Global disparity in the ecological benefits of reducing carbon emissions for coral reefs

Juan Carlos Ortiz[1,2]*, Yves-Marie Bozec[1,2], Nicholas H. Wolff[1,2], Christopher Doropoulos[1,2] and Peter J. Mumby[1,2]

Even if carbon emissions are reduced drastically in the next decade the amount of carbon already stored in the atmosphere would lead to the occurrence of extreme thermal events every three to four years between 2040 and 2080[1,2]. This time lag on the effect of reducing emissions suggests that the benefits of carbon emission reduction on the health of coral reefs will be noticeable only in the long term[2–4]. Here, we use a spatially explicit ecosystem model to compare the potential ecosystem benefits that Caribbean and Pacific reefs could gain from reductions in carbon emissions, and the timescale of these benefits. We found that whereas the effect of a reduction in emissions on Caribbean reefs will be modest and realized only in the long term (more than 60 years), Pacific reefs would start to show benefits within the first half of this century. Moreover, it seems that Pacific reefs have the potential to maintain their ecological integrity and ecosystem state in the mid- to long term if carbon emissions are reduced, but only if plate-like corals are present.

Since the early 1990s climate change has been identified as one of the main threats to coral reefs[1]. It has been shown repeatedly that the frequency and intensity of extreme thermal events will increase nonlinearly over the next 100 years[2,5]. Owing to the large pool of greenhouse gas (GHG) already stored in the atmosphere from decades of emissions, and lags in the ability of Earth systems to reabsorb these excesses, legacy impacts will be felt for years even if emissions are reduced drastically in the near future[5,6]. Even under climate scenarios that require strong and immediate emission reductions (reducing emissions to 1980s level by 2020, Representative Concentration Pathway (RCP) 2.6), there will still be extreme thermal events every three to four years between 2040 and 2080; only towards the end of the century will the frequency of these events start to decline[2,5,6]. Therefore, it is not clear how long it will take for the reduction in thermal stress to translate into an improvement in ecosystem state. Furthermore, the potential for synergistic effects and ecological feedbacks from the multiple stressors impacting reefs—such as overfishing, hurricanes, reduced calcification, and sedimentation—increase the risk of coral reefs losing resilience by the time the potential benefits of reducing GHG emissions are realized[7].

Most of the projections of the effect of thermal stress on coral reefs are based on the frequency and intensity of predicted future thermal disturbances[1,8], but relatively few studies have attempted to predict the ecosystem-level consequences in detail[9–12]. In particular, spatially explicit models that incorporate multiple coral taxa and their vital rates, as well as multiple ecological mechanisms (for example, herbivory and productivity), have mainly been applied to reefs in the Caribbean[3,4,13]. These studies support the idea that

reducing emissions will have only a small positive effect in the state of Caribbean reefs in the short to mid-term, with a predicted coral cover of less than 10% for most Caribbean reefs, and with coral cover trajectories that do not start to trend up by the end of the twenty-first century. However, available evidence, in terms of observed recovery rates[14], suggest that Pacific reefs have far greater resilience than those in the Caribbean. Thus, it is possible that Pacific reefs may respond earlier and more strongly to a change in climate policy.

Here, we present a spatially explicit ecosystem model for Pacific coral reefs and examine their response to alternate climate scenarios. We also compare the behaviour of Pacific reefs against those of the Caribbean, using a similar model from that region. The model includes six representative coral growth forms of the Pacific, each with different life history traits (Fig. 1). Model parameterization combines 40 published articles and new empirical data in addition to the 26 publications used in the parameterization of the Caribbean model. Full descriptions of parameters and model sensitivity analysis are provided in Supplementary Methods and Supplementary Analysis, respectively. Model performance was validated by reproducing 18 observed recovery trajectories from 14 reefs, spanning more than 1,200 km along the Great Barrier Reef (GBR; Fig. 2a).

The average recovery rate obtained from the model ($5.4 \pm 0.8\%$) fell within the variability of the rate observed in the field ($5.8 \pm 1.9\%$), and the two averages were not statistically different (Fig. 2b insert). A second test took individual species into account by comparing the predicted and observed community structure of reefs at the end of each recovery time series. Predicted communities had a high average similarity to observed communities, with a Bray–Curtis similarity average coefficient of 77% (Fig. 2c). Indeed, the similarity exceeded 80% for 11 of the 18 trajectories. The accuracy to predict both recovery rate and final community composition was independent of the initial coral cover (Fig. 2b,c).

Climate change is likely to affect the frequency, intensity and geographic distribution of large storms (cyclones), but the results of different climate models are variable and rarely disaggregated for different regions of the Southern Hemisphere[15]. Therefore, reef projections were run in the absence of cyclones to focus on the direct effect of climate change drivers, but the results remain directly appropriate for low-latitude reefs, such as those in the northern GBR and southern Caribbean that rarely experience such conditions. The impact of climate change is simulated through coral bleaching only because it is the best-understood of the three identified coral stressors driven by climate change (coral bleaching, ocean acidification and chronic thermal stress). The effects of ocean acidification and thermal stress on calcification were not included because of the great uncertainty that remains over their effects at reef

[1]Marine Spatial Ecology Lab, School of Biological Sciences, The University of Queensland, Brisbane St Lucia, Queensland 4072, Australia. [2]ARC Centre of Excellence for Coral Reef Studies, The University of Queensland, Brisbane St Lucia, Queensland 4072, Australia. *e-mail: j.ortiz@uq.edu.au

Figure 1 | Life history parameters of Pacific coral 'species'. Colours represent relative values of each parameter (1 = the highest value of a particular parameter among the six coral types). Absolute values are provided in the Supplementary Methods.
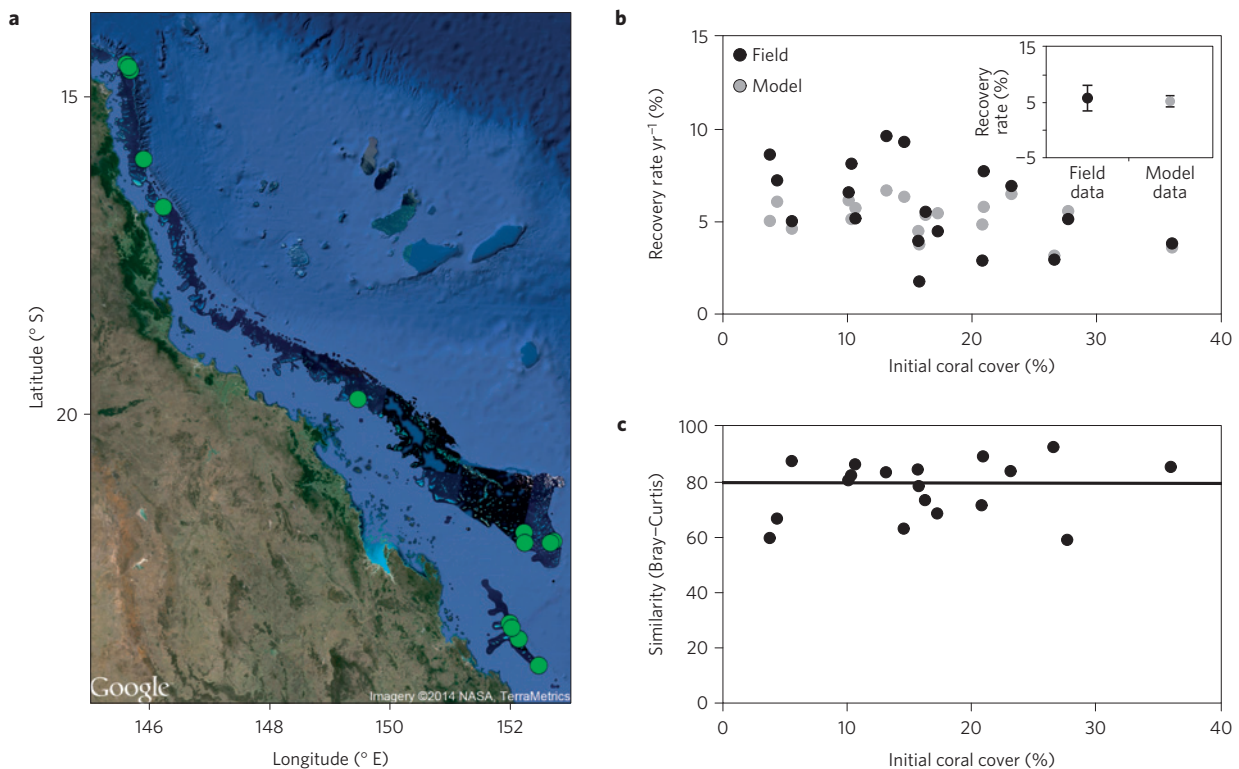

Figure 2 | Model validation. a, Location of the 14 reefs used for the field validation of the model along the Great Barrier Reef, Australia. **b**, Yearly recovery trajectory of modelled and field data versus initial coral cover. Insert shows the average and standard deviation. **c**, Bray–Curtis similarity of each pair of final community compositions (field and modelled) against initial coral cover.

scales[16] and the paucity of data on thermal impacts on the multiple taxa we model here.

In the absence of coral bleaching, the initial reef growth/recovery rate was nearly ten times greater on Pacific systems than those in the Caribbean (8.12 [±0.8] yr^{-1} versus 0.91% [±0.7] yr^{-1}) (Fig. 3a,b). The faster recovery rate of Pacific corals can be attributed to a combination of a higher growth rate of branching corals in the Pacific than in the Caribbean, as well as the lower productivity potential of macroalgae in the Pacific[14]. Despite the large difference in recovery trajectories, both Caribbean and Pacific reefs collapsed under business-as-usual climate emissions scenarios (Fig. 3c,d). The

trajectories of decline differed, being smooth in the Caribbean, whereas the Pacific began with rapid periods of recovery punctuated with large impacts of bleaching. However, the trajectory of decline eventually became smooth once the frequency of thermal events overwhelmed the recovery potential of the reefs, by around 2050 (Fig. 3d). High-amplitude dynamics occur on Pacific reefs because both the recovery rate and susceptibility of corals to bleaching are greater in this region (Supplementary Methods). Interestingly, the post-2050 scenarios under business-as-usual greenhouse gas (GHG) emissions are remarkably similar between regions, with no recovery trajectories and a final average coral cover of ~3[±0.2]%.
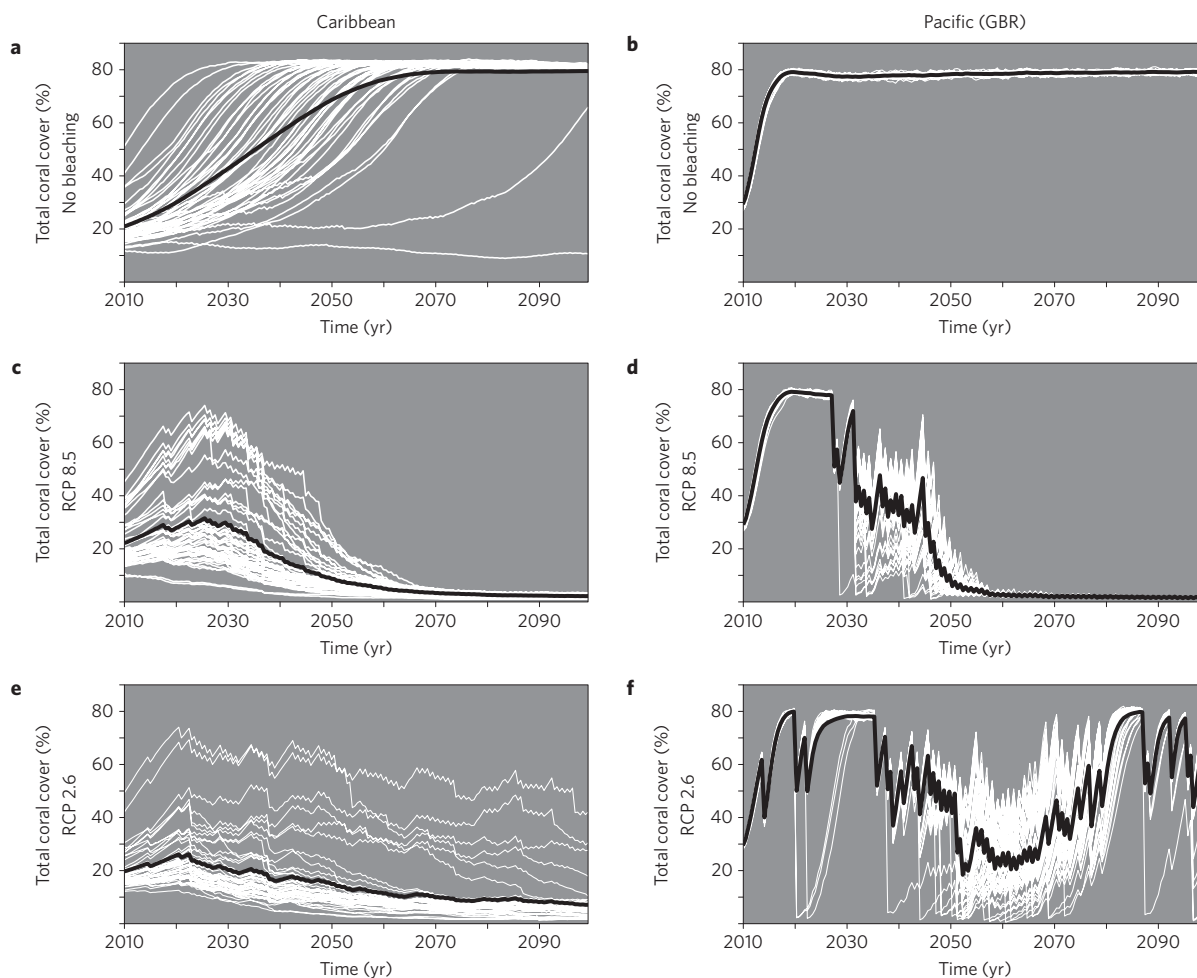
Figure 3 | Trajectory of coral cover under different climate change scenarios. a,c,e, Caribbean simulations for the three climate change scenarios: no bleaching (**a**); high GHG emissions (**c**); and low GHG emissions (**e**). **b,d,f,** Pacific simulations for the three climate change scenarios: no bleaching (**b**); high GHG emissions (**d**); and low GHG emissions (**f**). Black lines represent average cover among simulations. White lines represent the trajectory of each of the 50 simulations in each case.

Under a far more optimistic scenario of GHG mitigation (RCP2.6), the trajectories of Pacific and Caribbean systems differed substantially throughout the century (Fig. 3e,f). The Caribbean still shows a net decline, but to a final state that has approximately three times higher cover than the business-as-usual trajectory (~10%[±0.5]). Although this is still low, it might be adequate to avoid the reef shifting to net erosion[17]. In the Pacific, although there remains a period of reef decline at around 2050 (as was seen under RCP8.5), the reefs then improve towards the end of the century. The final projected average coral cover was ~70%, about 20 times higher than under the business-as-usual scenario.

We point out that these model simulations do not consider the potentially synergistic additional effects of cyclones, crown-of-thorns starfish, or effects of thermal stress on calcification[18], so it is unlikely that coral cover will average 70% towards the end of the century under RCP2.6. However, the contrast in reef dynamics and average state between alternative GHG emissions is remarkable. Our results also suggest that reducing GHG emissions can have a positive effect on Pacific reefs (relative to business-as-usual) within 20–30 years. Furthermore, the benefit that GHG reductions confer to reefs significantly reduces the possibility that synergistic effects of additional disturbances (COTS outbreaks, storms, overfishing, and so on) could lead to a collapse of Pacific reefs. However, our model suggests that coral cover will be severely reduced on Pacific reefs by the end of the century under RCP8.5, even in the absence of

additional stressors, emphasizing the importance in reducing GHG from the current RCP8.5 trajectory.

Furthermore, even though the likelihood of a phase shift towards macroalgal-dominated reefs seems to have been far lower in the Pacific than the Caribbean[14], avoidance of a prolonged period of low coral cover should help maintain lower risks of phase shift. An important mechanism of macroalgal phase shift is the reduction of grazing intensity to levels where macroalgae can 'escape' from turfs and form a relatively unpalatable canopy that is difficult to remove[19]. Grazing intensity can decline under persistent low coral cover because fish distribute their grazing across proportionally more dead substrate and because the associated reduction of reef structural complexity have a severe deleterious impact on fish density[20].

Even though the Pacific model was initialized with equal abundances of all six coral 'types', tabular corals maintained the highest cover throughout the simulation period (Fig. 4a). This pattern is also seen on most of the observed recovery trajectories in the GBR long-term monitoring data set (14 of the 18 time series), and other empirical studies from the region[21,22]. By the end of the simulated period tabular corals represented half of the total coral cover, followed by small massive corals and corymbose acroporids, while the final cover of other morphologies was similar to initial levels. The fast growth and high recruitment rate, combined with a relatively high average colony size, confer tabular coral competitive advantages over other coral types[23] (Fig. 1). Despite their high
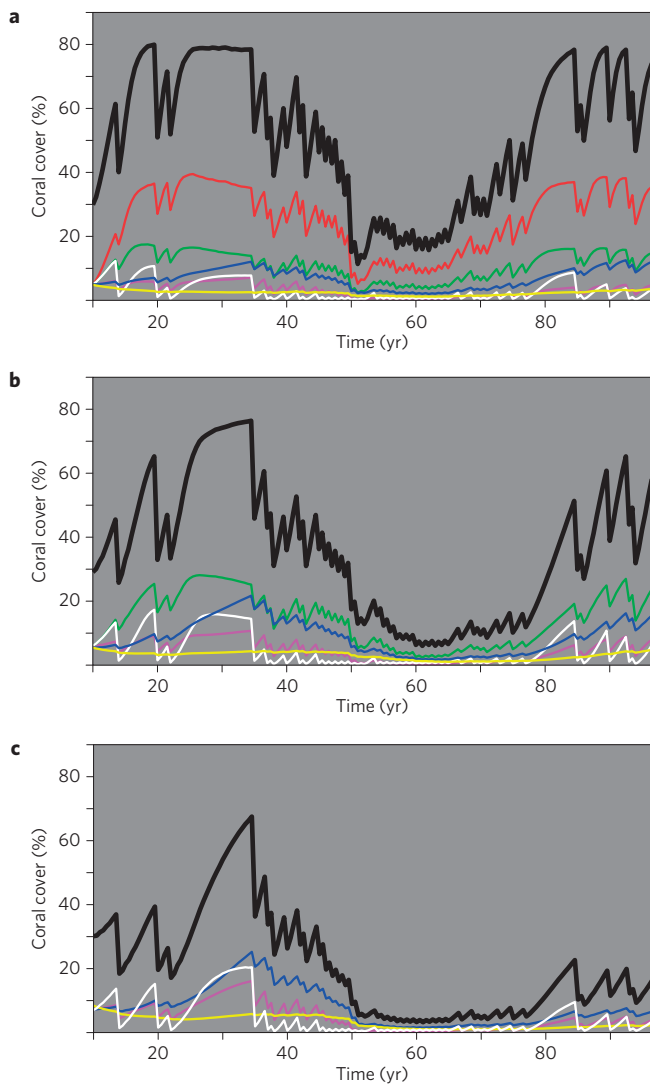
Figure 4 | Relative contribution of each coral type to total coral cover.
a, With all coral types. **b**, Without tabular corals. **c**, Without tabular corals or corymbose acroporids. Black line represents total coral cover; pink, branching corals; red, tabular corals; green, corymbose acroporids; white, corymbose other; blue, small massives; yellow, large massives. All cases reflect the RCP2.6 scenario.

growth rate, thicket-forming branching corals did not contribute significantly to recovery trajectories, either in the model or field data, probably owing to their relatively low recruitment rate[24] and high sensitivity to bleaching[25,26].

Strong reliance on a single growth form of corals—tabular corals—might constitute a level of community vulnerability. Tabular corals are particularly susceptible to the epizootic white syndrome[27], and epizootics have decimated acroporid populations in some regions, most notably the Caribbean[28]. To explore this concern, we repeated model simulations under the RCP2.6 scenario in the absence of several key species. An absence of tabular corals is projected to have a significant impact on total coral cover and dynamics (Fig. 4b). Even though the potential final coral cover is only 12% lower than the scenario that included tabular corals, a period of 30 years exists in the middle of the simulation where coral cover remains below 20%, with 15 consecutive years below 10%. Again, given the lack of additional disturbances in these simulations, these long periods of low coral cover increase significantly the risk of profound declines in coral. Towards the end of the simulation

corymbose acroporids start to recover, becoming dominant at the end of the time series. Indeed, the final cover of corymbose acroporids is 46% higher than the scenario that included tabular corals, a superior competitor.

Going one step further, if both tabular corals and corymbose acroporids are lost, the functional redundancy of the ecosystem—at least at a morphological level—becomes heavily depleted, and the coral cover trajectory becomes similar to that predicted for the Caribbean under reduced GHG emissions (Fig. 3d and Fig. 4c). Coral cover remains below 5% for 30 consecutive years, and only small recoveries are shown towards the end of the simulation. Moreover, none of the remaining coral types (two branching and two massive) show signs of strong recovery. These results suggest that not all branching corals contribute similarly to the recovery potential of Pacific reefs, despite their high growth rate, and that protecting tabular corals, and to a lesser degree corymbose acroporids, is of paramount importance for the resilience of Pacific reefs. It is important to note that a lack of empirical data prevents us from modelling changes in the interaction strengths among coral morphologies and between corals and macroalgae, as a consequence of differential responses to climate change. Although macroalgae might become stronger competitors under an acidifying ocean, some species also suffer at higher temperatures, and the net outcome remains uncertain[16].

We find that diverse Pacific coral assemblages have the potential to benefit from a reduction in GHG emissions in the mid-term and maintain their ecological integrity; whereas Caribbean reefs will realize the benefit of reduction in GHG emissions only in the long term, with a higher likelihood of functional ecosystem collapse. Moreover, it seems that tabular corals, and to a lesser degree corymbose acroporids, play a key role in maintaining the recovery potential of Pacific reefs, suggesting that reefs that have already lost these functional groups—or where they were never abundant—may have a higher risk of losing their ecological integrity even if GHG emissions are drastically reduced. Thus, tabular corals and corymbose acroporids might be assigned elevated weight in resilience assessments. We predict that society could experience the ecosystem benefits of vastly reducing GHG emissions on Pacific reefs within the lifetime of the current human generation.

Methods

The simulation model employed in the present study was designed to represent mid-depth (6–15 m) *Orbicella*-dominated forereefs in the Caribbean, which are the predominant coral-rich habitat in the region[29] and 6–12 m forereefs in the Pacific. Because white-band disease has depleted populations of large, branching corals[30] in the Caribbean, stylized massive growth forms of coral were simulated together for the forereefs. Six different growth forms were included in the Pacific model, with rates of recruitment, growth, reproduction and mortality. The model is a square lattice of 2,500 cells, each of which approximates $1\,m^2$ of reef, and can be occupied by a mixture of living and dead substrata. Although the reef has a toroidal lattice of 2,500 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 (cropped algae). Competitive interactions between corals and macroalgae reduce the growth rate of each taxon and are the only processes modelled to occur across cell boundaries. The 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 $1–60\,cm^2$), juveniles ($61–250\,cm^2$), and adults ($>250\,cm^2$). All simulations assume no stock-recruitment relationship and corals recruit at maximum levels irrespective of stock size (that is, up to 12 recruits per $m^{-2}\,yr^{-1}$). Individual cells in the lattice are updated in random sequence using discrete intervals of six months. The parameterization was based on reefs with little sediment deposition; therefore no effect of sediment on recruitment is incorporated. All parameters were fitted from empirical studies.

Fifty simulations were run for each scenario for a duration of 180 time steps (90 years), as this is the length of the available climate projections[3]. These projections extend to the year 2100.

Thermal stress. Thermal stress is implemented in the model as bleaching events following a previous application of the Caribbean model[3]. Bleaching events are triggered when the summer modelled sea surface temperature generates more than 4 degree heating weeks (DHW) in a summer season. When a bleaching event is triggered there is partial and total colony mortality associated with it. Mortality rates are species specific, size specific, and consider whether a colony has experienced previous bleaching or not. Total mortality due to bleaching is calculated as a function of the intensity and duration of the thermal stress using empirical relationships[3].

Climate scenarios. Background scenarios were considered where only natural partial and total mortality affected the reefs. These scenarios were included to compare disturbance-free recovery trajectories between the two provinces. Two climate change scenarios were considered for the calculation of partial and total coral mortality owing to bleaching events[3]. The low GHG emissions scenario (RCP2.6) represents the future trajectory of sea surface temperature anomalies considering an immediate drastic reduction in greenhouse gas emissions. This scenario implies a peaking of about 450 ppm CO_2 equivalent (CO_2e) by 2040 and 380 ppm CO_2e by 2100. The business-as-usual emissions scenario (RCP8.5) represents a high emissions situation where emissions continue to grow and little action is taken to reduce emissions in the near future. In this scenario, CO_2 concentrations increase linearly, reaching 1,200 ppm CO_2e by 2100. All climate variables were provided as a spatial mean across the Caribbean Sea for the Caribbean model, and the GBR for the Pacific model.

Coral species. Because white-band disease has depleted populations of large, branching corals in the Caribbean[30], four coral types (representing different growth forms) were simulated for the forereefs. Six coral types (representing different growth forms) were included in the Pacific model, with specific rates of recruitment, growth, reproduction and mortality for each coral type in both regions (see Supplementary Methods for details).

Model validation. The yearly average recovery rate of 18 trajectories from 14 reefs included in the Australian Institute of Marine Science Long-Term Monitoring Program (Permanent transects in 98 reefs along the Great Barrier Reef between 1992 and 2012) were compared against simulated recovery rates using the same initial conditions observed in the 18 field observations. (The 18 observations included every time series of at least four consecutive years without a reduction in coral cover (average length six years) from the whole data set.) A linear mixed model was used to statistically compare the average recovery rate between field and modelled trajectories. Bray–Curtis similarity was used to compare the final community structure of field and modelled data. The detailed parameterization and sensitivity of the model are presented in Supplementary Methods and Supplementary Analysis, respectively.

References

1. Hoegh-Guldberg, O. *et al.* Coral reefs under rapid climate change and ocean acidification. *Science* **318,** 1737–1742 (2007).
2. Donner, S. D., Skirving, W. J., Little, C. M., Oppenheimer, M. & Hoegh-Guldberg, O. Global assessment of coral bleaching and required rates of adaptation under climate change. *Glob. Change Biol.* **11,** 2251–2265 (2005).
3. Edwards, H. J. *et al.* How much time can herbivore protection buy for coral reefs under realistic regimes of hurricanes and coral bleaching? *Glob. Change Biol.* **17,** 2033–2048 (2011).
4. Ortiz, J., González-Rivero, M. & Mumby, P. An ecosystem-level perspective on the host and symbiont traits needed to mitigate climate change impacts on Caribbean coral reefs. *Ecosystems* **17,** 1–13 (2013).
5. Frieler, K. *et al.* Limiting global warming to 2 °C is unlikely to save most coral reefs. *Nature Clim. Change* **3,** 165–170 (2012).
6. Matthews, H. D. & Caldeira, K. Stabilizing climate requires near-zero emissions. *Geophys. Res. Lett.* **35,** L04705 (2008).
7. Bozec, Y-M. & Mumby, P. J. Synergistic impacts of global warming on the resilience of coral reefs. *Phil. Trans. R. Soc. B* (in the press).
8. Graham, N. A. J., Cinner, J. E., Norström, A. V. & Nyström, M. Coral reefs as novel ecosystems: Embracing new futures. *Curr. Opin. Environ. Sustain.* **7,** 9–14 (2014).
9. Kreyling, J., Jentsch, A. & Beier, C. Beyond realism in climate change experiments: Gradient approaches identify thresholds and tipping points. *Ecol. Lett.* **17,** 125–e1 (2014).
10. Fung, T., Seymour, R. M. & Johnson, C. R. Warning signals of regime shifts as intrinsic properties of endogenous dynamics. *Am. Nat.* **182,** 208–222 (2013).
11. Anthony, K. R. N. *et al.* Ocean acidification and warming will lower coral reef resilience. *Glob. Change Biol.* **17,** 1798–1808 (2011).
12. Kubicek, A., Muhando, C. & Reuter, H. Simulations of long-term community dynamics in coral reefs — how perturbations shape trajectories. *PLoS Comput. Biol.* **8,** e1002791 (2012).
13. Ortiz, J. C., González-Rivero, M. & Mumby, P. J. Can a thermally tolerant symbiont improve the future of Caribbean coral reefs? *Glob. Change Biol.* **19,** 273–281 (2013).
14. Roff, G. & Mumby, P. J. Global disparity in the resilience of coral reefs. *Trends Ecol. Evol.* **27,** 404–413 (2012).
15. Mendelsohn, R., Emanuel, K., Chonabayashi, S. & Bakkensen, L. The impact of climate change on global tropical cyclone damage. *Nature Clim. Change* **2,** 205–209 (2012).
16. Mumby, P. J. & vanWoesik, R. Consequences of ecological, evolutionary and biogeochemical uncertainty for coral reef responses to climatic stress. *Curr. Biol.* **24,** R413–R423 (2014).
17. Kennedy, E. V. *et al.* Avoiding coral reef functional collapse requires local and global action. *Curr. Biol.* **23,** 912–918 (2013).
18. Ban, S. S., Graham, N. A. & Connolly, S. R. Evidence for multiple stressor interactions and effects on coral reefs. *Glob. Change Biol.* **20,** 681–697 (2014).
19. Mumby, P. J. The impact of exploiting grazers (scaridae) on the dynamics of Caribbean coral reefs. *Ecol. Appl.* **16,** 747–769 (2006).
20. Bozec, Y. M., Yakob, L., Bejarano, S. & Mumby, P. J. Reciprocal facilitation and non-linearity maintain habitat engineering on coral reefs. *Oikos* **122,** 428–440 (2013).
21. Halford, A., Cheal, A., Ryan, D. & Williams, D. M. Resilience to large-scale disturbance in coral and fish assemblages on the Great Barrier Reef. *Ecology* **85,** 1892–1905 (2004).
22. Linares, C., Pratchett, M. & Coker, D. Recolonisation of *Acropora hyacinthus* following climate-induced coral bleaching on the Great Barrier Reef. *Mar. Ecol. Prog. Ser.* **438,** 97–104 (2011).
23. Connolly, S. R. & Muko, S. Space preemption, size-dependent competition, and the coexistence of clonal growth forms. *Ecology* **84,** 2979–2988 (2003).
24. Wallace, C. C. Reproduction, recruitment and fragmentation in 9 sympatric species of the coral genus *Acropora. Mar. Biol.* **88,** 217–233 (1985).
25. Ortiz, J. C., Gomez-Cabrera, M. D. & Hoegh-Guldberg, O. Effect of colony size and surrounding substrate on corals experiencing a mild bleaching event on Heron Island reef flat (southern Great Barrier Reef, Australia). *Coral Reefs* **28,** 999–1003 (2009).
26. Van Woesik, R., Sakai, K., Ganase, A. & Loya, Y. Revisiting the winners and the losers a decade after coral bleaching. *Mar. Ecol. Prog. Ser.* **434,** 67–76 (2011).
27. Roff, G. *et al.* The ecology of 'acroporid white syndrome', a coral disease from the southern Great Barrier Reef. *PLoS ONE* **6,** e26829 (2011).
28. Bythell, J. & Sheppard, C. Mass mortality of Caribbean shallow corals. *Mar. Pollut. Bull.* **26,** 296–297 (1993).
29. Mumby, P. J. *et al.* Coral reef habitats as surrogates of species, ecological functions, and ecosystem services. *Conserv. Biol.* **22,** 941–951 (2008).
30. Aronson, R. B. & Precht, W. F. White-band disease and the changing face of Caribbean coral reefs. *Hydrobiologia* **460,** 25–38 (2001).

Author contributions

J.C.O. designed the study, analysed the data and wrote the manuscript; Y-M.B. assisted in writing the model code, assisted in analysing the data and edited the manuscript; N.H.W. processed the empirical data for the validation, processed the GBR climate change scenarios data and assisted in writing the manuscript; C.D. provided empirical data for the parameterization of the Pacific model and edited the manuscript; P.J.M. conceived and helped design the study and co-authored the manuscript.

Additional information

Supplementary information is available in the online version of the paper. Reprints and permissions information is available online at www.nature.com/reprints. Correspondence and requests for materials should be addressed to J.C.O.

Competing financial interests

The authors declare no competing financial interests.