_{h2} =51.3%/day. Using values of L_{c1}=.95, and L_{c2}=.05 equations 15 and 16 can be solved leading to f= 0.471. The feedback experiments were designed to create optimal conditions for consumption (e.g. highly palatable algae, readily accessible) such that we could effectively determine relative rates between community states. This comparison of herbivory assays between community states offers a reasonable method to estimate the spatial fidelity parameter *f*, but is less well suited to evaluating absolute consumption rates of diverse (and possibly defended) algal species. Observed consumption rates would completely deplete highly palatable algae in less than a two-week time step, so to obtain a more conservative estimate of herbivory pressure that better reflects a varied algal community we assumed total consumption would occur, but over the course of an entire time step. Thus we set λ_{h1} and λ_{h2} at 1 and solved for *h* in eq. 10 and eq. 11. However, those produce somewhat different estimates of *h* because of the different values of N_h so we used their average, providing an intermediate estimate of *h* = 1.022.

Similarly we calculated nutrient recycling efficiency (*e*) and global nutrient supply (*n*) from the algal growth assays by using the algal growth rates measured in adjacent coral-dominated and algal-dominated patches (unenriched samples in Fig. 3-1) as values for λ_a in eq. 6, creating the system of equations:

$$\lambda_{a1} = \sigma_a N\big(1 + (eL_{a1})\big)(1 - H)\ eq.18.$$

$$\lambda_{a2} = \sigma_h N\big(1 + (eL_{a2})\big)(1 - H)\ \ eq.19.$$

In the ambient nutrient treatment of the growth assays (Fig. 3-1b) we measured algal growth rates of 6.28±0.46 and 9.00±0.49 %/day for the coral-dominated and algal-dominated states respectively. Scaling these rates to a two-week time step we calculated values λ_{a1}=49.0 %/time step, λ_{a2}=86.3 %/time step, L_{a1}=.05, and L_{a2}=.95, and H=0 (because growth rates were measured in an experiment where algae were protected from herbivory) we solved to find $e = 0.884$ and $n = 1.630$.

Other parameters were estimated from long-term monitoring and experiments done in the ETP during P. Glynn's NSF funded research cruises. In experiments at Isla Uva (a similar *Pocillopora* dominated ETP reef with comparable community composition), algal growth rates measured in patches cleared of algae showed reductions of nutrient facilitation on the scale of 0.3 m and herbivory rates measured at various positions suggested spatial fidelity on the scale of ~1m (Fong, *unpublished data*). Using that data we estimated facilitation distances of $d_n=3$ and $d_h=10$ assuming cells that are 10x10cm. Based on observations over 20 years from long term monitoring plots in the ETP we estimated a recruitment rate of 0.55 colonies/m^2 per year which translates to a value of $r = 0.0002$ recruits/(cell*timestep) (Glynn, *unpublished data*). Using data from a separate experiment at Suecas reef (Chapter 2) we measured the number of new algal patches that arose within a set of plots over a 10-week period, which we used for estimates of the rate of settlement of algal propagules (λ_p). Using those estimates of λ_p, values for L_a measured in each plot, the values of e and n calculated for Isla Contadora, and assuming H=0 because the plots had herbivore exclosures, we calculated local nutrient supply (N) from eq. 2 which we then used to calculate the supply of algal propagules (p) from eq. 7. Measurements from 5 plots yields an estimate of $p = 0.020$ propagules/(cell*time step).

The simulated reefs were created by model runs initialized with a randomly assorted landscape of cells (400 x 400). This significantly larger scale was used to better reflect the scale of real reefs at Isla Contadora and to provide enough space so that spatial patterns could be evaluated analogously to our empirical benthic cover surveys. The initial proportion of cells in the live coral state was chosen as a uniform random variate on the interval from 0 to 1, and these coral cells were distributed randomly with respect to space; the remaining cells were given one of the 3 algal states (M_1, M_2 or T) with equal probability. Simulations were then allowed to run for 1 year (26 time steps). The paths of all runs were plotted in Fig. 3-4a and simulated reefs with overall coral cover within 10% of the average value of coral cover observed in benthic cover surveys at Isla Contadora (58.75%) were selected for further evaluation of spatial patterning. Coral abundance was measured in 156 randomly-placed 10x10 cells, replicating the design and sample size of our field surveys. Simulated reefs that were not close enough to the empirically-observed coral abundance provided an inappropriate comparison to the empirical data due to the overall differences in coral abundance, rather than their spatial patterning, and so were discarded. Replicate simulations were conducted until there were 100 appropriate simulated reefs to be sampled. Figure 3-4c shows a histogram of the average coral cover for each bin across all simulations (error bars represent ± SE). In addition, to test the importance of positive feedbacks on spatial patterning, a similar ensemble of reefs was simulated using the same methods and environmental parameters but with no positive feedbacks (e=0, f=0) and results are shown in Fig. 3-4d. While bistability only occurs within a certain range of conditions, spatial patterning occurs broadly whenever positive feedbacks are present.

Supplemental Tables

Table 3-S1 Probabilities of transitions between states for individual cells based on probabilities of specific processes (from equations 11-15). Intersection symbols (⋂) indicate that both processes must occur and the combined probability is calculated such that $P(A \cap B) = P(A)P(B)$. Union symbols (⋃) indicate that either process can occur and probabilities are calculated such that $P(A \cup B) = P(A) + P(B) - P(A \cap B)$. Terms with arrows indicate the probability of a transition between states calculated in another cell.

	To L state	**To M_1 state**	**To M_2 state**	**To T state**
From L state	$1 - P(algal\ growth \cup algal\ settlement)$	$P(algal\ growth \cup algal\ settlement)$	0	0
From M_1 state	$P(consumption)$	0	$1 - P(consumption)$	0
From M_2 state	0	0	$1 - P(consumption)$	$P(consumption)$
From T state	$P(coral\ growth \cup coral\ recruitment)$	0	$P(algal\ growth \cup algal\ settlement) - P((T \rightarrow L) \cap (algal\ growth \cup algal\ settlement))$	$1 - P((T \rightarrow L) \cup (T \rightarrow M_2))$

Table 3-S2 List of parameters used in model equations and values used for different simulations. Ranges for environmental variables (*n, h*) in the bistability analysis and feedback values indicate separate simulations were run at multiple parameter values. Two sets of values are shown for *n* and *h* in the hysteresis analysis to represent the separate analyses with variable herbivore abundance (Fig. 3-S3) versus variable nutrient supply (Fig. 3-S4) and the ranges represent the set of conditions individual simulations move through. Empirical estimates were used in the creation of simulated reefs used to evaluate spatial patterns (section 3.4). Information in parentheses indicates the source of data used to estimate parameters.

Parameter	**Symbol**	**Values in bistability analysis**	**Values in hysteresis analysis**	**Empirical estimate (derived from)**
Herbivore abundance	h	0-2	0-2; 0.5	1.051 (herbivory experiments)
Global nutrient supply	n	0-1	0.4; 0-1	1.630 (growth experiments)
Efficiency of algal nutrient cycling	e	0-8	0-8	0.884 (growth experiments)
Herbivore spatial fidelity	f	0-1	0-1	0.471 (herbivory experiments)
Nutrient facilitation distance	d_n	1	1	3 (Fong unpublished data)
Herbivory facilitation distance	d_h	1	1	10 (Fong unpublished data)
Algal propagule supply	p	0.01	0.01	0.020 (Chapter 2)
Coral recruit supply	r	0.01	0.01	0.0002 (Glynn unpublished data)
Consumption scaling factor	σ_h	1.386	1.386	1.386 (Chapter 2, herbivory experiments)
Algal growth scaling factor	σ_a	0.288	0.288	0.288 (Chapter 2, growth experiments)
Algal settlement scaling factor	σ_p	1	1	1
Coral growth scaling factor	σ_c	0.257	0.257	0.257 (Chapter 2)

Table S3 List of derived quantities used in model equations. Values are calculated independently for each cell and updated at every timepoint.

Derived quantities	**Symbol**	**Calculated by**
Local herbivory pressure	H	Eq. 3
Local nutrient supply	N	Eq. 2
Local neighborhood coral abundance	L_c	Proportion of coral cells in the neighborhood up to d_h cells away
Local neighborhood algal abundance	L_a	Eq. 1
Directly adjacent coral	A_c	Number of directly adjacent coral cells
Directly adjacent algae	A_a	Number of directly adjacent macroalgae cells
Consumption rate	l_b	Eq. 11
Algal growth rate	l_a	Eq. 12
Algal settlement rate	l_p	Eq. 13
Coral growth rate	l_c	Eq. 14
Coral recruitment rate	l_r	Eq. 15

Supplemental Figures

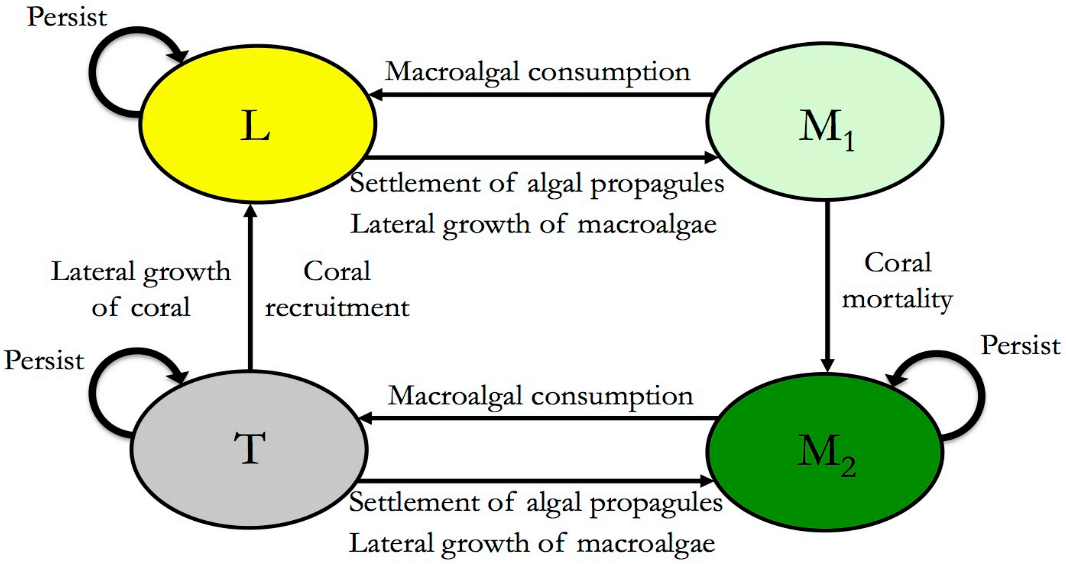


Fig. 3-S1 Flow diagram of model. Colored ovals represent states in which individual cells can exist. Directional arrows represent transition processes.

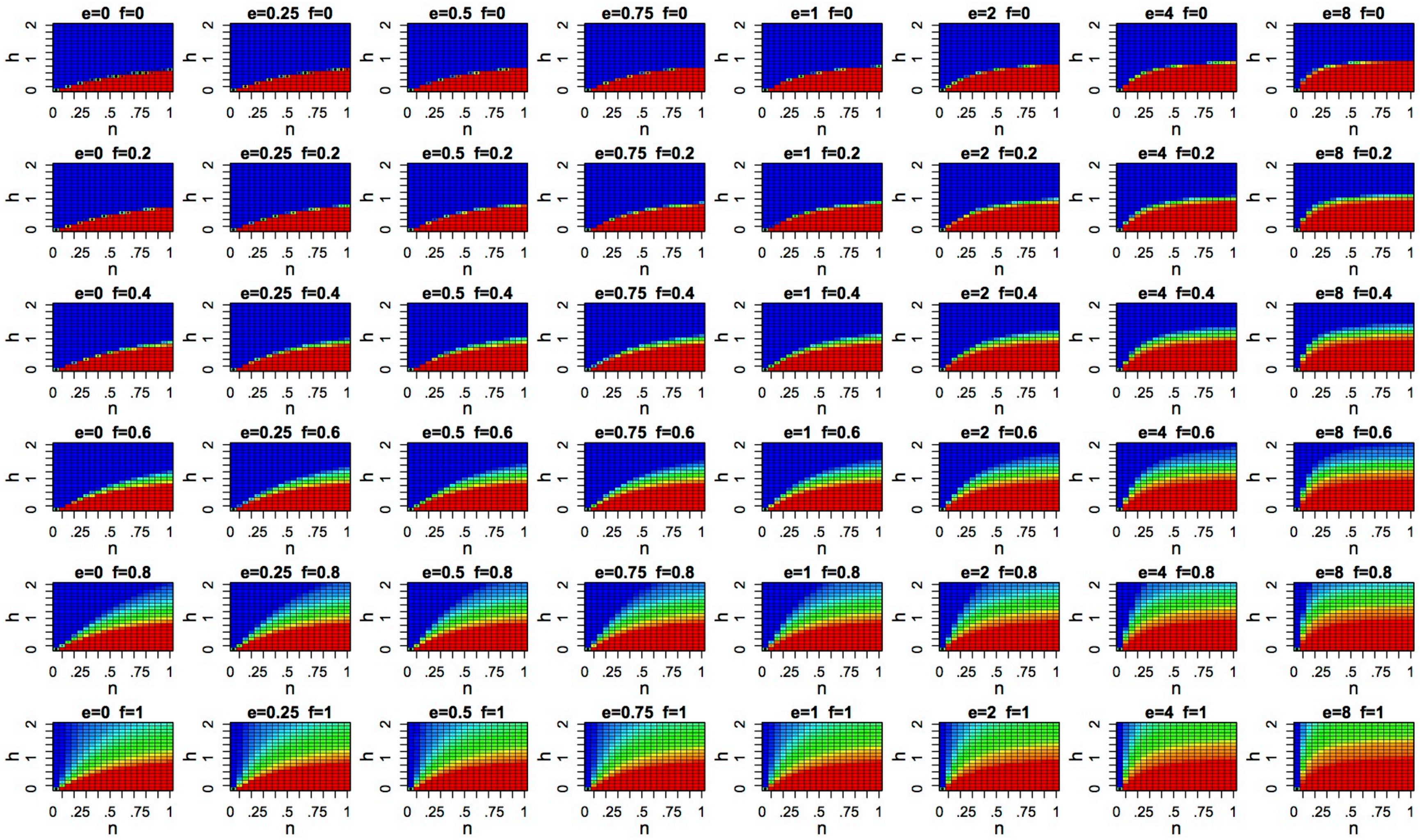


Fig. 3-S2 Bistability analysis across a range of feedback strengths. Heatmaps show the percent of simulations that ended with more than 50% coral cover for each set of parameters. Individual cells in each heatmap represent a unique parameter set with global nutrient supply

(*n*) increasing along the x axis and herbivore abundance (*h*) increasing on the y axis. Separate heatmaps indicate simulations conducted with different feedback strengths with the efficiency of algal nutrient cycling (*e*) and spatial fidelity of herbivores (*f*) indicated above each heatmap. Dark blue squares indicate conditions where all simulations ended in a coral-dominated state, red squares indicate all ended in an algal-dominated state, and intermediate colors denote outcomes were split between states. The size of the black dot in each cell represents the proportion of runs that ended with intermediate (25%-75%) coral cover. Thus only intermediate colored squares with small or no dots represent bistability as opposed to noise.

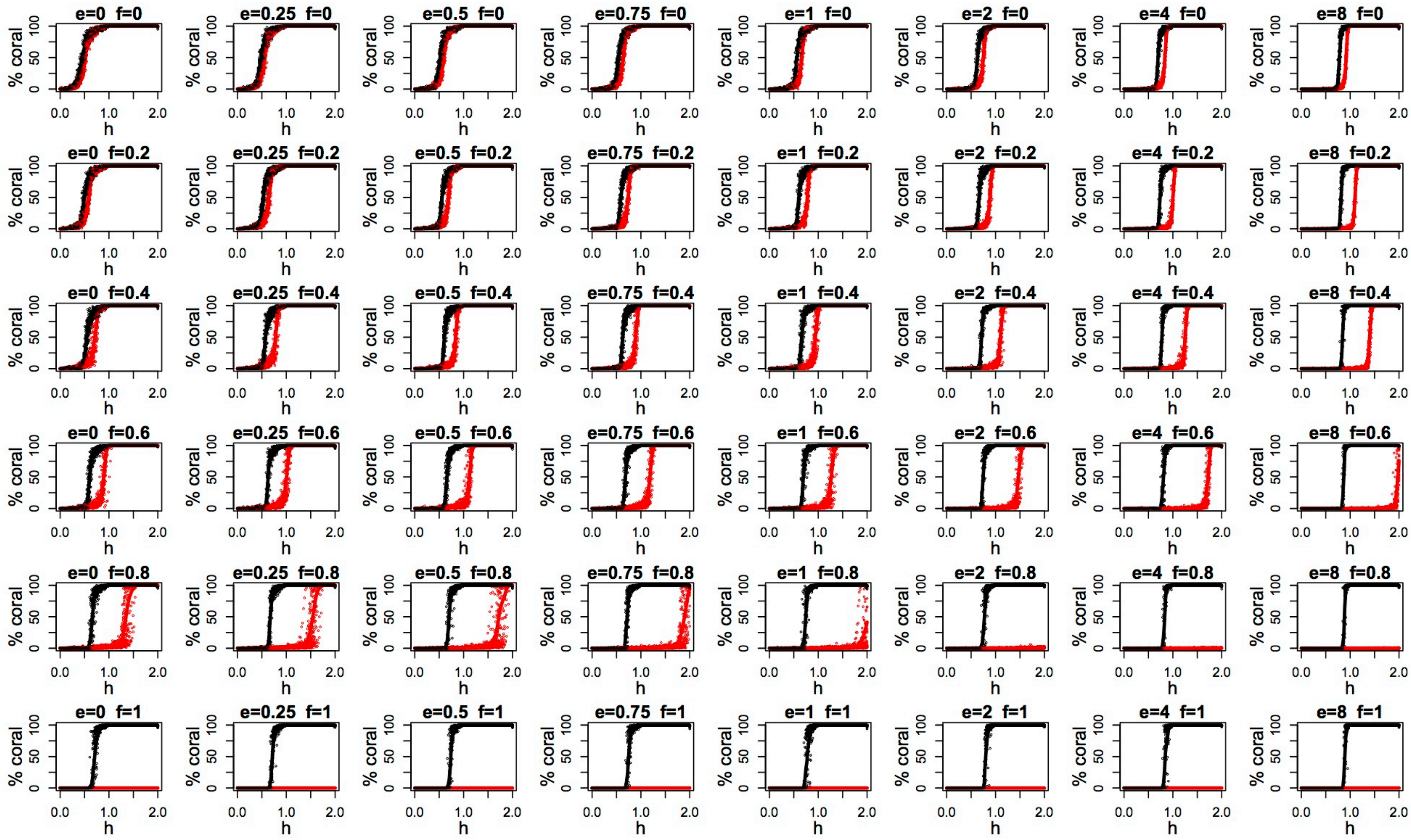
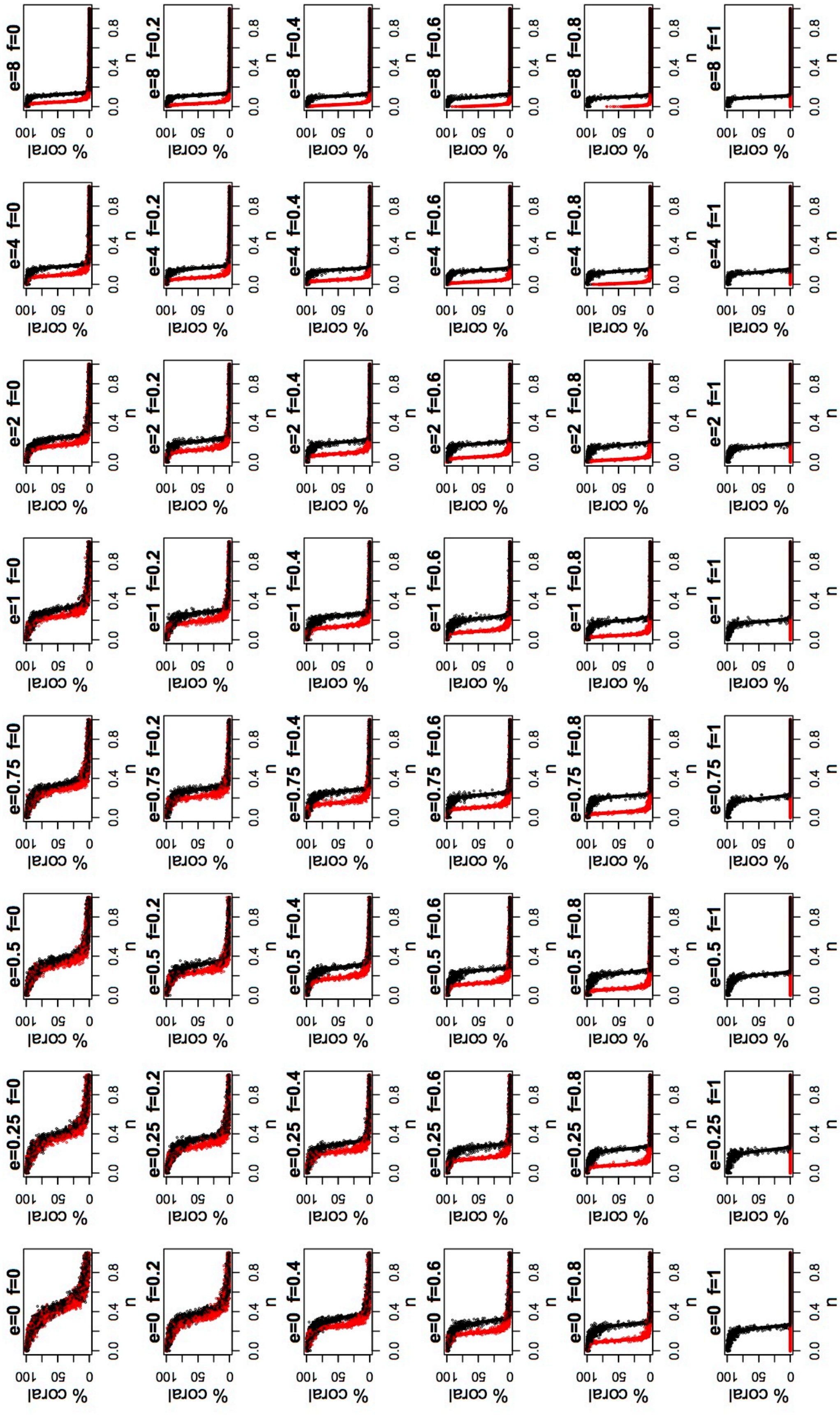


Fig. 3-S3 Hysteresis analyses across a range of feedback conditions where degredation occurs via overharvesting of herbivores. Dots represent % coral cover for each of 25 replicate simulations at intervals of 20 time steps as the simulation moves through a range of

herbivore abundances ($h=2$ to $h=0$). Black dots represent values as abundance decreases (successive time steps move rightward) while red are values as conditions recover (successive time steps move leftward). Lines show the average value across all replicates. Each separate plot indicates simulations conducted with different feedback strengths with the efficiency of algal nutrient cycling (e) and spatial fidelity of herbivores (f) indicated above the plot. When feedback strengths are particularly high (*e.g.* $f=1$) once the community transitions to an algal-dominated state it is unable to recover even if environmental conditions return to the “pristine” state. Hence the red lines remain at 0% coral cover through the entire simulation.



e=0 f=0
e=0 f=0.2
e=0 f=0.4
e=0 f=0.6
e=0 f=0.8
e=0 f=1
e=0.25 f=0
e=0.25 f=0.2
e=0.25 f=0.4
e=0.25 f=0.6
e=0.25 f=0.8
e=0.25 f=1
e=0.5 f=0
e=0.5 f=0.2
e=0.5 f=0.4
e=0.5 f=0.6
e=0.5 f=0.8
e=0.5 f=1
e=0.75 f=0
e=0.75 f=0.2
e=0.75 f=0.4
e=0.75 f=0.6
e=0.75 f=0.8
e=0.75 f=1
e=1 f=0
e=1 f=0.2
e=1 f=0.4
e=1 f=0.6
e=1 f=0.8
e=1 f=1
e=2 f=0
e=2 f=0.2
e=2 f=0.4
e=2 f=0.6
e=2 f=0.8
e=2 f=1
e=4 f=0
e=4 f=0.2
e=4 f=0.4
e=4 f=0.6
e=4 f=0.8
e=4 f=1
e=8 f=0
e=8 f=0.2
e=8 f=0.4
e=8 f=0.6
e=8 f=0.8
e=8 f=1
% coral
0
50
100
n
0.0
0.4
0.8

Fig. 3-S4 Hysteresis analyses across a range of feedback conditions where degredation occurs via increasing global nutrient supply. Dots represent % coral cover for each of 25 replicate simulations at intervals of 20 time steps as the simulation moves through a range of global nutrient supply (*n*=0 to *n*=1). Black dots represent values as abundance decreases (successive time steps move rightward) while red are values as conditions recover (successive time steps move leftward). Lines show the average value across all replicates. Each separate plot indicates simulations conducted with different feedback strengths with the efficiency of algal nutrient cycling (*e*) and spatial fidelity of herbivores (*f*) indicated above the plot. When feedback strengths are particularly high (*e.g.* *f*=1) once the community transitions to an algal-dominated state it is unable to recover even if environmental conditions return to the "pristine" state. Hence the red lines remain at 0% coral cover through the entire simulation.

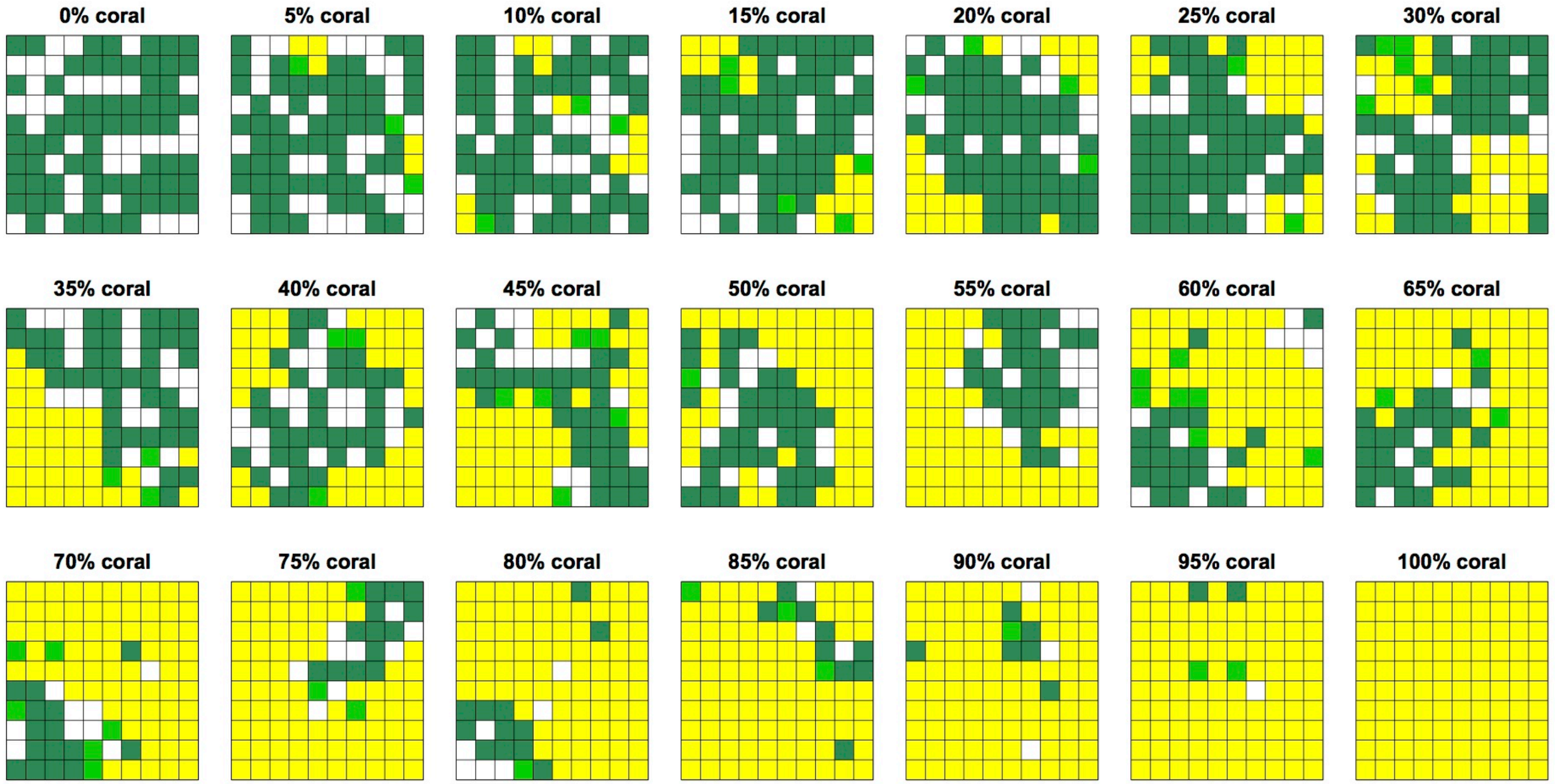


Fig. 3-S5 Examples of initial landscapes. Individual 10x10 grids show one of the 25 landscapes for each of the 21 levels of initial coral abundance that were used to initialize simulations. Cell colors represent different possible states: yellow (L), light green (M_1), dark green (M_2), and white (T). The 0% coral condition still has variability in the placement and relative abundances of different algal types, while the

100% coral condition has no initial variability.

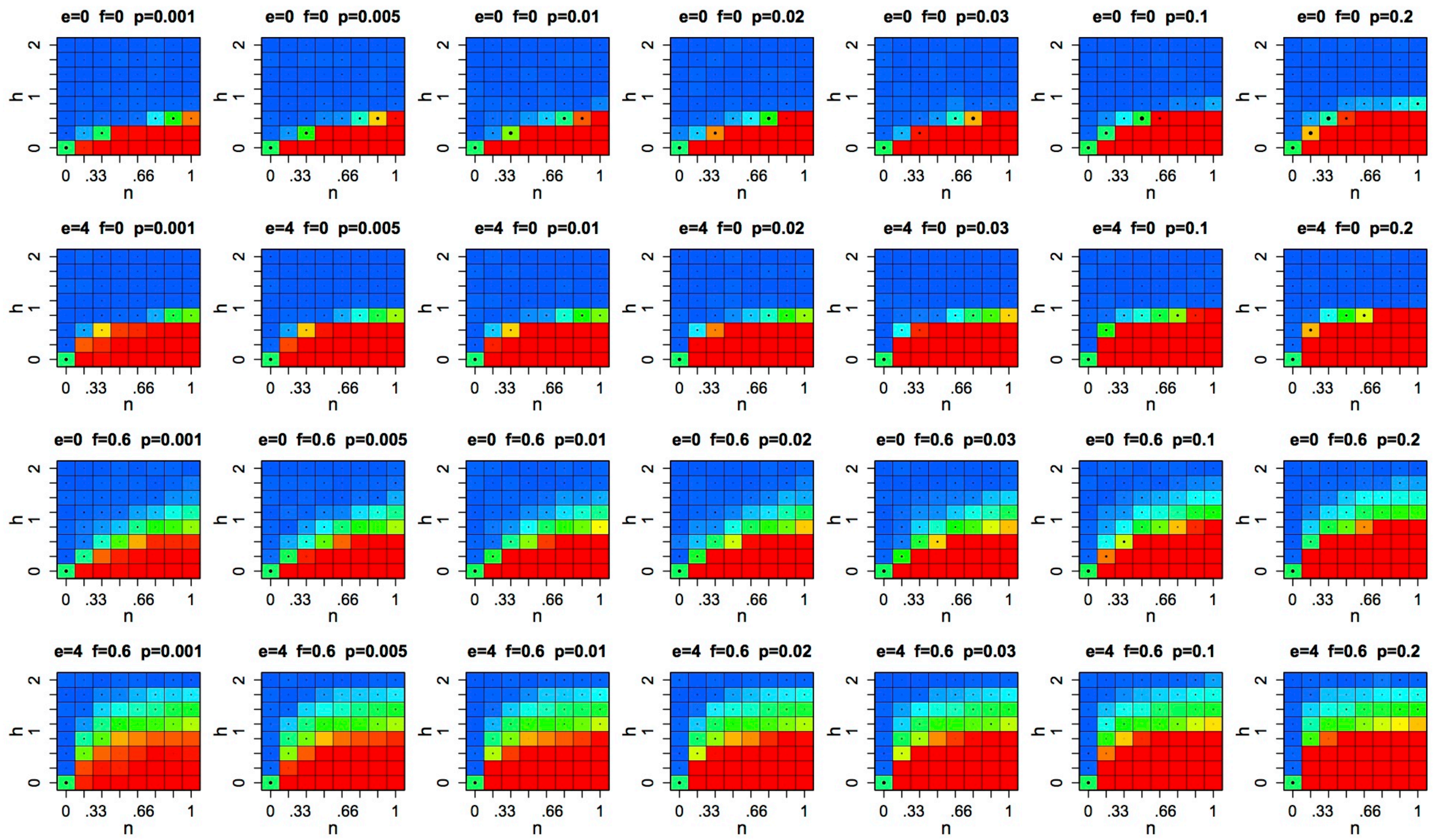


Fig. 3-S6 Sensitivity analysis for algal propagule supply. Plots are similar to bistability analysis above but simulations were run under more limited conditions for computational efficiency. Simulations were only run for 100 time steps, only 8 levels of herbivore abundance (*h*) and

global nutrient supply (*n*) and for only 4 feedback strength scenarios (*e* and *f*). For each of those parameter sets bistability analyses were conducted for 7 values of propagule supply (*p*) ranging over multiple orders of magnitude. Different levels of *p* are shown in successive columns of heatmaps and levels are indicated above each plot. The middle column (*p*=.02) reflects the values used in the main bistability analyses (Figs. 2 and S2) and does not qualitatively differ from other values of *p*.

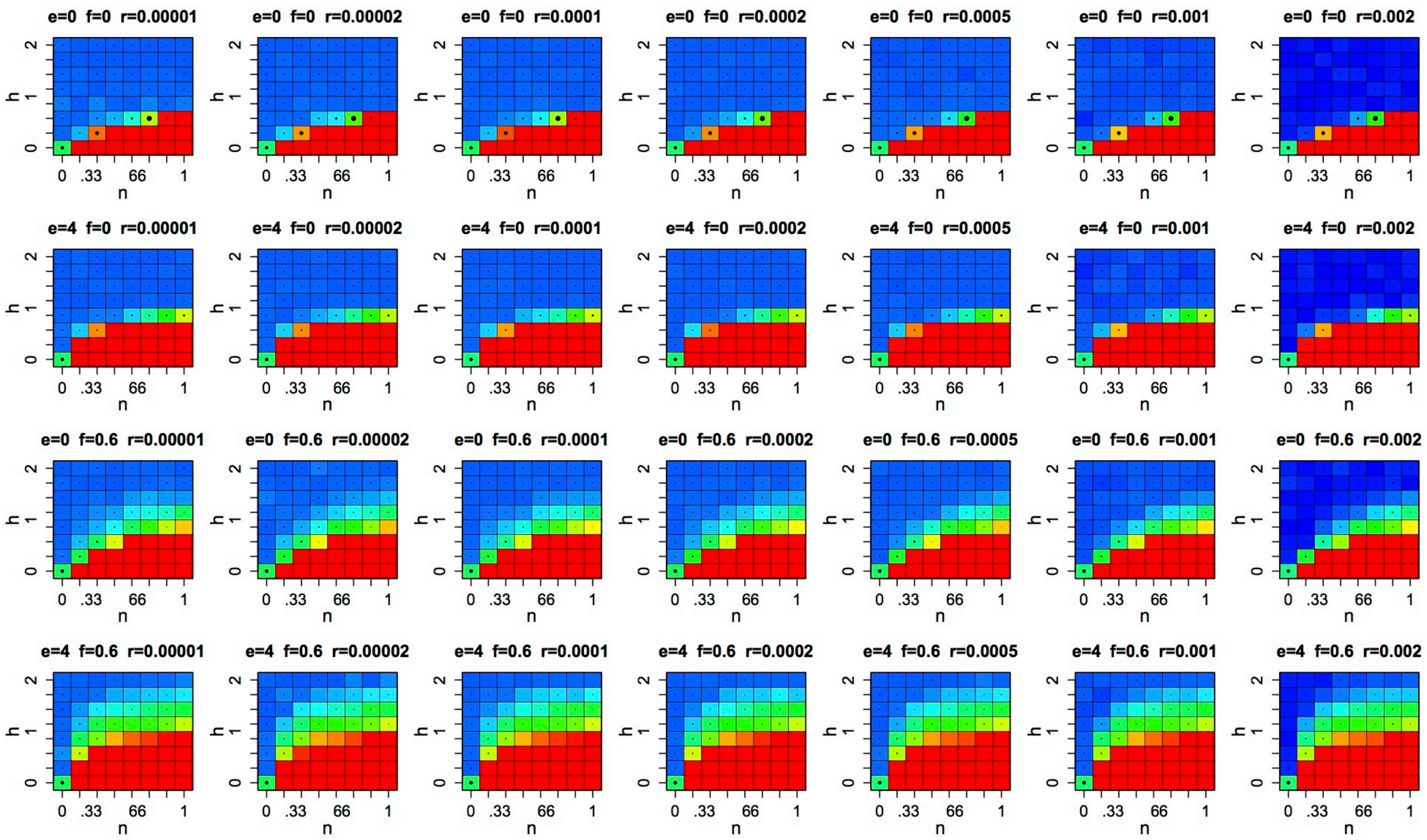


Fig. 3-S7 Sensitivity analysis for coral recruits. Using the same parameter sets as in Fig. 3-S5 bistability analyses were conducted for 7 values of coral recruits (*r*) ranging over multiple orders of magnitude. Different levels of *p* are shown in successive columns of heatmaps and

levels are indicated above each plot. The middle column (r=.0002) reflects the values used in the main bistability analyses (Figs. 2 and S2) and does not qualitatively differ from other values of r.

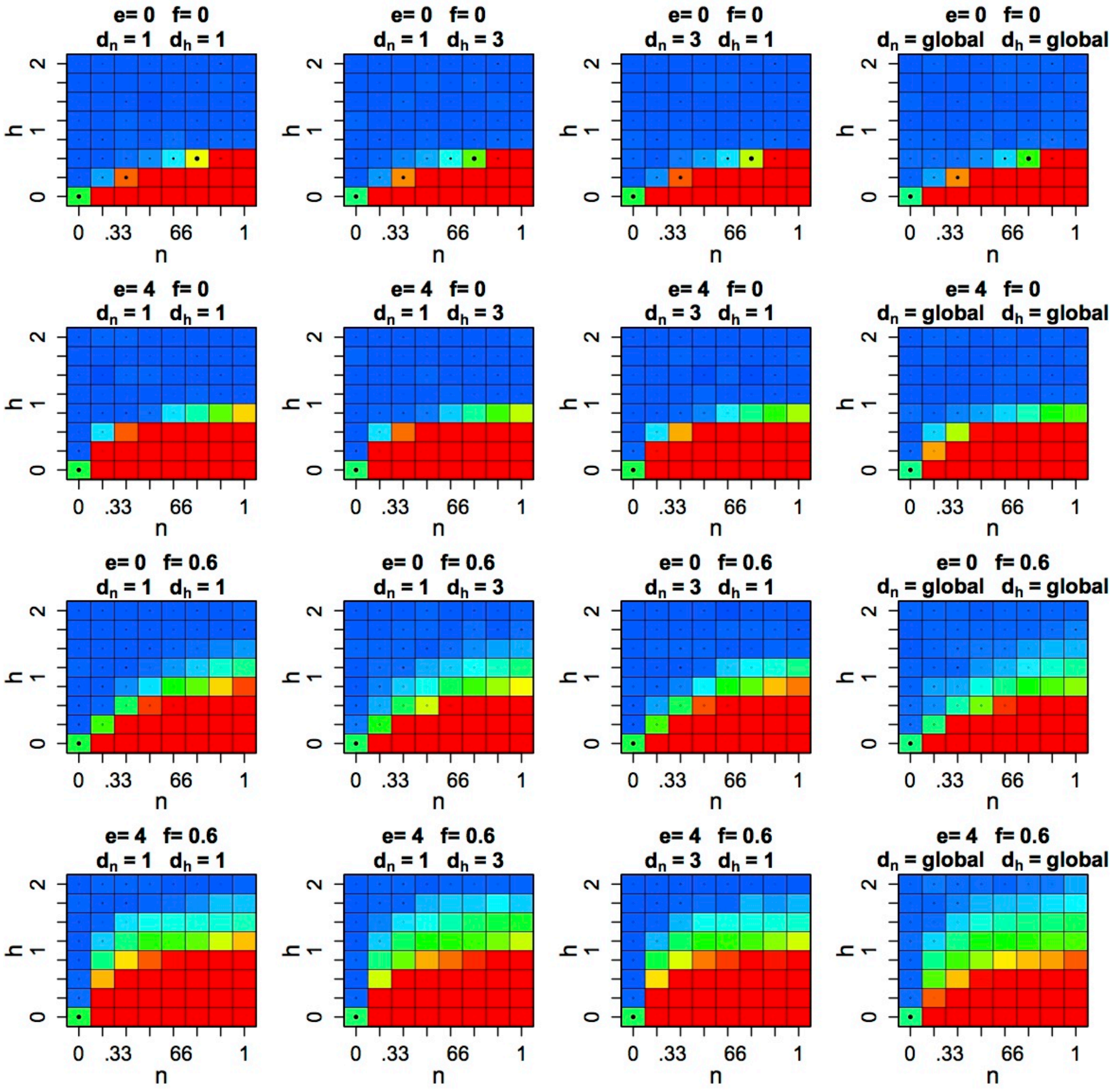


Fig. 3-S8 Sensitivity analysis for herbivory and nutrient facilitation distances. Using the same parameter sets as in Fig. 3-S5 bistability analyses were conducted for 4 sets of facilitation distances. Distances are are shown in successive columns of heatmaps and levels are indicated above each plot. The third column (d_n=1, d_h=3) reflects the values used in the main bistability analyses (Figs. 2 and S2) and does not qualitatively differ from other facilitation distance values.

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