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Synergistic impacts of global warming on the resilience of coral reefs

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Recent epizootics have removed important functional species from Caribbean coral reefs and left communities vulnerable to alternative attractors. Global warming will impact reefs further through two mechanisms. A chronic mechanism reduces coral calcification, which can result in depressed somatic growth. An acute mechanism, coral bleaching, causes extreme mortality when sea temperatures become anomalously high. We ask how these two mechanisms interact in driving future reef state (coral cover) and resilience (the probability of a reef remaining within a coral attractor). We find that acute mechanisms have the greatest impact overall, but the nature of the interaction with chronic stress depends on the metric considered. Chronic and acute stress act additively on reef state but form a strong synergy when influencing resilience by intensifying a regime shift. Chronic stress increases the size of the algal basin of attraction (at the expense of the coral basin), whereas coral bleaching pushes the system closer to the algal attractor. Resilience can change faster—and earlier—than a change in reef state. Therefore, we caution against basing management solely on measures of reef state because a loss of resilience can go unnoticed for many years and then become disproportionately more difficult to restore.

1. Introduction

In the past three decades, many Caribbean coral reef ecosystems have undergone a profound phase (regime) shift in community composition from coral to macroalgal dominance [1–3]. It has been hypothesized that this shift in community state was accompanied by a novel susceptibility to alternative attractors (i.e. stable equilibria), such that reef (community) state can follow either a coral-dominated basin of attraction or an algal-dominated attractor [4,5]. This hypothesis is based on the predictions of field-tested simulation models [6,7], the empirical discovery of divergent reef trajectories either side of modelled (predicted) bifurcation thresholds [5], and mechanistic difficulties with the alternative, single attractor hypothesis, advanced by Dudgeon *et al.* [8] (see also [5]). A key prediction of this theory is that multiple attractors only became feasible once disease decimated populations of two of the most important species on Caribbean reefs: first, the dominant herbivorous urchin *Diadema antillarum*, which died off in 1983/1984 [9], and second, the dominant reef-building coral *Acropora* spp., which died off throughout the 1980s [10]. Neither species has made a significant regional recovery although a few areas have seen local increases in abundance [11]. As a result, the average coral cover in the Caribbean has declined considerably since the late 1970s [1].

With relatively few corals capable of rapid growth, and a paucity of herbivores, fleshy macroalgae, such as *Lobophora variegata*, have increased in abundance on Caribbean reefs [12,13]. Because macroalgae compete with corals for space, the combined relaxation of top-down controls on algal abundance and the weakened community recovery of corals have created the possibility of multiple attractors with hysteresis (figure 1). Moreover, grazing levels have often been reduced further by the fisheries exploitation of the remaining herbivores, which primarily include the reef fish families parrotfish and surgeonfish [14–16]. Thus, the existence of multiple attractors is primarily

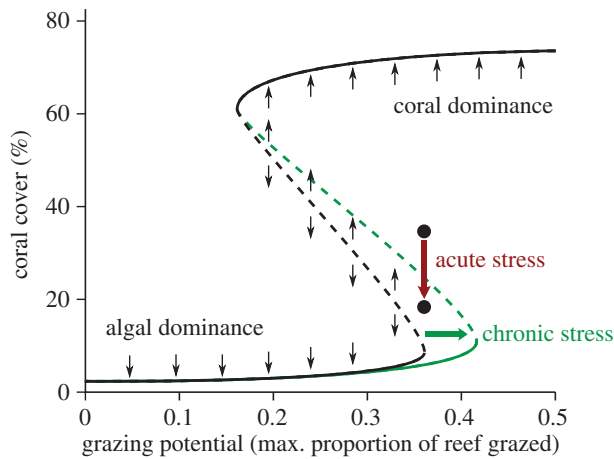


Figure 1. Schematic phase portrait of Caribbean reef resilience exhibiting hysteresis with stable (lines) and unstable equilibria (dashed lines). The phase portrait delineates two basins of attraction (coral-dominated and algal-dominated attractors) which determine the direction of change (black arrows) of the reef community state (coral cover) in the absence of acute stress and for a fixed grazing rate. Acute stress (e.g. bleaching) affects reef state (black dot) by pushing down coral cover (red arrow). Chronic stress (e.g. reduction in coral growth) may shift unstable equilibria (green arrow) on the grazing scale towards higher herbivory levels. The two effects combined are likely to push the system into the algal-dominated basin, impairing the recovery potential of corals.

hypothesized to have a biological origin, triggered by disease of two functionally important species, and has then been reinforced by harvesting of the remaining herbivores.

The ability of coral reefs to exhibit alternative attractors has been highlighted in several key papers on ecosystem resilience [17–20]. To date, most studies of reef resilience have focused on either ecological drivers such as the effects of fishing on herbivory [6,7,21], chronic local physical drivers such as nutrient enrichment [7,21,22] or the effect of periodic physical hurricane disturbance [23,24]. However, because corals usually tolerate only a narrow range of sea temperatures, the consequences of global warming have become one of the greatest concerns for the future of coral reef health [25]. Indeed, anomalous warming events, such as the 1998 El Niño–Southern Oscillation, have resulted in global outbreaks of coral bleaching (i.e. the partial or complete mortality of coral colonies due to a loss of symbiotic algae [26,27]) which caused a massive loss of living corals worldwide [28]. This raises the question, how might elevated sea temperatures generate regime shifts on Caribbean reefs, now that multiple attractors have become feasible?

Most models of the response of coral reefs to global warming have focused on reef state (usually expressed as the percentage of living coral) or the frequency of bleaching events that can maintain coral cover at low levels [24,29,30]. Reef state is important because it underpins a series of ecosystem functions [31,32]. However, few studies have explicitly studied the effect of climate change on coral reef resilience *per se*. One exception is Anthony *et al.* [21], who found that the combined effects of increased greenhouse gas (GHG) emissions reduced the resilience of Pacific corals, thereby increasing their susceptibility to local stressors.

Climate change impacts on coral reefs present an interesting opportunity for studies of resilience. Firstly, reefs are among the first ecosystems to experience severe impacts of climate change so the lessons learnt may prove insightful for

other ecosystems that are yet to experience severe impacts of global warming. Secondly, a single climate-related driver can exert multiple impacts on a reef system. A good example is rising sea surface temperature (SST). Global SST has risen 0.74°C over the twentieth century [33] and appears likely to have had a chronic negative impact on the calcification and growth of the massive coral *Porites* spp. on the Great Barrier Reef, causing a 14% reduction in calcification since 1990 [34]. Rising SST is also responsible for coral bleaching: exceptionally high summer SST, often only of +1°C, can cause mass mortality at regional to global scales [35]. The frequency and magnitude of acute bleaching events is expected to increase as SST continues to rise [30]. Thus, rising SST has both a chronic and an acute impact on reef ecosystems. The chronic impact affects the rate of extension of the carbonate skeleton of some corals, and therefore influences size-dependent mortality rates, ecological interactions and population recovery rate. Changes to these ecological parameters are expected to influence the unstable equilibria of the ecosystem (figure 1), potentially reducing the size of the coral basin of attraction and increasing the likelihood that reefs will shift towards an alternative attractor. The acute impact causes sudden mortality which can push a system closer to, or even across, the unstable equilibrium, which again reduces resilience (figure 1). Each impact is likely to occur on a different time scale and will vary among species. There is, therefore, the potential for complex dynamics emerging from a single driver (SST), and it is unclear whether the duality of its effects will be additive, synergistic or possibly antagonistic.

Here, we study the complex effects of rising SST on the resilience of Caribbean coral reefs. We simplify the ecosystem to represent two contrasting life-history strategies of extant corals and allow the dual effects of SST to affect each differently as they do *in situ*. We ask whether the chronic and acute impacts of rising SST interact synergistically, additively or antagonistically. We then compare the dual effects of this driver on both ecosystem state and resilience. State is included because of its functional importance and the ubiquity of its usage in studies of reef health and resilience [36]. To calculate the effect on resilience, we adopt the probabilistic framework developed by Mumby *et al.* [5,6,37] to quantify the ability of coral reefs to remain within their coral basin of attraction, essentially operationalizing Holling's [38] original concept of the ability of a system to remain within one (of multiple) basins of attraction. Resilience is sensitive to the initial state of the system, its environment and the disturbance regime to which it is subjected. As a result, the underlying unstable equilibria that separate alternative basins of attraction are dynamic, changing in response to the effects of climate change on coral growth.

2. Material and methods

(a) Model overview

A spatially explicit model of coral populations [6,22] was used to simulate the dual effects of chronic and acute thermal stress, both individually and in combination. The model is individual-based and simulates the population dynamics of corals of a typical mid-depth (5–15 m) Caribbean foreereef system. The model is designed as a regular square lattice of 400 cells, each approximating 1 m² of a reef. Individual cells can be occupied by multiple coral colonies of different species and patches of cropped algae

(a mixture of coralline algae and short turf) or macroalgae. Each coral colony is defined by its cross-sectional basal area on the square lattice. Colony area is updated every six-month time step following systematic and probabilistic rules which reflect processes of coral population dynamics (recruitment, colony growth, predation and natural mortality), macroalgal populations (growth and grazing from herbivores) and competitive interactions among corals and between corals and macroalgae. In the present model application, coral populations are demographically open with a constant supply of larvae. Corals are subjected to rising sea temperature, which has a deleterious impact on coral calcification in addition to causing acute mortality events due to bleaching. Model outputs include the cover (%) of each coral and algal species over time, averaged over a number (typically 100) of stochastic simulations.

For the past two to three decades, the branching coral *Acropora* spp. has become scarce on Caribbean reefs, mostly because of disease [10]. Today, massive and encrusting corals dominate many Caribbean ecosystems and two of the most abundant species are the *Orbicella* (previously *Montastraea* [39]) *annularis* complex and *Porites astreoides*. The *O. annularis* complex includes three sibling species (*O. annularis*, *O. franksi* and *O. faveolata*) which tend to form large, mound-like colonies. By contrast, *P. astreoides* exhibits encrusting or small boulder-shaped colonies which provide little architectural complexity to the reef framework. These two species are representative of opposed life-history strategies generally developed by coral organisms: while *O. annularis* is a broadcast spawner, with a very low recruitment success and a moderate rate of colony (lateral) extension, *P. astreoides* is a brooding coral with high recruitment levels but a low extension rate (see details in the electronic supplementary material). While *O. annularis* is a historically dominant reef-framework builder on Caribbean reefs, recent observations indicated a shift in dominance with significant rises of *P. astreoides* populations [40]. Projecting the responses of those two species in the future may thus inform on the ability of Caribbean reefs to maintain a functional reef habitat structure in the face of climate change. A full description of model components adapted to this study is provided in the electronic supplementary material.

(b) Thermal stress regime

Thermally induced disturbances were implemented according to future SST as predicted by the UK Hadley Centre Global Environmental Model HadGEM1 [41]. Global warming follows the RCP8.5 GHG emission trajectory, a baseline scenario representing high GHG emissions 'business as usual' without any specific mitigation target [42]. Similar to Edwards *et al.* [24], we used the Caribbean basin mean SST calculated monthly from 2010 to 2060 (figure 2) to project global warming. Future SST anomalies were used to calculate cumulative degree heating months within a four month window [29], and then converted to degree heating weeks (DHWs) to determine the probability of coral bleaching. To retain a focus on the impact of acute thermal stress, hurricanes were not included in the model.

(c) Coral response to chronic thermal stress: reduced extension rate

Corals extend their skeleton through the precipitation of calcium carbonate (CaCO_3). The rate at which CaCO_3 is deposited is affected by many factors but temperature is particularly important [43–46]. Experimental studies have shown that many coral species have an optimal temperature at which calcification rate is maximal [43,45]. Using radiographic analyses, Carricart-Garnivet *et al.* [47] quantified recent calcification rates in *P. astreoides* and two species of the *O. annularis* complex in the Mexican Caribbean. For *P. astreoides*, they observed a negative

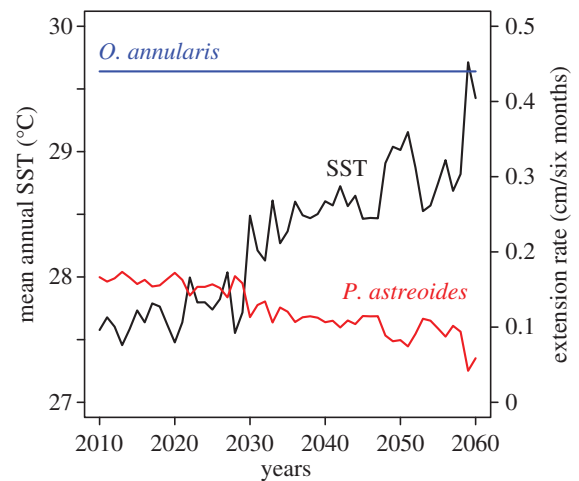


Figure 2. Mean annual SST (black line) as predicted by the HadGEM1 climate model for the Caribbean basin and projected rates of lateral extension of *O. annularis* (constant rate, blue line) and *P. astreoides* (variable rate, red line) for the 2010–2060 period.

correlation between mean annual calcification rate and yearly averaged SST (range 27.7–28.5°C). This relationship was extrapolated to estimate the rate of linear extension of *P. astreoides* as a function of the predicted annual changes of SST. First, we determined changes in relative calcification with SST assuming calcification rate of *P. astreoides* is maximum (100%) at 27°C, which corresponds to the first mean annual SST value (27.6°C) of our 2010–2060 time series. We assume that relative calcification is 100% at the start of simulations. Changes in relative calcification were then converted directly into changes in relative extension (figure 2). This assumption, that a change in calcification rate translates into a corresponding change in skeletal extension, is supported by strong correlations between calcification and linear extension reported for *P. astreoides* colonies [47,48] and for massive *Porites* in the Indo-Pacific [49]. One explanation is that *P. astreoides* invests calcification into skeletal extension to maximize population growth and space colonization [48]. As a result, *P. astreoides* linear extension changes in our simulations on an annual basis as a proportion of their present-day extension rate. Further details on calculations are provided in the electronic supplementary material.

By contrast, linear extension of *O. annularis* was assumed to be unaffected by global warming (i.e. extension rate is constant, figure 2). Coral species of the *O. annularis* complex construct denser skeletons possibly for increased resistance to bioerosion [46]. As a result, variations in calcification and extension rates appear to be weakly correlated in *O. annularis* colonies along a gradient of SST [46]. In addition, Carricart-Garnivet *et al.* [47] obtained a weaker correlation between mean annual calcification rate and SST for *O. annularis* than for *P. astreoides*. Thus, we hypothesize that a slight reduction in relative calcification would mostly affect skeletal density, rather than skeletal extension, and therefore the impact of chronic thermal stress on *O. annularis* has negligible influence on growth rate. We do not attempt to include the additional impact of ocean acidification on coral calcification as this would obscure results and its combined effect with temperature on skeletal extension rate remains uncertain.

(d) Coral response to acute thermal stress: bleaching mortality

In the model, bleaching mortality is dependent upon the magnitude and duration of thermal stress [24]. For a given summer, a DHW of more than 4°C triggers a bleaching event that generates

whole- and partial-colony mortalities in corals. Details of the calculation of bleaching probabilities are provided in the electronic supplementary material. Briefly, whole-colony mortality is modelled based on empirical observations collected throughout the wider Caribbean during the 2005 bleaching event [50]. The probability of partial-colony mortality follows observations collected during the 1995 bleaching event that occurred in Belize [51], with coral brooders and spawners having a 7% and 8% risk, respectively. The extent of partial mortality is set at 30% of tissue area, following McField *et al.* [51]. Corals that had previously been exposed to elevated SST have a lower risk of mortality during subsequent bleaching events [52]. Juvenile corals (cross-sectional area less than 60 cm²) are not affected by bleaching [53].

In this study, the differential bleaching response of brooders and spawners was further enhanced to better represent the contrasting susceptibility exhibited by *P. astreoides* and the *O. annularis* complex. Bleaching impact studies have shown that the *O. annularis* complex has a greater bleaching prevalence compared with *P. astreoides* [51,54]. In addition, bleached colonies of the *O. annularis* complex appear to suffer greater subsequent mortality due to diseases [54]. In the absence of a robust quantification of relative bleaching prevalence and subsequent mortality for the two model species, we considered a simple scenario where bleaching-induced mortality for the *O. annularis* complex was twice that of *P. astreoides*.

(e) Assessing the effects of thermal stresses

A simulation-based experimental approach was developed to assess the separate and combined effects of the two thermal stresses on reef state and resilience. Four groups of simulations were designed: (i) a control treatment without any stress (no climate change); (ii) a regime consisting only of acute stress (bleaching under the RCP8.5 climate scenario); (iii) a regime of chronic stress but no acute bleaching (reduced growth of *P. astreoides* under the RCP8.5 climate scenario); and (iv) a combined regime of acute and chronic stress. For each treatment, 100 replicate simulations were run for 50 years (from winter 2010 to summer 2060). For all simulations, the model was initialized with a 20% total coral cover (10% for each species), a 10% cover of ungrazable substrate (e.g. sand), 20% macroalgal cover, 50% of cropped algae and a high fish grazing rate that maintained up to 36% of the reef in a grazed state, representative of a reef with unfished parrotfish populations [55].

Reef state was quantified using total coral cover (%). Reef resilience was calculated at every time step as the probability that the reef lies above the unstable equilibrium (figure 1), meaning that the reef is on a recovery trajectory. This requires building the phase portrait of a reef in order to determine the locations of unstable equilibria, i.e. the coupled values of coral cover and grazing rate that separate the two alternative basins of attraction. Note that positions of the unstable equilibria are influenced by many processes even though only two are plotted in figure 1. In our simulation experiments, algal productivity, ungrazable substrate and grazing are kept constant, but the growth rate of *P. astreoides* varies deterministically with changing SST and the relative proportion of the two coral species evolves through the simulation. To account for these changing conditions, we built a phase portrait for 11 combinations of coral species' relative abundance and for each decade of climate change, during which the growth rate of *P. astreoides* declined (i.e. using the average SST for each decade). For each phase portrait, unstable equilibria were found by running 100 stochastic simulations for every combination of grazing rate and initial total coral cover over a period of 100 years. External perturbations were switched off during this process, because the aim is to determine which attractor is operating or whether the reef is at equilibrium. Positions on the phase portrait that clearly fall below the unstable

equilibrium (i.e. within the algal-dominated basin) would never experience an increase in coral cover. By contrast, simulations from positions that lie above the unstable equilibrium (i.e. within the coral-dominated basin) would always exhibit an increase in coral cover. Theoretically, the state of a reef would remain unchanged for all 100 years if it lays precisely at the unstable equilibrium. However, the existence of stochastic ecological processes means that the unstable equilibrium is in fact probabilistic. We captured this variability in our calculation of the phase portrait by determining the percentage of 100 simulations that exhibited coral recovery for each initial starting position. A reef near the unstable equilibrium will follow the coral attractor 50% of the time and the algal attractor 50% of the time.

For each simulation of the four treatments, we extracted the probability of recovery from the relevant phase portrait, based on coral species composition and decade. At every time step, ecological resilience was calculated as the mean recovery probability over the 100 simulations. Note that these simulations differ to those used to create the phase portrait; here, the simulations can include acute disturbances (i.e. for the two scenarios that include bleaching). Resilience for a given year can be thought of as the probability that a reef remains within the coral-dominated attractor and is therefore able to exhibit recovery.

Our approach allowed us to measure the effect of each treatment by comparison with the control group. Effect sizes $E^{(t)}$ for a given treatment relative to the control were calculated at every time step as follows:

$$E_{\text{treatment}}^{(t)} = \frac{X_{\text{control}}^{(t)} - X_{\text{treatment}}^{(t)}}{X_{\text{control}}^{(t)}}$$

where $X^{(t)}$ is the variable of interest (i.e. total coral cover or resilience) at time step t in the simulated control or treatment group. Effect sizes thus quantify the variation of $X^{(t)}$ in the treatment relative to the control. A positive effect indicates a lower $X^{(t)}$ value in treatment compared with the control. Mean treatment effects and standard deviations were calculated from the 10 000 possible pairwise values of $X^{(t)}$ between each replicated ($n = 100$) control and treatment simulations. As a result, treatment effects can be tracked over time by their mean value and 95% confidence limits.

To investigate whether the two stressors have additive, antagonistic or synergistic effects on total coral cover and resilience, we calculated a predictive additive effect following a multiplicative model defined as [56,57]:

$$\hat{E}_{\text{combined}}^{(t)} = E_{\text{acute}}^{(t)} + E_{\text{chronic}}^{(t)} - E_{\text{acute}}^{(t)} \times E_{\text{chronic}}^{(t)}$$

A multiplicative expectation (e.g. a multiplicative loss) assumes that one stress can be enhanced by the other [58] so that the two effects are not independent [56–58]. If the combined treatment effect is found to be significantly higher than the (additive) expectation, then the interaction is synergistic. If the observed effect is less than the expectation, then the stressors are acting antagonistically [58]. If the response matches the predicted, then the two effects are simply additive (as calculated using a multiplicative model).

3. Results

(a) Chronic and acute effects of thermal stresses on reef state

Under a baseline scenario where corals are not affected by any thermally induced perturbations, coral cover invariably increases over time (figure 3*a–c*). The addition of acute disturbances, i.e. bleaching events as predicted under the

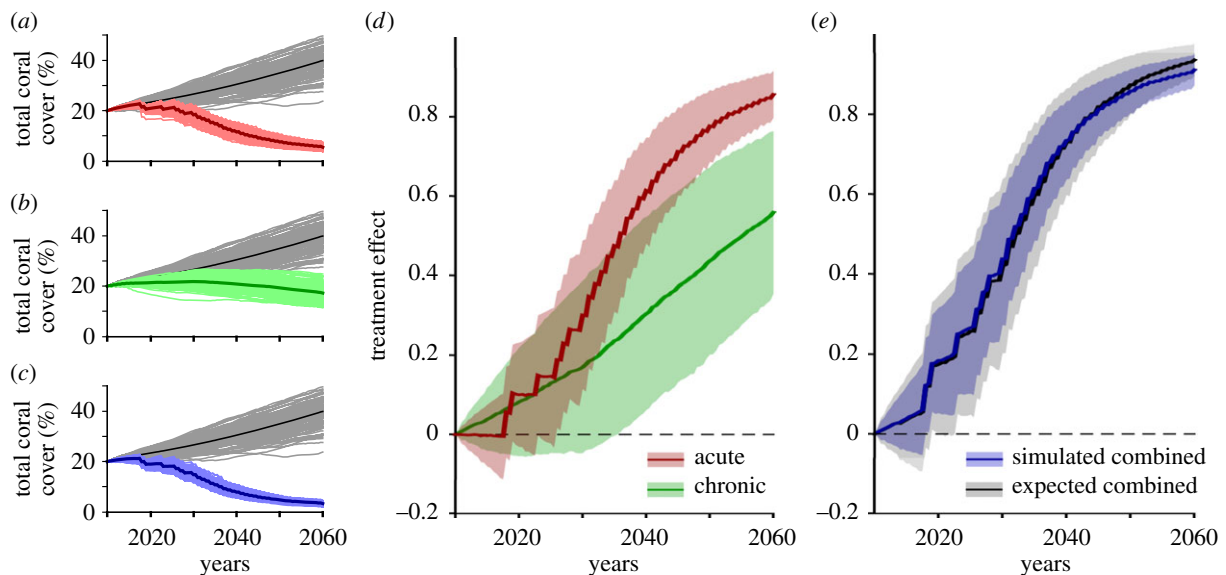


Figure 3. (a–c) Individual (shaded lines) and mean (plain lines) trajectories of total coral cover (%) from 2010 to 2060 for each simulated scenario: acute stress (i.e. bleaching mortality, red lines), chronic stress (i.e. reduced growth, green lines) and the two stresses combined (blue lines). The control scenario (black lines) is represented on each plot. (d,e) Mean effect sizes and 95% confidence intervals for each simulated treatment over time. The zero line (dotted line) indicates no effect of stress relative to the mean trajectory of the control treatment. All simulations were run for a grazing level of 0.36 and 20% starting coral cover (10% for each coral species).

RCP8.5 scenario, considerably reduces the total cover of corals to *ca* 20% of the baseline by 2060 (figure 3a), with an effect becoming significant (i.e. the 95% confidence interval does not overlap with 0) by 2025 (figure 3d). A chronic reduction of *P. astreoides* growth rate has a smaller effect on reef state than bleaching (figure 3b,d) but becomes significant by 2035. The predicted combined effects of the two stressors closely matched the simulated combined-stressor effect (figure 3e), indicating that the two stressors act additively on reef state, without synergism or antagonism.

(b) Chronic effects of thermal stress on coral/grazing unstable equilibria

Under a scenario of elevated SST, which reduces the extension rate of *P. astreoides*, the position of unstable equilibria in the coral/grazing phase portrait (figure 4) is progressively shifted to the right, thus reducing the size of the coral basin of attraction. This indicates that higher herbivory is required to maintain future Caribbean reefs in the coral-dominated basin. Species composition of the initial coral assemblage (i.e. the relative cover of *P. astreoides* at initial step) also affected the location of the critical thresholds by steepening the hysteresis curve with increasing dominance of the brooding species, *P. astreoides*. This implies that a given loss of coral in *P. astreoides* can have a greater impact on system resilience than a loss of *O. annularis*.

(c) Chronic and acute effects of thermal stresses on reef resilience

In the absence of thermal stress, reefs are fully resilient (i.e. probability of recovery is 1) for the designated initial coral cover (20%) and grazing level of 0.36 (figure 5a–c). Acute bleaching progressively erodes reef resilience to the extent that reefs have a 50% chance of losing their facility to show any recovery by 2060 (figure 5a). The chronic effects of global

warming lower resilience to a lesser extent (figure 5b,d) such that resilience remains at 70% by the end of the simulations (figure 5b). Resilience decreases dramatically in 2030, which corresponds to a significant increase in SST during the decade 2030–2040. When combined, acute and chronic stresses have a much greater effect than expected (figure 5e), indicating synergism in the reduction of resilience. The recovery potential exhibits a dramatic drop off in 2030 and becomes nearly null by 2040. All reefs switched to the algal basin of attraction at the end of the time frame.

4. Discussion

We used a spatially explicit model to simulate the complex response of Caribbean coral reefs to global warming under a ‘business as usual’ scenario for GHG emissions. Coral community structure was reduced to *O. annularis* and *P. astreoides*, two species relatively abundant on Caribbean reefs in the absence of *Acropora* spp. This simplification allowed us to retain a focus on the impact of thermal stress on two representative life-history coral strategies. Warming influences reefs through multiple pathways and the nature of their interaction changes depending on the ecosystem metric considered. The chronic and acute impacts of warming were simply additive on reef state while their interactions generated a multiplicative synergism (*sensu* [58]).

In our simulations, global warming increased the frequency and intensity of acute coral bleaching events, which led to a rapid deterioration of reef state because of repeated coral losses. Reef state is highly sensitive to bleaching because bleaching causes partial and whole-colony mortality in medium-sized to larger corals which have the most important contribution to coral cover (figure 6). Chronic impacts of global warming, acting through the reduction of *P. astreoides* growth rate, have indirect and delayed effects on coral cover. Coral cover will decline if the processes that increase cover—recruitment of new corals and the somatic growth of all

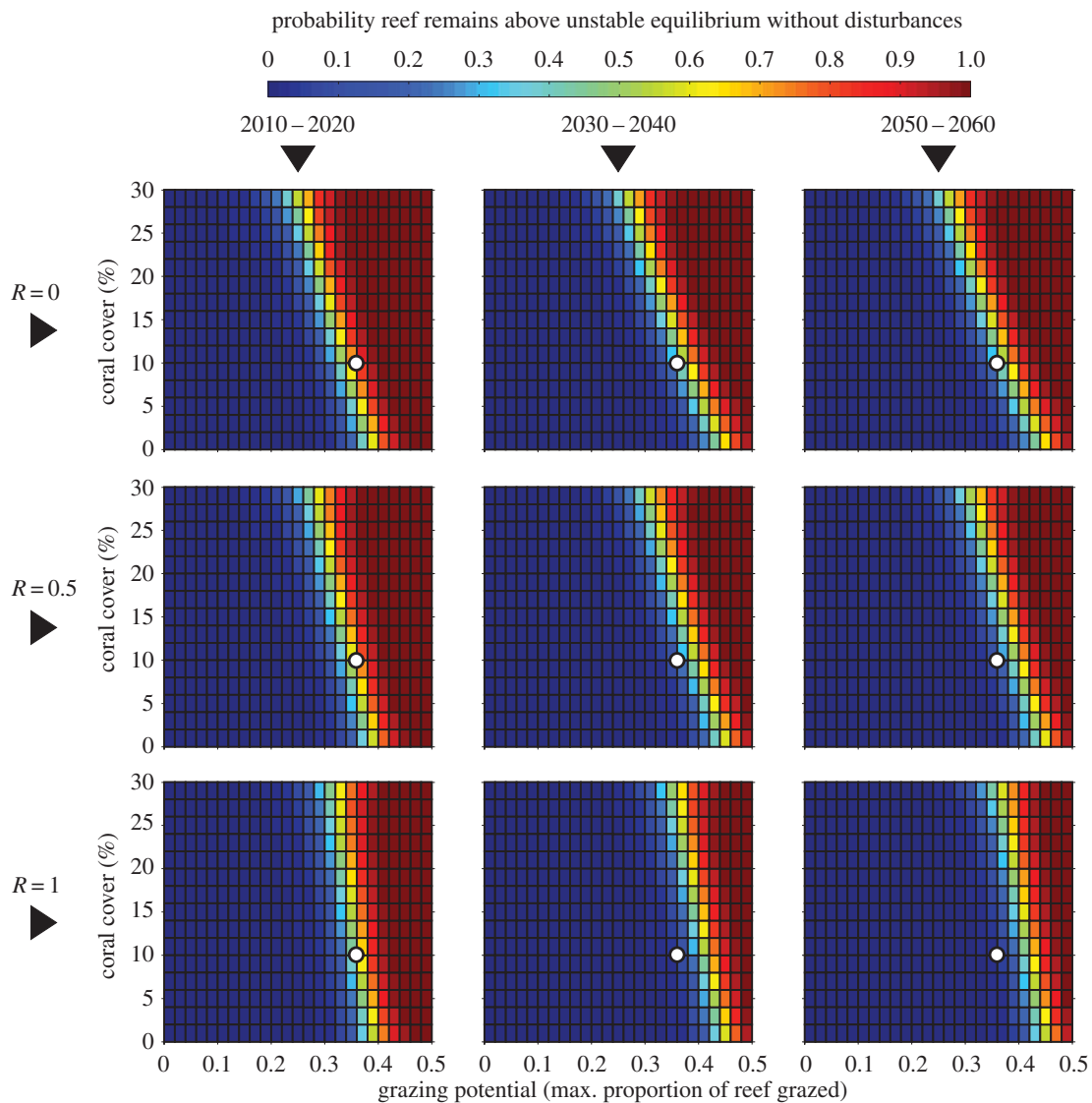


Figure 4. Some decadal-average phase portraits of Caribbean reefs (left to right) modelled with a changing relative cover (R) of *P. astreoides* in the initial coral assemblage (top to bottom) in the absence of acute disturbances. A zone of variation lies between red (recovery is certain) and blue areas (recovery is impossible) that delineates uncertainty in the location of unstable equilibria. The circled white dot indicates a reef with 10% total coral cover and a grazing potential of 0.36 (as fixed in this study) to highlight the shifting position of unstable equilibria due to elevated temperatures and initial species composition. Note that the relative cover of the two coral species varies over time, so that a scenario starting with a null cover of *P. astreoides* does not imply that its cover is 0 throughout the simulated time frame (100 years).

corals—are outweighed by the processes that remove cover. In the absence of acute mortality, the only processes that remove cover are natural whole- and partial-colony mortalities. The first impact of chronic stress is to reduce recruitment by increasing the mortality of young corals (figure 6). A slower individual growth rate prolongs the exposure of coral recruits and juveniles to competition from macroalgae, which can smother such small corals relatively easily [59,60]. Increased mortality of these diminutive corals has barely any direct, short-term effect on coral cover because their combined areal coverage is virtually negligible. However, when the reduction of recruitment is combined with slower somatic growth across all *P. astreoides*, the rate of replenishment of coral cover can become impaired. This effect is delayed for two reasons. First, population recovery exceeds loss in early parts of the time series because growth rates are still high and recruitment is not limiting the adult population. Second, as chronic stress only influences *P. astreoides*, the magnitude of the impact should become increasingly notable if *Porites* dominates the

community. In the early years, *O. annularis* are still relatively abundant but they are progressively outcompeted by *Porites*, whose recruitment rate is an order of magnitude higher [55,61]. Thus, the gradual shift in species composition further delays the point when chronic stress has a significant impact on coral cover.

Interestingly, chronic and acute stresses have an additive effect on reef state, as evidenced by the perfect fit of the multiplicative model. Stressors combine additively because chronic stress acts to reduce the rate of coral recovery between successive bleaching events. The interaction between stressors is indirect, because one has a direct effect on mortality (acute stress) and the other has a direct effect on growth rate (chronic stress). While reef state projections are drawn for an average Caribbean reef system, similar impacts of increasing SST on coral colony growth may be expected in other regions [25,34]. In addition, future SST projections suggest that temperature anomalies will occur worldwide so that bleaching will continue to be a widespread phenomenon [30,62]. This strongly suggests that thermal stress,

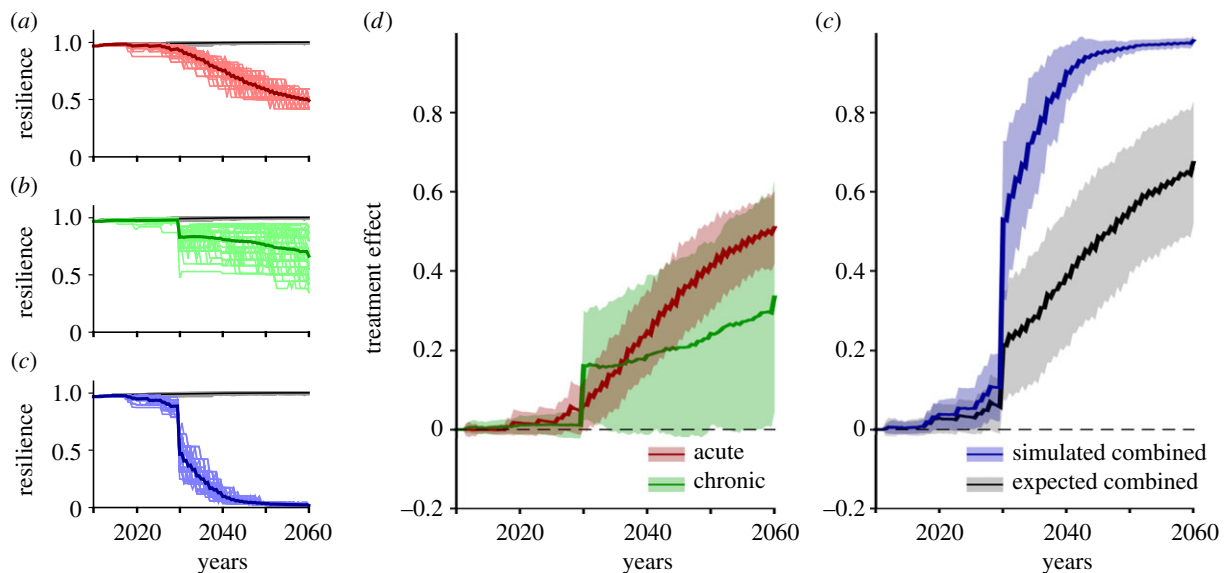


Figure 5. (a–c) Individual (shaded lines) and mean (plain lines) trajectories of ecological resilience from 2010 to 2060 for each simulated scenario: acute stress (i.e. bleaching mortality, red lines), chronic stress (i.e. reduced growth, green lines) and the two stresses combined (blue lines). The control scenario (black lines) is represented on each plot. (d,e) Mean effect sizes and 95% confidence intervals for each simulated treatment over time (see figure 3 legend).

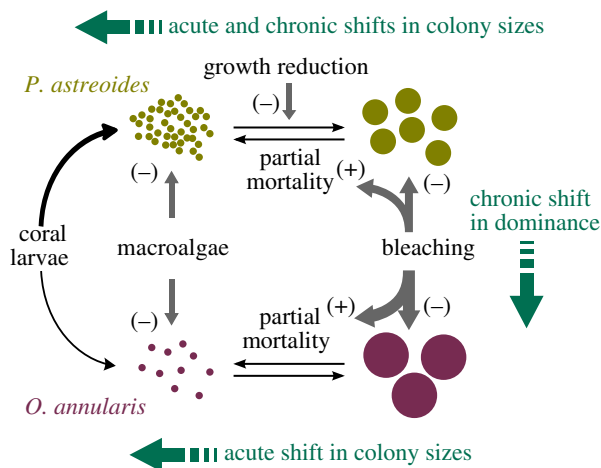


Figure 6. Schematic diagram showing the mechanisms affected by acute and chronic thermal stresses in juvenile (small circles) and adult (large circles) populations of the two modelled coral species.

induced by climate change, will become an important driver of coral reef state in the next 50 years. More detailed projections of Caribbean reefs, which include other stressors, can be found elsewhere (e.g. [24,32]).

Unlike reef state, the interaction between chronic and acute stress is synergistic on resilience. Both stressors work in concert to push reef state closer to, and eventually over, the unstable equilibrium. Chronic stress moves the bifurcation threshold to the right (figure 4), which effectively raises the threshold level of coral cover for the unfished grazing rate of 0.36 and increases the likelihood that bleaching-induced losses of coral will push the system across the threshold. Shifts in unstable equilibria that affect the size of a basin of attraction have been already described in other systems with multiple attractors [63,64]. Because coral reefs are subject to multiple stressors, there are many potential pathways by which external disturbances can gradually shift a critical threshold towards increased susceptibility to acute stress (e.g. [7]). For instance, our simulations did not consider sublethal effects of bleaching events, such as the prolonged

reduction of somatic growth and reproductive capacity of bleached colonies [27], or the effects of other stressors, such as hurricanes, fishing, nutrients and ocean acidification. Considering synergism among stressors is therefore of paramount importance to envision the future impacts of climate change on coral reef resilience. While there is no evidence that coral reefs other than those in the Caribbean exhibit alternative attractors, there is no guarantee that reefs of the Indo-Pacific will not eventually succumb to multiple attractors, particularly if climate change and/or ocean acidification continue to reduce coral calcification and growth [21].

A key difference between reef state and resilience is the time scale over which they change. Once reef state lies near the unstable equilibrium, a small change in state can have a catastrophic and immediate impact on resilience. Resilience measures whether there is sufficient recruitment and growth to allow net coral recovery from the current reef state. Imagine, for example, that state moves to a point where the balance between processes of recovery versus natural mortality just becomes negative. In the short term, this will have a barely detectable effect on state because the rate of coral decline might be very low. But the effect on resilience is immediate, because the derivation of the phase portrait is based on 100-year simulations and these would easily detect that the coral population has become unsustainable. Thus, resilience can change considerably faster—and earlier—than a change in reef state [65].

Our analysis focused only on a single stressor on coral reefs, albeit one with dramatic impacts, which include the 1998 global bleaching event. While we do not attempt to provide a comprehensive analysis of all stressors acting on corals, we learn that reef state and resilience respond differently and are largely decoupled. This has important implications for management interventions. Currently, reef state plays an important role in the monitoring of reefs and is commonly included as ‘indicator’ of resilience [36]. There is nothing wrong in this because reef state does contribute to resilience by determining the proximity of the unstable equilibrium and species composition does influence the phase portrait. However, if management interventions are

based solely on state, then a loss of resilience could go unnoticed [66]. This is because resilience can respond rapidly to an incremental change in state. Worse, the hypothesized existence of hysteresis means that it may become disproportionately more difficult to restore resilience as state continues to decline [67]. Resilience has been operationalized for Caribbean coral reefs by combining an extended version of the simulation model used here with a wider range of spatially realistic disturbances and an assessment of how management measures, such as marine reserves, can influence the resilience under a 'business as usual' scenario [37]. However, further modelling efforts are required to account for various growth strategies and thermal susceptibilities in the

assessment of coral reef resilience and to integrate connectivity among coral populations. Operationalizing resilience has its challenges [37,67] but is particularly important in the context of climate change because it can help identify, and ideally repair, ecosystem dysfunction before stress levels have risen to the point that degradation becomes potentially irreversible [19,68].

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