

# Avoiding Coral Reef Functional Collapse Requires Local and Global Action

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## Results and Discussion

Coral reefs provide a wealth of ecosystem services, including the provision of coastal protection, commercial fishing, tourism, animal protein, sand production, and the highest biodiversity in the oceans [7]. Many of these services are ultimately founded on the healthy functioning of living corals and the habitat structures they create. Through their growth, corals generate skeletons of calcium carbonate (limestone) that provide a natural breakwater and the complex three-dimensional habitat needed to sustain biodiversity. Natural, ongoing erosion of this carbonate substrate generates sand accumulation on beaches and islands. The long-term maintenance of reef structures requires that the production of carbonate exceeds its rate of erosion; i.e., that the carbonate budget is positive [5]. However, carbonate budgets are acutely threatened by the combined effects of climate change and local anthropogenic stressors [8], and a recent study concluded that 21% of Caribbean reefs surveyed were experiencing net decline [9]. Rates of coral production may decline because of a suite of detrimental processes, including coral bleaching [10], ocean acidification [1], diseases [11, 12], and a reduction in reef resilience [13]. Further, rates of erosion are projected to increase as ocean acidification slows coral growth, weakens reefs [14], and enhances sponge driven biochemical dissolution of the carbonate substrate [15].

Here, we couple models of climate change, ecosystem dynamics, and carbonate processes to ask whether reefs could shift to net erosional states and consider how threat mitigation at global and local scales might avoid this undesirable trajectory. We focus on Caribbean reefs for four reasons. First, much of the pioneering research on carbonate budgets was carried out in this region [6, 16, 17], thereby providing a benchmark to develop models and gauge changes in budgets over recent decades. Second, the low diversity of this region simplifies the challenge of modeling reef dynamics and carbonate budgets [13]. Third, Caribbean reefs have experienced profound levels of disturbance and degradation [2], and fourthly, these anthropogenic impacts have served as a bellwether for declines seen subsequently in other regions [18], meaning that there is an urgent need to understand future trajectories of ecosystem functioning.

Evidence suggests that Caribbean reefs have been losing architectural structure since the late 1970s (Figure 1A) [19] and that contemporary carbonate production rates on many reefs are now lower than those measured in core records over the last ~8,000 years [9]. These changes have been caused by widespread coral mortality, and while the drivers of mortality differ among sites, coral disease, hurricanes, overfishing, urchin die-off, and episodic bleaching events have all contributed. To explore the implications of these well-documented ecological events on the dynamics of reef structures, we developed several characteristic scenarios (Figures 1A and 1C) ranging from “healthy” intact ecosystems documented in the 1960s through to the present day (model specification provided in [Supplemental Experimental Procedures](#) available online). Key ecological events are (1) depletion of reef fish by fishing, (2) loss of large branching *Acropora*

## Summary

Coral reefs face multiple anthropogenic threats, from pollution and overfishing to the dual effects of greenhouse gas emissions: rising sea temperature and ocean acidification [1]. While the abundance of coral has declined in recent decades [2, 3], the implications for humanity are difficult to quantify because they depend on ecosystem function rather than the corals themselves. Most reef functions and ecosystem services are founded on the ability of reefs to maintain their three-dimensional structure through net carbonate accumulation [4]. Coral growth only constitutes part of a reef’s carbonate budget; bioerosion processes are influential in determining the balance between net structural growth and disintegration [5, 6]. Here, we combine ecological models with carbonate budgets and drive the dynamics of Caribbean reefs with the latest generation of climate models. Budget reconstructions using documented ecological perturbations drive shallow (6–10 m) Caribbean forereefs toward an increasingly fragile carbonate balance. We then projected carbonate budgets toward 2080 and contrasted the benefits of local conservation and global action on climate change. Local management of fisheries (specifically, no-take marine reserves) and the watershed can delay reef loss by at least a decade under “business-as-usual” rises in greenhouse gas emissions. However, local action must be combined with a low-carbon economy to prevent degradation of reef structures and associated ecosystem services.

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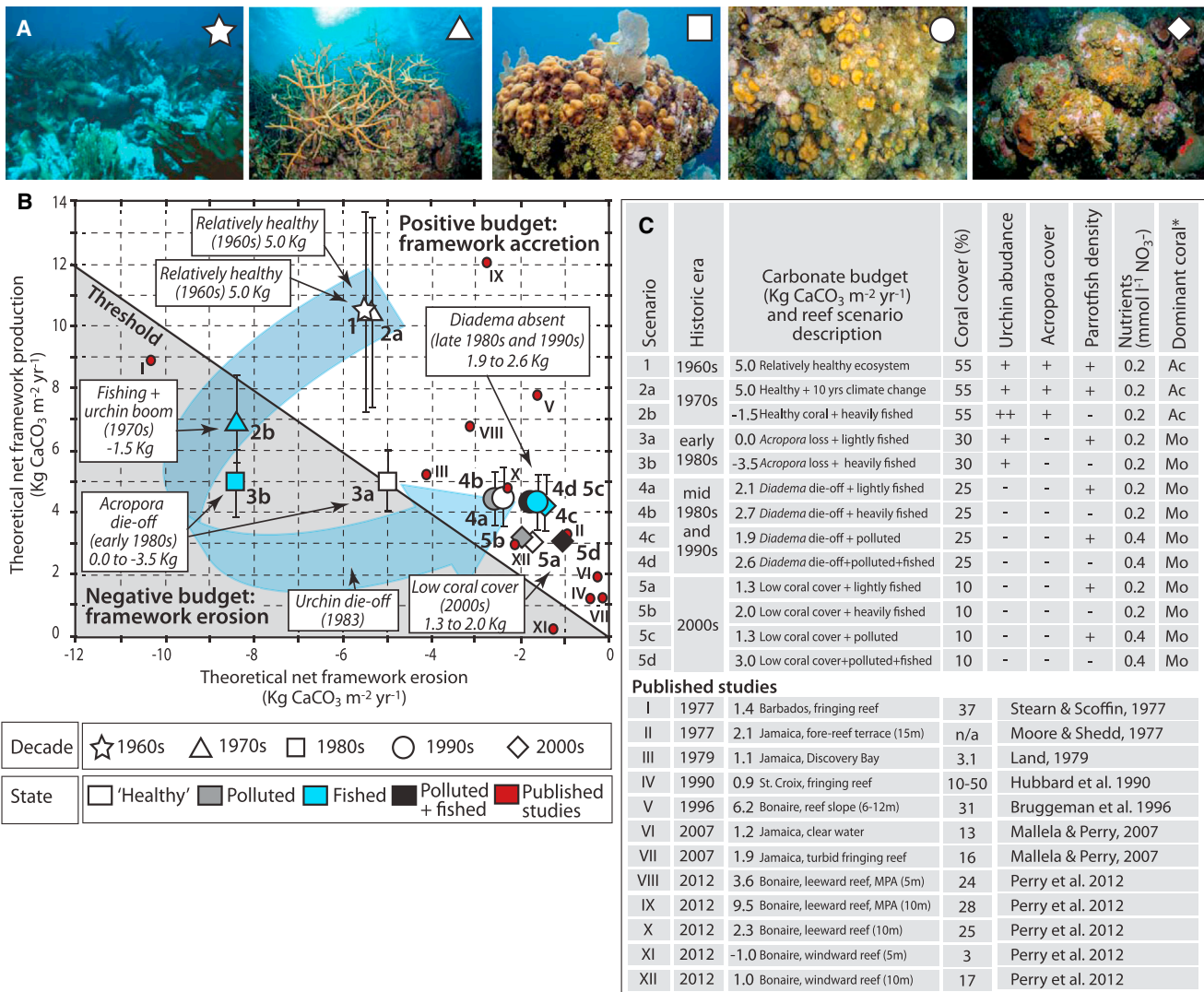


Figure 1. Changes in Caribbean Framework Bioerosion versus Carbonate Production over the Past Half Century

(A) Photographs of Caribbean reefs typifying states of degradation used to illustrate historical scenarios (1 to 5). From left to right: scenario 1, a relatively healthy reef (considered typical of the 1960s to early 1970s) with high abundance and diversity of corals and fish; scenario 2 (1970s), in some cases overfished; scenario 3 (1970s to early 1980s), reefs have lost most branching Acroporids and are often heavily fished with reduced coral cover; scenario 4, *Diadema*-depauperate reef with low coral cover and diversity from the mid-1980s to 1990s; scenario 5 (2000s), a degraded reef with low coral cover.

(B) Model reconstructions of carbonate budgets with mean net accretion values (kg CaCO<sub>3</sub> m<sup>-2</sup> year<sup>-1</sup> ± SD). Parameter values were allowed to vary based on empirical data. Arrow shows chronological trajectory of net reef budget. Other published reef carbonate budgets from the Caribbean region are plotted for comparison.

(C) The table lists the plotted scenarios and their descriptors: -, absent; +, present; ++, overabundance; \*Ac, *Acropora*; Mo, *Montastraea*.

See also Figures S1, S4, and S9 and Tables S1 and S2.

*palmata* and *A. cervicornis*, primarily because of disease, (3) hyperabundance of the urchin *Diadema antillarum* when its predators were overfished, (4) loss of *Diadema* because of disease, (5) poor watershed management leading to eutrophication, and (6) ongoing climate change from the 1960s onward. We also model the recuperation of some ecological processes through improved reef management or natural recovery [20].

#### Historical Changes in Caribbean Reef Carbonate Budgets

Although reef ecosystems were not pristine in the 1960s, our reconstruction of the environment and ecological structure yielded high mean rates of net carbonate production at 5.0 (±3.2) kg CaCO<sub>3</sub> m<sup>-2</sup> y<sup>-1</sup>, and a maximum of 17.7 kg CaCO<sub>3</sub>

m<sup>-2</sup> y<sup>-1</sup> (Figure 1B, scenario 1). By convention, the term G is used for net carbonate production with units kg CaCO<sub>3</sub> m<sup>-2</sup> y<sup>-1</sup> [21]. Moving forward to the 1970s, carbonate budgets show little difference when only greenhouse gas-driven changes in temperature and ocean acidification (OA) were added (Figure 1B, scenario 2a). These hind-casted budgets of net reef carbonate production are almost identical to those rates measured in several classic studies from the 1970s (Supplemental Experimental Procedures), which found that Caribbean reefs existed in positive budgetary states, primarily because of high rates of production by the species *A. palmata* and *A. cervicornis*. Measured rates ranged from 4.5 G [6], to 2.1 G [22] in Barbados and 1.1 G in Jamaica [17]. Similarly, a synthesis of regional foreereef carbonate production measures

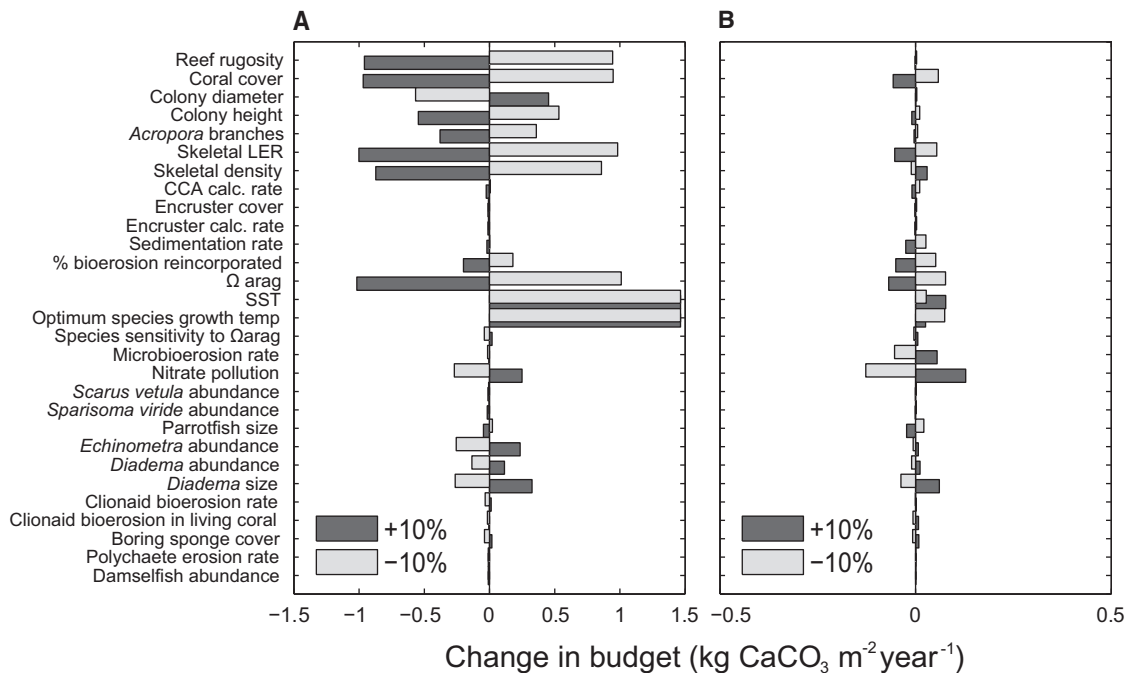


Figure 2. Sensitivity of Model Caribbean Reefs to Simulated Disturbance Events

Absolute change in carbonate budget output (x axis) brought about by 10% change in selected variable (y axis) for a relatively healthy reef (scenario 1) with 55% coral cover, healthy abundances of urchins and fish, and a reference budget of 5.0 kg CaCO<sub>3</sub> m<sup>-2</sup> year<sup>-1</sup> (A) and a present-day degraded Caribbean reef (scenario 5) with 10% coral cover, low diversity, few fish, and no urchins accreting at 2.0 kg CaCO<sub>3</sub> m<sup>-2</sup> year<sup>-1</sup> (B). Note that the x axes differ between the panels.

from this period suggested that gross carbonate production rates in the region ranged from ~10–17 G [23].

Many reefs had already experienced heavy fisheries exploitation by the 1960s and 1970s, resulting in depauperate fish communities and rapidly expanding populations of urchins, which were freed from their predators [24]. Under these circumstances, we found that the hyperabundance of bioeroding *Diadema* shifted reefs toward a net loss of reef structure (–1.5 G; Figure 1B, scenario 2b). However, we add a cautionary note about this result for those systems that had a high abundance of crustose coralline algae (CCA). A Jamaican study site that exhibited a hyperabundance of *Diadema* (15 m<sup>-2</sup>) in 1978 was also dominated by CCA (55%) and 30% live coral [25]. For CCAs to be surviving under this grazing intensity, the reef could not have been in a net erosional state as would have been predicted by several carbonate budgets [26], including our own. Models usually calculate the erosive capacity of herbivores separately and then subtract this from observed rates of carbonate production for CCAs (and other carbonate producers). However, most measurements of CCA carbonate production implicitly include ambient erosion by fish and invertebrates, yet this is rarely quantified or considered further. Thus, models run the risk of overestimating the erosion of CCAs because observed CCA production is often net CCA production after herbivory. Empirical studies are needed to determine the accretion of CCA under a wide range of herbivore assemblages so that double-accounting can be avoided.

In the 1980s, two epizootics shaped the ecology of Caribbean reefs dramatically. First, both species of the branching coral, *Acropora*, experienced region-wide decline because of white band disease. Our early 1980s scenarios reflect this event through dramatic reductions in net carbonate production, such that even lightly fished reefs were pushed close to

carbonate equilibrium (Figure 1B, scenario 3a, –0.01 G). Overfished reefs in the early 1980s show the most negative budget of –3.5 G, driven by high urchin bioerosion (–11.1 G) and reduced coral productivity (2.6 G). This budget is similar to that calculated on heavily exploited reefs in the tropical eastern Pacific (–0.6 to –3.6 G) [27]: sites at which extensive loss of reef structure was documented.

The second major epizootic was the regional mass mortality of the urchin *D. antillarum* in 1983–1984 [28]. The loss of this important herbivore generated a well-documented increase in algal abundance [24, 29], but the cessation of *Diadema* bioerosion also returned the reef to net carbonate accretion, albeit at lower levels than predicted for the 1960s (Figure 1). Positive budgets were possible, in part, because coral cover remained modest (Figure 1B, scenarios 4a–4d). Although internal bioerosion doubled under polluted scenarios (Figure 1B, scenarios 4c and 4d), the increase was insufficient to shift the system into net erosion (net budget +0.30 G). Again, modeled values of net carbonate production (1.9 to 2.7 G) were comparable to empirical estimates at the time, such as that from Saint Croix (0.9 G) [16].

Net carbonate budgets in archetypal reefs of the 1990s are positive, but the decline in coral after bleaching events in 1998 and 2005 [30–32] led to increasingly marginal carbonate production in the 2000s (Figure 1B). However, although net production remained positive, it is important to recognize that absolute levels of carbonate production and bioerosion have declined, principally because of reduced coral production and a loss of urchin and sometimes parrotfish bioerosion. The ecosystem therefore has lower rates of carbonate processes (Figure 2). In accordance with previous decades, modeled budget estimates are comparable to recent studies from Jamaica [33] and exposed sites of Bonaire [5].

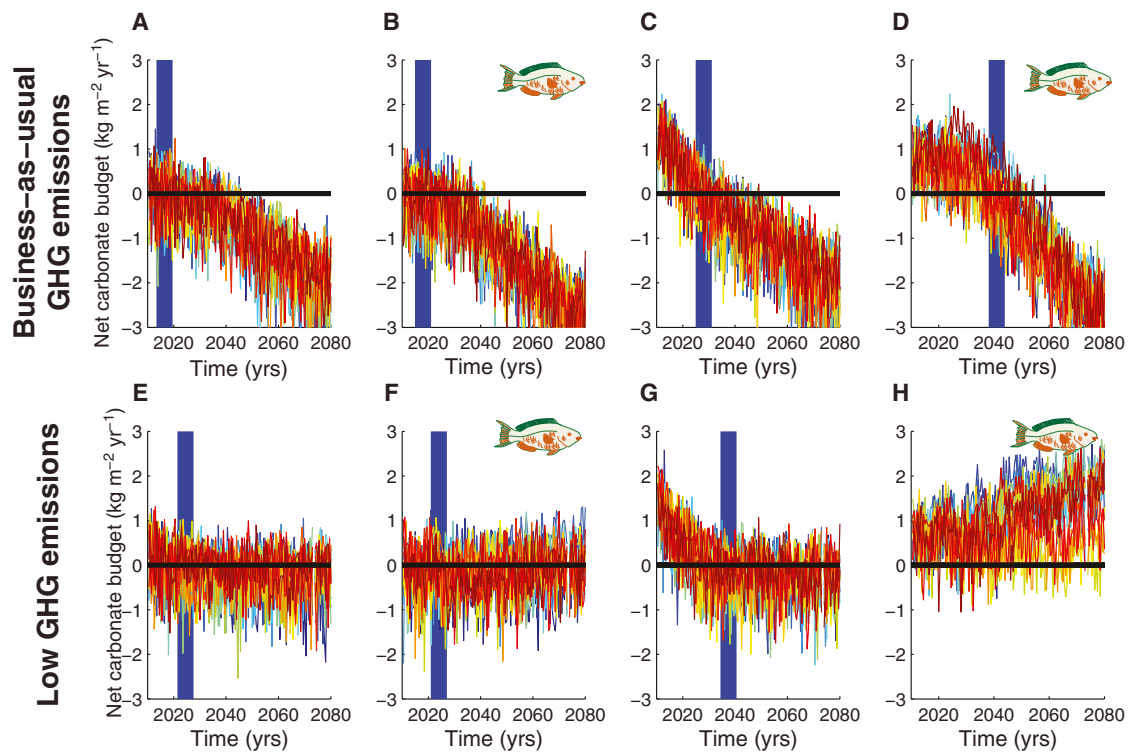


Figure 3. Future Carbonate Budgets of a Caribbean Forereef under Climate Change and Ocean Acidification with and without Local Conservation of Herbivores

The top panel represents scenarios under realistic greenhouse gas (GHG) emissions (RCP 8.5), whereas the bottom panel represents aggressive reduction of GHGs (RCP 2.6). Initial conditions of reefs are either degraded with 10% coral cover (A, B, E, and F) or healthier with 20% coral (C, D, G, and H). Herbivorous fish are either overfished or protected (denoted with parrotfish symbols). Each plot displays 20 simulations, with outputs generated at 6 month intervals and run for years 2010–2080. Vertical blue bars indicate point at which the projected budget becomes negative ( $<-0.1$  kg for  $>5$  years). See also Figures S3 and S6–S8.

### Key Drivers of Carbonate Budgets

To identify how the key drivers of carbonate dynamics have changed over time, we ran model sensitivity analyses for the “healthy” reefs of scenario 1 and “unhealthy” reefs of scenario 5 (Figure 2). Each sensitivity analysis calculated the difference in budget associated with a  $\pm 10\%$  change in the mean value of each of the 115 input variables. Healthy, coral-dominated reefs were most sensitive to changes in coral production brought about by variability in the physical drivers of calcification (sea surface temperature and carbonate saturation state, Figure S3), as well as intrinsic skeletal density and linear extension rate (Figure 2A). As coral cover declined (Figure 2B), the system became less sensitive to drivers of calcification and responded to drivers of bioerosion such as nitrate level (a proxy for eutrophication), sponge bioerosion rate, and the size and abundance of urchins. Indeed, nitrate level was ranked the most important factor for degraded reef budgets such that a 10% increase led to a 33% decline in net carbonate production. Nutrification can benefit the growth of microendoliths [34] and filter-feeding macrobioeroders, such as molluscs and sponges [35, 36], while also reducing coral calcification and extension rates [37, 38].

### Ensuring Reef Function in Future: Local Management versus Global Action on Greenhouse Gas Emissions

The maintenance of a positive carbonate budget is a fundamental prerequisite to sustain many reef functions, such as the provision of habitat for biodiversity and fishery resources.

To assess the action needed to sustain net carbonate production, we separated interventions to reduce local stressors from global efforts to mitigate greenhouse gas emissions. Our first analysis considered the local action of protecting grazing parrotfishes, which have been found to reduce levels of seaweed on forereefs [39] and assist coral recovery [40]. We also contrasted a “business-as-usual” scenario of greenhouse gas emissions (based on HadGEM-2ES Earth System model scenario Representative Concentration Pathway, RCP 8.5 [41]) with a progressive move toward a low carbon economy (RCP 2.6), a scenario based low emissions and radiative forcing, that aims to keep global mean temperature increases below  $2^{\circ}\text{C}$ . In this first analysis, we assumed that the catastrophic losses of *Acropora* and the urchin *Diadema* persist and also compare the outlook for reefs with a “relatively healthy” 20% coral cover and a more degraded 10% cover, based on a synthesis of Caribbean coral cover values [42]. While scope exists for coral adaptation to rising stress [43], the extent of adaptation is uncertain [44], and we make the conservative assumption of no adaptation.

Only one set of interventions maintained substantial positive carbonate budgets until the end of simulations in 2080: local maintenance of grazing by protecting parrotfishes and concerted global action to reduce greenhouse gas emissions (Figure 3H). Moreover, clear positive budgets required reefs to start with relatively healthy coral as those starting with only 10% coral remained close to equilibrium (Figure 3F). If greenhouse gas emissions follow the business-as-usual trend

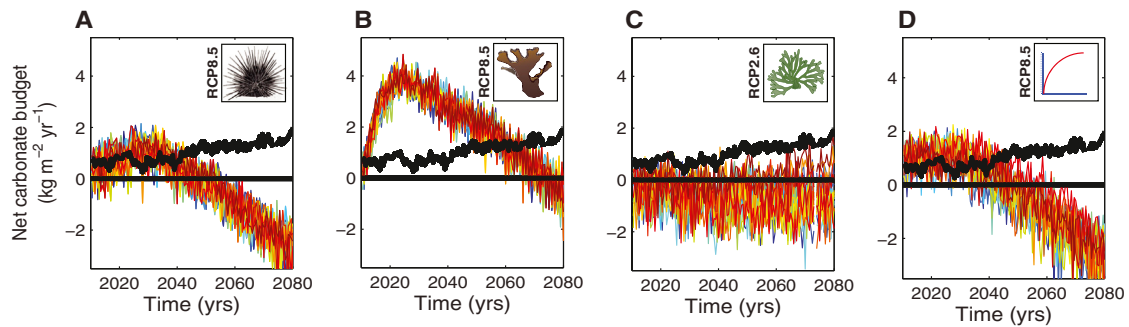


Figure 4. Alternative Scenarios for Future Carbonate Budgets

The effect of simulated *Diadema* recovery (A), combined *Diadema* and *Acropora* recovery (B), chronic eutrophication (C), and weaker effects of ocean acidification (D) with nonlinear [54] rather than linear [55] calcification response curves. A representative concentration pathway (RCP) for each set of simulations is given in the insets. For comparison, the solid black line represents predicted based case from Figure 3H. See also Figure S2.

(RCP 8.5), then reefs eventually exhibit strong net erosion irrespective of local conservation measures (Figures 3A–3D). However, conservation of parrotfish managed to delay the onset of net erosion by approximately a decade, providing that the reef started with higher coral cover (Figures 3C and 3D). A nonlinear benefit of parrotfish protection with initial coral cover (Figures 3G and 3H) occurred because of ecosystem hysteresis [45]. At 20% initial cover, grazing intensity was high and coral recruitment was successful. However, 10% coral led to reduced grazing intensity because herbivores had a larger area in which to feed. Reduced grazing intensity allowed macroalgae to increase and reduce coral recruitment to the extent that coral populations were no longer sustainable. Under RCP 8.5, however, even high initial coral cover did not confer sufficient resilience, and the system was eventually overwhelmed by frequent coral bleaching.

The outlook for carbonate budgets improves when greenhouse gases are mitigated aggressively. Although only one scenario led to clear reef growth, the alternatives hovered near carbonate equilibrium under RCP 2.6 (Figures 3E–3G).

The impact of parrotfish conservation on more degraded reefs helps resolve the putative “negative” impact of parrotfish as a source of bioerosion from their positive impact in reducing the algal competitors of corals [46]. After parrotfish stocks are heavily fished, rates of bioerosion are lower and net carbonate production is initially greater (Figure 1B, scenarios 5a and 5b, and Figures 3E and 3F). However, because coral cover declines rapidly in the functional absence of parrotfish (Supplemental Experimental Procedures), the long-term consequence of fishing is worse for the reef because a decline in coral skeletal production leads to a lower overall carbonate budget (Figures 3E and 3F).

The benefits of local action are not confined to managing parrotfish. Poor management of agricultural runoff and waste water can increase nutrient levels and influence macroalgal growth [47], coral calcification [48, 49], and rates of bioerosion [50–52]. Indeed, eutrophication is likely to be highly influential on the balance between carbonate production and erosion [35, 53]. We found qualitatively similar results simulating the effects of eutrophication in which an increase in nitrate concentration of  $0.22 \mu\text{mol liter}^{-1}$  prevented long-term net carbonate production even under RCP 2.6 (Figure 4C).

It has been argued that the lack of resilience of Caribbean reefs is strongly associated with the disease-induced absence of the fast-growing coral, *A. cervicornis*, and/or the urchin, *Diadema* [42]. We simulated their recovery under RCP 8.5

but found that neither allowed sustained positive reef growth, although reefs fared better with *A. cervicornis* (Figures 4A and 4B). Whether these key species can make a full recovery is highly uncertain. Ambiguity also surrounds the effects of ocean acidification on coral net calcification and growth [56, 57]. Most simulations assumed linear reductions in net calcification with falling aragonite saturation state. However, much less extreme reductions in calcification have also been reported [58]. We repeated the business-as-usual greenhouse gas emissions but substituted a more benign impact of ocean acidification on net calcification (Figure 4D). Although carbonate budgets improved, the overall result remained unchanged; even with parrotfish protection, no eutrophication, and an initial cover of 20% coral, carbonate budgets eventually became strongly negative (see also Figure S2). This is likely because the effects of ocean acidification on corals appeared to be considerably less influential in driving the negative budget projections than rising SSTs, agreeing with other recent work [59].

The assessment of coral reefs for management has largely focused on ecological variables such as coral cover, coral size distribution, and fish abundance [5]. Yet the ultimate goals of most management are founded on the functions delivered by reefs as three-dimensional geological structures. We propose that carbonate budgets could be used to set target levels of coral, water quality, and herbivory that enable reefs to be maintained in positive accretion and therefore better able to deliver the biodiversity and livelihood goals of reef management. Although better local management should always favor reef function, there was no a priori reason to expect that the combination of local and global interventions would have the potential to sustain net carbonate accretion in the 21<sup>st</sup> century. Yet our results suggest that local interventions are far from futile [60], and indeed are essential for assuring sustained ecosystem functioning. Unfortunately, only three countries in the region have taken steps to protect herbivorous fish throughout their coastal zone (Belize, Bermuda, and Bonaire), so protection is usually confined to small no-take marine reserves. We also provide unambiguous evidence that local efforts must be accompanied by rigorous global action to mitigate climate change.

#### Experimental Procedures

A simulation model was created in Matlab (MATLAB 7.1, The MathWorks, Natick, MA, 2000). Model parameters were drawn from published literature

on Caribbean reefs, some unpublished data, and climate data from IPCC AR5 earth system models (see Figure S3). One hundred fifteen parameters were defined in total, and each was assigned a mean value and a standard deviation (Table S1). All model parameters and scenarios are provided in detail in the Supplemental Experimental Procedures.

#### Supplemental Information

Supplemental Information includes nine figures, four tables, and Supplemental Experimental Procedures and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2013.04.020>.

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#### References

1. Hoegh-Guldberg, O., Mumby, P.J., Hooten, A.J., Steneck, R.S., Greenfield, P., Gomez, E., Harvell, C.D., Sale, P.F., Edwards, A.J., Caldeira, K., et al. (2007). Coral reefs under rapid climate change and ocean acidification. *Science* 318, 1737–1742.
2. Gardner, T.A., Côté, I.M., Gill, J.A., Grant, A., and Watkinson, A.R. (2003). Long-term region-wide declines in Caribbean corals. *Science* 301, 958–960.
3. Bruno, J.F., and Selig, E.R. (2007). Regional decline of coral cover in the Indo-Pacific: timing, extent, and subregional comparisons. *PLoS ONE* 2, e711.
4. Done, T.J., Ogden, J.C., Wiebe, W.J., and Rosen, B.R. (1996). Biodiversity and ecosystem function of coral reefs. In *Functional roles of biodiversity: A global perspective*, H.A. Mooney, J.H. Cushman, E. Medina, O.E. Sala, and E.-D. Schulze, eds. (Chichester, UK: John Wiley & Sons).
5. Perry, C.T., Edinger, E.N., Kench, P.S., Murphy, G.N., Smithers, S.G., Steneck, R.S., and Mumby, P.J. (2012). Estimating rates of biologically driven coral reef framework production and erosion: a new census-based carbonate budget methodology and applications to the reefs of Bonaire. *Coral Reefs* 31, 853–868.
6. Stearn, C.W., Scoffin, T.P., and Martindale, W. (1977). Calcium carbonate budget of a fringing reef on the west coast of Barbados. Part 1: Zonation and Productivity. *Bull. Mar. Sci.* 27, 479–510.
7. Knowlton, N., Brainard, R.E., Fisher, R., Moews, M., Plaisance, L., and Caley, M.J. (2010). Coral Reef Biodiversity. In *Life in the World's Oceans*, A. McIntyre, ed. (Oxford: Wiley-Blackwell).
8. Perry, C.T., Spencer, T., and Kench, P.S. (2008). Carbonate budgets and reef production states: a geomorphic perspective on the ecological phase-shift concept. *Coral Reefs* 27, 853–866.
9. Perry, C.T., Murphy, G.N., Kench, P.S., Smithers, S.G., Edinger, E.N., Steneck, R.S., and Mumby, P.J. (2013). Caribbean-wide decline in carbonate production threatens coral reef growth. *Nat Commun* 4, 1402.
10. Donner, S.D., Skirving, W.J., Little, C.M., Oppenheimer, M., and Hoegh-Guldberg, O.V.E. (2005). Global assessment of coral bleaching and required rates of adaptation under climate change. *Glob. Change Biol.* 11, 2251–2265.
11. Rogers, C. (2009). Coral bleaching and disease should not be underestimated as causes of Caribbean coral reef decline. *Proc. Biol. Sci.* 276, 197–198, discussion 199–200.
12. Weil, E., and Rogers, C.S. (2011). Coral reef diseases in the Atlantic-Caribbean. In *Coral Reefs: An Ecosystem in Transition*, Z. Dubinsky and N. Stambler, eds. (Dordrecht, The Netherlands: Springer), pp. 465–491.
13. Mumby, P.J., Hastings, A., and Edwards, H.J. (2007). Thresholds and the resilience of Caribbean coral reefs. *Nature* 450, 98–101.
14. Manzello, D.P., Kleypas, J.A., Budd, D.A., Eakin, C.M., Glynn, P.W., and Langdon, C. (2008). Poorly cemented coral reefs of the eastern tropical Pacific: possible insights into reef development in a high-CO<sub>2</sub> world. *Proc. Natl. Acad. Sci. USA* 105, 10450–10455.
15. Wisshak, M., Schönberg, C.H.L., Form, A., and Freiwald, A. (2012). Ocean acidification accelerates reef bioerosion. *PLoS ONE* 7, e45124.
16. Hubbard, D.K., Miller, A.I., and Scaturro, D. (1990). Production and cycling of calcium-carbonate in a shelf-edge reef system (St. Croix, United States Virgin Islands): applications to the nature of reef systems in the fossil record. *J. Sediment. Petrol.* 60, 335–360.
17. Land, L.S. (1974). Growth rate of a West Indian (Jamaican) reef. In *Proceedings of the 2nd International Symposium on Coral Reefs*, Volume 2, A.M. Cameron, B.M. Cambell, A.B. Cribb, R. Endean, J.S. Jell, O.A. Jones, P. Mather, and F.H. Talbot, eds. (Brisbane, Australia), pp. 409–412.
18. De'ath, G., Fabricius, K.E., Sweatman, H., and Puotinen, M. (2012). The 27-year decline of coral cover on the Great Barrier Reef and its causes. *Proceedings of the National Academy of Sciences*.
19. Alvarez-Filip, L., Dulvy, N.K., Gill, J.A., Côté, I.M., and Watkinson, A.R. (2009). Flattening of Caribbean coral reefs: region-wide declines in architectural complexity. *Proc. Biol. Sci.* 276, 3019–3025.
20. Hughes, T.P., Graham, N.A.J., Jackson, J.B.C., Mumby, P.J., and Steneck, R.S. (2010). Rising to the challenge of sustaining coral reef resilience. *Trends Ecol. Evol.* 25, 633–642.
21. Kinsey, D.W. (1985). Metabolism, calcification and carbon production. In *Proceedings of the 5th International Coral Reef Congress*, C. Gabrie and B. Salvat, eds. (Tahiti).
22. Moore, C.H., and Shedd, W.W. (1977). Effective rates of sponge bioerosion as a function of carbonate production. In *Proceedings of the 3rd International Coral Reef Symposium*, Volume 2, D.L. Taylor, ed. (Miami, Florida), pp. 499–505.
23. Vecsei, A. (2001). Fore-reef carbonate production: development of a regional census-based method and first estimates. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 175, 185–200.
24. Hughes, T.P. (1994). Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* 265, 1547–1551.
25. Steneck, R.S. (1994). Is herbivore loss more damaging to reefs than hurricanes? Case studies from two Caribbean reef systems (1978–1988). In *Global Aspects of Coral Reefs: Health, Hazards, and History*, R.N. Ginsburg, ed. (Florida: University of Miami), pp. C32–C37.
26. Stearn, C.W., and Scoffin, T.P. (1977). Carbonate budget of a fringing reef, Barbados. In *Proceedings of the 3rd International Coral Reef Symposium*, Volume 1. (Miami: Rosenstiel School of Marine and Atmospheric Sciences), pp. 471–476.
27. Eakin, C.M. (1996). Where have all the carbonates gone? A model comparison of calcium carbonate budgets before and after the 1982–1983 El Niño at Uva Island in the eastern Pacific. *Coral Reefs* 15, 109–119.
28. Lessios, H.A. (1988). Mass mortality of *Diadema antillarum* in the Caribbean: What have we learned? *Annu. Rev. Ecol. Syst.* 19, 371–393.
29. Steneck, R.S. (1994). Is herbivore loss more damaging to reefs than hurricanes? Case studies from two Caribbean reef systems (1978–1988). In *Global Aspects of Coral Reefs: Health, Hazards and History*, R.N. Ginsburg, ed. (Miami, FL: University of Miami), pp. C32–C37.
30. Wilkinson, C., and Souter, D. (2008). Status of Caribbean coral reefs after bleaching and hurricanes in 2005. *Global Coral Reef Monitoring Network, and Reef and Rainforest Research Centre*. (Townsville, Australia: Global Coral Reef Monitoring Network).
31. Miller, J., Muller, E., Rogers, C., Waara, R., Atkinson, A., Whelan, K.R.T., Patterson, M., and Witcher, B. (2009). Coral disease following massive bleaching in 2005 causes 60% decline in coral cover on reefs in the US Virgin Islands. *Coral Reefs* 28, 925–937.
32. Eakin, C.M., Morgan, J.A., Heron, S.F., Smith, T.B., Liu, G., Alvarez-Filip, L., Baca, B., Bartels, E., Bastidas, C., Bouchon, C., et al. (2010). Caribbean corals in crisis: record thermal stress, bleaching, and mortality in 2005. *PLoS ONE* 5, e13969.
33. Mallela, J., and Perry, C.T. (2007). Calcium carbonate budgets for two coral reefs affected by different terrestrial runoff regimes, Rio Bueno, Jamaica. *Coral Reefs* 26, 129–145.
34. Carreiro-Silva, M., McClanahan, T.R., and Kiene, W.E. (2005). The role of inorganic nutrients and herbivory in controlling microbioerosion of carbonate substratum. *Coral Reefs* 24, 214–221.

35. Hallock, P. (1988). The role of nutrient availability in bioerosion: Consequences to carbonate buildups. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 63, 275–291.
36. Rose, C.S., and Risk, M.J. (1985). Increase in *Cliona delitrix* infestation of *Montastraea cavernosa* heads on an organically polluted portion of the Grand Cayman fringing reef. *Mar. Ecol. (Berl.)* 6, 345–363.
37. Ferrier-Pagés, C., Gattuso, J.P., Dallot, S., and Jaubert, J. (2000). Effect of nutrient enrichment on growth and photosynthesis of the zooxanthellate coral *Stylophora pistillata*. *Coral Reefs* 19, 103–113.
38. Marubini, F., and Davies, P.S. (1996). Nitrate increases zooxanthellae population density and reduces skeletogenesis in corals. *Mar. Biol.* 127, 319–328.
39. Mumby, P.J., Dahlgren, C.P., Harborne, A.R., Kappel, C.V., Micheli, F., Brumbaugh, D.R., Holmes, K.E., Mendes, J.M., Broad, K., Sanchirico, J.N., et al. (2006). Fishing, trophic cascades, and the process of grazing on coral reefs. *Science* 311, 98–101.
40. Mumby, P.J., and Harborne, A.R. (2010). Marine reserves enhance the recovery of corals on Caribbean reefs. *PLoS ONE* 5, e8657.
41. Collins, W.J., Bellouin, N., Doutriaux-Boucher, M., Gedney, N., Halloran, P., Hinton, T., Hughes, J., Jones, C.D., Joshi, M., Liddicoat, S., et al. (2011). Development and evaluation of an Earth-System model – HadGEM2. *Geoscientific Model Development* 4, 1051–1075.
42. Roff, G., and Mumby, P.J. (2012). Global disparity in the resilience of coral reefs. *Trends in Ecology & Evolution* 27, 404–413.
43. Van Oppen, M.J.H., Souter, P., Howells, E.J., Heyward, A., and Berkelmans, R. (2011). Novel Genetic Diversity Through Somatic Mutations: Fuel for Adaptation of Reef Corals? *Diversity* 3, 405–423.
44. Mumby, P.J., Elliott, I.A., Eakin, C.M., Skirving, W., Paris, C.B., Edwards, H.J., Enríquez, S., Iglesias-Prieto, R., Cherubin, L.M., and Stevens, J.R. (2011). Reserve design for uncertain responses of coral reefs to climate change. *Ecol. Lett.* 14, 132–140.
45. Mumby, P.J., Steneck, R.S., and Hastings, A. (2013). Evidence for and against the existence of alternate attractors on coral reefs. *Oikos* 122, 481–491.
46. Rotjan, R.D., and Lewis, S.M. (2008). Impact of coral predators on tropical reefs. *Mar. Ecol. Prog. Ser.* 367, 73–91.
47. Smith, J.E., Runcie, J.W., and Smith, C.M. (2005). Characterization of a large-scale ephemeral bloom of the green alga *Cladophora sericea* on the coral reefs of West Maui, Hawai'i. *Mar. Ecol. Prog. Ser.* 302, 77–91.
48. Marubini, F., and Atkinson, M.J. (1999). Effects of lowered pH and elevated nitrate on coral calcification. *Mar. Ecol. Prog. Ser.* 188, 117–121.
49. Anthony, K.R.N. (1999). Coral suspension feeding on fine particulate matter. *J. Exp. Mar. Biol. Ecol.* 232, 85–106.
50. Holmes, K.E. (1997). Eutrophication and its effect on bioeroding sponge communities. In 8th International Coral Reef Symposium, Volume 2, H.A. Lessios and I.G. MacIntyre, eds. (Smithsonian Tropical Research Institute, Panama).
51. Ward-Paige, C.A., Risk, M.J., Sherwood, O.A., and Jaap, W.C. (2005). Clonid sponge surveys on the Florida Reef Tract suggest land-based nutrient inputs. *Mar. Pollut. Bull.* 51, 570–579.
52. Carreiro-Silva, M., McClanahan, T.R., and Kiene, W.E. (2009). Effects of inorganic nutrients and organic matter on microbial euendolithic community composition and microbioerosion rates. *Mar. Ecol. Prog. Ser.* 392, 1–15.
53. Kinsey, D.W., and Davis, P.J. (1979). Effect of elevated nitrogen and phosphorus on coral reef growth. *Limnol. Oceanogr.* 25, 935–940.
54. Gattuso, J.P., Frankignoulle, M., Bourge, I., Romaine, S., and Buddemeier, R.W. (1998). Effect of calcium carbonate saturation of seawater on coral calcification. *Global Planet. Change* 18, 37–46.
55. Langdon, C., Takahashi, T., Sweeney, C., Chipman, D., and Goddard, J. (2000). Effect of calcium carbonate saturation state on the rate of calcification of an experimental coral reef. *Global Biogeochem. Cycles* 14, 639–654.
56. Pandolfi, J.M., Connolly, S.R., Marshall, D.J., and Cohen, A.L. (2011). Projecting coral reef futures under global warming and ocean acidification. *Science* 333, 418–422.
57. Erez, J., Reynaud, S., Silverman, J., Schneider, J., and Allemand, D. (2011). Coral calcification under ocean acidification and global change. In *Coral Reefs: An Ecosystem in Transition*, Z. Dubinsky and N. Stambler, eds. (Berlin: Springer), pp. 151–176.
58. Gattuso, J.P., Frankignoulle, M., and Wollast, R. (1998). Carbon and carbonate metabolism in coastal aquatic ecosystems. *Annu. Rev. Ecol. Syst.* 29, 405–434.
59. Chan, N.C.S., and Connolly, S.R. (2013). Sensitivity of coral calcification to ocean acidification: a meta-analysis. *Glob. Change Biol.* 19, 282–290.
60. Bradbury, R.H. (2012). A world without coral reefs. *The New York Times*, July 14, 2012. A17. <http://www.nytimes.com/2012/07/14/opinion/a-world-without-coral-reefs.html>.