

LETTERS

Thresholds and the resilience of Caribbean coral reefs

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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 regions¹. 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 coral⁵. 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 parameter⁶. 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 hysteresis¹². 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 problem¹², we discover multiple stable equilibria by using a mechanistic model of the ecosystem¹³.

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 Islands¹⁴, southern Caribbean^{15,16} and Central America¹⁷. Brooding and spawning forms of coral recruit at a size of 1 cm² 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 growth¹⁸ or to overgrow living coral when in direct proximity¹⁹. 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 parrotfishes¹⁶. Comparing model predictions to an exceptionally long time series of independent field data from Jamaica¹⁰, 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,

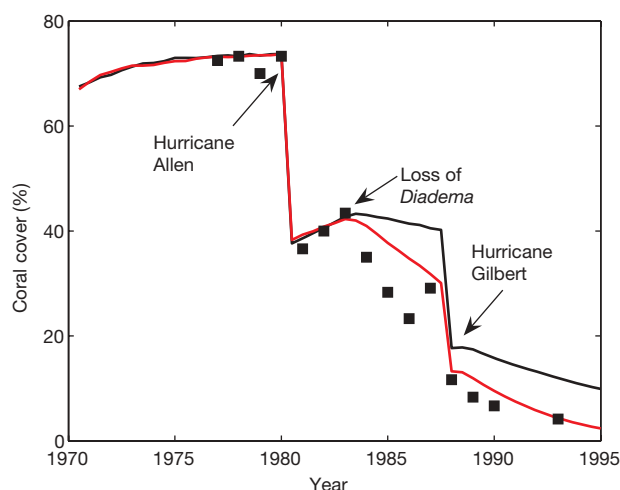


Figure 1 | Comparison between model predictions and Hughes' empirical data for the trajectory of structurally complex forereefs in Jamaica at a depth of 10 m. Predictions are denoted by lines and empirical data are denoted by black squares. The model that was run with a median algal–coral overgrowth rate of 8 cm² yr^{−1} is shown with a black line and the upper rate of 14 cm² yr^{−1} is shown with a red line.

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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 plane²¹ 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 bleaching²² 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

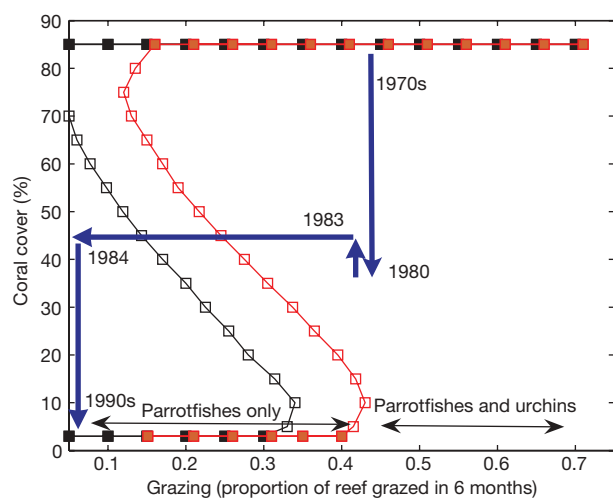


Figure 2 | Stable and unstable equilibria for Caribbean coral reefs at two levels of algal–coral overgrowth. Stable and unstable equilibria are denoted by solid and open squares, respectively. Black denotes $8 \text{ cm}^2 \text{ yr}^{-1}$, red denotes $14 \text{ cm}^2 \text{ yr}^{-1}$. Blue lines, marked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

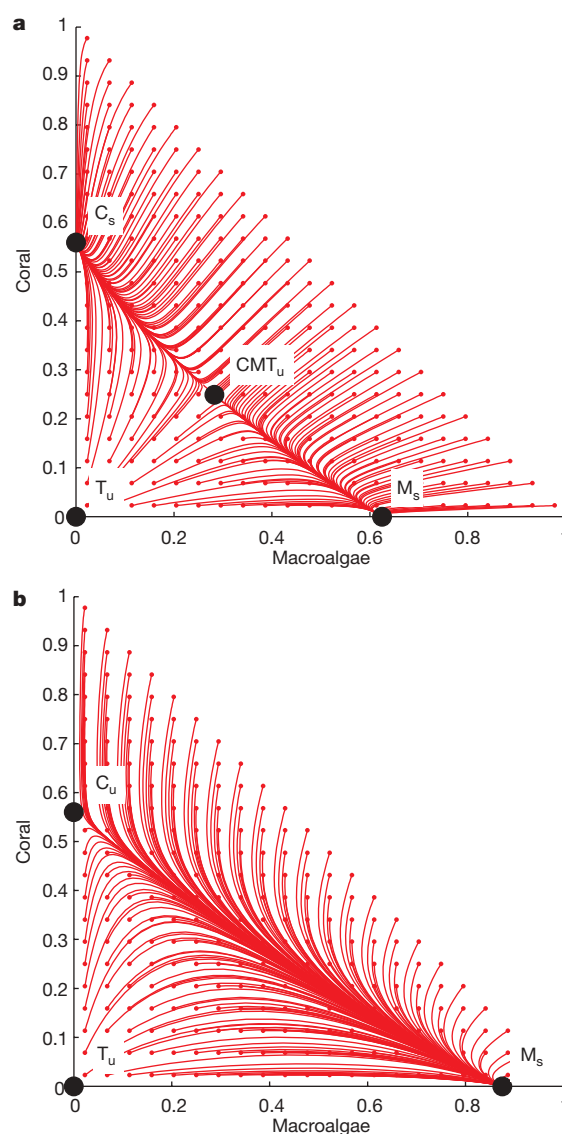


Figure 3 | Phase plane showing equilibrium covers of macroalgae and corals and trajectories over time. a, b, Equilibrium covers are denoted by black circles; trajectories are shown in red for grazing intensities of 0.3 (a) and 0.1 (b). Trajectories may be thought of as arrows beginning at different initial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

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 $\sim 75\%$ (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 goal²⁰. Recent reports of *Diadema* recovery²³ 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 plagues²⁴. 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 regime²⁵. 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.

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 means²¹. Trajectories were plotted using numerical integration with 4th- and 5th-order Runge–Kutta formulae²⁶. 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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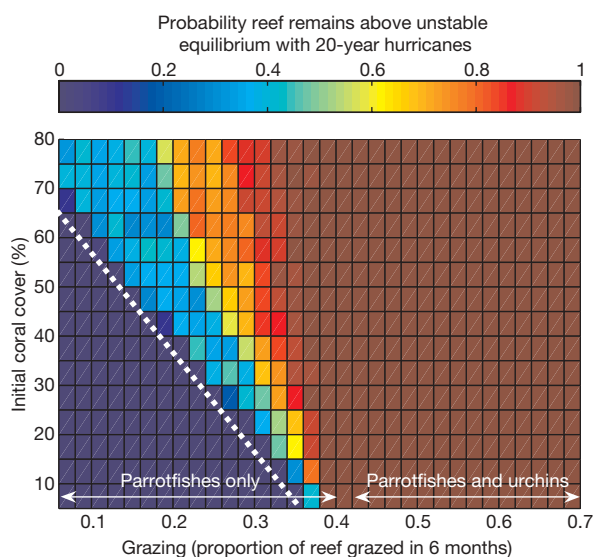


Figure 4 | Probability that reefs of given initial state will remain above the unstable equilibrium during a 25-year period. The physical disturbance regime includes stochastic hurricanes with a 20-year periodicity and the algal–coral overgrowth rate is $8\text{ cm}^2\text{ yr}^{-1}$. The unstable equilibrium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

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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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