Towards a multi-stressor theory for coral reefs in a changing world

Running head: Coral reef ecology under global change

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Abstract

Coral reefs are facing a constant barrage of human impacts, including eutrophication, overharvesting and climate change. However, research and management are just beginning to depart from a single-dominant-stressor paradigm and a holistic ecosystem-based understanding of these systems is still in its infancy. We expand on a well-known theoretical model to motivate an integrated multi-stressor framework for coral reefs by incorporating empirical evidence of multi-stressor impacts (overfishing, eutrophication and climate-driven mortality) as well as general ecological and theoretical concepts. We show that: i) the geometry of a simple, empirically-motivated model suggests nutrients and harvesting can operate similarly in driving shifts from coral- to algae-dominated reefs; ii) these impacts increase nonlinearly when acting concurrently, resulting in clear context-dependent management implications; and iii) this same geometry suggests climate-driven coral mortality (temperature-stress, cyclonic storms) can drive the presence of long transients and climate-driven alternate states, even in moderately-impacted ecosystems. These results imply that reefs that appear to be in a “safe space” may in fact be in danger of being pushed into a degraded algae-dominated state as storms and bleaching events are increasing in frequency and magnitude. Altogether, we find that responses in benthic composition as “signatures of change” to multi-stressors allows us to develop a predictive multi-stressor framework for coral reefs. In line with this theory, we detail empirical evidence from Barbados that highlights the context-dependent nature of coral reefs in a changing world. Our results present novel and generalizable insights into the functioning of coral reefs, that draw from classic theoretical and ecological concepts such as keystone predation theory, ecological succession and life history theory, as well as the emerging fields of long transients and early warning signals. By bridging coral reef ecology and general ecological concepts, we can better understand ecosystem functioning and resilience in these important yet highly threatened systems.

Keywords: *coral reefs, multi-stressors, ecological theory, transients, global change, marine conservation*

Introduction

Various axes of global change are increasing rapidly(Steffen et al. 2015) and imposing a suite of multi-stressor impacts on ecosystems around the world, most notably coastal ecosystems such as coral reefs(Halpern et al. 2019). For coral reefs, three major stressors have been identified as playing important roles in determining coral reef structure and ecosystem functioning: climate change, nutrient loading/water pollution, and overfishing, and these stressors have been studied extensively in isolation(Norström et al. 2016, Harborne et al. 2017, Hughes et al. 2017). As coral reefs appear to be classic examples of ecosystems under heavy multi-stressor impacts(Scheffer et al. 2015), researchers have begun to argue that they should no longer be studied from a single-impact perspective(Ban et al. 2014, Pendleton et al. 2016). For example, climate change and temperature-induced coral bleaching is often, and understandably, targeted as the most important stressor threatening the future of coral reefs. While addressing anthropogenic climate change at the global scale is undoubtedly critical, it is important we simultaneously consider the influence of regional- and local-scale management actions that may improve coral reefs' resilience(Hughes et al. 2017, Donovan et al. 2020, 2021, Guan et al. 2020, Abelson 2020). This is especially true if multiple stressors interact to nonlinearly increase negative impacts on coral reef function and would allow a more balanced, context-dependent approach to local management that could have dramatically more positive impacts.

At a local scale, the role of herbivory has been a dominant focus of coral reef research(Brandl et al. 2019). Researchers have argued for decades that losses in herbivory can drive phase shifts from healthy coral-dominated reefs to degraded algal-dominated states(Mumby et al. 2007), pointing to empirical examples of declining herbivores in reefs around the world to support this mechanism(Done 1992, Hughes 1994, Hughes et al. 2007, Mumby et al. 2007, Steneck et al. 2014, Jouffray et al. 2015). This has been argued to be caused by the overfishing of herbivores(McManus et al. 2000, Hughes et al. 2007, Mumby and Steneck 2008) as well as sudden reductions in other grazers not directly linked to fishing, such as the widespread *Diadema antillarium* die-off that occurred throughout the Caribbean in the 1980s(Lessios 1988, Hughes 1994, Mumby et al. 2007). Importantly, loss of hard corals and shifts to algae-dominated reefs result in highly degraded systems with the concomitant loss of important ecosystem services. As a result of these patterns, common management actions are to implement fishing restrictions through marine protected areas (MPAs) or bans on harvesting specific grazers(Bruno et al. 2019, McClanahan and Muthiga 2020). While MPAs have shown some potential to increase coral reef resilience to disturbances(Mellin et al. 2016, Steneck et al. 2019), other research has suggested that MPAs are likely not a universally effective strategy due to unpromising results for restoring herbivores and increasing coral cover(McClanahan et al. 2011, Cox et al. 2017, Bruno et al. 2019, McClanahan and Muthiga 2020). Additionally, regional and global assessments of MPA effectiveness showed there is overall weak association between MPAs and coral reef resilience(Suchley et al. 2016, Arias-González et al. 2017, Bruno et al. 2019). Consistent with a recent argument for multi-stressor approaches in coral reefs, these empirical results imply that restoring herbivory is likely a necessary, but not always sufficient, condition to preserve or restore the structure and function of coral reef ecosystems(Suchley and Alvarez-Filip 2018).

Relative to the role of herbivory, coastal development and watershed pollution have been allocated less attention and management action, even though researchers and managers generally agree that coastal pollution is a major problem along with overfishing(Wear and Thurber 2015, Wear 2016). Nutrients – nitrogen loading and changes in associated stoichiometry (elevated N:P ratio) in particular(Wiedenmann et al. 2013, Lapointe et al. 2019) – have been shown to alter important biological parameters that mediate coral reef ecosystem dynamics, decrease coral calcification rates(Shantz and Burkepile 2014), and increase corals' susceptibility to and severity of bleaching and disease(Bruno et al. 2003, Wooldridge 2009, Wiedenmann et al. 2013, Vega Thurber et al. 2014, Zaneveld et al. 2016, Wang et al. 2018, Lapointe et al. 2019, DeCarlo et al. 2020, Donovan et al. 2020). Additionally, nutrients have a positive impact on algae growth rates, and so nutrient loading can ultimately shift the dominant competitor from coral to algae(Lapointe 1999, Smith et al. 2001).

Importantly, these collective biological responses to multiple stressors suggest there may be an interactive effect of nutrients, fishing pressure and climate variation in coral reef ecosystems and the competitive interaction between coral and algae(Hughes et al. 2017), and therefore context-dependent outcomes to management actions(Mumby et al. 2006). Indeed, the Relative Dominance Model was developed over 35 years ago(Littler and Littler 1984, Lapointe 1997) to describe the combined impacts of grazing reduction and nutrient loading on coral reef structure. Additionally, empirical research has more recently found that the recovery of coral reefs after bleaching events appears to be highly dependent on multiple stressors including nutrient loading and herbivory(Robinson et al. 2019), and these stressors both appear to act together to change the rate and stages of algal succession following climatic disturbances(Hixon and Brostoff 1996, Mcclanahan 1997, Ceccarelli et al. 2011). However, despite this longstanding conceptual model and clear empirical support of multi-stressor interactions(Burkepile and Hay 2006), there remains considerable debate among researchers regarding how multi-stressors interactively govern coral reef structure and functioning(Ban et al. 2014, Muthukrishnan and Fong 2014, Cote et al. 2016). Some researchers have begun to incorporate multiple stressors into theoretical and modelling approaches(Mumby et al. 2006, Anthony et al. 2011, Fung et al. 2011, Blackwood et al. 2011, 2018, Arias-González et al. 2017), often done with either site-specific parameterizations and large amounts of detail or only incorporating one to two major stressors in more general ways. These studies have shown that multi-stressors can indeed interact and together contribute to increasing rates of hard coral decline. However, as a result of the disparity in approaches a generalizable understanding of multi-stressors impacts on coral reef functioning is still in its infancy.

While the nuances of coral reef dynamics and the multitude of anthropogenic impacts altering them are understandably not easy to discern, researchers have begun to call for a holistic multi-stressor approach to coral reef science and management appropriate for a changing world(Norström et al. 2009, Ban et al. 2014, Pendleton et al. 2016, Mumby 2017). Here, as a step towards this goal, we expand on existing top-down-focused theory(Mumby et al. 2007) to demonstrate the context-dependency of management outcomes for coral reefs under multi-stressor impacts. We do this by integrating the combined influence of overfishing (i.e., loss/reduced herbivory), decreasing water quality (nutrient loading) and climate change (temperature stress and cyclonic storm damage) on coral reef structure and function within a theoretical multi-stressor framework (Figure 1A), and highlight the importance of highly responsive r-strategy life histories in changing, heavily impacted systems (Figure 1B). Our approach integrates general ecological concepts (e.g., ecological succession, keystone predation theory) with our current understanding of individual processes in coral reef ecosystem functioning and emerging theoretical insight into the role of noise in transient dynamics and ecosystem resilience. We end by evaluating empirical evidence from Barbados within our framework that corroborates the importance of considering an integrated multi-stressor perspective for coral reef management. Our results suggest a predictable, context-dependent response of coral reef ecosystems to multi-stressors and in turn a context-dependent approach to management.

Methods

We employ a simple multi-stressor extension to the well known Mumby et al.(Mumby et al. 2007) model. Here, we follow recent evidence from the literature that suggests coral calcification is inhibited by increased nutrients(Shantz and Burkepile 2014), and similarly making the intuitive assumption that nutrients increase the rate at which macroalgae (a primary producer) can overtake coral (i.e., its growth rate), as well as decreases coral's resistance to macroalgae overgrowth and competitive ability(Lapointe 1999, McClanahan et al. 2003). Figure 1A shows a schematic summarizing our model and the interactions between state variables. As such, our new nutrient-dependent model is as follows:

$$dM/_{dt} = M(aC\left({N_t}/_{(N_0 + N_t)}\right) - \,{g}/_{(M + B)} \; + \gamma B)$$

(1)

$$dC/_{dt} = C(r(1 - cN_t)B - m - aM\left({N_t}/_{(N_0 + N_t)}\right)) \qquad (2)$$

Here, M represents macroalgae, C represents coral, and B represents other benthic r-strategists that instantaneously fill empty space left by dead coral and grazed macroalgae. Since B is assumed to instantaneously fill any space (r-strategists act on much faster time scales relative to the other state variables), B = 1 – M – C and the model can therefore be reduced to two dimensions. The original model by Mumby et al.(Mumby et al. 2007) referred to this variable as turf algae, a fast-growing r-strategist, however, we argue that nutrients and grazing rates would determine the composition of other components of benthic cover(Lapointe 1997, Lapointe et al. 2018) (Figure 1A). Towards this end, we include a simple extension that includes algal life history traits. Specifically, we include growth-palatability trade-offs in algal community composition to represent the role of r-strategists in response to disturbances and grazing pressure (Figure 1). High grazing rates suppress late-succession, palatable macroalgae while simultaneously selecting for fast-growth and less-palatable life strategies (through physical and chemical defenses) within early succession r-strategists. Here, we consider r-strategists as algae functional groups that colonize disturbed reefs quickly relative to thick, fleshy macroalgae (late succession K-strategists relative to other functional forms of algae, but of course all are fast relative to corals). We argue that within the group of early succession r-strategists there is a variety of life history strategies, that will be differentially selected for based on grazing rates. High grazing rates favour less-palatable life strategies and fast growth rates that can withstand these grazing levels. At moderate-high grazing rates, fast-growing r-strategists can withstand the grazing rates, explaining why we see a lot of turf algae and some less-palatable algae like CCA in some reefs. However, at extremely high grazing rates (e.g., extremely high *Diadema* densities), only low palatability organisms will be able to survive. While some unpalatable algal types like CCA are slow growing in terms of biomass, they are relatively quick colonizers and can thus be considered similar to r-strategists in the face of disturbances. As a simple extension, we include a linear 1:1 relationship between grazing rates and the proportion of more/less palatable r-strategists composing the benthic r-strategist guild. We refer to highly palatable fast-growing r-strategists (e.g., filamentous turf) as r1-strategists, and slightly less palatable (but still fast-growing relative to K-strategists) r-strategists (e.g., CCA) as r2-strategists (Figure 1B). Therefore, $B = r1 + r2$, where $r2 = gB$ and $r1 = (1-g)B$. These assumptions relate to well-known relationships between high grazing rates and less palatable algae(Sammarco 1982, Chiappone et al. 2006), as well as research showing that grazing rates (among other drivers such as nutrients) can alter the rates and stages of succession in coral reefs(Hixon and Brostoff 1996, Mcclanahan 1997).

Here, a is the rate that macroalgae overgrows coral, and thus can be thought of as an algal-coral competition rate. g represents the grazing rate from herbivores, which is scaled by densities (or % cover since $M + C + B = 1$) of both M and B. y is the rate that macroalgae overgrows benthic r-strategists (B; which could also include open space), r is the coral growth rate (again over B or open space), and m is the natural mortality rate of coral.

Nutrients (N_t) alter the algal-coral overgrowth rate (competition) in the Mumby model (a), based on the assumptions made above. We also assume that this competitive advantage eventually saturates and therefore N_0 is a saturation constant that determines the effect of nutrients (N_t) on algal-coral competition (a). Additionally, c is the calcification rate – scaled by nutrient loading, N_t – which alters the coral growth rate (r) in response to nutrient loading. An important distinction between this model and Mumby et al.'s original model is that the parameter *a* can now be thought of as a_{max} and *r* similarly as r_{max} due to their scaling by nutrients.

With these equations, we can symbolically solve for the model isoclines as follows:

$$ {dM}/_{dt} = 0: \quad M = 1 - C + \frac{aC}{y}\left({N_t}/_{(N_0 + N_t)} \right) - \frac{g}{y(1-C)} \tag{3} $$

$$ {dC}/_{dt} = 0: \quad M = {(N_0 + N_t)(m - r(1 - cN_t)(1 - C))}/_{r(N_0 + N_t)(cN_t - 1) - aN_t} \tag{4} $$

Immediately, we can see that both grazing (g) and nutrient loading (N_t) alter the isocline geometry (grazing via (3) and nutrients via both (3) and (4)) and thus equilibrium structure. These parameters both drive qualitatively similar changes in the isocline geometry (Supplement A.1) shown in Figure 1 and can cause both saddle node and transcritical bifurcations.

All analyses were done using Wolfram Mathematica (version 12.1.0.0) and numerical simulations were evaluated using the built-in ODE solver "NDSolve" with integration method "StiffnessSwitching" (switches from explicit to implicit methods if stiffness is detected) when needed for non-deterministic simulations. We incorporated noise (discrete disturbances) using a flow-kick method(Meyer et al. 2018), by inducing repeated pulse perturbations to coral cover (-50% cover) at variable frequencies, which allowed us to evaluate the effect of noise on transients and asymptotic behaviour in comparison to deterministic simulations.

Results

Towards a Multi Stressor Theory for Coral Reef Ecology

Previous theoretical studies have highlighted the importance of using a multi-stressor approach, however, they have largely focused on one or two stressors and thus the combination of local stressors (grazing and nutrients) and global climatic patterns (increasing frequency of bleaching events and hurricane damage) is not well understood. Alternatively, larger-scale simulation exercises with high levels of detail and site specificity have shown that these stressors interact in important ways, but as a trade-off with the simpler theoretical exercises they lose generality. Here, we synthesize many of these ideas that have either been evaluated separately or in less general simulation exercises as an important step towards developing a general and mechanistic understanding of coral reef ecosystems under multi-stressor impacts. To model the dynamics of coral reefs, we expand on a single-stressor (herbivory) model first introduced by Mumby et al.(Mumby et al. 2007) by incorporating the synergistic effects of overfishing (grazing), nutrient loading (algal competition and coral physiological stress) and climate change (coral mortality). This model has been widely used and extended by many researchers to include additional complexity (reviewed in detail by Blackwood et al.(Blackwood et al. 2018)), such as grazer dynamics(Blackwood et al. 2011, 2012), additional benthic components (e.g., sponges)(González-Rivero et al. 2011, Briggs et al. 2018), spatial dynamics(Andréfouët et al. 2002, Mumby 2006, Mumby et al. 2006, 2014) and, like us, multiple stressors(Anthony et al. 2011, Fung et al. 2011, Arias-González et al. 2017).

Here, following empirical evidence, multi-stressors alter the biological rates and interactions included in the original model as illustrated in Figure 1A (see Methods for equations), and we explore the role of variations in faster algal life history strategies along a growth-palatability gradient (r1 and r2 compared to K-strategist, M) in response to multi-stressors (e.g., grazing resistance, growth rates), as demonstrated in Figure 1B. Notably, nutrients are incorporated following recent evidence from the literature that suggests coral calcification is inhibited by increased nutrients(Shantz and Burkepile 2014) (Figure 1A – coral per capita rates of increase decline with elevated nutrients), and similarly that nutrients increase the growth rate of macroalgae as well as decrease coral's resistance to macroalgae overgrowth and competitive ability(Lapointe 1999) (Figure 1A; macroalgae's ability to overgrow coral increases to a maximum with nutrients). While others have included nutrients in their models, this is generally done by only influencing algal growth rates(Mumby et al. 2006, Anthony et al. 2011, Hughes et al. 2017). We note that since our model does not consider other aspects of water quality such as sedimentation, our results may be similar to others who have included this stressor in their models to negatively influence coral growth(Fung et al. 2011, Gurney et al. 2013, Arias-González et al. 2017). However, sedimentation of course would have other effects on coral recruitment and various algal functional forms which we do not discuss here(Gurney et al. 2013). Furthermore, our simple extension of benthic r-strategists allows us to explore the role of various fast algal life history strategies along a growth-palatability gradient (r1 and r2 compared to K-strategist, M) in response to multi-stressors (e.g., grazing resistance, growth rates; Figure 1B). Research has shown that algal community dynamics are important in overall coral reef ecosystem functioning(Renken and Mumby 2009, Renken et al. 2010, Bozec et al. 2016, Briggs et al. 2018), and our goal is to integrate general ecological concepts into this literature (e.g., life history, keystone predation theory). Although a simple extension, our model formulation is a starting point for understanding the importance of algal life histories in general. Towards understanding multi-stressors as an integrated whole, we start by first looking at the individual stressors of herbivory (top-down) and nutrients (bottom-up) in the absence of climate-driven coral mortality. We then examine the interaction of these three stressors together.

i. Bottom-up and Top-down: The Geometry of Nutrients and Grazing Impacts on Coral Collapse

Our choice of a simple model formulation allows us to use traditional phase plane techniques to mathematically explore the dynamic outcomes of this coral reef model. As such, we can immediately see that both increasing nutrient loading and overfishing of herbivores (i.e., reduced grazing) drive a qualitatively similar sequence of dynamic outcomes in this model (Figure 2A). Assuming we start in a pristine coral reef scenario (pink coral zone; Figure 2Ai), increasing nutrients or fishing pressure alter the geometry of the isoclines (see Supplement A.1 for individual stressor effects) driving bistabilty (yellow, light green, Fig. 2Aiii, iv) and finally complete loss of coral (dark green zone, Figure 2Av). This initial result suggests that bottom-up factors like nutrients alone, under an otherwise relatively pristine system (e.g., MPA), can shift coral reefs to an algae-dominated state (bistability, Fig. 2Aiii, iv), and with high enough nutrients drive the complete loss of the coral-only stable equilibrium (Figure 2Av). Thus, simple empirically-motivated extensions of this classic coral model find that both top-down and bottom-up impacts, in isolation, have qualitatively identical impacts on coral ecosystems.

This similarity in response immediately implies that when both stressors are increased simultaneously there is a strong tendency for the collapse of the coral state to occur under lower individual stressor values, compared to when each stressor is altered alone (Fig. 2B; follow the colored dots to see a multi-stressor trajectory). While a simple geometric extension of Mumby et al.(Mumby et al. 2007), these results importantly suggest that we should expect context-dependent management outcomes, for example to fisheries regulations (e.g., herbivore bans, MPA implementation; Figure 2B,C), such that low nutrient cases may be more prone to success (e.g. Figure 2B, scenario 1) than nutrient enriched areas (e.g., Figure 2B, scenario 2) as shown in Fig. 2C. In other words, fishing regulations may be ineffective if other stressors, like nutrient levels, are too high (Fig. 2C). This first result is aligned with Bruno et al.'s(Bruno et al. 2019) meta-analytic paper which shows extremely variable coral reef ecosystem recovery responses to MPAs, strongly suggesting that other factors are involved and may even be the primary driver of coral reef structure and functioning(Suchley and Alvarez-Filip 2018), as well as other simulation results suggesting context-dependency of MPA success(Mumby et al. 2006). This is not to say that herbivory is not important, however an emphasis on it alone has little chance of significant success in the face of other stressors, and could lead to dangerous implications for ecosystem services provided by coral reefs and those whose livelihoods depend on their fisheries(Aronson and Precht 2006).

ii. Long Transients and Climate-driven Coral Collapse

With our geometric understanding of how nutrients and fishing alter coral ecosystems we next turn to consider the impact of how climate intersects with these stressors to alter coral reef dynamics. We explore this by considering deterministic isocline arrangements that yield only a healthy coral reef state (i.e., the deterministic skeleton(Higgins et al. 1997) is not bistable; Fig. 3AB.i), but specifically focus on the very plausible scenario that there is some deterioration via both nutrients and fishing (i.e., Fig. 2Aii.), which we will refer to as **moderate local impacts**. While under apparently "healthy" conditions (i.e., only a coral-dominated stable state), we note that the geometry implies that the two isoclines are relatively close to intersecting, and therefore near a saddle-node bifurcation (e.g., Fig.2Aii, 3A). Under such a biologically plausible condition (i.e, at least some human impact), we find that climate-induced coral mortality (i.e., adding stochasticity) greatly alters reef dynamics (e.g., Fig. 3A-B,ii).

First, even without climate-induced mortality events, we see that the time to reach equilibrium (the coral axial solution) is highly dependent on initial values (Figure 3Ai.), such that in certain cases (i.e., trajectory 3) the system is initially pulled to lower coral densities before eventually approaching the equilibrium. We also see that benthic r-strategists play an important role during these transient periods (Figure 3Bi), something we elaborate on more below. Second, when adding climate-induced mortality events (i.e., stochasticity) under moderate local impacts, not all trajectories have the same outcome (Figure 3A.ii). Here, once again depending on the initial values, some trajectories get stochastically "entangled" in the region where the isoclines are close (dark red, trajectory 3), while others avoid this and eventually approach the coral axial equilibrium (though they notably take longer due to the noise). This is an example of **climate-driven bistability**, such that there appears to be two different outcomes once climatic disturbances are incorporated into the simulations. Again, Figure 3B.ii shows this third trajectory as a time series, where the system ends up in an algae-dominated alternate state. Here, some coral persists but the system is largely dominated by macroalgae and other benthic r-strategists. Note that while we focus here on a state of moderate impact, disturbances could of course cause local extinctions of coral in more degraded (i.e., bistable) ecosystems by knocking the system out of the basin of attraction to the coral equilibrium (bistable configurations in Fig. 2A iii and iv).

Taken altogether, these results suggest that climate-driven coral mortality has the potential to greatly increase the presence of bistability, especially in a world already plagued by varying levels of nutrient loading and overfishing. Effectively, disturbances shift the resilience boundary for coral reefs(Meyer et al. 2018), and the interaction of all three stressors operates nonlinearly to decrease coral reef resilience. Note that there is a possibility that some of these stochastic trajectories, such as trajectory 3, are extremely long transients that eventually squeeze through this region of entanglement (our climate-driven alternate state) if given enough time between mortality events. However, on ecological and management time scales this result remains functionally bistable, and with the increasing frequency of coral mortality events these states may become more common. Further, depending on initial values and the frequency of disturbances, we can indeed see extremely long transients that eventually reach the coral-only attractor (Supplement A.2). On the other hand, coral collapse may have the potential to take an extremely long time. If this is the case, it may seem like coral might persist, or even recover, before eventually disappearing (Supplement A.2), which would importantly suggest the possibility of extinction debt(Tilman et al. 1994) in degraded coral reef ecosystems (i.e., whereby species are doomed to slow extinction even if the ecosystem deteriorates no more). This interesting result suggests that the interactions between moderate levels of multiple stressors may enhance the likelihood of bistability and long transients, both states that are incredibly hard to manage.

Interestingly, we can begin to explain these unexpected results using the geometry of our simple model (Figure 3A). While beyond the scope of this paper to fully investigate, we note that these results are consistent with phenomena recently described in the theoretical literature(Hastings et al. 2018, 2021, Morozov et al. 2020). Specifically, we see a unique combination of what have been known in the theoretical literature as “ghost attractors” and “crawl-bys”, such that the system is influenced by what is effectively the memory of a nonexistent equilibrium – in this case a saddle point – which we will refer to here as a “ghost saddle” (Figure 3). Hastings et al.(Hastings et al. 2018) and Morozov et al.(Morozov et al. 2020) provide more detailed information on long transients, ghost attractors and crawl-bys. Importantly, both of these phenomena can lead to long transients and slow shifts between states, which can have important implications in the face of stochasticity and we indeed see here (Figure 3). Here, the geometry of this intermediate multi-stressor state explains both the change in direction of the trajectories shown in Figure 3A, as well as the “slow down” causing long transients and the emergence of a climate-driven algae dominated state seen in Figure 3A,B.ii.

iii. Algal Trait Responses

Finally, and in order to pull out the different signatures of multi-stressors, we show how the relationship between stressors impacts algal community composition. From Figure 3B, the role of benthic (B) r-strategists is clearly important during long transients following a disturbance (Figure 3B.i), as well as when frequent disturbances lead to a climate-driven alternate state (Figure 3B.ii). Here, we once again focus on the case of moderate local impacts (Fig. 2Aii), to examine how multiple stressors interact to influence the benthic algae composition in this state of uncertainty. Depending on grazing, nutrient levels and frequency of climate perturbations, different benthic r-strategists (B) will dominate primary succession following large mortality events (Figure 4).

To elucidate these outcomes within our model, we performed a single climate pulse perturbation under different multi-stressor conditions (i.e., relatively low grazing and low nutrients versus relatively high grazing and high nutrients), within this moderate local impact geometrical configuration (Figure 4A). We see that grazing-mediated algae selection strongly influences the composition of benthic algae cover (r1- (i.e., highly-palatable, fast growing) vs. r2- (less-palatable, fast growing) vs. K- (palatable, slow growing) strategists), and all three stressors – nutrients, grazing, and climate – mediate the relative dominance of total benthic cover including coral (Figure 4A; see both post-disturbance transient responses as well as equilibrium composition). Notably, these results are exacerbated when frequent climate-induced mortality events are considered (Figure 4B). Frequent disturbances can permanently alter benthic composition by continuously suppressing coral recovery and impeding full algal community succession, while also compounding the effect of multi-stressors on the relative dominance of benthic composition (Figure 4B). Note that in Figure 4B.i we see that frequent disturbances in a relatively low-nutrients and low-grazing scenario drive coral to extinction and cause a shift to a macroalgae-dominated state. In the relatively higher-nutrient, higher-grazing scenario shown in Figure 4B.ii, coral can persist but is largely suppressed to the benefit of (mostly low-palatability) benthic r-strategists. These results again demonstrate the existence of climate-driven bistability as shown in Figure 3, making this region one of high uncertainty driven by the interactions between multi-stressors. Importantly, our theory suggests that monitoring benthic cover responses critically allows us to differentiate the role of multi-stressors and aid management decisions.

Theoretical Synthesis: A framework for coral reef composition in a changing world

We have seen that multi-stressors have the potential to cause interactive, synergistic and non-linear effects, as well as potentially unexpected outcomes in impacted systems. Our theoretical results also predict that moderate local impacts ought to generally display bistability in a world with lots of climate variation. Indeed, increasing the frequency of climate-induced mortality events enlarges the area of bistability and therefore increases the chances of algal dominance (i.e., grey region in Figure 2B; see Supplement A.2 for simulation data). As a result, our region of moderate local impacts in parameter space (Figure 2) becomes a region of **climate-driven uncertainty**, which is likely characterized by a large presence of benthic r-strategists (r1 and r2) when faced with real world climatic noise and perturbations. Additionally, climatic variation increases the likelihood of climate-induced state shifts (Supplement A.2), essentially meaning that all regions of bistability and algal dominance in the deterministic model will likely result in algae-dominated reefs.

Here, we summarize our theoretical results as a multi-stressor framework describing the relative dominance of coral reefs for a changing world, highlighting this important region of climate-driven uncertainty and noting the importance of multi-stressor impacts on determining benthic composition (Figure 5). Importantly, algal composition gives us a signature of the degree of top-down control in coral reefs. Specifically, high amounts of relatively less-palatable benthic organisms like CCA suggest significant top-down grazing pressure and therefore point to the fact that other stressors – such as climate and/or nutrient loading – are likely playing a larger role in driving the proliferation of algae and reduction of coral. In rapidly changing environments, this framework allows us to make qualitative predictions about the trajectories of benthic composition change – in other words, signatures of change – in coral reefs based on different levels of multi-stressor impacts.

Linking empirical evidence to our theoretical framework

Our theoretical framework importantly allows us to test predictions about changes in benthic cover under multi-stressor impacts and identify underlying drivers of change in coral reefs. As such, we now highlight evidence from the Caribbean within our theoretical framework. Reefs across the Caribbean notably underwent significant changes in the 1980s with a general loss of hard corals(Gardner et al. 2003) corresponding with the culmination of damaging hurricanes (e.g., Hurricane Allen in 1980), the widespread loss of *Diadema* in 1982/83, as well as ongoing eutrophication from land-based urban and agricultural runoff, untreated wastewater, and widespread overfishing in the region(Jackson et al. 2014). As a first step of linking our theoretical framework to empirical accounts of changing reef conditions, we do this by integrating multiple studies from reefs along the west coast of Barbados (Supplement B) that demonstrate changes in benthic cover and associated trends in nutrients and grazing rates. The west coast of Barbados has a long history of human impacts including heavy fishing and nutrient runoff from urban and agricultural areas(Allard 1994, Bell and Tomascik 1994, Tosic et al. 2008, Gill et al. 2019). Barbados also has a unique research history, in the sense that researchers with both a top-down (grazing) and bottom-up (nutrients) focus have dotted its history. Collectively, and with hindsight, this allows us a relatively broad perspective of the changing coral reefs during this period of drastic change.

Baseline accounts (qualitative descriptions(Lewis, John 1960) and quantitative surveys(Stearn et al. 1977)) of the west coast's fringing reefs suggest that live coral cover began declining as early as the 1960's, with particularly drastic declines throughout the 1970's, during which time algae began taking over(Tomascik and Sander 1987a) (Figure 6A,B). Coral was further depleted following Hurricane Allen in 1980, and this appears to have largely benefitted less-palatable CCA along the entire coast(Mah and Stearn 1986) (Figure 6B). At this time (1982/83), and prior to the widespread *Diadema* die-off, Tomascik and Sander(Tomascik and Sander 1985, 1987a, 1987b) began sampling multiple reefs along the west coast in an attempt to understand the major drivers of change in Barbados' rapidly degrading coral reefs (Figure 6A; note high rates of change in Figure 6B). As a result of rapid development on land(Tomascik and Sander 1985) these surveys identified a north-south gradient of increasing eutrophication and decreasing *Diadema* densities, though average *Diadema* density was still quite high, even in the southern reefs as shown in Figure 6C(Tomascik and Sander 1987a). Along this eutrophication/grazing gradient, coral diversity, percent cover, growth, and overall recruitment all decreased(Tomascik and Sander 1987a, 1987b, Tomascik 1990, 1991, Hunte and Wittenberg 1992, Wittenberg and Hunte 1992, Mann 1994), and CCA cover – relative to turf and frondose macroalgae combined – increased with increasing *Diadema* densities (Figure 6C). These local patterns support our theoretical predictions, namely that coral was already rapidly declining before the reduction in grazing, possibly due to elevated nutrient levels, and that the still relatively high grazing rates meditated benthic algae composition (Figure 6B,C). Note that despite the apparent gradient, the majority of the coastline may have been nutrient saturated by the early 1980's(Tomascik and Sander 1985, Allard 1994), if not earlier(Sander and Moore 1979), based on various nutrient thresholds (Supplement B)(Lapointe 1997, Bell et al. 2014, Lapointe et al. 2019). This suggests that algae growth rates were likely already near or at a maximum by this time, and coral physiologically impaired and susceptible to storm-induced damage, disease and algal overgrowth along the entire coast(Lapointe 1999, Bruno et al. 2003, Wiedenmann et al. 2013, Lapointe et al. 2019) (Figure 1A, Supplement B). However, the persistent co-variation between eutrophication and *Diadema* grazing (Figure 6C) precluded identifying which of these two factors had a larger influence on coral reef composition and resilience at the time.

Following the 1983/84 *Diadema* die-off, Allard(Allard 1994) repeated Tomascik and Sander's(Tomascik and Sander 1987a) surveys along the coastal eutrophication/grazing gradient (which persisted into the 1990's, albeit with much lower grazing rates(Hunte and Wittenberg 1992, Wittenberg and Hunte 1992, Allard 1994, Mann 1994)) in an attempt to separate these effects, and found that the overall loss of *Diadema* led to a subsequent increase in more-palatable turf and macroalgae along the entire west coast (Figure 6B). This was used to conclude that *Diadema* grazing was in fact the dominant driver of benthic composition along the west coast, ruling out the importance of the eutrophication gradient(Allard 1994). While the reduction in *Diadema* would have certainly altered benthic composition along the west coast of Barbados, Allard didn't consider the already-severely-depleted state of coral by the early 1980s (Figure 6B) and we argue their conclusions instead reflected a shifting baseline rather than the full story of change along the coast(Allard 1994, Jackson 2001a, 2001b). Indeed, the observed increase in palatable turf and frondose macroalgae appears to have been largely at the expense of less-palatable CCA rather than coral, reflecting this shifting baseline (Figure 6B,C). Additionally, by the 1990s the eutrophication/grazing gradient no longer helped explain variation in benthic composition between reefs as they were already in such a depleted state and there was much less variation in stressors along the coastline (Figure 6C). Grazing rates at this point were nearly homogeneous, the entire coastline was nutrient saturated, and the reefs were well-established as algae-dominated reefs. Collectively, these results highlight the context-dependency of our ability to detect multi-stressor effects on benthic composition in field studies and the importance of historical baselines.

Importantly, the patterns from Barbados' west coast reefs support our theoretical predictions given changes to the multi-stressor landscape in both time and space, and do so at two spatial scales (i.e., along the entire coastline, Figure 6B, and between sites, Figure 6C). Accordingly, we map these patterns in space and time as a trajectory of change within our multi-stressor framework (i.e., Figure 5), showing how the evolution of benthic cover over time in Barbados is best explained as a function of both eutrophication and grazing (Figure 7). Based on the timing of multi-stressor change described above, nutrients initially pushed the system through our "region of uncertainty" (likely also around the time of Hurricane Allen in 1980) and into an algae-dominated state (Figure 7). The subsequent *Diadema* die-off was the final straw that further pushed the system well-into the algae-dominated region within our framework, and significantly altered the algae community composition (Figure 7). While the specific placement and timing of this trajectory within our framework is not quantitative (grazing and nutrient thresholds are still debated and likely site specific), we argue that this qualitative approach to viewing changes in multi-stressor impacts provides an important step towards a holistic understanding of coral reefs under global change, and allows us a way of piecing apart the roles of various drivers of change (e.g., the role of Barbados' eutrophication/grazing gradient within this multi-stressor space). Here, we emphasize again the importance of baseline information as well as ongoing monitoring, and consideration of scale for disentangling the relative (and likely changing) influence of various drivers spatially and temporally.

Discussion

Even with our relatively simple model used here, we have highlighted the important context-dependency of life histories, disturbance frequencies, and simultaneous multi-stressor impacts in highly disturbed coral reef ecosystems. Immediately, our empirically-motivated coral reef model shows that changes in grazing, nutrients and climate-driven coral mortality events (temperature stress, cyclonic storms) can independently invoke shifts to algae-dominated states and increase uncertainty in the face of global change. We also show that these three axes of global change operate synergistically to increase the likelihood of long transients and phase shifts to unwanted algal equilibrium states such that when all are conspiring together, we see even greater likelihood of deteriorated ecosystem structure and functioning. Our analysis found climate-driven mortality can drive shifts to algal domination even when in a moderately weakened state (i.e., nutrients and fishing are moderately high; Figure 2Aii) that would not be expected based on the deterministic skeleton. This novel theoretical result is related to recent theoretical literature on long transients(Hastings et al. 2018, 2021), and importantly highlights the potential for unexpected results when considering noise in our mathematical models. Furthermore, we show that our theoretical results rely on the geometry of our model and thus are highly general. That is, any combination of parameters that leads to the geometric configuration discussed throughout our manuscript (specifically, what we refer to as "moderate local impacts") will lead to these results. Our results are intentionally general for this reason, but this of course implores us to use empirical approaches to find out the current state of reef resilience under system-specific parameterizations and multi-stressor impacts. Together, our results immediately indicate context-dependent responses to global change and highlight the importance of considering multi-stressors in a more holistic approach to management decisions.

Our results also suggest the intriguing notion that the rise of different benthic r-strategists give us signatures of the dominant underlying stressor, matching a variety of empirical and conceptual accounts of benthic cover in coral reefs(Littler and Littler 1984, Lapointe 1997). Notably, fast-growing benthic r-strategists play important roles in highly disturbed coral reefs (Fig. 3) and benthic composition is dependent on multi-stressors, particularly grazing-mediated algal selection that selects for differential life history (growth and palatability) strategies (Figs. 1, 4). This is consistent with experimental and observational studies(Sammarco 1980, 1982, Chiappone et al. 2006), as well as theoretical concepts such as keystone predation theory(Leibold 1996). Here, less-palatable r2-strategists (e.g., CCA) garner a competitive advantage over more palatable fast-growth (r1) strategists when grazing rates are high, and vice versa. These life strategies are becoming even more important to consider in the face of global change and may offer us empirical insight into the mechanisms behind state shifts, including the potential for our "signature of change" to act as early warning signals for coral collapse and decreasing resilience (related, see (Nyström et al. 2008)). However, we note that further empirical research into underlying drivers is needed to establish more comprehensive signatures of multi-stressor impacts on benthic composition, as well as expand this model to include life history trade-offs within other taxa such as different macroalgae genera(Renken and Mumby 2009, Renken et al. 2010, Bozec et al. 2016, Briggs et al. 2018), (hard and soft) corals(Zinke et al. 2018, Toth et al. 2019), sponges(González-Rivero et al. 2011), and cyanobacteria(de Bakker et al. 2017) for a more thorough representation of multi-stressor effects on benthic composition.

These signatures of multi-stressor impacts allow us to map changes in benthic composition within our predictive framework. Empirical evidence from Barbados shows promising consistency with our theoretical results and highlight the importance of accurate baseline data as well as monitoring multi-stressors simultaneously and with fine enough resolution to track changes and identify underlying drivers of change in coral reefs. Collectively, our empirical and theoretical results show that local stressors mediate coral reef resilience and can increase uncertainty in the face of climate-related mortality events, particularly as they are increasing in frequency and severity.

While climate change is undoubtedly a massive threat to coral reefs, our results suggest that scientists and managers must simultaneously consider that local and regional management actions can enable at least some coral reef resilience (resistance to and recovery after disturbances). Here, we have shown how varying levels of multi-stressors can lead to very different trajectories of change in coral reefs (Figure 6), and would in turn have drastically different responses to singular management actions (e.g., Figure 2B,C). In times of rapid and drastic global change, research and management need to move away from isolating individual impacts and develop ways to address multiple stressors where nonlinear interactions are likely the rule not the exception. This way we can manage for ecosystem resilience and sustainability in the face of uncertainty(Anthony et al. 2015, Roberts et al. 2017, Mcleod et al. 2019). We also need effective management so that peoples' livelihoods are not unnecessarily limited or sacrificed under the guise of conservation(Aronson and Precht 2006). It's easy to point the finger at local fishing communities, for example, when in reality there is likely a much more nuanced problem that must be acknowledged. Ecosystem stability and sustainability ultimately means protecting important ecosystem services necessary for food and livelihood security and human wellbeing.

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All authors contributed to the development of ideas through workshops and discussions. CB and KSM designed the theoretical model and CB created the figures. Data collection from Barbados and creation of Figure 6 was done by HV. CB and KSM wrote the initial draft of the manuscript and all authors contributed to editing subsequent revisions.

Competing Interests

The authors declare no competing interests.

Data and Code Availability

Data from Barbados presented in Figure 6 and in the Supplementary Material were collected from various literature sources. Citations can be found in the manuscript and in the Supplement B. analyses and simulations were performed in Wolfram Mathematica (version 12.1.0.0); code is available at: https://github.com/carlingbieg/corals

References

Abelson, A. 2020. Are we sacrificing the future of coral reefs on the altar of the “climate change” narrative? ICES Journal of Marine Science 77:40–45.

Allard, P. 1994. Changes in Coral Community Structure in Barbados: Effects of Eutrophication and Reduced Grazing Pressure. McGill University.

Andréfouët, S., P. Mumby, M. McField, C. Hu, and F. Muller-Karger. 2002. Revisiting coral reef connectivity. Coral Reefs 21:43–48.

Anthony, K. R. N., P. A. Marshall, A. Abdulla, R. Beeden, C. Bergh, R. Black, C. M. Eakin, E. T. Game, M. Gooch, N. A. J. Graham, A. Green, S. F. Heron, R. van Hooidonk, C. Knowland, S. Mangubhai, N. Marshall, J. A. Maynard, P. Mcginnity, E. Mcleod, P. J. Mumby, M. Nyström, D. Obura, J. Oliver, H. P. Possingham, R. L. Pressey, G. P. Rowlands, J. Tamelander, D. Wachenfeld, and S. Wear. 2015. Operationalizing resilience for adaptive coral reef management under global environmental change. Global Change Biology 21:48–61.

Anthony, K. R. N., J. A. Maynard, G. Diaz-Pulido, P. J. Mumby, P. A. Marshall, L. Cao, and O. Hoegh-Guldberg. 2011. Ocean acidification and warming will lower coral reef resilience. Global Change Biology 17:1798–1808.

Arias-González, J. E., T. Fung, R. M. Seymour, J. R. Garza-Pérez, G. Acosta-González, Y.-M. Bozec, and C. R. Johnson. 2017. A coral-algal phase shift in Mesoamerica not driven by changes in herbivorous fish abundance. PLOS ONE 12:e0174855.

Aronson, R. B., and W. F. Precht. 2006. Conservation, precaution, and Caribbean reefs. Coral Reefs 25:441–450.

de Bakker, D. M., F. C. van Duyl, R. P. M. Bak, M. M. Nugues, G. Nieuwland, and E. H.

Meesters. 2017. 40 Years of benthic community change on the Caribbean reefs of Curaçao and Bonaire: the rise of slimy cyanobacterial mats. Coral Reefs 36:355–367.

Ban, S. S., N. A. J. Graham, and S. R. Connolly. 2014. Evidence for multiple stressor interactions and effects on coral reefs. Global Change Biology 20:681–697.

Bell, P. R. F., I. Elmetri, and B. E. Lapointe. 2014. Evidence of Large-Scale Chronic Eutrophication in the Great Barrier Reef: Quantification of Chlorophyll a Thresholds for Sustaining Coral Reef Communities. AMBIO 43:361–376.

Bell, P. R. F., and T. Tomascik. 1994. The demise of the fringing coral reefs of Barbados and of regions in the Great Barrier Reef (GBR) lagoon - impacts of eutrophication. Proceedings of the colloquium on global aspects of coral reefs, Miami, 1993:319–325.

Blackwood, J. C., A. Hastings, and P. J. Mumby. 2011. A model-based approach to determine the long-term effects of multiple interacting stressors on coral reefs. Ecological Applications 21:2722–2733.

Blackwood, J. C., A. Hastings, and P. J. Mumby. 2012. The effect of fishing on hysteresis in Caribbean coral reefs. Theoretical Ecology 5:105–114.

Blackwood, J. C., C. Okasaki, A. Archer, E. W. Matt, E. Sherman, and K. Montovan. 2018. Modeling alternative stable states in Caribbean coral reefs. Natural Resource Modeling 31:1–17.

Bozec, Y. M., S. O'Farrell, J. H. Bruggemann, B. E. Luckhurst, and P. J. Mumby. 2016. Tradeoffs between fisheries harvest and the resilience of coral reefs. Proceedings of the National Academy of Sciences of the United States of America 113:4536–4541.

Brandl, S. J., D. B. Rasher, I. M. Côté, J. M. Casey, E. S. Darling, J. S. Lefcheck, and J. E. Duffy. 2019. Coral reef ecosystem functioning: eight core processes and the role of biodiversity. Frontiers in Ecology and the Environment 17:445–454.

Briggs, C. J., T. C. Adam, S. J. Holbrook, and R. J. Schmitt. 2018. Macroalgae size refuge from herbivory promotes alternative stable states on coral reefs. PLoS ONE 13:1–14.

Bruno, J. F., I. M. Côté, and L. T. Toth. 2019. Climate Change, Coral Loss, and the Curious Case of the Parrotfish Paradigm: Why Don't Marine Protected Areas Improve Reef Resilience? Annual Review of Marine Science 11:307–334.

Bruno, J. F., L. E. Petes, C. D. Harvell, and A. Hettinger. 2003. Nutrient enrichment can increase the severity of coral diseases. Ecology Letters 6:1056–1061.

Burkepile, D. E., and M. E. Hay. 2006. Herbivore vs. nutrient control of marine primary producers: Context-dependent effects. Ecology 87:3128–3139.

Ceccarelli, D. M., G. P. Jones, and L. J. McCook. 2011. Interactions between herbivorous fish guilds and their influence on algal succession on a coastal coral reef. Journal of Experimental Marine Biology and Ecology 399:60–67.

Chiappone, M., D. Swanson, S. Miller, and M. Science. 2006. One-year Response of Florida Keys Patch Reef Communities to Translocation of Long-spined Sea Urchins (Diadema antillarum). Sites The Journal Of 20Th Century Contemporary French Studies:319–344.

Cote, I. M., E. S. Darling, and C. J. Brown. 2016. Interactions among ecosystem stressors and their importance in conservation. Proceedings of the Royal Society B: Biological Sciences 283:1–9.

Cox, C., A. Valdivia, M. McField, K. Castillo, and J. F. Bruno. 2017. Establishment of marine protected areas alone does not restore coral reef communities in Belize. Marine Ecology Progress Series 563:65–79.

DeCarlo, T. M., L. Gajdzik, J. Ellis, D. J. Coker, M. B. Roberts, N. M. Hammerman, J. M.

Pandolfi, A. A. Monroe, and M. L. Berumen. 2020. Nutrient-supplying ocean currents modulate coral bleaching susceptibility. Science Advances 6:1–8.

Done, T. J. 1992. Phase shifts in coral reef communities and their ecological significance. Hydrobiologia 247:121–132.

Donovan, M. K., T. C. Adam, A. A. Shantz, K. E. Speare, K. S. Munsterman, M. M. Rice, R. J. Schmitt, S. J. Holbrook, and D. E. Burkepile. 2020. Nitrogen pollution interacts with heat stress to increase coral bleaching across the seascape. Proceedings of the National Academy of Sciences of the United States of America 117:5351–5357.

Donovan, M. K., D. E. Burkepile, C. Kratochwill, T. Shlesinger, S. Sully, T. A. Oliver, G. Hodgson, J. Freiwald, and R. van Woesik. 2021. Local conditions magnify coral loss after marine heatwaves. Science 372:977–980.

Fung, T., R. M. Seymour, and C. R. Johnson. 2011. Alternative stable states and phase shifts in coral reefs under anthropogenic stress. Ecology 92:967–982.

Gardner, T. A., I. M. Côté, J. A. Gill, A. Grant, and A. R. Watkinson. 2003. Long-term region-wide declines in Caribbean corals. Science 301:958–960.

Gill, D. A., H. A. Oxenford, R. A. Turner, and P. W. Schuhmann. 2019. Making the most of data-poor fisheries: Low cost mapping of small island fisheries to inform policy. Marine Policy 101:198–207.

González-Rivero, M., L. Yakob, and P. J. Mumby. 2011. The role of sponge competition on coral reef alternative steady states. Ecological Modelling 222:1847–1853.

Guan, Y., S. Hohn, C. Wild, and A. Merico. 2020. Vulnerability of global coral reef habitat suitability to ocean warming, acidification and eutrophication. Global Change Biology 26:5646–5660.

Gurney, G. G., J. Melbourne-Thomas, R. C. Geronimo, P. M. Aliño, and C. R. Johnson. 2013. Modelling coral reef futures to inform management: Can reducing local-scale stressors conserve reefs under climate change? PLoS ONE 8:1–17.

Halpern, B. S., M. Frazier, J. Afflerbach, J. S. Lowndes, F. Micheli, C. O'Hara, C. Scarborough, and K. A. Selkoe. 2019. Recent pace of change in human impact on the world's ocean. Scientific Reports 9:1–8.

Harborne, A. R., A. Rogers, Y.-M. Bozec, and P. J. Mumby. 2017. Multiple Stressors and the Functioning of Coral Reefs. Annual Review of Marine Science 9:445–468.

Hastings, A., K. C. Abbott, K. Cuddington, T. B. Francis, Y. C. Lai, A. Morozov, S. Petrovskii, and M. Lou Zeeman. 2021. Effects of stochasticity on the length and behaviour of ecological transients. Journal of the Royal Society Interface 18.

Hastings, A., K. C. Abbott, K. Cuddington, T. Francis, G. Gellner, Y. C. Lai, A. Morozov, S. Petrovskii, K. Scranton, and M. Lou Zeeman. 2018. Transient phenomena in ecology. Science 361.

Higgins, K., A. Hastings, J. N. Sarvela, and L. W. Botsford. 1997. Stochastic Dynamics and Deterministic Skeletons: Population Behavior of Dungeness Crab. Science 276:1431–1435.

Hixon, M. A., and W. N. Brostoff. 1996. Succession and herbivory: Effects of differential fish grazing on hawaiian coral-reef algae. Ecological Monographs 66:67–90.

Hughes, T. P. 1994. Catastrophes, Phase Shifts, and Large-Scale Degradation of a Caribbean Coral Reef. Science 265:1547–1551.

Hughes, T. P., M. L. Barnes, D. R. Bellwood, J. E. Cinner, G. S. Cumming, J. B. C. Jackson, J. Kleypas, I. A. Van De Leemput, J. M. Lough, T. H. Morrison, S. R. Palumbi, E. H. Van Nes, and M. Scheffer. 2017. Coral reefs in the Anthropocene. Nature 546:82–90.

Hughes, T. P., M. J. Rodrigues, D. R. Bellwood, D. Ceccarelli, O. Hoegh-Guldberg, L. McCook, N. Moltschaniwskyj, M. S. Pratchett, R. S. Steneck, and B. Willis. 2007. Phase Shifts, Herbivory, and the Resilience of Coral Reefs to Climate Change. Current Biology 17:360–365.

Hunte, W., and M. Wittenberg. 1992. Effects of eutrophication and sedimentation on juvenile corals II. Settlement. Marine Biology 114:625–631.

Jackson, J. B. C. 2001a. What was natural in the coastal oceans? Proceedings of the National Academy of Sciences 98:5411–5418.

Jackson, J. B. C. 2001b. Historical Overfishing and the Recent Collapse of Coastal Ecosystems. Science 293:629–637.

Jackson, J., M. Donovan, K. Cramer, and V. Lam. 2014. Status and trends of Caribbean coral reefs: 1970-2012. Gland, Switzerland.

Jouffray, J. B., M. Nyström, A. V. Norström, I. D. Williams, L. M. Wedding, J. N. Kittinger, and G. J. Williams. 2015. Identifying multiple coral reef regimes and their drivers across the hawaiian archipelago. Philosophical Transactions of the Royal Society B: Biological Sciences 370:1–8.

Lapointe, B. E. 1997. Nutrient thresholds for bottom-up control of macroalgal blooms on coral reefs in Jamaica and southeast Florida. Limnology and Oceanography 42:1119–1131.

Lapointe, B. E. 1999. Simultaneous top-down and bottom-up forces control macroalgal blooms on coral reefs (Reply to the comment by Hughes et al.). Limnology and Oceanography 44:1586–1592.

Lapointe, B. E., R. A. Brewton, L. W. Herren, J. W. Porter, and C. Hu. 2019. Nitrogen enrichment, altered stoichiometry, and coral reef decline at Looe Key, Florida Keys, USA: a

3-decade study. Marine Biology 166:1–31.

Lapointe, B. E., J. M. Burkholder, and K. L. Van Alstyne. 2018. Harmful Macroalgal Blooms in a Changing World: Causes, Impacts, and Management. Pages 515–560 Harmful Algal Blooms. John Wiley & Sons, Ltd, Chichester, UK.

Leibold, M. A. 1996. A Graphical Model of Keystone Predators in Food Webs: Trophic Regulation of Abundance, Incidence, and Diversity Patterns in Communities. The American Naturalist 147:784–812.

Lessios, H. A. 1988. Mass mortality of Diadema antillarum in the Caribbean: what have we learned? Annual review of ecology and systematics. Vol. 19:371–393.

Lewis, John, B. 1960. The coral reefs and coral communities of Barbados, W.I. Canadian Journal of Zoology 38:1133–1152.

Littler, M., and D. Littler. 1984. Models of tropical reef biogenesis: the contribution of algae.

Mah, A. J., and C. W. Stearn. 1986. The effect of Hurricane Allen on the Bellairs fringing reef, Barbados. Coral Reefs 4:169–176.

Mann, G. S. 1994. Distribution, abundance and life history of the reef coral Favia fragrum (Esper) in Barbados: effects of eutrophication and of the black sea urchin Diadema antillarum (Philippi). McGill University.

McClanahan, T., and N. Muthiga. 2020. Change in fish and benthic communities in Belizean patch reefs across a parrotfish ban in and out of a fisheries closure. Marine Ecology Progress Series 645:25–40.

Mcclanahan, T. R. 1997. Primary succession of coral-reef algae: Differing patterns on fished versus unfished reefs. Page Journal of Experimental Marine Biology and Ecology.

McClanahan, T. R., N. A. Muthiga, and R. A. Coleman. 2011. Testing for top-down control: Can post-disturbance fisheries closures reverse algal dominance? Aquatic Conservation: Marine and Freshwater Ecosystems 21:658–675.

McClanahan, T. R., E. Sala, P. A. Stickels, B. A. Cokos, A. C. Baker, C. J. Starger, and S. H. Jones IV. 2003. Interaction between nutrients and herbivory in controlling algal communities and coral condition on Glover's Reef, Belize. Marine Ecology Progress Series 261:135–147.

Mcleod, E., K. R. N. Anthony, P. J. Mumby, J. Maynard, R. Beeden, N. A. J. Graham, S. F. Heron, O. Hoegh-Guldberg, S. Jupiter, P. MacGowan, S. Mangubhai, N. Marshall, P. A. Marshall, T. R. McClanahan, K. Mcleod, M. Nyström, D. Obura, B. Parker, H. P. Possingham, R. V. Salm, and J. Tamelander. 2019. The future of resilience-based management in coral reef ecosystems. Journal of Environmental Management 233:291–301.

McManus, J. W., L. A. B. Meñez, K. N. Kesner-Reyes, S. G. Vergara, and M. C. Ablan. 2000. Coral reef fishing and coral-algal phase shifts: implications for global reef status. ICES Journal of Marine Science 57:572–578.

Mellin, C., M. Aaron Macneil, A. J. Cheal, M. J. Emslie, and M. Julian Caley. 2016. Marine protected areas increase resilience among coral reef communities. Ecology Letters 19:629–637.

Meyer, K., A. Hoyer-Leitzel, S. Iams, I. Klasky, V. Lee, S. Ligtenberg, E. Bussmann, and M. Lou Zeeman. 2018. Quantifying resilience to recurrent ecosystem disturbances using flow–kick dynamics. Nature Sustainability 1:671–678.

Morozov, A., K. Abbott, K. Cuddington, T. Francis, G. Gellner, A. Hastings, Y. C. Lai, S. Petrovskii, K. Scranton, and M. Lou Zeeman. 2020. Long transients in ecology: Theory and applications. Physics of Life Reviews 1.

Mumby, P. J. 2006. The impact of exploiting grazers (Scaridae) on the dynamics of Caribbean coral reefs. Ecological Applications 16:747–769.

Mumby, P. J. 2017. Embracing a world of subtlety and nuance on coral reefs. Coral Reefs 36:1003–1011.

Mumby, P. J., A. Hastings, and H. J. Edwards. 2007. Thresholds and the resilience of Caribbean coral reefs. Nature 450:98–101.

Mumby, P. J., J. D. Hedley, K. Zychaluk, A. R. Harborne, and P. G. Blackwell. 2006. Revisiting the catastrophic die-off of the urchin Diadema antillarum on Caribbean coral reefs: Fresh insights on resilience from a simulation model. Ecological Modelling 196:131–148.

Mumby, P. J., and R. S. Steneck. 2008. Coral reef management and conservation in light of rapidly evolving ecological paradigms. Trends in Ecology & Evolution 23:555–563.

Mumby, P. J., N. H. Wolff, Y. M. Bozec, I. Chollett, and P. Halloran. 2014. Operationalizing the resilience of coral reefs in an era of climate change. Conservation Letters 7:176–187.

Muthukrishnan, R., and P. Fong. 2014. Multiple anthropogenic stressors exert complex, interactive effects on a coral reef community. Coral Reefs 33:911–921.

Norström, A. V., M. Nyström, J. B. Jouffray, C. Folke, N. A. J. Graham, F. Moberg, P. Olsson, and G. J. Williams. 2016. Guiding coral reef futures in the Anthropocene. Frontiers in Ecology and the Environment 14:490–498.

Norström, A. V., M. Nyström, J. Lokrantz, and C. Folke. 2009. Alternative states on coral reefs: Beyond coral-macroalgal phase shifts. Marine Ecology Progress Series 376:293–306.

Nyström, M., N. A. J. Graham, J. Lokrantz, and A. V. Norström. 2008. Capturing the cornerstones of coral reef resilience: Linking theory to practice. Coral Reefs 27:795–809.

Pendleton, L. H., O. Hoegh-Guldberg, C. Langdon, and A. Comte. 2016. Multiple stressors and ecological complexity require a new approach to coral reef research. Frontiers in Marine Science 3:1–5.

Renken, H., and P. J. Mumby. 2009. Modelling the dynamics of coral reef macroalgae using a Bayesian belief network approach. Ecological Modelling 220:1305–1314.

Renken, H., P. J. Mumby, I. Matsikis, and H. J. Edwards. 2010. Effects of physical environmental conditions on the patch dynamics of Dictyota pulchella and Lobophora variegata on Caribbean coral reefs. Marine Ecology Progress Series 403:63–74.

Roberts, M., N. Hanley, S. Williams, and W. Cresswell. 2017. Terrestrial degradation impacts on coral reef health: Evidence from the Caribbean. Ocean and Coastal Management 149:52–68.

Robinson, J. P. W., S. K. Wilson, and N. A. J. Graham. 2019. Abiotic and biotic controls on coral recovery 16 years after mass bleaching. Coral Reefs 38:1255–1265.

Sammarco, P. W. 1980. Diadema and its relationship to coral spat mortality: grazing, competition, and biological disturbance. Journal of Experimental Marine Biology and Ecology 45:245–272.

Sammarco, P. W. 1982. Effects of grazing by Diadema antillarum Philippi (Echinodermata: Echinoidea) on algal diversity and community structure. Journal of Experimental Marine Biology and Ecology 65:83–105.

Sander, F., and E. Moore. 1979. Significance of ammonia in determining the N:P ratio of the sea water off Barbados, West Indies. Marine Biology 55:17–21.

Scheffer, M., S. Barrett, S. R. Carpenter, C. Folke, A. J. Green, M. Holmgren, T. P. Hughes, S. Kosten, I. A. Van De Leemput, D. C. Nepstad, E. H. Van Nes, E. T. H. M. Peeters, and B. Walker. 2015. Creating a safe operating space for iconic ecosystems: Manage local stressors to promote resilience to global change. Science 347:1317–1319.

Shantz, A. A., and D. E. Burkepile. 2014. Context-dependent effects of nutrient loading on the coral-algal mutualism. Ecology 95:1995–2005.

Smith, J., C. Smith, and C. Hunter. 2001. An experimental analysis of the effects of herbivory and nutrient enrichment on benthic community dynamics on a Hawaiian reef. Coral Reefs 19:332–342.

Stearn, C. W., T. P. Scoffin, and W. Martindale. 1977. Calcium carbonate budget of a fringing reef on the west coast of Barbados Part I- zonation and productivity. Bulletin of Marine Science 27:479–510.

Steffen, W., W. Broadgate, L. Deutsch, O. Gaffney, and C. Ludwig. 2015. The trajectory of the anthropocene: The great acceleration. Anthropocene Review 2:81–98.

Steneck, R. S., S. N. Arnold, R. Boenish, R. de León, P. J. Mumby, D. B. Rasher, and M. W. Wilson. 2019. Managing recovery resilience in coral reefs against climate-induced bleaching and hurricanes: A 15 year case study from Bonaire, Dutch Caribbean. Frontiers in Marine Science 6:1–12.

Steneck, R. S., S. N. Arnold, and P. J. Mumby. 2014. Experiment mimics fishing on parrotfish: Insights on coral reef recovery and alternative attractors. Marine Ecology Progress Series 506:115–127.

Suchley, A., and L. Alvarez-Filip. 2018. Local human activities limit marine protection efficacy on Caribbean coral reefs. Conservation Letters 11:e12571.

Suchley, A., M. D. McField, and L. Alvarez-Filip. 2016. Rapidly increasing macroalgal cover not related to herbivorous fishes on Mesoamerican reefs. PeerJ 4:e2084.

Tilman, D., R. M. May, C. L. Lehman, and M. A. Nowak. 1994. Habitat destruction and the extinction debt. Nature 371:65–66.

Tomascik, T. 1990. Growth rates of two morphotypes of Montastrea annularis along a eutrophication gradient, Barbados, W.I. Marine Pollution Bulletin 21:376–381.

Tomascik, T. 1991. Settlement patterns od Caribbean scleractinian corals on artificial substrata along a eutrophication gradient, Barbados, West Indies. Marine Ecology Progress Series 77:261–269.

Tomascik, T., and F. Sander. 1985. Effects of eutrophication on reef-building corals I. Growth rate of the reef-building coral Montastrea annularis. Marine Biology 87.

Tomascik, T., and F. Sander. 1987a. Effects of eutrophication on reef-building corals - II. Structure of scleractinian coral communities on fringing reefs, Barbados, West Indies. Marine Biology 94:53–75.

Tomascik, T., and F. Sander. 1987b. Effects of eutrophication on reef-building corals - III. Reproduction of the reef-building coral Porites porites. Marine Biology 94:77–94.

Tosic, M., R. B. Bonnell, P. Dutilleul, and H. A. Oxenford. 2008. Runoff Water Quality, Landuse and Environmental Impacts on the Bellairs Fringing Reef, Barbados. Pages 521–553 Remote Sensing and Geospatial Technologies for Coastal Ecosystem Assessment and Management. Springer Berlin Heidelberg.

Toth, L. T., A. Stathakopoulos, I. B. Kuffner, R. R. Ruzicka, M. A. Colella, and E. A. Shinn. 2019. The unprecedented loss of Florida’s reef-building corals and the emergence of a novel coral-reef assemblage. Ecology 100:1–14.

Vega Thurber, R. L., D. E. Burkepile, C. Fuchs, A. A. Shantz, R. Mcminds, and J. R. Zaneveld. 2014. Chronic nutrient enrichment increases prevalence and severity of coral disease and bleaching. Global Change Biology 20:544–554.

Wang, L., A. A. Shantz, J. P. Payet, T. J. Sharpton, A. Foster, D. E. Burkepile, and R. V. Thurber. 2018. Corals and their microbiomes are differentially affected by exposure to elevated nutrients and a natural thermal anomaly. Frontiers in Marine Science 5:1–16.

Wear, S. L. 2016. Missing the boat: Critical threats to coral reefs are neglected at global scale. Marine Policy 74:153–157.

Wear, S. L., and R. V. Thurber. 2015. Sewage pollution: Mitigation is key for coral reef stewardship. Annals of the New York Academy of Sciences 1355:15–30.

Wiedenmann, J., C. D'Angelo, E. G. Smith, A. N. Hunt, F. E. Legiret, A. D. Postle, and E. P. Achterberg. 2013. Nutrient enrichment can increase the susceptibility of reef corals to bleaching. Nature Climate Change 3:160–164.

Wittenberg, M., and W. Hunte. 1992. Effects of eutrophication and sedimentation on juvenile corals I. Abundance, mortality and community structure. Marine Biology 112:131–138.

Wooldridge, S. A. 2009. Water quality and coral bleaching thresholds: Formalising the linkage for the inshore reefs of the Great Barrier Reef, Australia. Marine Pollution Bulletin 58:745–751.

Zaneveld, J. R., D. E. Burkepile, A. A. Shantz, C. E. Pritchard, R. McMinds, J. P. Payet, R. Welsh, A. M. S. Correa, N. P. Lemoine, S. Rosales, C. Fuchs, J. A. Maynard, and R. V. Thurber. 2016. Overfishing and nutrient pollution interact with temperature to disrupt coral reefs down to microbial scales. Nature Communications 7:1–12.

Zinke, J., J. P. Gilmour, R. Fisher, M. Puotinen, J. Maina, E. Darling, | Michael Stat, Z. T. Richards, T. R. Mcclanahan, M. Beger, | Cordelia Moore, N. A. J. Graham, M. Feng, J.-P. A. Hobbs, S. N. Evans, | Stuart Field, G. Shedrawi, | Russ, C. Babcock, S. K. Wilson, and C. T. Macarthur. 2018. Gradients of disturbance and environmental conditions shape coral community structure for south-eastern Indian Ocean reefs. Diversity and Distributions:24.

Figure Legends

Figure 1. A) Summary of the model, interactions between state variables, and the incorporation of grazing (overfishing), nutrients and climate-induced mortality into scaling the model. Nutrients are incorporated into the model such that coral calcification is inhibited by increased nutrients (coral per capita rates of increase, r, decrease linearly with nutrients), and that nutrients also increase the growth rate of macroalgae as well as decrease coral's resistance to macroalgae overgrowth and competitive ability (algal overgrowth rate, a, increases with nutrients up to a saturation point). Finally, we assume that climate change effectively alters coral mortality through stochastic events (pulse perturbations at increasing frequencies, which is similar to the increasing frequency and autocorrelation of extreme climate events such as bleaching events (i.e., temperature stress) and destructive weather events like cyclonic storms). **B)** Summary of grazing-mediated algae composition in coral reefs based on growth-palatability trade-offs. High grazing rates suppress late-succession, palatable macroalgae while simultaneously selecting for less-palatable life strategies (through physical and chemical defenses) within the early-succession algal r-strategists. Here we consider r-strategists as algae functional groups that colonize disturbed reefs quickly relative to thick, fleshy macroalgae (K-strategists relative to other functional forms of algae). We argue that within the group of benthic (B) r-strategists there are a variety of life history strategies that will be differentially selected for based on grazing rates. Note though that at moderate-high grazing rates, palatable fast-growing r-strategists may be able to withstand the grazing rates if their productive capacity simply outweighs grazing rates, however, at extremely high grazing rates (e.g., extreme *Diadema* densities), the relatively fast low-palatability organisms (e.g., CCA; r2) will thrive.

Figure 2. Interaction between grazing rates and nutrient loading on alternate states and management implications. **A)** Geometry of the model isoclines equilibrium structure, and all possible (qualitative) configurations along a gradient of impact from coral-dominated reefs, through bistable configurations, to algae-dominated reefs. **B)** Regions of parameter space that correspond to geometrical configurations show in (a), highlighting regions of bistability. Grey regions show the area of parameter space where alternate states exist (yellow and light green), and the black region has only a 0-0 solution. Nutrients and grazing both drive a shift along this impact gradient, and they interact nonlinearly such that this shift is exacerbated. a = 2.0, y = 0.7, m = 0.15, N_0 = 0.5, r = 1.8, and cal = 0.25. Black arrows (1 & 2) represent trajectories within this parameter space of management actions aimed at restoring herbivory and suggest context-dependent outcomes. **C)** Context-dependent restoration effects of management actions on benthic cover when reducing fishing pressure (e.g., MPA introduction) to increase grazing rates at low (1) and high (2) nutrient scenarios (represented by solid black arrows in B; 1, 2). Here, restoring grazers sufficiently allows for coral recovery in a low nutrient scenario (1) but remains in an algae-dominated state under higher nutrients (2).

Figure 3. A) Isocline geometry and phase plane trajectories under moderate local impacts in (i) deterministic (no climate-induced noise) and (ii) stochastic simulations starting at different initial values (numbered trajectories). Since there is only one stable equilibrium (the coral axial equilibrium), all deterministic solutions (i) eventually reach equilibrium. However, we can have drastically different outcomes in the face of repeated climate-induced disturbances (ii). Note this state (moderate local impacts) is near a bifurcation point where nutrients and grazing can quickly

drive a saddle-node bifurcation, creating two new equilibria (one stable and one unstable) where the isoclines intersect. Our trajectories appear be influenced by a nonexistent (but soon to be real) saddle point (the unstable equilibrium that appears after a saddle-node bifurcation), such that the vector field effectively has "memory" of it (notice the vector field pulls toward the region of entanglement). Note that while saddle points are an unstable equilibrium, they characteristically attract in one direction while repelling in another direction. Behavior like this has been referred to as a "ghost attractor" where the system mimics the dynamics as if the attractor were there(Hastings et al. 2018, Morozov et al. 2020). Furthermore, saddles are known to cause what have been referred to as "crawl-bys" whereby trajectories can become effectively entangled as the system spends a long time near a saddle before slowly moving away in another direction(Hastings et al. 2018). In our case, we have an interesting example of a "ghost saddle" where the system is influenced by the ghost of a saddle point. Here, we see that ghost saddles can cause long-transients and disturbance-driven alternate states.

B) Time series of trajectory 3 (from part A i and ii) showing that benthic r-strategists flourish during these transients and periods of coral suppression. Here, a = 2.0, y = 0.7, m = 0.15, g = 0.4, $N_t = 0.53$, $N_0 = 0.5$, r = 1.8, and cal = 0.25. In ii) disturbance frequency is every 5 time units, and results in an instantaneous loss of 50% coral cover.

Figure 4. Benthic cover in a moderately impacted system (long transients after a perturbation) is altered by multiple stressors, through grazing-mediated algae composition and differential trajectories of coral recovery. Higher grazing rates select for fast-growing but relatively less palatable benthic r-strategists (e.g., r2 strategists such as CCA) that can productively withstand grazing, whereas lower grazing rates allow for more palatable (and likely even faster growing)

benthic r-strategists dominate (e.g., r1 strategists like turf algae). Grazing of course also suppresses palatable macroalgae (K-strategist). **A)** The effect of single perturbations on benthic composition during transients (post-disturbance), and **B)** frequent climate-driven mortality events, such as temperature-induced bleaching events and cyclonic storm damage, can permanently alter benthic composition. Simulations in A) and B) have the same parameter values. In all cases a = 2.4, y = 0.7, m = 0.15, N_0 = 0.5, r = 1.8, and cal = 0.25. Nutrients and grazing are varied as follows: i) g = 0.24, N_t = 0.16; and ii) g = 0.7, N_t = 2.31. In B) disturbance frequency is every 5 time units, and results in an instantaneous loss of 50% coral cover.

Figure 5. A summary of our theoretical results as a framework for coral reef composition in a changing world. Reef benthic cover depends on grazing, nutrients, and climate-related coral mortality. The region of multi-stressor space for coral-dominated reefs decreases with increased disturbance frequency (replaced by a region of climate-driven uncertainty), while the composition of algae (both slower-growing and late succession thick macroalgae, as well as early succession r-strategists) is mediated by grazing rates. Here, pie charts display the changing nature of benthic composition due to grazing-induced selection. Increasing disturbance frequency reduces the possibility of coral persistence by increasing the susceptibility to other stressors, decreasing the basin of attraction to the coral-dominated equilibrium when in a bistable configuration, and increasing the likelihood of climate-driven state shifts. We therefore argue that anything below the region of climate-driven uncertainty would be an algae-dominated system in a noisy world.

Figure 6. Changes in benthic composition of fringing reefs along the west coast of Barbados in space and time. **A)** Location of eight fringing reefs on the west coast of Barbados studied between 1972 and 1993. The triangle symbol shows the location of the North Bellairs reef, which was here used as baseline for 1972(Stearn et al. 1977) (pre-hurricane and pre-*Diadema* die off) and 1981(Mah and Stearn 1986) (post-hurricane but pre-*Diadema* die off) whereas the square symbols represent seven other fringing reefs surveyed(Tomascik and Sander 1987a, Allard 1994), including South Bellairs reef (BRI), which is located only meters away from North Bellairs reef. From North to South: SR = Sandridge, GS = Greensleeves, North Bellairs Reef (triangle), BRI = Bellairs Research Institute (South Bellairs Reef), SL = Sandy Lane, FV = Fitts Village, SG = Spring Gardens, BR= Brighton; **B)** Temporal changes in the per cent cover of hard coral, CCA and turf + frondose algae in the fringing reefs, as well as changes in *Diadema* densities (95%CI when coastal average shown) and a schematic showing overall nutrient concentrations relative to eutrophication thresholds (see Supplement B.1 for individual nutrient measurements and thresholds); **C)** Multi-panels showing spatial correlations across the seven aforementioned reefs showing a gradient of decreasing *Diadema* density and increasing eutrophication (north-south gradient), as well as correlations between *Diadema* density and three benthic variables (hard coral cover, CCA and turf + frondose algae), and between reef eutrophication rank and the three aforementioned benthic variables. Note that data in (c) are shown for the pre-*Diadema* die-off period (1982/1983) and for the post-*Diadema* die off period (1992-1993). Significant Spearman rank correlations ($p<0.05$) are identified with bold font and solid trend lines.

Figure 7. Mapping the trajectory of change of coral reefs along Barbados' west coast within our theoretical multi-stressor framework. Approximate trajectory over time is represented by the dashed red line, with average reef composition at each time period displayed in pie charts (data described above and in Figure 6). In 1982/83 and 1992/93 surveys of multiple reefs were conducted along the coastline, following a gradient in eutrophication and grazing rates, with site-level variation shown by smaller transparent charts.

Figure 1

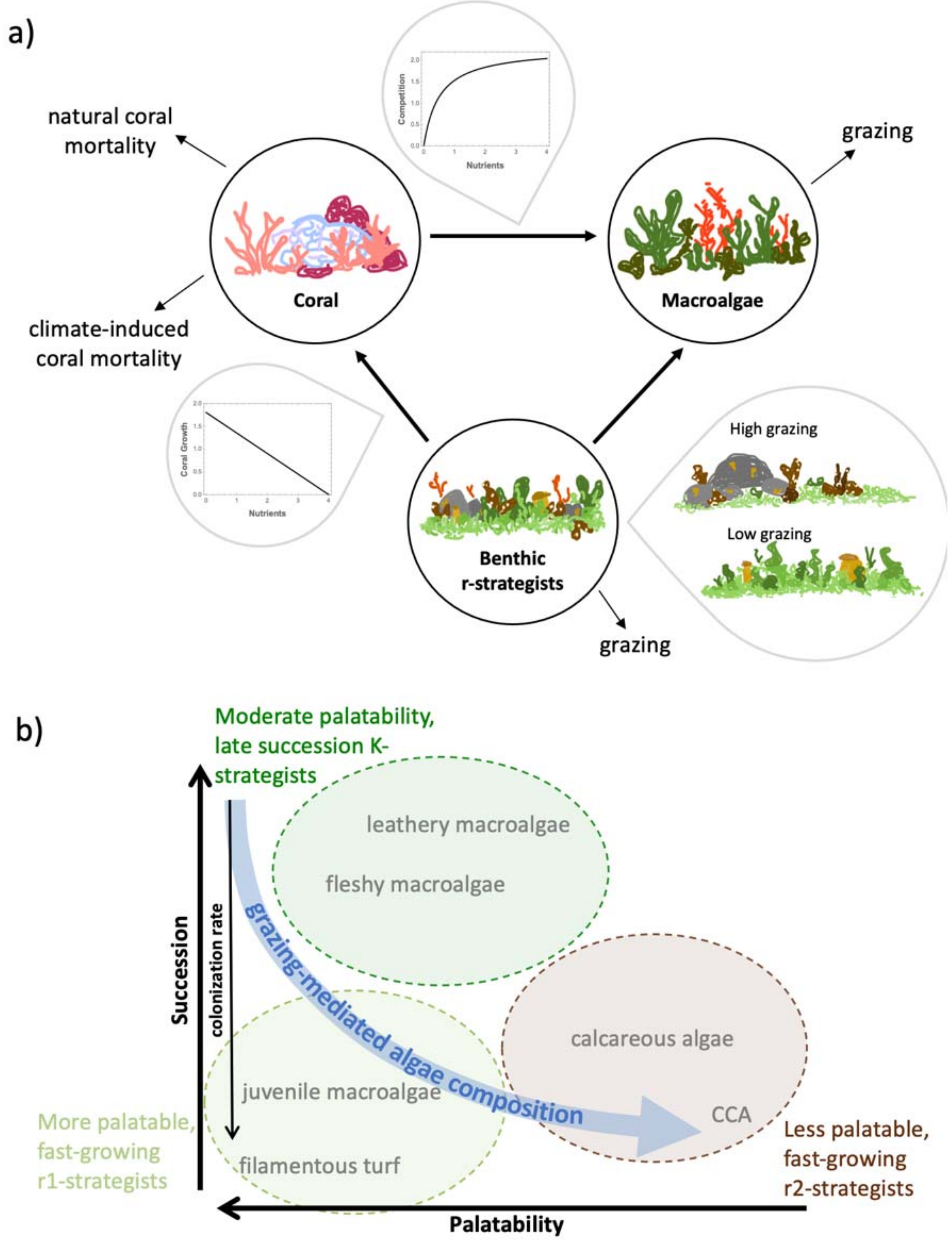

a)
Competition
0.0
0.5
1.0
1.5
2.0
0
1
2
3
4
Nutrients
natural coral mortality
grazing
Coral
Macroalgae
climate-induced coral mortality
Coral Growth
0.0
0.5
1.0
1.5
2.0
0
1
2
3
4
Nutrients
Benthic r-strategists
High grazing
Low grazing
grazing
b)
Moderate palatability, late succession K-strategists
leathery macroalgae
fleshy macroalgae
Succession
colonization rate
grazing-mediated algae composition
calcareous algae
juvenile macroalgae
CCA
More palatable, fast-growing r1-strategists
filamentous turf
Less palatable, fast-growing r2-strategists
Palatability

Figure 2

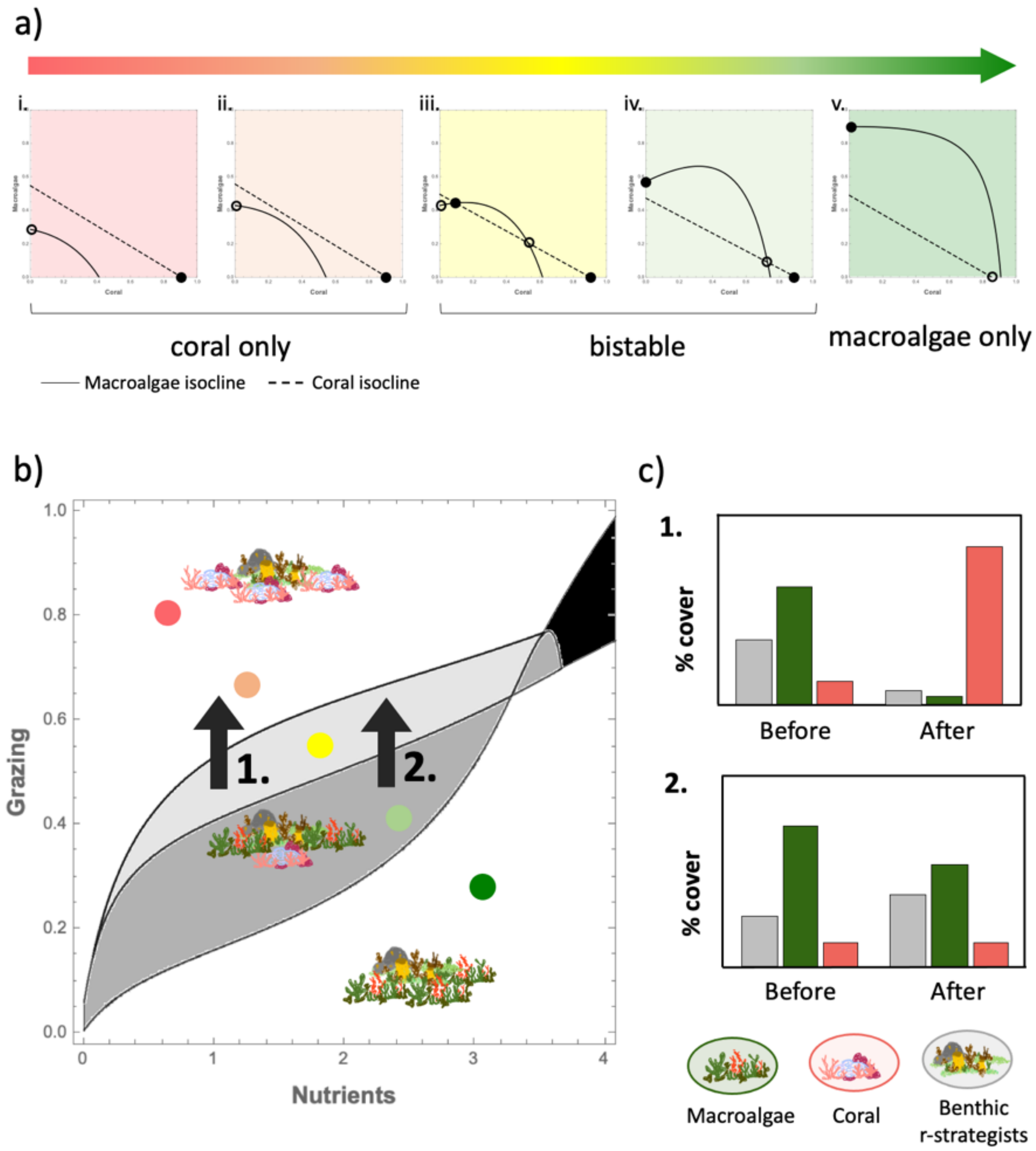

a)
i.
ii.
iii.
iv.
v.
Macroalgae
Coral
coral only
bistable
macroalgae only
Macroalgae isocline
Coral isocline
b)
1.0
0.8
0.6
0.4
0.2
0.0
Grazing
0
1
2
3
4
Nutrients
1.
2.
c)
1.
% cover
Before
After
2.
% cover
Before
After
Macroalgae
Coral
Benthic r-strategists

Figure 3

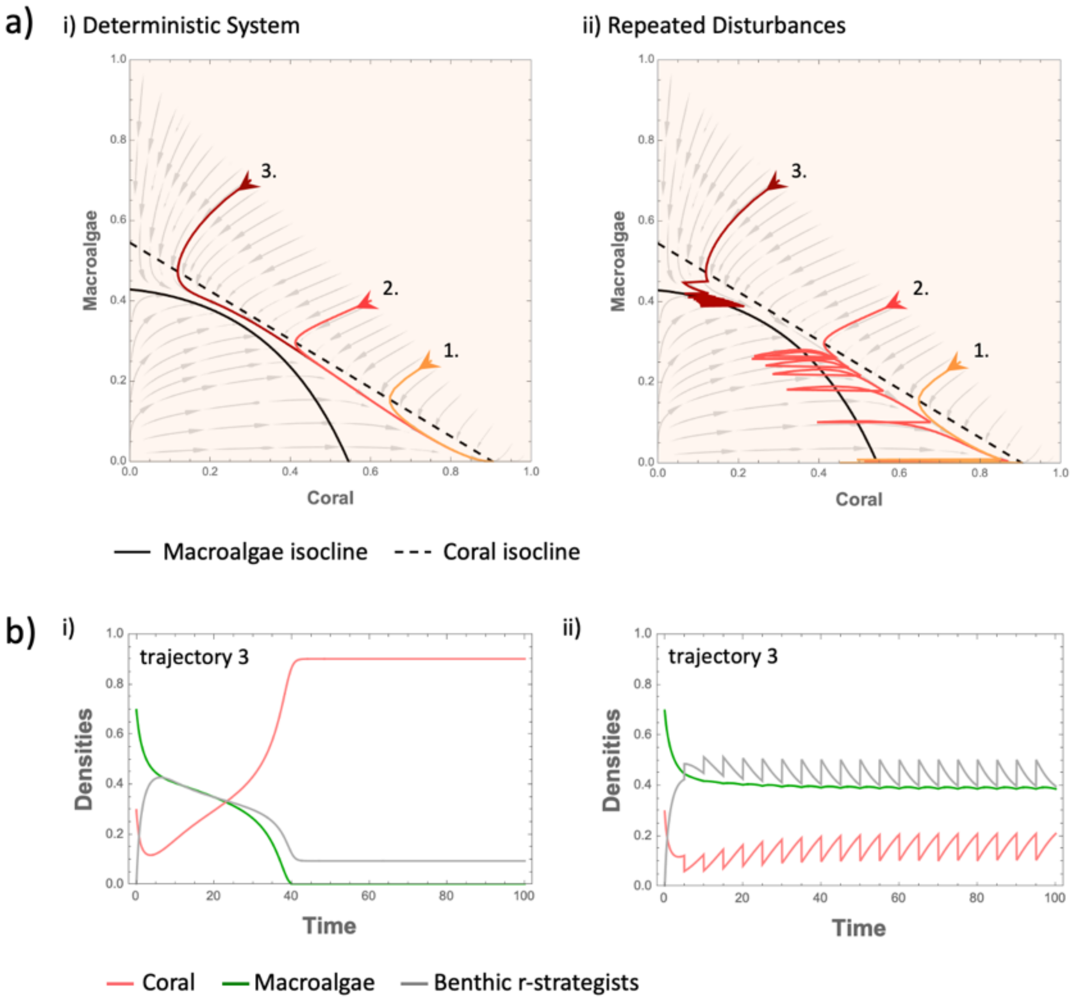
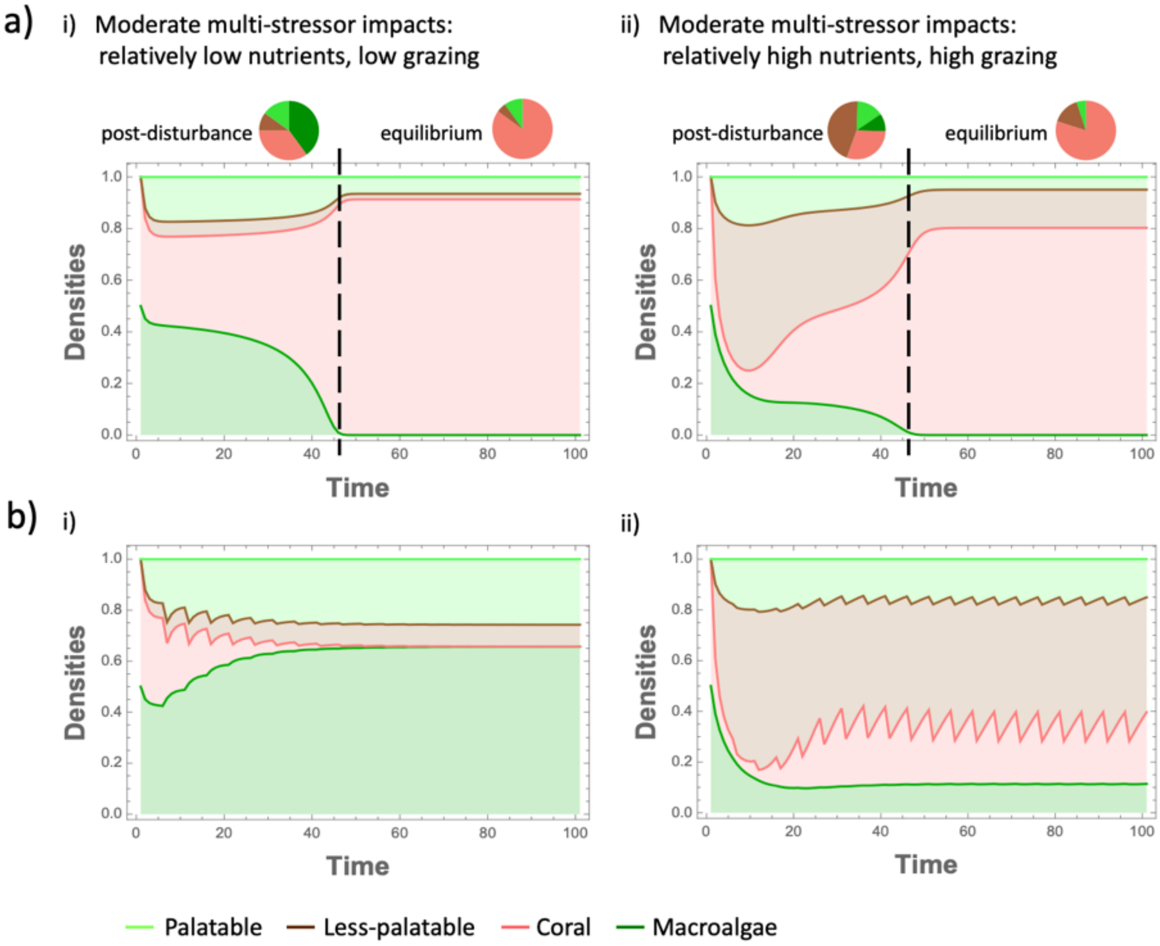
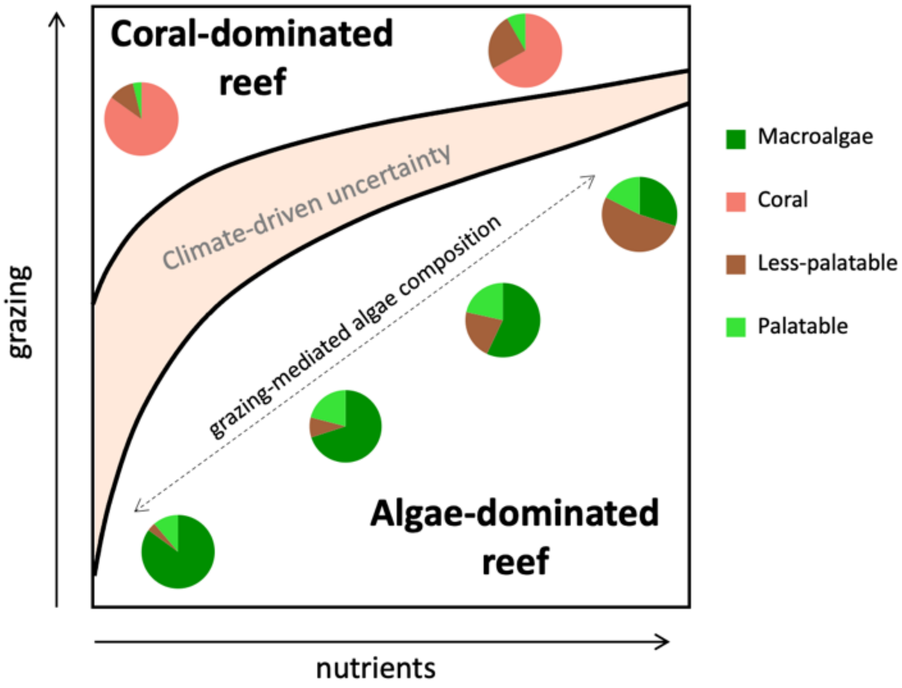

a)
i) Deterministic System
ii) Repeated Disturbances
Macroalgae
Coral
1.
2.
3.
0.0
0.2
0.4
0.6
0.8
1.0
Macroalgae isocline
Coral isocline
b)
i)
ii)
trajectory 3
Densities
Time
0
20
40
60
80
100
Coral
Macroalgae
Benthic r-strategists

Figure 4


a)
i) Moderate multi-stressor impacts:
relatively low nutrients, low grazing
ii) Moderate multi-stressor impacts:
relatively high nutrients, high grazing
post-disturbance
equilibrium
Densities
Time
0
20
40
60
80
100
0.0
0.2
0.4
0.6
0.8
1.0
b)
i)
ii)
Palatable
Less-palatable
Coral
Macroalgae

1074 **Figure 5**



1075

Figure 6

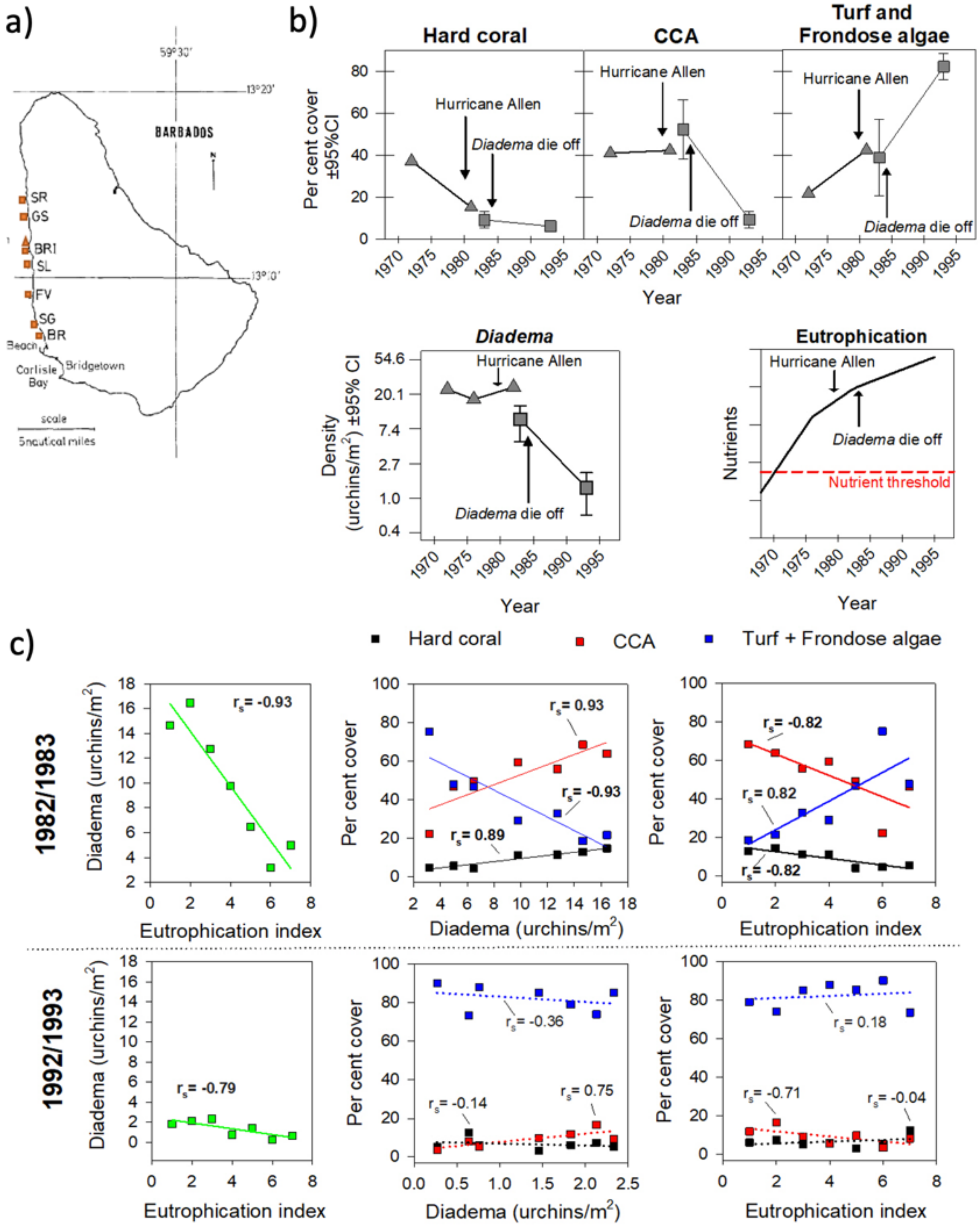
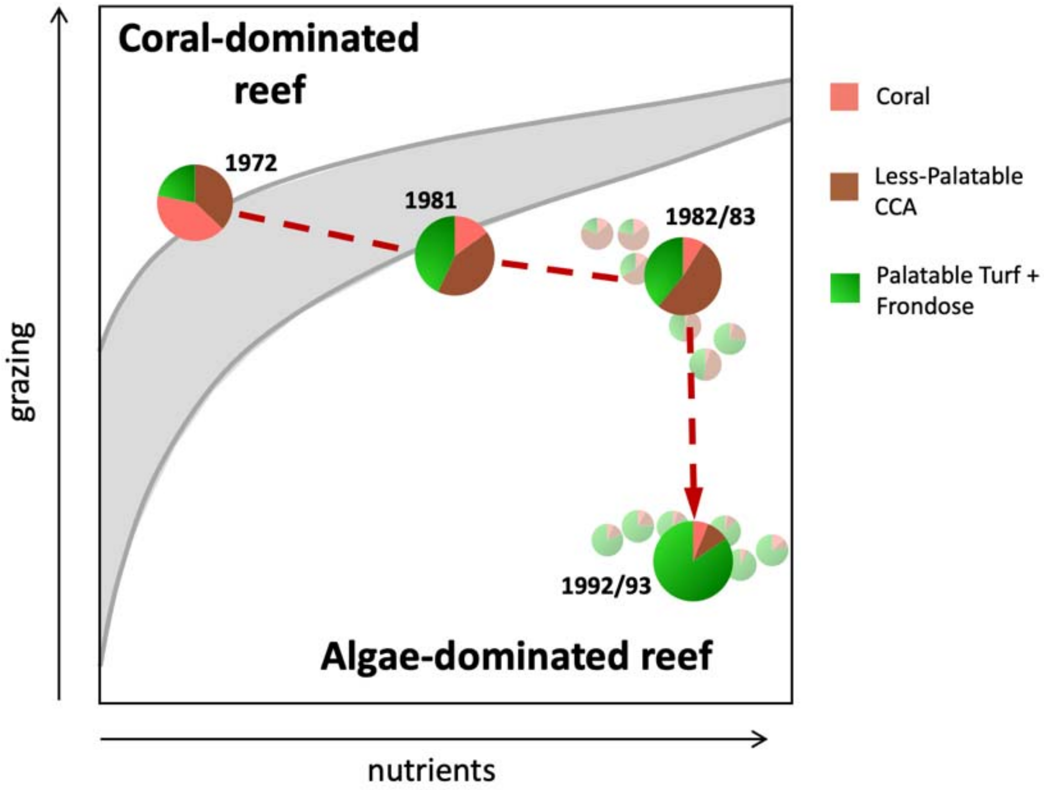

a)
59°30'
13°20'
BARBADOS
N
SR
GS
BRI
SL
13°10'
FV
SG
BR
Beach
Carlisle Bay
Bridgetown
scale
5nautical miles
b)
Hard coral
CCA
Turf and Frondose algae
Per cent cover ±95%CI
Hurricane Allen
Diadema die off
Year
Diadema
Density (urchins/m²) ±95% CI
54.6
20.1
7.4
2.7
1.0
0.4
Eutrophication
Nutrients
Nutrient threshold
1970 1975 1980 1985 1990 1995
c)
Hard coral
CCA
Turf + Frondose algae
1982/1983
1992/1993
Diadema (urchins/m²)
Per cent cover
Eutrophication index
Diadema (urchins/m²)
rs= -0.93
rs= 0.93
rs= -0.93
rs= 0.89
rs= -0.82
rs= 0.82
rs= -0.82
rs= -0.79
rs= -0.36
rs= -0.14
rs= 0.75
rs= 0.18
rs= -0.71
rs= -0.04

Figure 7


Coral-dominated reef
1972
1981
1982/83
1992/93
Algae-dominated reef
grazing
nutrients
Coral
Less-Palatable CCA
Palatable Turf + Frondose