

Coral reefs in the Anthropocene

Terry P. Hughes¹, Michele L. Barnes¹, David R. Bellwood¹, Joshua E. Cinner¹, Graeme S. Cumming¹, Jeremy B. C. Jackson^{2,3}, Joanie Kleypas⁴, Ingrid A. van de Leemput⁵, Janice M. Lough^{1,6}, Tiffany H. Morrison¹, Stephen R. Palumbi⁷, Egbert H. van Nes⁵ & Marten Scheffer⁵

Coral reefs support immense biodiversity and provide important ecosystem services to many millions of people. Yet reefs are degrading rapidly in response to numerous anthropogenic drivers. In the coming centuries, reefs will run the gauntlet of climate change, and rising temperatures will transform them into new configurations, unlike anything observed previously by humans. Returning reefs to past configurations is no longer an option. Instead, the global challenge is to steer reefs through the Anthropocene era in a way that maintains their biological functions. Successful navigation of this transition will require radical changes in the science, management and governance of coral reefs.

A defining feature of the emerging Anthropocene era is the escalation of numerous pressures, including climate change, globalization and migration, on society and the world's ecosystems^{1–4}. Many coastal coral reefs have already been degraded by centuries of overfishing and pollution, and anthropogenic climate change is exerting further stress, even on remote reefs where local pressures are low or absent^{5–9}. Increasingly, coral reef scientists and managers encounter previously unseen configurations of species^{10–12}. The challenges now are to identify and maintain the ecosystem functions that are crucial for sustaining coral reefs, and to secure the ecosystem services that highly altered reef assemblages can provide to people in the future¹³. Central to this endeavour is an improved understanding of ecosystem functioning and of the types of management and governance that are effective.

In this Review, we explore the future prospects for coral reefs in the Anthropocene. First, we examine the implications for coral reefs of a worldwide shift away from business-as-usual emissions of greenhouse gases (as agreed at the 2015 United Nations Climate Change Conference (COP 21) in Paris) and reassess the future threat of global warming and ocean acidification to reef biodiversity. Second, we consider whether current experimental evaluations of the impact of rising temperatures and ocean acidification are appropriately calibrated for simulating future conditions. Third, we scrutinize the strengths and weaknesses of conventional scientific approaches to understanding the cumulative, interacting effects of numerous stresses or drivers of change on the trajectories of coral reefs. Fourth, we present a conceptual framework that offers innovative insight into these cumulative impacts and their effects on the complex dynamics of interlinked social and ecological systems. Last, we develop a suite of future options for the governance and management of new and unfamiliar coral reef ecosystems. Sustaining reef biodiversity will require a conceptual shift away from the current emphasis on protection, conservation or restoration of stable coral ecosystems at equilibrium, to a reality in which ecosystems are more dynamic and patchier, as well as increasingly different to anything that people have encountered before. Embracing this paradigm shift will necessitate a transformation in the governance and management of these high-diversity ecosystems.

Running the climate gauntlet

The accelerated effort towards global action on climate change calls for a reassessment of the environmental conditions that will test coral

reefs in the near future. The goal of the COP 21 Paris agreement¹⁴ on climate change is to constrain the increase in global average temperatures “to well below 2 °C above pre-industrial levels and to pursue efforts to limit the temperature increase to 1.5 °C”. Consequently, the scenario of 600–1,000 parts per million (p.p.m.) of atmospheric carbon dioxide, arising from unrestrained business-as-usual emissions, which underpins most of the scientific literature on the projected impacts of rising temperatures and ocean acidification on coral reefs, is no longer realistic — even if the Paris agreement is only partially successful¹⁵. However, it is almost certain that the 1.5 °C target will be exceeded for many decades^{16,17}. Restraining the rise in global temperatures to less than 2 °C (with a probability of 66%) would translate into an atmospheric carbon dioxide concentration of only 410–420 p.p.m. (Fig. 1a) — an amount that is likely to be surpassed in 3–4 years. Furthermore, representative concentration pathway (RCP) 2.6, which is the lowest (most optimistic) greenhouse gas emissions scenario assessed in the Intergovernmental Panel on Climate Change (IPCC) *Fifth Assessment Report*, indicates that coral reefs will run a gauntlet of hostile environmental conditions for several centuries, even with a rapid transition to zero emissions¹⁸. Reefs have already experienced three pan-tropical episodes of intense coral bleaching in the past three decades (1997–1998, 2010 and 2015–2016), triggered by an average global warming of close to 1 °C above pre-industrial temperatures^{8,19}.

The 1.5 °C and 2 °C targets, based on global average land and sea temperatures, are misleading metrics for understanding future changes to coral reefs because of differences in the amounts of warming that land and sea experience²⁰, steep latitudinal gradients in temperature, and regional discrepancies in rates of warming⁸. The global average temperature of about 14 °C has little relevance for tropical sea surface temperatures, which, in summer, are typically 27–30 °C, or higher. On the basis of the HadCRUT4 global temperature data set²¹, we calculate that the average tropical sea surface temperature rose by 0.57 °C between 1880 and 2015, which is substantially lower than the 0.88 °C increase in global average temperature for the same period. Furthermore, the observed increase in sea surface temperature in the tropics and subtropics since the late nineteenth century has varied substantially at the regional and local scales, with 71% of reefs worldwide warming by 0.25–0.75 °C, so far (Fig. 1b). This spatial heterogeneity suggests that there is no single ‘safe’ level, or planetary boundary², of global emissions for all coral reefs. Future increases in temperature will also vary greatly in space and time,

¹Australian Research Council Centre of Excellence for Coral Reef Studies, James Cook University, Townsville 4811, Queensland, Australia. ²Scripps Institution of Oceanography, University of California, San Diego, La Jolla, California 92093-0244, USA. ³Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington DC 20013, USA. ⁴National Center for Atmospheric Research, Boulder, Colorado 80307, USA. ⁵Department of Environmental Sciences, Wageningen University, PO Box 47, 6700 AA Wageningen, the Netherlands. ⁶Australian Institute of Marine Science, PMB 3, Townsville 4810, Queensland, Australia. ⁷Hopkins Marine Station, Department of Biology, Stanford University, Pacific Grove, California 93950, USA.

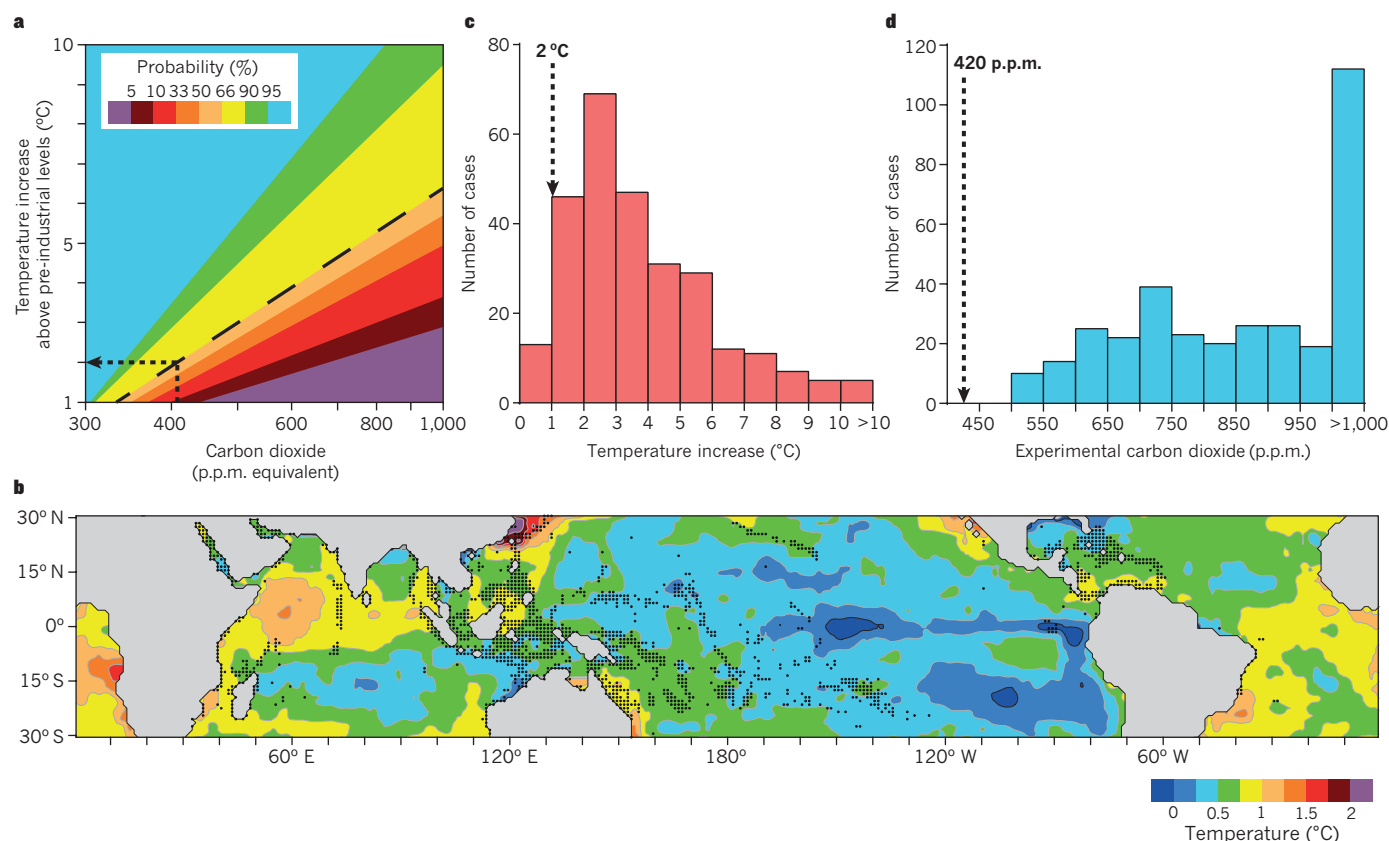


Figure 1 | The climate gauntlet faced by coral reefs. **a**, The relationship between stabilized concentrations of atmospheric carbon dioxide and stabilized increases in global average temperature above pre-industrial levels. The dashed line indicates a probability of 66%. Adapted from ref. 95. **b**, Global trends in tropical sea surface temperature from 1880 to 2015. Rates of warming of annual average sea surface temperature were calculated on the basis of linear trend analysis of the HadISST data set^{96,97} for all 1° latitude by 1° longitude boxes between 30.5° N and 30.5° S

(ref. 98) (the geographic zone in which coral reefs form). **c**, The range of temperature treatments used to experimentally simulate global warming on coral reef organisms. **d**, The range of atmospheric concentrations of carbon dioxide that correspond to experimental tests of ocean acidification on coral reefs. The arrows in **a**, **c** and **d** indicate the 2 °C target (with 66% probability) set by the 2015 Paris agreement on climate change. (See Supplementary Information Tables 1 and 2 for data used in **c** and **d**, respectively.)

which highlights the need for improved regional-scale modelling that incorporates more optimistic trajectories of emission reduction.

Future sea surface temperatures under the IPCC's RCP2.6 scenario are projected to increase in the short-term (2010–2039) in all major coral reef provinces, even as global emissions peak and begin to fall. Further warming projections for this period range from 0.32 °C in the eastern Indian Ocean to 0.48 °C in the Caribbean²². From 2039 to 2099, as sea surface temperatures begin to stabilize, temperatures are projected to change further in different reef provinces by +0.20 °C to −0.05 °C. Consequently, the longer-term warming trend, from 2010 to the end of the twenty-first century, under this low-emissions scenario varies from 0.30 °C to 0.68 °C between reef provinces, an increase that is roughly equivalent to the warming already observed over the past century.

Even if the 2 °C target of the Paris agreement is achieved, this projected level of warming will still have severe consequences for coral reefs — particularly when temperatures spike above the long-term summer maxima, leading to recurrent bleaching events²³. However, our knowledge of the chronic impacts of up to 1 °C of further warming on the physiology and demography of reef organisms is surprisingly limited because the temperatures used most commonly in recent thermal experiments are too high (Fig. 1c). Typically, these studies apply one or more treatments of elevated water temperatures, for periods that last from a day to a year (or sometimes even longer), to simulate long-term global warming on coral reefs. So far, the median manipulation of water temperatures above ambient controls represents an increase of 4 °C (or of almost 5 °C above the pre-industrial baseline temperature), and no study has experimentally examined the plausible biological responses to increases in the range of 0.30–0.68 °C that are projected for various coral

reef regions by RCP2.6 (Fig. 1c). Most manipulations also greatly exceed the spikes of 1–3 °C above baseline summer maximum temperatures that cause coral bleaching.

Similarly, shallow-water pH and the saturation state of aragonite, a form of calcium carbonate, which are crucial for calcification and other processes on coral reefs²⁴, are likely to change much less than the extremes that are predicted under higher-emission scenarios. The global average pH of ocean surface waters has declined in the last 200 years by about 0.1 units, from pH 8.21 to pH 8.10 (ref. 25). A further decrease of 0.3–0.4 units (to pH 7.7–7.8) would occur if atmospheric carbon dioxide concentrations reached 800 p.p.m., causing a contraction towards the Equator of optimal conditions for calcification²⁶. However, according to more recent modelling by the IPCC²², an equilibrium atmospheric concentration of 450 p.p.m. of carbon dioxide would maintain a pH of 7.9–8.1 in most tropical oceanic waters, sustaining a strongly supersaturated aragonite state throughout the tropics and the subtropics. So far, we find no evidence that the geographic range of calcifying species is contracting towards the Equator owing to ocean acidification. On the contrary, as temperatures rise, many species are expanding towards the north and south into the subtropics, despite small decreases in aragonite concentration^{27,28}.

Most experiments that are designed to explore the effects of ocean acidification on corals and other reef organisms have simulated extreme levels of atmospheric carbon dioxide that are designed to match conditions predicted for the end of the twenty-first century under unconstrained emissions of greenhouse gases (Fig. 1d). Typically, such experiments comprise a control, which corresponds to the present-day atmospheric carbon dioxide concentration of around 400 p.p.m., and

one or more treatments that manipulate pH or water chemistry. A broad range of physiological and demographic responses have been measured, including rates of calcification, growth, reproduction and survival. In 336 manipulations from a sample of 137 published studies (Supplementary Table 1), we found none that specifically simulated a future atmospheric carbon dioxide concentration of 400–500 p.p.m., the range that reefs are likely to experience for at least the next century. The lowest concentrations, which account for 32.7% of manipulations, ranged from 500 to 750 p.p.m. (Fig. 1d). Consequently, our knowledge of the effects of ocean acidification under conditions of less than 500 p.p.m. of carbon dioxide is built on the basis of interpolation between ambient controls and unrealistically high experimental treatments. Of the remaining manipulations, 33.9% studied concentrations of 750–1,000 p.p.m., and 33.3% evaluated concentrations that were even higher (Fig. 1c) — simulating atmospheric conditions that would generate temperatures of 6 °C or more that are lethal to corals (Fig. 1a). A similar challenge arises for field studies of ocean acidification that use naturally occurring locations with a consistently low pH, including volcanic vents or submarine springs, as a proxy for future climatic conditions. The water chemistry typically mimics an atmospheric carbon dioxide concentration of more than 1,000 p.p.m., but it is necessarily mismatched with current temperatures rather than those predicted for future global warming. Corals have already been affected by recurrent episodes of mass bleaching and mortality following exposure to warming of only 1–2 °C above baseline summer maximum temperatures for periods of 4–8 weeks^{8,19}. Consequently, whereas coral reefs already need to cope with severe global warming, they may never encounter the projected physiological and ecological impacts of severe ocean acidification that are simulated in the experimental literature (Fig. 1d).

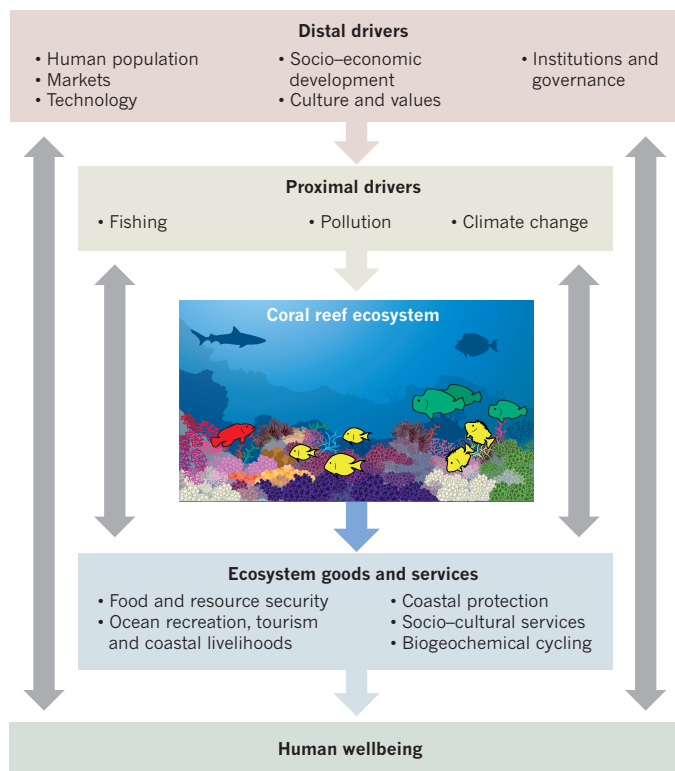


Figure 2 | Linkages and feedbacks between people and coral reefs. Distal drivers are traits in social systems that indirectly influence how people interact with coral reefs. Proximal drivers directly affect coral reef ecosystems (centre). Coral reefs provide important ecosystem services to people, which influence aspects of human wellbeing. Single-headed arrows indicate how the pathway flows from distal drivers to human wellbeing. Double-headed arrows show the complex linkages and feedbacks that also occur between the various components. Modified from ref. 39.

Clearly, our analysis (Fig. 1c, d) points to an urgent need to recalibrate both temperature and ocean-acidification experiments to better understand their interactive, combined impact on coral reefs under less extreme conditions. According to a statistical analysis of 25 experiments, the rate of calcification by corals declines on average by 15% per unit decrease in the aragonite saturation state (Ω), over the range of 2 to 4 Ω (ref. 29). However, atmospheric concentrations of carbon dioxide would have to double from 400 to 800 p.p.m. to reduce the present average aragonite saturation state of tropical surface waters (currently 3.01 Ω (ref. 26) by one unit. There is insufficient experimental evidence to accurately estimate how calcification would decline in response to a more modest emissions trajectory that peaks far below 800 p.p.m. However, interpolation of the available experimental evidence suggests that an average decrease in calcification of less than 10% is likely to occur with an increase in atmospheric carbon dioxide of up to 500–550 p.p.m. Although highly speculative, in the short term, rising average temperatures could promote coral growth and compensate partially for long-term shifts in aragonite concentrations³⁰. For example, on the most southerly subtropical coast of Western Australia, the calcification rate of corals from the genus *Porites* increased by 23.5% between 1900 and 2010, as temperatures rose by 0.10 °C per decade³⁰.

To resolve this uncertainty, there is an urgent need for future experiments to examine the synergy between warming and ocean acidification. This could be achieved by manipulating temperature and water chemistry incrementally, and by matching them to each other, over a more realistic range of projected levels of atmospheric carbon dioxide (400–500 p.p.m.). Recalibrating experimental approaches to global warming and ocean acidification will be challenging because smaller manipulations in temperature and water chemistry are more difficult to regulate, and the resulting biological responses will be harder to detect and quantify.

Although a modest level of oceanic acidification undoubtedly will have discernable effects, mass bleaching events owing to global warming, pollution and overfishing are likely to remain the most pressing challenges for reef biodiversity throughout the twenty-first century^{7,13,31,32}. We can therefore anticipate a rapid expansion of the geographic range of corals into higher latitudes^{27,28}, as well as continued shifts in species composition in response to differences in susceptibility to climate change and other anthropogenic drivers^{19,33}. The challenge worldwide is to steer reefs through this period of continued warming, a fundamentally different mindset to the current focus on managing to maintain the status quo of coral reefs.

Understanding social–ecological dynamics

In an era of rapid environmental shifts, social change and unprecedented economic development, the need for improved stewardship of natural systems worldwide has never been greater or more urgent². There is a growing awareness of the considerable influence of people on the functioning of all ecosystems^{31,34–36}, as well as a renewed evaluation of the dependence of human society on nature for food security, water, aesthetic and spiritual values, and other ecosystem services that contribute to human wellbeing (Fig. 2). Securing biodiversity and ecosystems for future generations requires new governance frameworks, or transformational changes to existing ones, and fresh approaches to ecosystem management. This task is probably greatest in the tropics, where the juxtaposition of billions of people with iconic hotspots of biodiversity presents an unprecedented challenge for securing both human development and conservation outcomes. Yet, until recently, ecologists have often ignored human behaviour as the ultimate (or distal) driver of environmental change, focusing instead on more proximal, smaller-scale drivers of change (Fig. 2). For example, in the coral reef literature, the grazing rate of herbivorous fishes is often considered to be an important driver of regime shifts from corals to macroalgae^{32,37}. However, grazing by herbivorous fishes is diminished by pressure from fishing, which is itself mediated by more distal social drivers such as poverty or market demands^{31,38}. Locally, the consumption of reef fish is

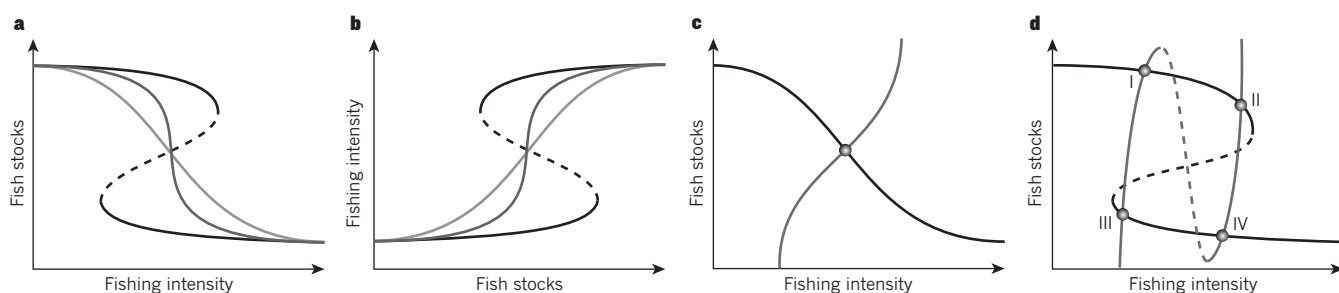
BOX 1

A framework for modelling social–ecological dynamics

Models that explicitly include feedbacks and nonlinear interactions within and between social and ecological systems are essential for understanding and analysing their intertwined dynamics. Here, we consider the hypothetical response of fish stocks to the intensity of fishing (Box 1 Fig. a) and vice versa (Box 1 Fig. b). In both cases, and depending on the strength of the feedbacks, a spectrum of responses (grey lines) is possible that range from linear to hysteretic (s-shaped curve; dotted sections indicate unstable regions). In a coupled social–ecological system, the simplest interaction (Box 1 Fig. c) is represented by two intersecting smooth responses, with a single stable equilibrium at intermediate levels of fishing intensity and stock size.

Depending on the shapes and intersections of the response curves, much more complicated dynamics can arise, including one, two, three or four stable states, and limit cycles. When both the ecological

and social elements exhibit hysteresis owing to strong feedbacks (Box 1 Fig. d), this can lead to four alternative stable equilibria (I–IV), which are classified according to the level of fish stocks and high fishing intensity. Subtle changes in either the social system or the ecological system can therefore produce profound differences in social–ecological dynamics. The most probable transitions between the four equilibria are directional, moving from II (the best-case scenario of both high fishing intensity and high fish stocks) to IV (fish stocks have collapsed and fishing remains high) then to III (both fish stocks and the fishery are degraded) and to I (fish stocks recover under light fishing). Consequently, the model suggests that the pathway to return to II (the best-case scenario) when the coupled system has collapsed to IV would be for both fish stocks and fishing intensity to decline to III and then shift to I before improving. Effectively, conditions are likely to get worse before they get better.



shaped by a combination of the size, socio–economic status and cultural norms of the human population³⁹. By emphasizing proximal drivers rather than more distal human ones, we often inadvertently simplify and re-scale a complex social–ecological problem into a subsystem that is entirely biological, which can distract from the underlying causes and ways to address them.

A social–ecological approach for sustaining ecosystems is beginning to emerge that explicitly links the resilience of ecosystems to governance structures, economies and society^{2,40–42}. Social–ecological models of various types have already been developed for a number of contexts, including forestry⁴³, freshwater lakes⁴⁴, fisheries⁴⁵ and agricultural abandonment⁴⁶. Combining human social systems and ecosystems in the same models reveals further complexity and a richer range of dynamics, which presents new possibilities for sustainable solutions (Box 1).

Death by a thousand cuts

Although climate change now dominates the discussion, it is clearly not the only threat in the Anthropocene to the biodiversity, ecological functions and ecosystem services of coral reefs^{7,13,31,32}. Approaches to understanding multi-causality — the interactions between multiple drivers — in coral reef science often categorize the effects of pairs of drivers as being additive, antagonistic or synergistic. For example, if climate change has effect x on the abundance of corals on a reef and overfishing has effect y , then climate change and overfishing together may, in theory, have an effect that is $x + y$, less than $x + y$ or greater than $x + y$ (ref. 47). In reality, however, the world is not so simple. Both the science and governance of coral reefs are in great need of stronger conceptual and methodological frameworks for understanding and managing multiple drivers and their combined impact.

Currently, the literature on multiple drivers and their impact on coral reefs focuses on three main strands: short-term laboratory or field experiments that manipulate two or, rarely, three stressors (for example, temperature and pH)²⁹; statistical analyses that correlate the

condition of reefs (for example, coral cover or fish biomass) at several locations or times with a number of factors^{48,49}; and global ecological assessments made on the basis of multi-layered geographic information systems maps (for example, ocean-health maps or Reefs at Risk maps)^{50,51}. Each strand can provide valuable insights, but all have considerable limitations. For example, experiments that manipulate drivers provide an in-depth understanding at only very small scales (from days to months, and usually in the laboratory) and are therefore unable to examine spatial dynamics or long-term interactions between species. Similarly, multiple regression analyses are often confounded by collinearity between explanatory variables. A tacit assumption in many such analyses, that the current condition of reefs can be explained by the mix and strength of present-day drivers, discounts the role of time lags between cause and effect in shaping the non-equilibrium trajectory of reefs⁵². Global maps also portray relative risks at large spatial scales, but they make the unrealistic assumption that stressors are only additive.

Analyses of interacting drivers and multi-causality have undergone more extensive development in terrestrial ecology, and their application has improved both the monitoring and management of ecosystems. For example, in savannas, an in-depth understanding of the interaction between fire, herbivory, predation, rainfall and vegetation has been central to developing strategies for the sustainable management of large herbivores⁵³. Others studies have proposed the formal use of a process of triangulation that compares and contrasts explorations of models, field studies and laboratory experiments⁵⁴ to cross-validate theories of causality. This builds on the idea that a rigorous understanding of multi-causality arises from testing hypotheses from a variety of perspectives.

Arguably, current thinking on the responses of ecosystems to one or more drivers is too linear. The ecological response to even a single stressor is often curved owing to positive or reinforcing feedbacks; small levels of drivers have no impact (for example, when pollution is too dilute or heat stress falls below a threshold) but higher amounts increasingly cause an ecological response⁵⁵. Thirty types of positive feedback

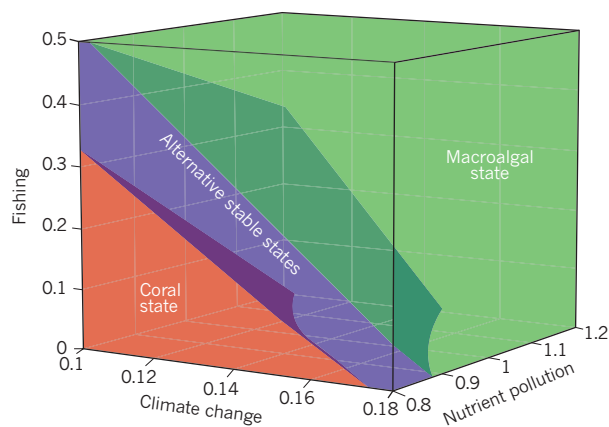


Figure 3 | The modelled response of coral reefs to multiple anthropogenic drivers. Depending on the strength and interaction between certain anthropogenic drivers (climate change, nutrient pollution and fishing), three outcomes are possible: when the drivers are weak, healthy coral-dominated assemblages form (coral state, red); when the drivers are strong, a state dominated by macroalgae with few corals forms (green); and when the drivers are intermediate, alternative states occur (purple). Interfaces between the coral, alternative and macroalgal states represent the tipping points or thresholds for each combination of drivers. The coral state collapses if the stress from any single driver is too strong and is eliminated entirely by the cumulative impacts of multiple drivers. The width and shape of the region of alternative stable states depends on the strength of interacting feedbacks. (See Supplementary Note 1 for further details about the model.)

have already been observed on coral reefs⁵⁶. Some are ecological or social and others are both. For example, when fish stocks decline, fishers without access to an alternative livelihood often increase their efforts and further suppress the stocks. A strong feedback produces a threshold response, and an even stronger one can cause hysteresis and precipitate a catastrophic collapse^{55,57}. When several weak feedbacks act simultaneously, they can collectively promote an unexpected regime shift as the effects of multiple drivers gradually increase⁵⁶.

An area that holds promise for understanding the role of multiple drivers and feedbacks in environmental change is the development of heuristic models. For example, when three drivers (climate change, overfishing and pollution) are modelled simultaneously (Fig. 3), their combined effects become more evident, which first results in transitions from a coral state to alternative states, in which both coral states and non-coral states can occur, and ultimately leads to conditions in which only a macroalgal state is possible. Consequently, the model identifies the concept of a generic 'safe operating space' for coral reefs²⁴, in which corals are dominant so long as multiple drivers are held in check below threshold levels that arise from their combined effects. This result is

particularly relevant to the widespread emergence of new drivers that affect ecosystems and add to the impact of pre-existing stressors, which themselves are likely to strengthen with time. For example, climate change and new coastal developments are adding to the now century-old pressures of overfishing and pollution on marine ecosystems. Here, modelling supports the proposal that local action to protect reefs from overfishing and pollution can boost the capacity of reef ecosystems to survive climate change^{57,10,49,58}. Therefore, the potential for making changes to social and ecological drivers and feedbacks is crucial when considering avenues for improved governance. Furthermore, the modelled result (Fig. 3) indicates that synergistic human impacts can reduce resilience and cause unexpected ecological collapse, even when individual drivers or stressors remain at levels that are considered to be safe.

Embracing change

The dynamics of coral reefs in the Anthropocene are already dominated by complex interactions between multiple anthropogenic drivers, which is resulting in new assemblages of species^{10,32,37}. Increasingly, we face a fundamentally different reality: it is no longer possible to restore coral reefs to their past configurations. For example, reefs in the Caribbean will never resemble the faunal composition of past centuries, owing to the ecological extinction of megafauna such as turtles and manatees, the massive decline of the once dominant branching corals of the genus *Acropora*, the irreversible introduction of the predatory lionfish (*Pterois volitans*) and the ongoing impact of coastal development, overfishing and climate change^{7,59}. Similarly, following a mass-bleaching event and unprecedented mortality in 2016, the corals of the remote northern Great Barrier Reef in Australia are unlikely to have sufficient time to fully recover their former species composition before further major bleaching events occur¹⁹. Instead of attempting to maintain or restore historical baseline assemblages, the governance and management of coral reefs will need to adapt continuously to the new conditions of the coming centuries.

Biodiversity in a changing world

In recent years, theoretical and empirical studies have provided a robust framework for understanding the relationship between biodiversity and ecosystem functioning⁶⁰. It is also now recognized widely that the morphologic, demographic and life-history traits of species play a central part in defining ecosystem functioning⁶¹ and that biodiversity is more than just counts of species; it also includes genetic, phylogenetic and functional diversity^{60,62–64}. However, considerable gaps in our knowledge remain — in particular, how ecosystem functions will respond to changing compositions of species that are the result of climate change and other anthropogenic drivers.

Despite their exceptionally high biodiversity, coral reefs are vulnerable to the loss of functionally important species^{31,63,64}. For example,

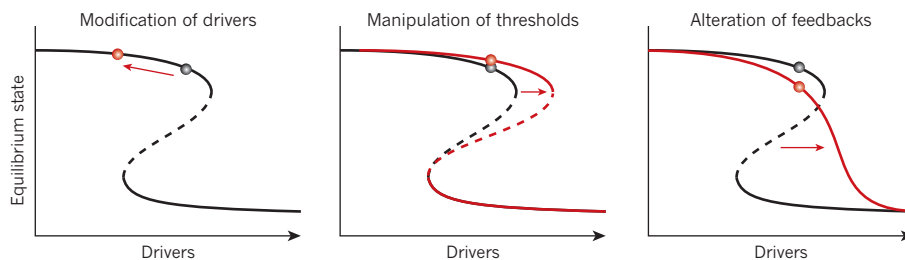


Figure 4 | A heuristic model of future management options for coral reefs. The x-axis represents one or more drivers of change, including climate change, pollution and overfishing, and the y-axis is the resultant state (at equilibrium) of the social or ecological system. Dashed lines indicate the intermediary range of drivers in which both healthy and degraded states are possible. Current stable states of the system are shown as black curves, whereas the red curves represent various potential approaches to reef management. The black and red dots indicate the state of the

ecosystem for a given strength of driver or drivers, and the arrows depict the change in trajectory that arises from present versus future management. The relative strength of multiple drivers could be reduced to move the system away from a dangerous threshold (left). The threshold could be manipulated to allow the system to handle higher levels of drivers without collapsing (centre). Multiple feedbacks could be managed to change the shape of the equilibrium response curve, eliminating the risk of surpassing a tipping point (right).

reefs support more than 6,000 species of fish, yet crucial functions are often delivered by just a handful of species. A global analysis of unique trait combinations of fish showed that about one-third of ecological functions are performed by only one species⁶³. The proportion of functional groups — sets of species performing the same function — that are depauperate is consistent regardless of regional species richness, which suggests that hotspots of high diversity on coral reefs are just as vulnerable as isolated reefs with low diversity. Consequently, it is becoming clear that biodiversity *per se* is less important for the maintenance of reefs than functional composition^{13,60,65}, and examples of this include the provision of a three-dimensional habitat by branching corals, the control of macroalgae by herbivores and the breakdown of dead corals by bioeroders. Identifying and targeting the functions that are required to maintain reef ecosystems offers an opportunity for fresh approaches to both the management and restoration of reefs.

Solution spaces

For coral reefs to survive and remain functional into the next century and beyond, we need to govern and manage them more effectively. Building on the emerging understanding of nonlinear responses, feedbacks and threshold dynamics in social–ecological systems (Box 1), we propose three complementary approaches to this endeavour.

First, a greater focus on reducing important drivers of change could help to avoid crossing thresholds that lead to environmental degradation (Fig. 4, left). Conversely, drivers that accelerate social change towards more sustainable practices⁶⁶ could be increased. The identification of how several drivers interact (for example, those shown in Fig. 3) is crucial for effective intervention. Current approaches to reef conservation, including marine reserves, often seek to limit fishing in selected areas but rarely address the distal causes of fishery overexploitation such as poverty and market demand⁴⁸ (Fig. 2). Understanding and tracking distal social drivers may provide an early warning of unsustainable impacts on reefs before they are detected by ecological indicators³⁸. The coupling of modern approaches to reef conservation with sustainable-development initiatives that target distal drivers, for example, by reducing poverty or encouraging shifts in social norms (the informal rules that shape people's attitudes and behaviours) such as compliance with fishing regulations, can produce both positive social⁶⁷ and ecological⁶⁸ outcomes.

Second, there could be opportunities to manipulate ecological thresholds so that stronger drivers are required to induce a regime shift or to cause unacceptable levels of degradation (Fig. 4, centre). This strategy seeks ways to ensure that a particular level of a driver, such as pressure from fishing or climate change, has less of an impact. Examples include: the introduction of technological innovations such as changes in fishing gear to reduce environmental damage⁶⁹; the fostering of social norms to reduce harmful practices^{66,70} and to encourage voluntary compliance with environmental laws and regulations⁷¹; investment in institutions and processes that help to buffer the deleterious effects that social drivers such as population size, consumption and access to markets have on cooperation and collective action⁷²; and altering the composition of ecosystems to increase the proportion of species that are more tolerant of escalating drivers (for example, heat-tolerant species that bleach and die at higher temperatures or species that recover faster). Ecosystem composition change is already occurring naturally, as corals respond and adapt to climate change (Box 2), and could be promoted further through efforts to actively manipulate ecosystem configurations. In social systems, shifts in the composition of society — for example, through enhanced education or a reduction in poverty — can also increase resilience to strong drivers such as climate change⁷³.

Last, feedbacks could be actively altered to flatten the slope of the response curve (Fig. 4, right), therefore reducing the risk of transgressing an unknown threshold or eliminating the threshold altogether. This approach could involve weakening positive feedbacks that result in a shift away from a coral-dominated state to an alternative, degraded ecosystem^{10,32,56,57}. Examples include providing government-backed

BOX 2

The acclimatization and adaptation of corals

It is becoming clearer that acclimatization and adaptation of corals to rapid changes in climate is already underway. Individual species of coral thrive in a variety of habitats and biogeographic locations because of their capacity to respond to a broad spectrum of temperatures, at both the physiological and population levels. Field studies using the reciprocal transplantation of coral clones also show that individual colonies have the ability to shift their temperature tolerance^{99,100}. These shifts are associated with changes in gene expression, the composition and density of symbionts, or colony growth patterns. Shifts towards partnerships with more heat-tolerant algal symbionts have also been recorded in individual colonies, especially after bleaching events¹⁰¹. However, populations of coral that live in different thermal regimes also show genetic fixed differences in heat tolerance that are not erased by acclimatization^{99,102}. Transplants along latitudes of the Great Barrier Reef¹⁰³ or from inshore to offshore populations¹⁰⁰ show a strong pattern of adaptation to their local thermal profile.

The mechanisms of local adaptation remain unclear. Genome scans and mating studies suggest that heat tolerance is influenced by the action of many genes^{102,104}. However, there are other opportunities for the evolution of fixed differences between coral populations besides the influence of classic natural selection on coral genes. Populations of corals in different reef microhabitats often differ in the type of symbiont that they acquire on settlement or following shifts caused by heat stress or the differential effects of bleaching¹⁰⁵. Epigenetic changes through DNA methylation generate heritable changes in gene expression in reef fish¹⁰⁶ and have also been documented in corals¹⁰⁷. These mechanisms, and the complex adaptive patterns that they produce, do not lend themselves to simple manipulation through genetic engineering.

Current data strongly show that reef corals exist as a mosaic of populations that respond physiologically to local heat stress to lessen damage from high temperatures¹⁰⁸. Microhabitats that experience periodic extremes of temperature can promote heat-resistant corals. Such corals will be crucial for the persistence of coral reefs through the upheavals of the Anthropocene.

incentives for fishers to exit a fishery when stocks decline or breaking the poverty-trap dynamics that encourage fishing despite low yields in an overexploited system^{39,70}. Understanding and manipulating feedbacks, thresholds and drivers at a number of scales will be integral to addressing the escalating problems that confront coral reefs.

Opportunities for action

Helping coral reefs to safely navigate the Anthropocene is a profound challenge for multiscale governance⁷⁴. In this context, reef governance refers to the myriad ways in which societies share knowledge and power, create policies, build legal frameworks and make decisions. By comparison, the management of coral reefs is the day-to-day business of reef protection, which is enabled by effective governance. At present, both the governance and management of coral reefs are typically focused at the local level and on the regulation of proximal drivers (for example, pressure from fishing or nearby coastal development). Attention to distal drivers, including migration, population growth or demand from global markets, is often limited, fragmented and ineffective³⁹. But in the Anthropocene, progression from local management and monitoring towards the multiscale governance of drivers, thresholds and feedbacks at relevant scales will be critically important. Here, we identify a number of potential

opportunities for overcoming this challenge for governance, many of which fall outside the comfort zone of reef scientists and managers.

Redefining management goals

As reefs continue to reconfigure and decline in the near future, it will be essential to reconsider management and conservation goals and how they can be achieved. Conventional management goals often focus on biodiversity, threatened species or the biomass of fish. Maintaining the ecological functions and ecosystem services of reefs, even as the species composition of the recent past becomes unattainable, will require a new focus that both builds on the current ecosystem-based model of management^{75–77} and recognizes more explicitly that ecosystems, and the people who depend on them, are changing rapidly. The emerging resilience-based approach^{10,32,40,78,79} is a step forward because it acknowledges the importance of ecological processes and the role of human drivers. In practical terms, process-based reef management could include reduction of corallivory (predation on corals) by the targeted culling of corallivores, enhancement of herbivory through the regulation of specific fisheries, or management of the connectivity of harvested functional groups by enhancing spillover from protected areas. A focus on processes, ecological functions, ecosystem services and human drivers therefore opens many more possibilities for active management interventions.

Manipulating ecosystems

A radical step, which is yet to be widely applied to coral reefs, entails a shift from passive ecosystem management to active ecosystem intervention^{55,80}. Conventionally, the management of coral reefs has been mostly passive, relying on an implicit assumption that if reefs are protected from human impacts, they will return to their original condition following a disturbance. In the Anthropocene, however, this fundamental assumption is void, and management and governance frameworks need to specifically embrace changes in the species composition of ecosystems or they will fail. So far, attempts at active intervention such as propagating coral fragments, assisted migration and selective breeding of corals^{81,82} have had limited success and are prohibitively expensive at meaningful spatial scales⁸³. For example, the US National Marine Fisheries Service estimates that a recovery plan for two species of the coral *Acropora* in the Caribbean territories of the United States would cost a minimum of US\$255 million and take more than 400 years to implement⁸⁴. Therefore, finding scalable, enduring and cost-effective interventions is an important and urgent research challenge. Efforts have typically focused on restoring populations of depleted species such as turtles or targeted corals, often without adequately addressing the drivers that caused their decline in the first place. A broader approach that seeks to reduce multiple pressures and repair key processes, including herbivory and larval recruitment, remains mostly unexplored.

Building institutions for governance

Multiscale governance is often fragmented and ineffective, and is challenged by issues of jurisdiction and legitimacy, complexity, scale and funding^{85–87}. More effective institutions for global governance could facilitate the reduction of important drivers (for example, the burning of fossil fuels or the trade in functionally important species) by assessing the scientific evidence, setting an agenda for action, managing compliance, building capacity and influencing social norms. Previous worldwide and transnational successes, including efforts to address ozone depletion and acid rain, demonstrate that it is feasible to meet the challenge of tackling global issues such as climate change⁶⁶. Further development of international agencies for the global stewardship of threatened ecosystems such as coral reefs could also expedite decision-making and action at national and local levels^{88,89}.

Fostering innovative partnerships

Local, national and transnational partnerships that involve civil society, development organizations and businesses can complement more

formal governance organizations^{72,90}. For example, the Coral Triangle Initiative on Coral Reefs, Fisheries and Food Security is a partnership of three major environmental non-government organizations (Conservation International, the World Wide Fund for Nature and The Nature Conservancy) and six national governments (Indonesia, Malaysia, Papua New Guinea, the Philippines, the Solomon Islands and Timor-Leste), which is aiming to achieve food security, sustainable fisheries and coral reef conservation at a regional scale⁶⁸. At the local scale, partnerships that build new alliances can also open up avenues for improving the governance and management of reefs, even in the absence of formal national governance^{67,74}.

Changing social norms

Governments, non-governmental organizations and social movements can actively encourage changes in social norms that lead to improved environmental behaviours^{66,91}. These changes can be promoted, for instance, through the imposition of taxes, the provision of incentives and subsidies, education and communication strategies⁹². Examples include communicating the risks and costs of environmental loss, education programmes that promote the value of marine parks and no-fishing zones, and providing subsidies to support the transition from fossil fuels to renewable energy.

The future for coral reefs

Confronting the global coral reef crisis will require immediate action to address the emission of greenhouse gases, as well as a clearer understanding of multiple drivers and ecosystem responses in the context of new, more realistic, scenarios of global climate change. We need to improve our grasp of the trajectories of interacting drivers and the responses of coral reefs to probable scenarios of shallow water temperatures and ocean pH. We should also incorporate the social sciences into our understanding of the dynamics of linked social-ecological systems. Anthropogenic drivers are becoming stronger and more diverse, as well as shifting in scale from local to global. Through globalization, coral reefs are becoming more accessible, which creates a variety of incentives for their exploitation but also has the potential to offer new solutions on the basis of multiscale governance, including international actions and policies. The challenge for the future is to steer away from the tipping points (Fig. 4) that are already manifesting at local scales^{13,93}. Future coral reef science should be re-oriented to test the effectiveness of policy and management solutions, to measure the success and failure of governance approaches and to modify them accordingly, and to guide the development of new policies⁹⁴.

We should not give up hope for the persistence of Earth's coral reefs. Importantly, governance approaches will need to integrate knowledge of human psychology and risk perception in ways that convey the seriousness of the challenges without generating hopelessness or despair. Progress in coral reef governance will require effective, multilevel institutions to coordinate and support action across multiple scales. Action to rein in distal drivers is needed at the global scale, yet there are few central authorities that operate effectively at such a scale⁸⁵. The Paris agreement¹⁴ is already reframing the possible futures of Earth's coral reefs and the science that underpins their management. To steer coral reefs through the next century, we will need to be bold, to embrace change and to recognize that securing essential services from coral reefs will require a new approach to science, management and governance. ■

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