LETTERS

Thresholds and the resilience of Caribbean coral reefs

Peter J. Mumby[1], Alan Hastings[2] & Helen J. Edwards[1]

The deteriorating health of the world's coral reefs threatens global biodiversity, ecosystem function, and the livelihoods of millions of people living in tropical coastal regions[1]. Reefs in the Caribbean are among the most heavily affected[2,3], having experienced mass disease-induced mortality of the herbivorous urchin *Diadema antillarum*[4] in 1983 and two framework-building species of coral[5]. Declining reef health is characterized by increases in macroalgae. A critical question is whether the observed macroalgal bloom on Caribbean reefs is easily reversible. To answer this question, we must resolve whether algal-dominated reefs are an alternative stable state of the ecosystem or simply the readily reversible result of a phase change along a gradient of some environmental or ecological parameter[6]. Here, using a fully parameterized simulation model in combination with a simple analytical model, we show that Caribbean reefs became susceptible to alternative stable states once the urchin mortality event of 1983 confined the majority of grazing to parrotfishes. We reveal dramatic hysteresis in a natural system[7,8] and define critical thresholds of grazing and coral cover beyond which resilience is lost. Most grazing thresholds lie near the upper level observed for parrotfishes in nature, suggesting that reefs are highly sensitive to parrotfish exploitation. Ecosystem thresholds can be combined with stochastic models of disturbance to identify targets for the restoration of ecosystem processes. We illustrate this principle by estimating the relationship between current reef state (coral cover and grazing) and the probability that the reef will withstand moderate hurricane intensity for two decades without becoming entrained in a shift towards a stable macroalgal-dominated state. Such targets may help reef managers face the challenge of addressing global disturbance at local scales.

Several studies have documented phase changes from coral- to algal-dominated states on Caribbean reefs[9–11] but none were designed to distinguish simple quantitative changes from the dramatic qualitative changes associated with multiple stable states and hysteresis[12]. Experimental evidence for multiple stable states would need to identify the emergence of multiple stable equilibria from a single parameter value. Given that ethical and logistical issues constrain an experimental approach to this problem[12], we discover multiple stable equilibria by using a mechanistic model of the ecosystem[13].

We modelled structurally complex forereef habitats of the Caribbean using a simulation that had the advantage of exploring reef dynamics with a minimum of simplifying assumptions (full details and parameters are in the Supplementary Information). All model parameters were derived from empirical studies in the Leeward Islands[14], southern Caribbean[15,16] and Central America[17]. Brooding and spawning forms of coral recruit at a size of 1 cm^2 and experience both chronic and acute mortality. Macroalgae, based on the dominant genera *Lobophora* and *Dictyota*, proliferate if dead coral is not sufficiently grazed and have a limited capacity either to arrest coral growth[18] or to overgrow living coral when in direct proximity[19]. An unexploited community of parrotfishes can maintain approximately 40% of the reef in a permanently grazed state but overfishing reduces this capacity to about 5% (refs 13, 20). Modest urchin populations are more effective grazers than parrotfishes[16]. Comparing model predictions to an exceptionally long time series of independent field data from Jamaica[10], we find that the model emulates coral dynamics faithfully even when the rate of algal–coral overgrowth is varied within published levels (Fig. 1).

The model suggests that Caribbean coral reefs did not exhibit an algal-dominated stable state when the urchin *Diadema* was present in the system (Fig. 2). At grazing levels exceeding 0.42, meaning that parrotfishes and urchins graze at least 42% of the reef every six months, all reefs, regardless of their state (coral cover), show an upward trajectory towards an equilibrium of high coral cover. However, two stable states emerged after the mass mortality of urchins in 1983 when grazing became dominated by parrotfishes (grazing intensity 0.05–0.4). The open squares in Fig. 2 represent unstable equilibria that join upper and lower stable equilibria. Reefs above and to the right of an unstable equilibrium follow a trajectory towards a stable equilibrium at high coral cover whereas those below and left of the line decline to a stable, macroalgal-dominated state with low coral cover (macroalgal cover not shown).

Multiple equilibria occur because of ecological feedbacks. For example, a decline in coral cover liberates new space for algal colonization. Once maximum levels of grazing have been reached, further increases in grazable area reduce the mean intensity of grazing and increase the probability that a patch of macroalgae will establish,

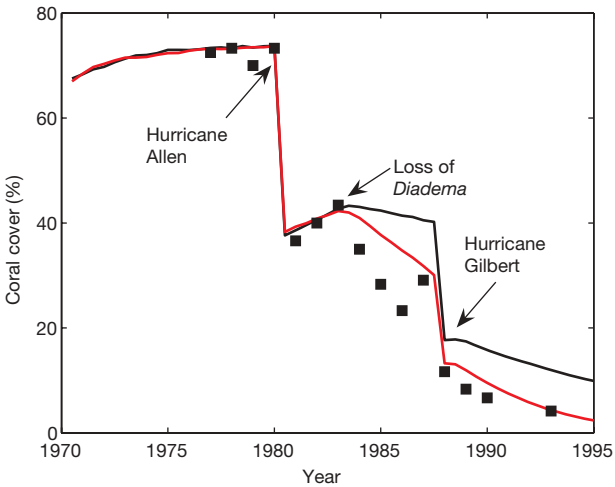

Figure 1 | Comparison between model predictions and Hughes' empirical data for the trajectory of structurally complex forereefs in Jamaica at a depth of 10 m. Predictions are denoted by lines and empirical data are denoted by black squares. The model that was run with a median algal–coral overgrowth rate of 8 $cm^2\,yr^{-1}$ is shown with a black line and the upper rate of 14 $cm^2\,yr^{-1}$ is shown with a red line.

[1]Marine Spatial Ecology Lab, School of BioSciences, University of Exeter, Prince of Wales Road, Exeter EX4 4PS, UK. [2]Environmental Science and Policy, University of California, Davis, California 95616, USA.

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ungrazed, from the algal turf. The resulting rise in macroalgal cover reduces the availability of coral settlement space and increases the frequency and intensity of coral–algal interactions, thereby reducing coral recruitment, reducing the growth rate of corals and causing limited mortality. The resulting increase in coral mortality further reduces the intensity of grazing, thereby reinforcing the increase in macroalgae. Importantly, hysteresis behaviour appears to be a fundamental property of the ecosystem. To confirm this and determine the features that are essential for the hysteresis effect, we simplified the ecosystem into a three-state analytical model with corals, macroalgae and short algal turfs.

Let C, T and M represent (as a fraction of the seabed available) the cover of corals, algal turfs and macroalgae respectively. Thus we assume that the sum $T+M+C$ is constant over time (here assumed to equal one), so only two equations are required to describe the dynamics of the reef (and we can express T as $1-M-C$):

$$\frac{dM}{dt} = aMC - \frac{gM}{M+T} + \gamma MT \quad (1)$$

$$\frac{dC}{dt} = rTC - dC - aMC \quad (2)$$

Grazers are assumed not to discriminate between algal types. Algal turfs arise when macroalgae are grazed ($gM/(M+T)$) and as a result of natural coral mortality ($-dC$). Corals recruit to and overgrow algal turfs at a combined rate r, constrained by the existing cover of turfs. Corals can be overgrown by macroalgae ($-aMC$) but macroalgae usually colonize dead coral by spreading vegetatively over algal turfs (γMT).

Our analysis of this system has been primarily numerical. The phase plane[21] in Fig. 3 shows all possible dynamical behaviour of the system. Each trajectory describes how populations change over time for a given initial state. All trajectories are attracted to a stable equilibrium, at which point the covers of coral and macroalgae remain constant. The dynamical behaviour of the system differs dramatically between high and low levels of grazing (compare Fig. 3a and Fig. 3b). Two stable states, with either coral (C_s) or macroalgal-domination (M_s) arise at high grazing, as predicted by the simulation model (Fig. 3a). In addition, there are two non-negative unstable equilibria including a saddle point with corals, macroalgae and turf (CMT_u), equivalent to the unstable equilibrium represented by the open squares in Fig. 2, and a system dominated by turf (T_u), which is never reached when reefs start with positive values of macroalgae or corals. In contrast, only a single stable equilibrium exists (M_s) when grazing levels are low (Fig. 3b) and C_s becomes an unstable saddle (C_u). The analytical model thus replicates the results of the simulation model in that the system may be driven to a high or low coral state and suggests that the essential interactions are those included in the analytical model, thereby confirming our explanation of the dynamics of the simulation model and the natural system.

The most appealing aspect of the hysteresis plot (Fig. 2) is that it helps define reef management objectives by explicitly integrating the impacts of disturbance with the effects of conservation action. The locations of thresholds and bifurcation points reflect the underlying ecosystem dynamics and are influenced by processes such as primary production and chronic coral mortality rates. Acute disturbance phenomena such as coral bleaching[22] cause sudden coral mortality and shift the state of a reef down the y axis, whereas periods of recovery allow the reef to move back up the y axis. Changes in grazing on the x axis represent the effects of fishing herbivores (shifts from right to left) and active herbivore management, such as marine

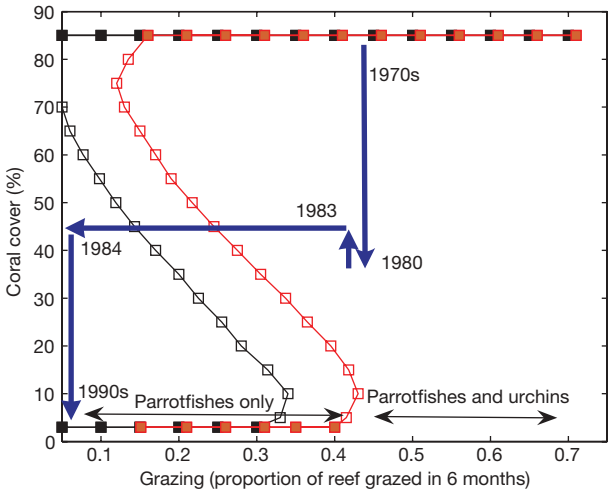

Figure 2 | Stable and unstable equilibria for Caribbean coral reefs at two levels of algal-coral overgrowth. Stable and unstable equilibria are denoted by solid and open squares, respectively. Black denotes 8 $cm^2 yr^{-1}$, red denotes 14 $cm^2 yr^{-1}$. Blue lines, marked with appropriate dates, represent model predictions of the trajectory of reefs in Jamaica (see also Fig. 1).

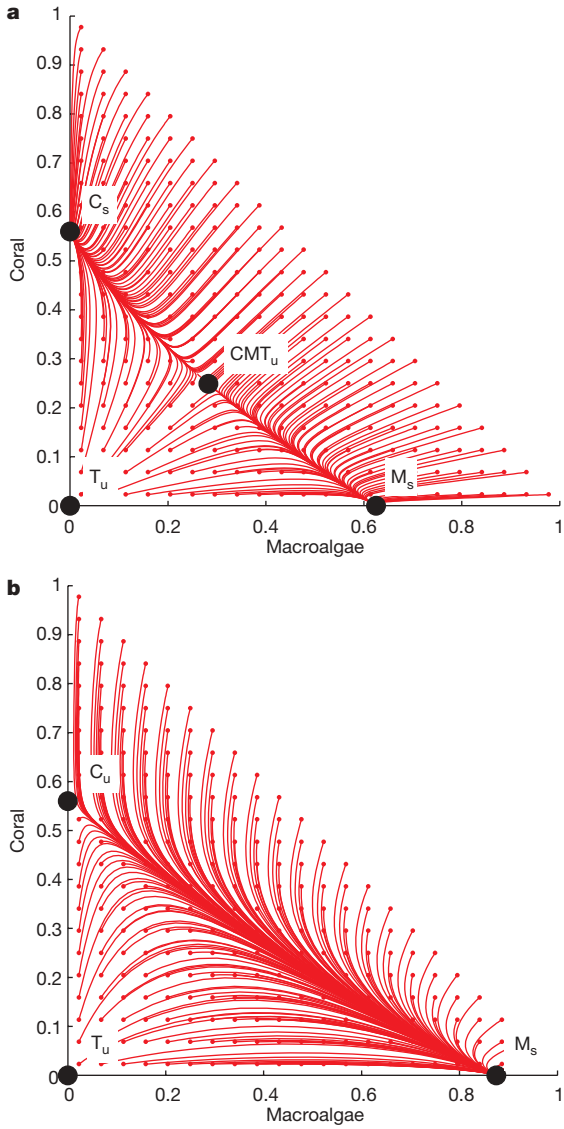

Figure 3 | Phase plane showing equilibrium covers of macroalgae and corals and trajectories over time. a, b, Equilibrium covers are denoted by black circles; trajectories are shown in red for grazing intensities of 0.3 (**a**) and 0.1 (**b**). Trajectories may be thought of as arrows beginning at different initial covers (red circles) and tending towards the stable (subscript s) rather than unstable (subscript u) equilibria.

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reserve implementation or the banning of fish traps (shifts from left to right).

The interpretation of such plots is easily illustrated for the decline in health of some Jamaican reefs between 1981 and 1993 (Fig. 2). By 1979, forereefs had not experienced a severe hurricane for 36 years and coral cover was high at ~75% (ref. 10). In 1980, a combination of coral disease and hurricane Allen reduced coral cover to around 38%, but because urchins were present, the reef began to recover. When the urchins died out in 1983, grazing levels were decimated, in part because long-term overfishing had removed larger parrotfishes. With a coral cover of approximately 44% and a grazing intensity of only 0.05–0.113, the reef began a negative trajectory towards algal domination that was exacerbated by further acute disturbance. By 1993, coral cover had fallen to less than 5%. A key feature of this graph is that reversing reef decline becomes ever more difficult as the cover of coral declines; as coral cover drops, the level of grazing needed to place the reef on the reverse trajectory (to the right of the unstable equilibrium) increases. Continuing the example of a simulated Jamaican reef, conservation action in the mid-1990s would require grazing levels to be elevated at least fourfold to the maximum observed levels for fishes in the Caribbean. In contrast, if action were taken a decade earlier when coral cover was still around 30%, target grazing levels would be more easily achievable, requiring only a two- to threefold increase.

Hysteresis plots from a field-tested simulation model may improve ecosystem management. Rather than suspecting that bistability occurs at some abstract level of grazing, which might be predicted by an analytical model, it now appears that fishing effects on parrotfish grazing may profoundly influence coral dynamics. Therefore, active management of parrotfishes is both highly desirable and a feasible conservation goal[20]. Recent reports of *Diadema* recovery[23] are promising given the high resilience conferred by the species, but the impact of urchins is only beneficial if their predators are not over-exploited, which would lead to undesirable urchin plagues[24]. Moreover, the hysteresis plot can be combined with stochastic model simulations to create a novel and explicit metric of resilience and set targets for restoration (for example, target levels of grazing). For a given level of grazing, a reef will be resilient if the net impact of disturbance and recovery does not force its state below the unstable equilibrium. This in turn depends on the local disturbance regime[25]. Using stochastic simulation, we can determine the probability that a reef will remain above the unstable equilibrium and an example is given for reefs in Central America that experience acute hurricanes with a 20-year periodicity (Fig. 4). In principle, this metric of resilience could be calculated for any physical environment, provided that a parameterization for disturbance events was available. For a given biophysical environment, our approach should help to identify the target levels of coral cover and grazing needed to reverse ecosystem decline and illuminate the efficacy of local conservation policy options against the threat of global climate change on coral reefs.

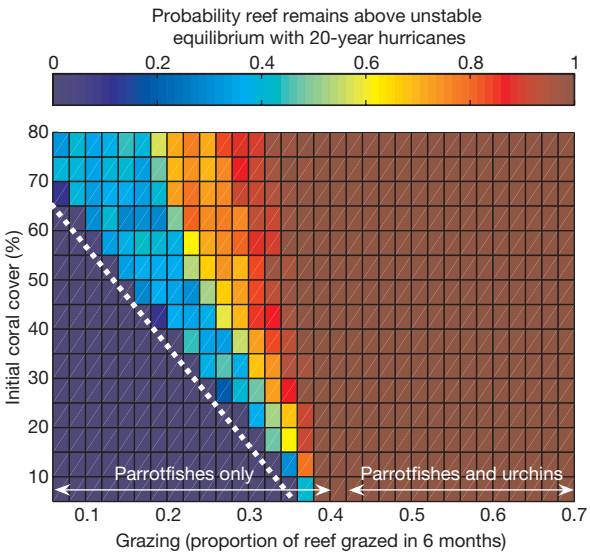

Figure 4 | Probability that reefs of given initial state will remain above the unstable equilibrium during a 25-year period. The physical disturbance regime includes stochastic hurricanes with a 20-year periodicity and the algal–coral overgrowth rate is 8 $cm^2 yr^{-1}$. The unstable equilibrium is denoted with a thick dashed white line.

METHODS SUMMARY

The simulation model followed the dynamics of individual coral colonies in discrete six-month steps. Although the reef has a toroidal lattice of 2,500 cells (each of size 0.25 m^2), the lattice merely helps to define probabilistic rules of coral recruitment and vegetative algal growth. Individual cells comprise multiple coral colonies and algal patches, so interactions occur at colony scales. Unstable equilibria were found by disabling acute disturbance and running simulations with a 25-year period. Initial coral cover was set at 5% intervals with an even mix of brooding and spawning taxa. Grazing was manipulated at intervals of 0.005 and unstable equilibria were defined as combinations of grazing and coral cover for which total cover remained within 2% of its initial level. A resilience plot was generated by conducting 100 simulations of a 25-year run and recording the probability that a reef drops below the mean unstable equilibrium. Hurricanes occurred stochastically but with a long-term 20-year periodicity. Sensitivity analyses reveal that perturbations to parameters and a full stochastic version of the model have little influence on the location of grazing thresholds. The model is most sensitive to the growth rate of brooding corals and changes in the rate of live coral overgrowth by macroalgae, for which extreme values are plotted in Fig. 2. However, variability in either parameter does not alter our conclusions because grazing thresholds are still found to coincide with the upper level of fish grazing.

Equilibria and their stability were determined for the analytic model by standard means[21]. Trajectories were plotted using numerical integration with 4th- and 5th-order Runge–Kutta formulae[26]. We use as simple a model as possible and ignore some time delays that must be present in natural systems (for example, we assume that algal turfs arise instantaneously after macroalgae are grazed). Such assumptions will not affect the equilibrium structure, and should have only limited effect on stability and dynamics.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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Author Contributions P.J.M. jointly conceived the study with A.H., designed and implemented the simulation model, and prepared the manuscript; A.H. created the analytic model with contributions from H.J.E. and P.J.M, supervised its analysis and edited the manuscript; H.J.E. analysed and described the analytic model, carried out the stochastic implementation of the simulation model, and edited the manuscript.

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Supplementary Information

Simulation model design, parameterisation and sensitivity analyses

Design and parameterisation

A simulation model was originally designed to represent mid-depth (6-20 m) forereefs which typically harbour the highest biomass and diversity of reef organisms[1,2]. Since white band disease has depleted populations of large, branching corals[3] stylised massive growth forms of coral were simulated together with rates of recruitment, growth, reproduction and mortality. The model is a square lattice of 2500 cells each of which approximates 0.25 m^2 of reef, and can be occupied by a *mixture* of living and dead substrata (Table 1). Although the reef has a toroidal lattice of 2500 cells, the lattice structure merely helps define probabilistic rules of coral recruitment and vegetative algal growth. Individual cells comprise multiple coral colonies and algal patches so interactions occur at colony scales as they do in situ. The reef has continuous boundaries, arranged as a torus. Corals can recruit to individual patches of cropped algae but not macroalgae. Macroalgae grow vegetatively and can overgrow corals. Grazing affects all algal classes and always results in the first grazed algal class. An unexploited community of parrotfishes can maintain up to 40% of the reef area in a grazed state every 6 months (Table 2). The effects of fishing, which change the density and size-structure of fishes[4], have been modelled previously[1] and deplete grazing to 5% of the reef. Grazing by the urchin *Diadema antillarum* is independent from that of parrotfishes and covers a maximum proportion of 53% of the reef area (Table 2). Competitive interactions between corals and macroalgae reduce the growth rate of each taxon and are the only process modelled to occur across cell boundaries (within a 4-cell von Neumann neighbourhood). The spatial arrangement of elements within an individual cell has no explicit spatial structure, but coral-coral competition can occur at intra-cellular scales. Corals are subjected to size-dependent fecundity and mortality, resulting in three functional categories: recruits (horizontal cross-sectional area 1-60 cm^2), pubescents (61-250 cm^2), and adults (>250 cm^2). All simulations assume no stock-recruitment relationship and corals recruit at maximum levels irrespective of stock size (i.e. up to 4 per 0.25m^{-2}). Individual cells in the lattice are updated in random sequence using discrete intervals of 6 months. Acute disturbance occurs from hurricanes. Although this is a simulation model, several of the parameters, such as coral growth rate, are entered as constants rather than allowed to vary probabilistically (but a probabilistic version is described below). This approach avoids unnecessary variation from relatively well-established parameters and is consistent with other models of reef processes[5,6]. The parameterisation was based on reefs with little or no mangrove connectivity and little sediment deposition. A full list of parameters is given in Table 2.

Table 1. Contents of individual cells (0.25 m^2) within the model. All substrata represented as area (cm^2). Area of U based on average value from Glovers Reef, Belize.

Substratum	Constraints	Range (cm^2)
Brooding coral (e.g. *Porites astreoides*), (BC)	up to three individuals per cell	$1 \leq BC \leq 2500$
Spawning coral (e.g. *Siderastrea siderea*), (SC)		$1 \leq SC \leq 2500$
Cropped algae [filamentous, coralline red algae, & short turfs (<5 mm height)], 0-6 months (A_6)		$0 \leq A_6 \leq 2500$
Cropped algae, 6-12 months (A_{12})		$0 \leq A_{12} \leq 2500$
Macroalgae (e.g. *Dictyota pulchella*, *Lobophora variegata*), 0-6 months (M_6)		$0 \leq M_6 \leq 2500$
Macroalgae, 6+ months (M_{12})		$0 \leq M_{12} \leq 2500$
Ungrazable substratum (e.g. sand), U	fills entire cell if present	U=0 or U=2500

Table 2. Parameterisation of simulation model

Parameter	**Details**
Coral recruitment	Corals recruit to cropped algae, A_6 and A_{12}, because algal turfs are not heavily sediment-laden. Recruit at size 1 cm^2. Recruitment rate of brooders and spawners (respectively): 2 and 0.2 per 0.25 m^2 of cropped algae per time interval. Recruitment rate was adjusted for rugosity (~2) and the cover of cropped algae at Glovers Reef[7]
Coral growth	Coral size is quantified as the cross-sectional, basal area of a hemispherical colony (cm^2). BC have a lateral extension rate of 0.8 cm yr^{-1} and SC grow slightly faster at 0.9 cm yr^{-1} (based on median rates for *Porites astreoides*, *P. porites*, *Siderastrea siderea*, *Montastraea annularis*, *Colpophyllia natans and Agaricia agaricites*)[8-12]
Coral reproduction	Excluded, assume constant rate of coral recruitment from outside reef (i.e. no stock-recruitment dynamics)
Colonisation of cropped algae	Cropped algae arises (i) when macroalgae is grazed and (ii) after all coral mortality events[13] except those due to macroalgal overgrowth (see coral-algal competition below).
Colonisation of macroalgae	Macroalgae have a 70% chance of becoming established if cropped algae are not grazed for 6 months (mostly *Dictyota*) and this increases to 100% probability after 12 mo of no grazing (mostly *Lobophora*). Rates acquired from detailed centimeter-resolution observations of algal dynamics with and without grazing[14,15]
Macroalgal growth over dead coral (cropped algae)	In addition to arising from cropped algae that are not grazed (above), established macroalgae also spread vegetatively over cropped algae (mostly *Lobophora* as *Dictyota* spread shows little pattern with grazing[15]). The probability that macroalgae will encroach onto the algal turf within a cell, $P_{A \rightarrow M}$, is given by (1) where M_{4cells} is the percent cover of macroalgae within the von Neumann (4-cell) neighbourhood[16]. This is a key method of algal expansion and represents the opportunistic overgrowth of coral that was extirpated by disturbance. $P_{A \rightarrow M} = M_{4cells}$ (1)
Competition between corals	If corals fill the cell (2500 cm^2), the larger coral overtops smaller corals (chosen at random if more than one smaller coral share the cell). If corals have equal size, the winner is chosen at random[17]
Competition between corals and cropped algae	Corals always overgrow cropped algae[13]

Competition between corals and macroalgae 1: effect of macroalgae on corals	a) Growth rate of juvenile corals (area <60 cm^2) set to zero if M_{4cells}>80%, and reduced by 70% if 60%<M_{4cells}<80%. Parameters based on both *Dictyota* and *Lobophora*[18] b) Growth rate of pubescent and adult corals (area≥60cm^2) reduced by 50% if M_{4cells}>60%[13,19] c) Limited direct overgrowth of coral by macroalgae can occur[20,21]. Nugues and Bak[22] found that the upper 95% CL of the mean area of overgrowth ranged from 0-18 cm^2 pa across a ~7cm length of coral edge, with an overall mean of 8 cm^2 pa. This translates to 4 cm^2 in each 6-mo time step of the model. Overgrowth (cm^2), $O_{C\rightarrow M}$, was scaled to entire colonies using (2) where M_{4cells} is the proportion of macroalgae in the von Neumann 4-cell neighbourhood and P_i is the perimeter of the coral. $O_{C\rightarrow M} = M_{4cells} \times P_i/7\times 4$ (2) Note that Nugues and Bak[22] did not find significant effects of *Lobophora* on all coral species studied. Whilst this was the correct interpretation of their data, the published results strongly suggest that an effect does exist and that a larger sample size may well have resulted in significant differences. Other studies have found negative effects of macroalgae on both massive[20] and branching corals[23].
Competition between corals and macroalgae 2: effect of corals on macroalgae	The vegetative growth rate of macroalgae, $P_{A\rightarrow M}$, is reduced by 25% when at least 50% of the local von Neumann neighbourhood includes coral[13,24] $proportion\ of\ \ coral, C = \frac{(BC+SC)}{2500}$ (3a) $P_{A\rightarrow M} = 0.75 \times M_{4cells}$ if $C \geq 0.5$ (3b) $P_{A\rightarrow M} = M_{4cells}$ if $C < 0.5$ (3c)

Grazing by fishes & impact of fishing	Grazing is spatially-constrained[1,4,25]. An unfished community of parrotfishes grazes a maximum of 40% of the seabed per 6 month time interval. The dynamic basis of this grazing threshold is poorly understood seeing as most measures of grazing take place at scales of seconds and most studies of algal dynamics take place on monthly scales (hence the use of a 6 month time step). Nonetheless empirical studies[1], and experimental results scaled to the complex forereef[25], have identified a grazing limit of 30%-40% of the reef during 6 months. This value allows for a numeric positive response by parrotfish after severe coral mortality events during which colonisation space for algae increases dramatically. For example, an increase in parrotfish biomass over 5 years maintained the cover of cropped algae at Glovers Reef at 30-40% after Hurricane Mitch caused extensive coral mortality and liberated new settlement space for macroalgae[15] (i.e. grazing impact remained at around 30% even though coral cover dropped from around 60% to 20%, suggesting that the approach is robust during phase changes). The reasons for this are not fully understood. All parrotfish species graze algal turfs and in doing so constrain the colonisation and vegetative growth of macroalgae. Direct removal of macroalgae occurs through the grazing of larger sparisomid species (up to 50% of bites in *S. viride*[26]) and natural fluctuations in algal dynamics including annual spawning events during which their cover is decimated[27]. Of course, macroalgae increase once the availability of settlement space exceeds the grazing threshold (e.g. as coral cover declines from disturbance). During a given time interval, cells are visited in a random order and all algae consumed until the total grazing impact is reached. This approach implies spatially-intensive grazing which appears to be more biologically-accurate than a spatially-extensive approach because parrotfish feed repeatedly at particular sites on time scales of days to weeks[26]. All turf and macroalgae are consumed (and converted to A_6) until the constraint is reached. A second, species-level model of parrotfish grazing was used to estimate the effect of fishing, which alters both the density and size-distribution of parrotfishes. The detailed parrotfish grazing model includes the species, size and life phase of individual fishes and predicts instantaneous grazing intensity; the total reef surface grazed per hour[1,4]. New data on the size distribution of parrotfishes from Jamaica were used to determine grazing intensity from heavily-fished sites[4]. Grazing intensities were found to be around one sixth that of unfished sites in Belize. Thus, fishing can reduce the instantaneous grazing intensity of parrotfish communities by at least six-fold. It was then assumed that this shift in grazing would hold linearly over a six month period and therefore the total proportion of reef effectively grazed over 6 months (i.e. the grazing parameter in the main simulation model) was reduced from 30-40% (unfished) to 5% (heavily fished).

Diadema antillarum	Urchin grazing is implemented in the same fashion as herbivorous fish. Up to 53% of the seabed can be grazed under normal conditions since studies of the impact of urchin die-off found that the contribution of urchin grazing was 4/3 that of parrotfish grazing in the USVI[28,29]. Urchins and fish can graze the same areas.
Partial-colony mortality of corals	Size-dependent, following empirical observations from Curaçao before major bleaching or hurricane disturbances[30]. State variables reported in literature converted to dynamic variables using least squares optimization until equilibrial state in model matched observed data. Implementation uses equations (4a) and (4b) where P_{pm} is the probability of a partial mortality event, A_{pm} is the area of tissue lost in a single event, and χ is the size of the coral in cm^2: $P_{pm} = 1-[60+(-12 \ln(\chi))]$ (4a) $\mathrm{Ln}[(A_{pm} \times 100)+1] = -0.5 + (1.1 \ln(\chi))$ (4b)
Whole-colony mortality of pubescent and adult corals	Incidence of mortality in pubescent corals (60-250 cm^2), 2% per time interval (~4% per annum). Halved to 1% (2% pa) for mature colonies (>250 cm^2)[31]. These levels of mortality occur in addition to macroalgal overgrowth. Algal overgrowth and predation affects juvenile corals (see above and below).
Predation on coral recruits	Instantaneous whole-colony mortality occurs from parrotfish predation at a rate of 15% each 6 month iteration of the model[18] Predation is confined to small corals of area ≤5cm^2, based on Meesters et al[30] where between 60% and 95% of bite-type lesions were of this size
Hurricane impact on pubescent & mature corals (>60 cm^2): whole-colony mortality	Whole-colony mortality of larger corals is represented using a quadratic function (5) where x is the cross-sectional basal area of colony[31,32]. Small colonies avoid dislodgement due to their low drag, intermediate-sized corals have greater drag and are light enough to be dislodged, whereas large colonies are heavy enough to prevent dislodgement $P_{hur} = -0.0000003x^2 + 0.0007x + 0.0551$ (5)
Hurricane impact on mature corals (>250 cm^2): partial-colony mortality	The extent of partial mortality, M_{hur}, is modelled using a Gaussian distribution with mean of 0.30 and standard deviation of 0.20. Each value of M_{hur} represents the percentage of original colony tissue that is lost due to the hurricane. If $M_{hur} \leq 0$, there is no mortality. If $M_{hur} \geq 1$, the entire colony is lost (though this is a rare event). Data from monitoring of impact of Hurricane Mitch in Belize[33]
Hurricane impact on juvenile corals (1-60 cm^2)	Scouring by sand during a hurricane may cause 80% whole-colony mortality in juvenile corals[7]
Hurricane impact on macroalgae	Hurricanes reduce the cover of macroalgae to 10% of its pre-hurricane level[15]
Hurricane frequency	Hurricanes were simulated using a binomial model which when implemented in discrete time approximates a poisson random distribution. Maximum long-term incidence of severe hurricanes ~10 years in Florida and 20 years in Mesoamerica[34,35]

Sensitivity analyses

Previous studies of the sensitivity of the model to various parameters concluded that changes in grazing had the greatest overall impact on model behaviour[1]. Furthermore, the model was found to be generally insensitive to changes in coral recruitment and dispersal parameters[1,36]. A new analysis of the model's sensitivity to underlying

assumptions is presented in Table 3. Sensitivity analyses were specifically focused on one of the most important outputs of the model: the threshold level of grazing required to enable coral recovery when cover is low at 10%. The first sensitivity analysis (Table 3) focused on the effects of perturbing individual parameters through either their published range or, if the range is poorly known, through a 10% variation either side of the parameter's standard value. Only one parameter was adjusted at a time, allowing a direct comparison of the relative impact of each parameter on the emergence of threshold dynamics. Each adjusted parameterisation was repeated 10 times for a 25 year period. Each simulation outputted the grazing level that best-defined the unstable equilibrium (threshold). This was defined as the grazing level that led to the minimal departure in total coral cover from the initial value of 10% after 25 years. The mean value of threshold grazing was then determined from the 10 simulations and compared to that of the standard parameterisation (Table 3).

A second sensitivity analysis investigated the consequences of implementing parrotfish grazing as a spatially-intensive process. Spatially-intensive grazing occurs on Caribbean reefs because parrotfishes tend to repeatedly graze individual algal patches whilst patrolling territories (P.J.M., unpublished data). The locations of such 'grazed patches' appear to change on longer time scales of months although the specific spatio-temporal scales are currently being quantified. Such spatially-intensive grazing was implemented by allowing parrotfish to consume all algae within randomly-chosen cells until the grazing threshold was reached. The pattern of grazing shifts each 6 month time step but the implication is that some cells will always have no macroalgal cover, which may facilitate the settlement and early post-settlement survival of corals. It is possible to simulate more homogeneous grazing, which might be appropriate in other ecosystems, by allowing fishes to graze throughout the reef during each time step. To investigate the effect of this we altered the grazing algorithm so that grazing was modelled to occur in each cell at the same intensity. Since grazers consume algae up to a maximum limit, this grazing intensity varied over time as a result of changes in the total percent cover of algae on the reef. The proportion of algae to be consumed within each cell was determined as the ratio of the maximum grazing limit to the total percent algal cover expressed as a proportion of the reef. For example, if the maximum grazing limit is 30% and percent algal cover sums to 40% of the reef, grazing intensity = 0.3/0.4=0.75 (75% of the algae within each grid cell).

The great sensitivity of the model to grazing is self-evident from the existence of threshold dynamics. Varying most model parameters had a minor impact on the threshold behaviour of the system, with absolute differences within a few percent of the standard behaviour (Table 3). Two parameters exerted larger impacts on threshold levels of grazing: the growth rate of brooding corals and the rate at which macroalgae overgrows live coral. The former result was surprising and will be investigated further as part of a study of ocean acidification effects, which can reduce coral calcification and therefore growth[37]. The latter was expected and was plotted explicitly in figures 1 and 2 of the main article. Furthermore, the shift to spatially-extensive grazing led to an increase in grazing thresholds (Table 3) because the post-settlement mortality of corals increased with fewer macroalgal-free patches. Although these parameters and grazing algorithms had relatively large impacts on the model, they did not affect our conclusions. Even when such parameters are modified, the model still predicts threshold dynamics at the upper levels observed for parrotfish communities in the Caribbean (i.e. ca 30% - 40% of the reef being grazed during each 6 month interval).

To explore the effects of potential variability in parameter values, a third sensitivity analysis was carried out that replaced the fixed value used in the standard parameterization with a probability distribution centered on this value. Each parameter was drawn from a truncated normal distribution with mean equal to the standard parameterization and standard deviation equal to half the difference between the standard parameterization and the adjusted (either minimum or maximum) value derived for the sensitivity analysis. The normal distribution for each parameter was truncated at two standard deviations (corresponding to the minimum and maximum values in Table 2.). This probabilistic approach was applied each time a parameter was used, thereby generating greater variability in the output of the model. To estimate the magnitude of such variability, we carried out 100 simulations and evaluated the variation in grazing threshold for 10% live coral cover (i.e. the same metric used in the first sensitivity analysis). The mean grazing threshold from such simulations was 36.5% which differs from the standard parameterization (34.6%) by less than 5%. Furthermore, the standard deviation of grazing threshold was only 0.8%. These results indicate that a probabilistic version of the model (i) does not cause significant departure from the mean behavior of the simpler parameterization and (ii) does not create excessive variability in model output. We conclude, therefore, that the model is generally robust in predicting threshold dynamics across a range of parameter space. Of course, stochastic simulations with acute disturbance phenomena (e.g. hurricanes) cause much greater variation in model output but these are excluded from the derivation of equilibrial properties and grazing thresholds.

Table 3. Sensitivity of model, defined as difference in threshold grazing at 10% live coral cover between standard parameterisation and that with adjusted parameter. Standard model has a grazing threshold of 34.6% (SE 0.2), implying that 34.6% of the reef must be grazed each 6 mo. to prevent the reef from falling below the unstable equilibrium. All sensitivity analyses report mean grazing threshold from 10 simulations. Absolute (Abs.) disparity expresses absolute difference in threshold as a percentage of the standard grazing threshold. Results given for both the minimum and maximum values of each parameter simulated except spatially-extensive grazing in which the model implementation was varied rather than parameter values.

Parameter	Value			Threshold grazing		Abs disparity	
	Min	Std	Max	Min	Max	Min	Max
Basal size at which corals become fully mature (cm^2)	225	250	275	34.5 (0.2)	35.0 (0.3)	0.3	1.2
Growth rate of brooders ($cm^2\ yr^{-1}$)	0.6	0.8	1.0	42.3 (0.3)	29.1 (0.1)	22.2	15.9
Growth rate of spawners ($cm^2\ yr^{-1}$)	0.7	0.9	1.1	36.1 (0.1)	33.3 (0.3)	4.3	4.6
Probability of macroalgal colonisation if cropped algae not grazed in 6 mo. (%)	60	70	80	33.6 (0.2)	35.6 (0.2)	2.9	2.9
Growth rate of coral recruits zero if M_{4cells} > X(%) where X is…	72	80	88	34.8 (0.2)	34.5 (0.1)	0.6	0.3
Growth rate of coral recruits reduced by X(%) if 60%<M_{4cells}≥80% where X is…	63	70	77	34.8 (0.2)	34.6 (0.1)	0.6	0.0
Growth rate of pubescent and adult corals reduced by X%...	45	50	55	34.7 (0.2)	33.9 (0.2)	0.3	2.0
Growth rate of pubescent and adult corals reduced by 50% if M_{4cells}<X%..	35	40	44	34.4 (0.1)	33.3 (0.2)	0.6	3.8
Effect of corals on macroalgal growth rate reduced by X%...	22.5	25	27.5	34.3 (0.2)	34.6 (0.3)	0.9	0.0
Effect of corals on macroalgae reduced by 25% when neighbourhood of coral>X(%)	45	50	55	37.4 (0.1)	37.3 (0.2)	8.0	7.8
Whole colony mortality of pubescent corals ($\%yr^{-1}$)	2	4	6	37.2 (0.2)	38.1 (0.2)	7.5	10.1
Whole colony mortality of mature corals ($\%yr^{-1}$)	1	2	3	32.3 (0.2)	36.6 (0.2)	6.6	5.7
Predation rate on coral recruits in each 6 mo. iteration of model (%)	13	15	17	36.4 (0.2)	36.6 (0.2)	5.1	5.8
Rate macroalgae overgrows live coral ($cm\ yr^{-1}$)	6	8	10	30.2 (0.2)	41.3 (0.1)	12.7	19.3
Spatially-extensive grazing		0.3		42.7 (0.2)		23.4	

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