Coral adaptive capacity insufficient to halt global transition of coral reefs into net erosion under climate change

Christopher Edward Cornwall
Victoria University of Wellington

Steeve Comeau
Sorbonne Université

Simon D. Donner
University of British Columbia

Chris Perry
University of Exeter

John Dunne
NOAA/OAR Geophysical Fluid Dynamics Laboratory

See next page for additional authors

Follow this and additional works at: https://digitalcommons.csumb.edu/marinescience_fac

Authors

Christopher Edward Cornwall, Steeve Comeau, Simon D. Donner, Chris Perry, John Dunne, Ruben van Hooidonk, James S. Ryan, and Cheryl A. Logan

RESEARCH ARTICLE

Global Change Biology WILEY

Coral adaptive capacity insufficient to halt global transition of coral reefs into net erosion under climate change

Christopher Edward Cornwall[1] | Steeve Comeau[2] | Simon D. Donner[3] | Chris Perry[4] | John Dunne[5] | Ruben van Hooidonk[6,7] | James S. Ryan[8] | Cheryl A. Logan[8]

[1]School of Biological Sciences and Coastal People Southern Skies, Victoria University of Wellington, Wellington, New Zealand

[2]Laboratoire d'Océanographie de Villefranche, CNRS-INSU, Sorbonne Université, Villefranche-sur-Mer, France

[3]Institute of Resources, Environment and Sustainability / Department of Geography, University of British Columbia, Vancouver, British Columbia, Canada

[4]Geography, Faculty of Environment, Science and Economy, University of Exeter, Exeter, UK

[5]NOAA/OAR Geophysical Fluid Dynamics Laboratory, Princeton, New Jersey, USA

[6]Cooperative Institute for Marine and Atmospheric Studies, Rosenstiel School of Marine and Atmospheric and Earth Science, University of Miami, Miami, Florida, USA

[7]Atlantic Oceanographic and Meteorological Laboratory, National Oceanic and Atmospheric Administration, Miami, Florida, USA

[8]Department of Marine Science, California State University, Monterey Bay, California, USA

Correspondence
Christopher Edward Cornwall, School of Biological Sciences and Coastal People Southern Skies, Victoria University of 7 Wellington, Wellington, New Zealand.
Email: christopher.cornwall@vuw.ac.nz

Funding information
Royal Society Te Apārangi, Grant/Award Number: VUW 1701

Abstract

Projecting the effects of climate change on net reef calcium carbonate production is critical to understanding the future impacts on ecosystem function, but prior estimates have not included corals' natural adaptive capacity to such change. Here we estimate how the ability of symbionts to evolve tolerance to heat stress, or for coral hosts to shuffle to favourable symbionts, and their combination, may influence responses to the combined impacts of ocean warming and acidification under three representative concentration pathway (RCP) emissions scenarios (RCP2.6, RCP4.5 and RCP8.5). We show that symbiont evolution and shuffling, both individually and when combined, favours persistent positive net reef calcium carbonate production. However, our projections of future net calcium carbonate production (NCCP) under climate change vary both spatially and by RCP. For example, 19%–35% of modelled coral reefs are still projected to have net positive NCCP by 2050 if symbionts can evolve increased thermal tolerance, depending on the RCP. Without symbiont adaptive capacity, the number of coral reefs with positive NCCP drops to 9%–13% by 2050. Accounting for both symbiont evolution and shuffling, we project median positive NCPP of coral reefs will still occur under low greenhouse emissions (RCP2.6) in the Indian Ocean, and even under moderate emissions (RCP4.5) in the Pacific Ocean. However, adaptive capacity will be insufficient to halt the transition of coral reefs globally into erosion by 2050 under severe emissions scenarios (RCP8.5).

KEYWORDS
adaptive capacity, calcium carbonate production, carbonate production, climate change, coral bleaching, coral reefs, marine heat waves, ocean warming, symbiont evolution, symbiont shuffling

1 | INTRODUCTION

Coral reefs provide crucial ecological services throughout coastal areas in the tropical and subtropical regions but are under threat from the emerging impacts of climate change (Cornwall et al., 2021; Hughes, Anderson, et al., 2018; Logan et al., 2021). Climate change is projected to increase marine heatwave (MHW) frequency, intensity and duration even under low greenhouse gas emission scenarios (Cooley et al., 2022; Frölicher et al., 2018; Laufkötter et al., 2020). Mass coral bleaching events are driven by MHWs, which rapidly cause high coral mortality over large areas of entire reefs, reducing coral cover, larval recruitment and rates of coral reef carbonate production over subsequent years (Hughes et al., 2017; Lange & Perry, 2019). Background ocean warming and acidification will further alter coral physiology (Kornder et al., 2018). Ocean acidification is the process of increasing absorption of anthropogenically derived CO_2 by the ocean's surface seawater, and results in shifts in seawater carbonate chemistry (including increasing H^+ and decreasing CO_3^{2-}) (Feely et al., 2004) that reduce the calcification rates of reef building taxa such as coral and calcareous algae while also increasing the rates of reef bioerosion and sediment dissolution (DeCarlo et al., 2015; Eyre et al., 2018; Kornder et al., 2018). Recent projections demonstrate the high likelihood that ocean warming, acidification and MHWs will combine to profoundly impact the ability of future coral reefs to produce calcium carbonate and accrete vertically (Cornwall et al., 2021).

The ability of coral reef structures to persist and to continuing to accrete vertically in the future will be strongly influenced by global greenhouse gas emissions and the ability of calcifying reef taxa to build resistance and resilience to increased heat stress and ocean acidification, even at reefs otherwise not strongly influenced by anthropogenic stressors. Scleractinian corals are the major reef building taxa, with other calcareous species such as coralline algae playing secondary roles on most reefs (Perry et al., 2018). Heat stress is predicted to be the major driver of coral decline in the future (Logan et al., 2021; van Hooidonk et al., 2020), and has already caused considerable negative impacts to coral reefs (Cooper et al., 2012; Hughes et al., 2017). Hence, the capacity of the coral or its dinoflagellate endosymbionts to increase their tolerance to progressive heat stress will strongly influence the ability of future reefs to persist and accrete.

Many corals have long generation times that likely could preclude some species from gaining tolerance to episodic heat stress and ongoing warming (Hoegh-Guldberg, 2012). For those corals with shorter generation times (1–2 years), there is emerging evidence that they could gain tolerance to such events (Bay et al., 2017; Howells et al., 2021; Humanes et al., 2022; Matz et al., 2018, 2020). However, the mechanisms responsible, causes of variation in effect sizes and the impacts of these mechanisms over multiple generations of exposure are still very uncertain. Conversely, corals' algal symbionts have relatively short generation times, large populations, and high genetic diversity, and their capacity to evolve more rapidly to tolerate future ocean conditions is relatively more certain (Buerger et al., 2020).

Likewise, some corals can shift their symbiont assemblages towards more heat tolerant genera ('symbiont shuffling') in response to heat stress (Baker, 2003; Berkelmans & van Oppen, 2006). Some evidence suggests that corals may also be able to pass down shuffled symbiont communities to their offspring (Quigley et al., 2019). While the effects of symbiont adaptive capacity on global coral cover have been quantified previously (Logan et al., 2021; van Hooidonk et al., 2020), it is unknown what consequences these adaptive processes would have on the ability of reefs to sustain rates of calcium carbonate production by maintaining higher coral cover in the future. Greater adaptive capacity under climate change could thus allow greater structural maintenance of reefs, increasing their ability to provide key functions such as habitat and food supply. How such adaptive capacity may influence carbonate production across a range of coral reefs that presently vary by community composition, reef health and geography is also unknown.

Here we integrate global-scale models of coral reef net calcium carbonate production (NCPP) (Cornwall et al., 2021) and coral reef ecological and evolutionary processes (Logan et al., 2021) to explore how the future outcomes for coral reef NCCP could be altered by the ability of symbionts to evolve greater heat tolerance, and/or for corals to shuffle their symbionts to those with greater heat tolerance across all ocean basins (see Section 2). Maintenance of higher coral cover under scenarios with adaptive capacity generally had favourable outcomes for NCCP. We find that symbiont adaptive capacity widens the window of persistent positive NCCP under minor to moderate emissions (representative concentration pathway RCP 2.6 and RCP4.5) by 2050 and even by 2100 via maintenance of higher coral cover, but will not afford continued persistence of positive NCCP under the most extreme emissions scenarios (RCP8.5) by 2050.

2 | METHODS

Here we combined two complementary models (Cornwall et al., 2021; Logan et al., 2021) to assess coral futures under ocean warming and acidification and use these to explore the critical question of how corals' natural adaptive capacity to warming may mitigate the impacts of warming and OA on reef carbonate budget states. Model one is an eco-evolutionary mechanistic model that assesses a full suite of outcomes for competing fast-growing/heat-sensitive corals ('branching') and slow-growing/heat-tolerant corals ('mounding') with no evolution, symbiont evolution, symbiont shuffling, and combined symbiont evolution and shuffling across coral reefs globally (Logan et al., 2021). Host evolution was not included here due to the relatively large uncertainties in parameterising these processes. Model two uses previous estimates of calcium carbonate production estimated from census-based and hydrochemical methods at more than 200 sites globally and employs a meta-analysis type model to estimate how ocean warming and acidification impact coral and coralline algal calcification, bioerosion and sediment dissolution rates (Cornwall et al., 2021). Both models use projections of RCP2.6, RCP4.5 and RCP8.5. Although both models project changes

through time, here we focus on combining models one and two to estimate how adaptive capacity of corals could protect from the effects of climate change at 2050 and 2100 under RCP scenarios 2.6, 4.5 and 8.5.

We briefly summarize each of the two models below and then describe how they were combined. In model one (Logan et al., 2021), symbiont-mediated adaptive capacity is simulated in two competing coral morphotypes through (1) natural selection of symbiont populations ('evolution') and (2) shifts between heat-sensitive and heat-tolerant symbiont communities ('shuffling'). Sea surface temperature (SST) and the thermal tolerance of both the symbiont and the coral host drives symbiont population dynamics, and symbiont density then influences coral population dynamics (e.g. growth and mortality). The model is comprised of differential equations for symbiont and coral population dynamics that are numerically integrated over time, with or without evolution, and with one or two symbiont populations. Model outputs includes coral and symbiont population size, symbiont 'genotype' or optimal temperature (°C), and change in relative coral cover over time. For models with evolution, natural selection is simulated using a quantitative genetic model, originally described in Baskett et al. (2009), resulting in thermal tolerance increases of 0.3–1.8°C by 2100 depending on climate scenario and reef location. For models with symbiont shuffling, a second heat-tolerant symbiont population is added with a thermal growth optimum +1°C above that of the original population that becomes competitively superior under warming. Due to documented trade-offs in coral growth associated with symbiont shuffling (e.g. Jones & Berkelmans, 2010), corals hosting shuffled heat-tolerant symbionts incur a 50% growth penalty (Cunning et al., 2015). Model one is applied to projected monthly bias-corrected SSTs from NOAA Geophysical Fluid Dynamics Laboratory's ESM2M for 1925 reef cells under RCP2.6, RCP4.5 and RCP8.5 to estimate relative coral cover between 1860 and 2100. The dynamics of the two adaptive mechanisms result in slower increases in coral thermal tolerance in evolution scenarios compared with shuffling scenarios by 2050, but both mechanisms lead to similar increases in thermal tolerance of remaining corals by 2100 (Logan et al., 2021). In this study, relative coral cover from model one was then extracted for the corresponding 210 reef locations used in model 2, described below. We use the measured coral covers in model two as our baseline, rather than projecting how these may have changed since 1860 due to increased uncertainty in such an estimate.

Model two (Cornwall et al., 2021), although previously described, warrants additional explanation of its main details here. NCCP for entire reefs are calculated by adding coralline algal gross production and coral gross production minus bioerosion rates. Model two uses meta-analysis derived responses of coral and coralline algal calcification to ocean warming, ocean acidification, and their responses to the interactive effects of the two. This includes 985 responses from 125 studies. For ocean warming, we project the impacts of increasing temperatures at each of our 201 sites under each RCP and time point. We then estimate the impacts of increasing temperatures beyond the summer maximum monthly mean for each study in our

meta-analysis approach (e.g. studies that recorded responses to simulated warming on coral and coralline algal calcification rates when combined with ocean acidification). We then calculated the mean of these effects to create modifiers for each reef, at each time point and RCP that were derived from coral and coralline algal responses to specific temperature and pH combinations. In this study, unlike in the previously published model two, we only assessed the responses to combined ocean warming and acidification. This acts as a proportional modifier that reduces any resident coral and coralline algal calcification. Resident coralline algal calcium carbonate production is determined by its gross calcium carbonate production calculated in model two multiplied by this modifier for RCP and year. However, for corals this is more complex, and functions as above, except that we remove the impacts of MHWs/mass coral bleaching events calculated in model two and replace them with calculations from model one. We describe this in further detail below.

For the bioerosion rates, we calculate similar reef by RCP by year modifiers under the combined impacts of ocean warming and acidification as above from model two. Initial bioerosion rates from model two are comprised of parrotfish, sea urchin, macro bioeroders (e.g. endolithic bivalves, sponges), and micro-bioeroders (e.g. cyanobacteria) at each site, and where site-specific estimates were not possible, means of ocean basins were taken. Here, only the macro- and micro-bioeroders were modified by the proportional effects of ocean warming and acidification, as there were insufficient data on tropical sea urchins and parrotfish responses to inform the model.

To calculate the impacts on potential vertical reef accretion, model two followed the methods of Perry et al. (2018). This combined the sediment infilling potential of sediment generated by resident parrotfish and sea urchins with NCCP, divided by the porosity of the accumulating framework components of the reef (accretion (mm year^{-1}) = infilling potential + NCCP/porosity). Infilling potential (CaCO$_3$ kg^{-1} m^{-2} year^{-1}) on each reef was estimated as ¼ of parrotfish bioerosion rates (CaCO$_3$ kg^{-1} m^{-2} year^{-1}) plus half of sea urchin and macro-eroder bioerosion rates (CaCO$_3$ kg^{-1} m^{-2} year^{-1}) (Perry et al., 2018). We then apply a proportional modifier based on meta-analysis derived rates of sediment dissolution. However, we add two important caveats here which are useful in interpreting what we refer to as vertical accretion potential. First, we acknowledge that there is much research required until rates of accretion can be accurately estimated from different components of the carbonate and sediment budgets, as large uncertainties presently exist in our scientific knowledge. The outputs of currently used approaches are also highly optimistic because they cannot factor for physical framework removal processes (waves, storms). Second, our sediment dissolution rates were derived mostly from 16 lagoon and laboratory-based experiments. More research is required to estimate how reef-generated sediments influence vertical accretion, and to accurately measure how rates of sediment dissolution and production on coral reefs will be impacted by climate change. Thus, we present vertical accretion only in the supplementary material as an indicator of impacts upon potential vertical accretion, and here we mostly focus on NCPP in our main manuscript.

To combine these models for the present study, we replace model two's projections of coral cover with differing DHWs with model one's projections of relative coral cover under different RCP and symbiont evolution/shuffling scenarios. Although we have branching and mounding coral cover at each of 201 sites from model two, future outcomes under model one are not tied to the initial cover of branching versus mounding corals at these real reefs, as model one deals with hypothetical reef cells in terms of coral cover extent relative to a pre-industrial time period. In addition, the underlying rates of coral gross carbonate production at these 201 reefs are difficult to separate into mounding and branching at every site, and often parameters other than their morphology influence gross carbonate production. Thus, we take the mean of both coral morphotypes NCCP. We then take the total relative coral cover produced by model one in 2050 and 2100, multiply the starting coral cover by this modifier from model two to obtain gross carbonate production of corals at each reef. For example, if model one projects 30% reductions in coral cover at a site under a specific scenario, and its initial coral cover was 50%, we multiple 0.3×0.5 to obtain the resulting coral cover. Lastly, we overlap the same effects of ocean warming and acidification at each reef on coral and coralline algal metabolism, bioerosion and sediment dissolution on remaining reef organisms.

3 | RESULTS

We project that the severity of the combined impacts of climate change on NCCP will be dictated primarily by the emissions scenario,

with adaptive capacity and location also influencing the severity of these impacts in lower emissions scenarios. In the absence of symbiont adaptive capacity, we project that reefs in the Atlantic and Indian Ocean regions will transition to net erosion of coral reef structures by 2050 under all three of the assessed RCP scenarios. Importantly, symbiont adaptive capacity via evolution and/or shuffling only provides significant buffering against the impacts of climate change in all ocean basins under RCP2.6, and to a lesser extent also provides benefits under RCP4.5 in the Pacific Ocean only (Figure 1). This projected resilience in the Pacific is due to higher initial NCCP, where many of our sites had lower bioerosion and higher coral cover (Cornwall et al., 2021).

Adaptive capacity via maintenance of higher coral covers affords some buffering against the impacts of climate change on NCCP under RCP2.6 and RCP4.5. For example, 19%–35% of coral reefs are still projected to have net positive NCCP in the evolution scenarios by 2050 (and 13%–24% by 2100), versus 9%–13% in scenarios without symbiont adaptive capacity by 2050 (and 4%–14% by 2100). Symbiont shuffling alone or combined shuffling and evolution, results in relatively higher NCCP in 2050 compared with symbiont evolution. However, by 2100, symbiont evolution keeps better pace with warming and confers the highest NCCP values across all basins and RCPs except RCP4.5 in the Indian Ocean. In locations with positive NCCP without adaptive capacity (e.g. Pacific Ocean under RCP2.6 and 4.5 in 2050), symbiont adaptive capacity has a relatively smaller effect on NCCP. However, the model projects non-linear changes between 2050 and 2100 in RCP2.6 due to increasing heat tolerance driven by symbiont adaptive capacity and enhanced recovery as warming plateaus. In this
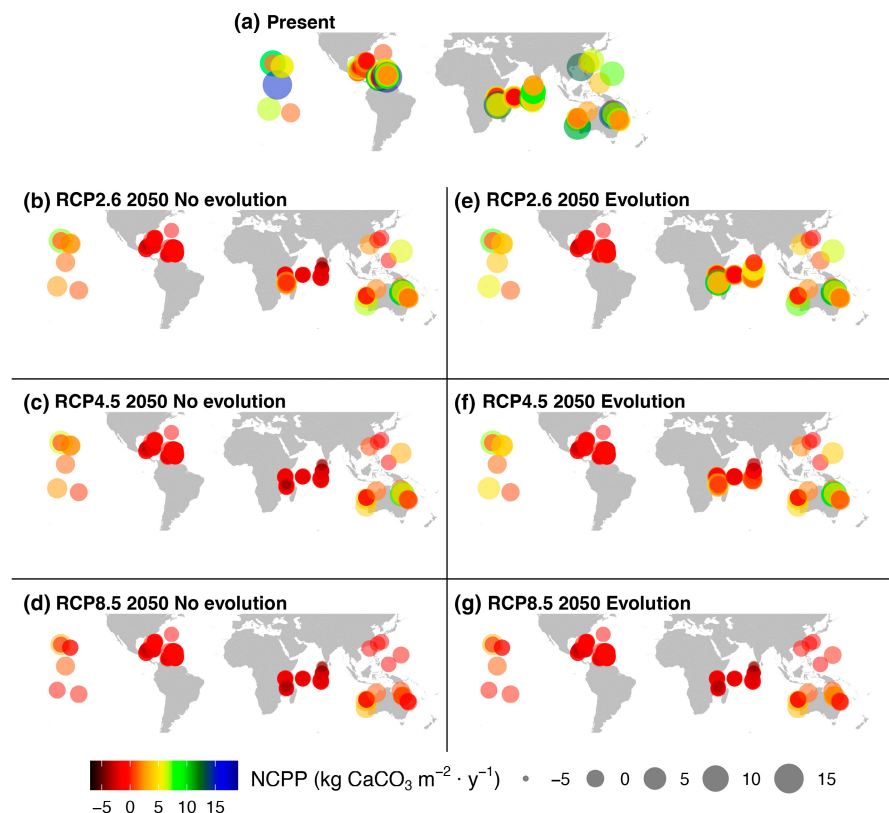

FIGURE 1 Locations of study reefs and their NCCP (net calcium carbonate production: kg CaCO$_3$ m^{-2} year^{-1}) (a) presently from Cornwall et al. (2021), and under scenarios of no evolution (b–d) and symbiont evolution (e–g) at RCP2.6 (b, e), RCP4.5 (c, f) and RCP8.5 (d, g) by 2050.

scenario, coral reefs will continue to act as sites of positive NCCP, albeit at very low rates, and with slight upturns after 2050, in line with previous model results of changes in coral cover from which this model is based (Logan et al., 2021).

Projected NCCP is sensitive to the simulated mechanisms of adaptive capacity, with inclusion of both symbiont evolution and shuffling of symbiont assemblages with greater heat tolerance generally leading to higher rates of NCCP across all ocean basins (Figure 2). However, the combined shuffling and evolution simulations are the least realistic, as some coral species may have limited or no capacity to undergo symbiont shuffling (Logan et al., 2021). Even in those simulations, coral reefs in every ocean basin are projected to be in net erosional states (<0 kg CaCO$_3$ m^{-2} year^{-1}) on average by 2100 under RCP8.5 (Figure 2; Figure S1). Only 6 of our 201 reefs are projected to still be producing calcium carbonate without adaptive capacity by 2100 (Figure S2).

4 | DISCUSSION

These results highlight that while symbiont adaptive capacity could ensure that coral reefs persist as sites of positive NCCP under climate change for a few decades, there is an immediate need to reduce greenhouse gas emissions for coral reefs to sustain NCCP long term. The ability to maintain NCPP will strongly influence the capacity of coral reefs to maintain physical structures that are essential in providing important ecosystem services into the future. Importantly, we project that symbiont adaptive capacity will not be a silver bullet that allows the persistence of normal coral reef functions as ocean warming and acidification intensifies, and as associated MHWs cause more frequent, widespread and intense bleaching events. The projected NCCP without symbiont adaptive capacity is even lower than in previous projections (Cornwall et al., 2021), which capped reductions in coral cover in response to MHWs, rather than the more physiological-based response to heat stress employed here and in other recent work (Bay et al., 2017; Logan et al., 2021; Matz et al., 2020; Walsworth et al., 2019). However, our results suggest that limiting warming to less than 2°C above the 1850–1900 level will allow many coral reefs to persist as sites of NCPP into the future.

While previous models have quantified the impacts of climate change and adaptive capacity on the proportional survival, cover and other components of coral physiology (Bay et al., 2017; Logan et al., 2014, 2021; McManus et al., 2021), this work additionally quantifies the impacts on NCCP. Other projections show more favourable
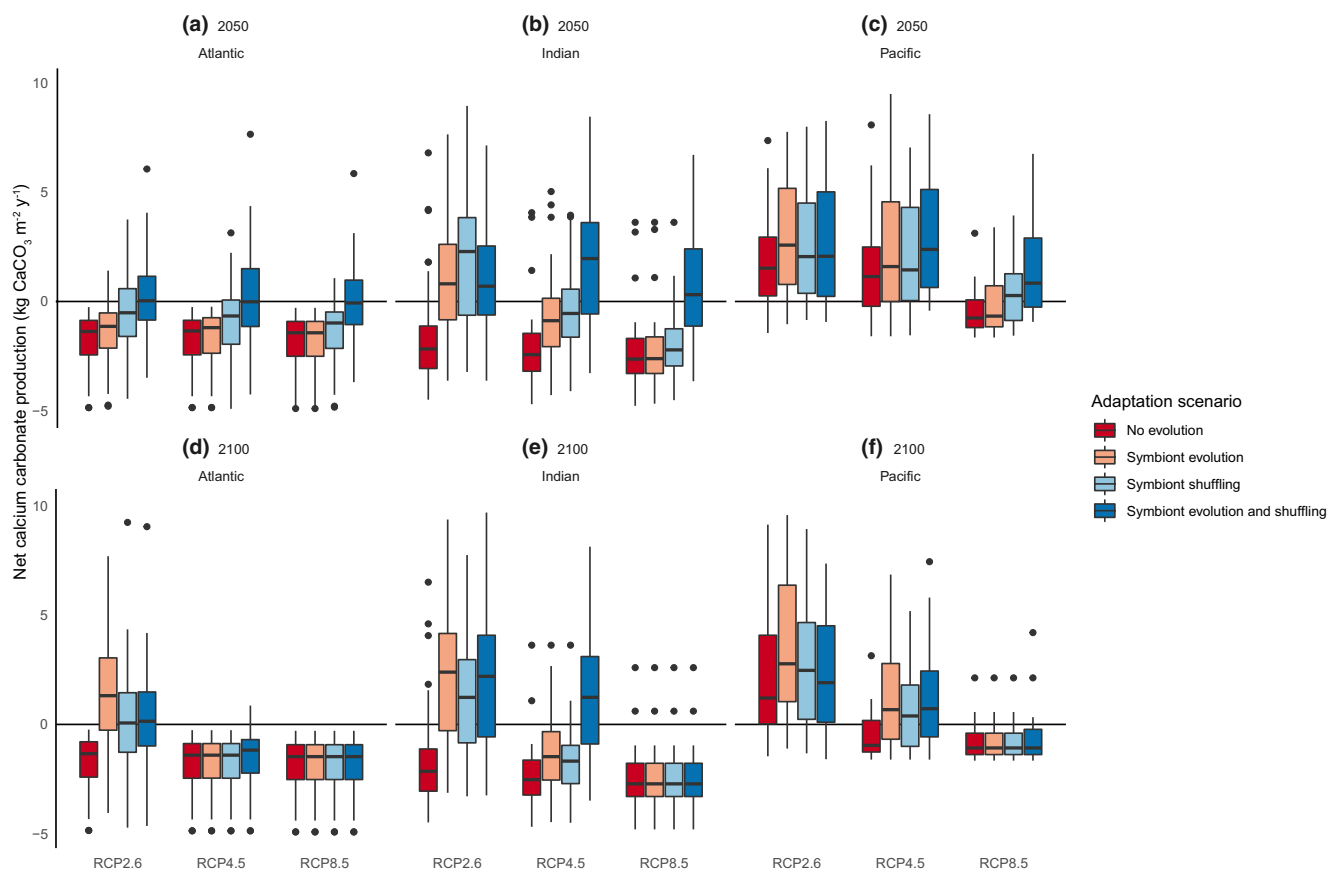
FIGURE 2 Projected net calcium carbonate production (NCCP) rates (kg CaCO$_3$ m^{-2} year^{-1}) in the Atlantic (a, d), Indian (b, e) and Pacific (c, f) Oceans by 2050 (a–c) and 2100 (d–f), allowing for four levels of adaptive capacity: no evolution, symbiont evolution only, symbiont shuffling only, and symbiont evolution and shuffling combined under RCP2.6, 4.5 ad 8.5. Medians, quartiles and 95% whiskers displayed across 201 coral reefs.

outcomes under simulated symbiont shuffling and evolution, but they focus on coral responses in isolation, not the responses of the entire reef. For example, under RCP4.5 relative coral cover shows relatively minor reductions by 2100 if symbiont evolution occurs as reported in past work, but at the expense of shifts in coral community composition (Logan et al., 2021). However, under RCP4.5 and beyond we demonstrate symbiont adaptive capacity likely will be insufficient to buffer from the effects of climate change on entire coral reefs. This is because coral reefs are not solely pressured by coral loss, but also by increasing sediment dissolution in lagoons (Eyre et al., 2018), bioerosion of reef substrate (DeCarlo et al., 2015), and metabolic depression of surviving corals and coralline algae (Comeau et al., 2019). Thus, NCCP in the future may be even lower than rates estimated here as the effects of climate change on these factors are poorly constrained. Furthermore, incorporation of different forms of natural adaptive capacity (e.g. coral host genetic adaptation, epigenetics, shifts in the microbiome) may also result in different abilities to buffer corals from declines in NCCP. This is highlighted here: the faster acting mechanism of symbiont shuffling is more advantageous to NCCP over the short term (e.g. by 2050), compared with the slower process of symbiont evolution that only keeps pace with warming over longer timescales if carbon emissions are curtailed.

Our results highlight that many reefs in the Pacific Ocean may continue to persist through 2100 with NCCP at reasonable rates with symbiont adaptive capacity even under RCP4.5. Indeed, there is some emerging evidence from sites in the Pacific that repeated bleaching events can result in reduced impacts of successive events (Harrison et al., 2019), inferring possible increases in heat tolerance (Pratchett et al., 2013). However, this is site specific, and other mitigating factors such as upwelling of cold and nutrient rich water cannot be discounted in some instances (DeCarlo & Harrison, 2019). In our model, coral reefs in the Pacific Ocean had higher initial NCCP due to higher coral cover, lower bioerosion and higher contribution to NCCP by coralline algae. We did not apply reduced coralline algal cover due to MHWs here, as much emerging work indicates that coralline algae are usually much more resistant to the effects of MHWs than corals, and can even increase in cover after such events (Cornwall et al., 2019). However, future research should focus on quantifying the response of coralline algal cover to MHWs of differing intensities in the field, as an array of work has already done with corals. Some coralline algae have short generation times, and thus it is possible they might also possess greater adaptive capacity than corals (Cornwall et al., 2020), though extensive further research is required to properly quantify this across a range of climate change stressors.

There are several improvements that could be made to better predict outcomes of coral reef NCCP under climate change. We consider that improving estimates of coralline algal gross calcium carbonate production and bioerosion rates in general would be the optimal first step. This is not only true within our model, but also in the field of measuring NCCP in general (Lange et al., 2020). Gross production by coralline algae is complex to measure accurately in the field, due to difficulties associated with identification and differences between how their gross production is measured, that is it is often measured via production on settlement plates. This means that their gross production also contains recruitment or density dependence issues that coral production is not hampered by, where linear extension of existing adults is measured. Likewise, most estimates of bioerosion are conducted either on experimentally deployed blocks of coral (Tribollet & Golubic, 2005) or on scanned coral cores (DeCarlo et al., 2015). Improving estimates of all these processes at numerous scales and identifying environmental patterns would increase the accuracy of future models. By combining two models here, we gained a wider range of scenarios over which we can observe possible future outcomes of climate change on coral reef NCCP. However, future models could that project changes in temperature variability, carbonate chemistry variability, oxygen concentrations at reef-scales presently could provide an even wider range of scenarios to view NCCP outcomes. In addition, sea-level rise will cause changes in coral reef ecosystems through increasing inundation of backreef habitats, and through very subtle decreases in irradiance due to water increases in water depth, with these reductions in irradiance being significant if wave activity also elevates turbidity through increases in sediment resuspension. However, we consider that the more scenarios/factors that are added, the larger the range of uncertainty would become. Especially for factors such as carbonate chemistry variability and oxygen concentrations, the effects of which are presently poorly constrained on coral reef taxa (Johnson et al., 2021; Rivest et al., 2017).

Adaptive capacity in the coral host was not included here due to the greater uncertainty in estimating its mechanistic effects across an ecologically realistic number of coral species. However, this is an emerging field of research that demonstrates that transgenerational changes in individual coral tolerances to successive MHWs and ongoing ocean warming and acidification is possible (Putnam & Gates, 2015; Torda et al., 2017). This is either through short-term transgenerational acclimatization that includes processes such as epigenetic changes in gene expression (Kenkel & Matz, 2016; Putnam et al., 2016; Putnam & Gates, 2015), or through long-term changes in allele frequencies that will be partially determined by the magnitude of stress and the heritably of traits related to increasing tolerance to such events (Quigley & van Oppen, 2022). Such effects have not been measured in coral populations beyond F1 generations exposed to such stressors. However, increasing tolerance to ocean acidification relative to controls has been measured in one tropical coralline algal species after six generations of exposure (Cornwall et al., 2020). The next step forward in projecting future coral reef futures will need to adequately quantify the magnitude of these effects while identifying the mechanisms responsible over more than just the F0–F1 generations in multiple coral and coralline algal species. Once that is completed, future modelling could advance existing methods (e.g. Bay et al., 2017; Logan et al., 2021; McManus et al., 2021) to better project future of coral reef NCCP across a broader range of holobiont adaptive responses.

Given the near-term threat to coral reefs, there is increasing attention to active management interventions which can help coral reefs and the services they provide persist in the face of climate change (Hoegh-Guldberg et al., 2018). For example, climate-smart marine-protected area design can focus on locations which may be more resilient to heat stress due to frequent exposure to heat stress (Beyer et al., 2018; Khen et al., 2022), local meteorological or oceanographic conditions (Gonzalez-Espinosa & Donner, 2021; Storlazzi et al., 2020), or presence of sufficient coral cover (e.g. Darling et al., 2019). Marine protection and past management approaches (passive restoration, reduction of other stressors) may be insufficient to protect coral cover and diversity beyond 1.5°C of global warming (Cooley et al., 2022; figure 3.25). More active interventions, like transplanting of heat tolerant colonies or assisted evolution, are therefore receiving greater attention (National Academies of Sciences, Engineering & Medicine, 2019).

The results of this study indicate that efforts to restore coral reefs by propagating heat-tolerant taxa, species or populations should also select those with high rates of NCCP and morphologies favouring reef accretion. Otherwise, active restoration efforts may be unsuccessful at maintaining positive NCCP and key ecosystem services like wave attenuation and habitat provision. However, this is challenge because many of the taxa with high rates of carbonate production are also the most thermally sensitive (Hughes, Kerry, et al., 2018; Kornder et al., 2018; Lange et al., 2020). For example, many prostrate corals also have high thermal tolerances (e.g. favids from coralline algal reefs in the northern Western Australia; Cornwall and Comeau unpublished data) but would provide much lower rates of NCCP than branching corals (Perry & Alvarez-Filip, 2019).

Our results indicate that symbiont-driven adaptive capacity of corals is not likely to keep pace with the impacts of climate change on the majority of reefs without limiting warming well below 2°C. In the Atlantic basin, we find that even immediate action to mitigate greenhouse gas emissions (RCP2.6) does not relieve net erosion except in the most optimistic case of adaptation at mid-century, but results in net deposition in all adaptation cases by end of century. In the Pacific, moderate mitigation of greenhouse gas emissions (RCP4.5) allows net deposition through the end of century if some form of symbiont-mediated adaptation occurs. Thus, immediate action is required to mitigate greenhouse gas emission or face the high likelihood that many coral reefs will shift into net erosional states.

CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest.

DATA AVAILABILITY STATEMENT

All data submitted to dryad https://doi.org/10.5061/dryad.5hqbz kh9v.

ORCID

Christopher Edward Cornwall https://orcid.org/0000-0002-6154-4082

Steeve Comeau https://orcid.org/0000-0002-6724-5286

Simon D. Donner https://orcid.org/0000-0003-0600-7388

Chris Perry https://orcid.org/0000-0001-9398-2418

John Dunne https://orcid.org/0000-0002-8794-0489

James S. Ryan https://orcid.org/0000-0003-0119-7960

Cheryl A. Logan https://orcid.org/0000-0001-7639-4956

REFERENCES

Baker, A. C. (2003). Flexibility and specificity in coral-algal symbiosis: Diversity, ecology, and biogeography of symbiodinium. *Annual Review of Ecology, Evolution, and Systematics*, 34(1), 661–689. https://doi.org/10.1146/annurev.ecolsys.34.011802.132417

Baskett, M. L., Gaines, S. D., & Nisbet, R. M. (2009). Symbiont diversity may help coral reefs survive moderate climate change. *Ecological Applications*, 19(1), 3–17. https://doi.org/10.1890/08-0139.1

Bay, R. A., Rose, N. H., Logan, C. A., & Palumbi, S. R. (2017). Genomic models predict successful coral adaptation if future ocean warming rates are reduced. *Science Advances*, 3(11), e1701413. https://doi.org/10.1126/sciadv.1701413

Berkelmans, R., & van Oppen, M. J. H. (2006). The role of zooxanthellae in the thermal tolerance of corals: A 'nugget of hope' for coral reefs in an era of climate change. *Proceedings of the Royal Society B: Biological Sciences*, 273(1599), 2305–2312. https://doi.org/10.1098/rspb.2006.3567

Beyer, H. L., Kennedy, E. V., Beger, M., Chen, C. A., Cinner, J. E., Darling, E. S., Eakin, C. M., Gates, R. D., Heron, S. F., Knowlton, N., Obura, D. O., Palumbi, S. R., Possingham, H. P., Puotinen, M., Runting, R. K., Skirving, W. J., Spalding, M., Wilson, K. A., Wood, S., … Hoegh-Guldberg, O. (2018). Risk-sensitive planning for conserving coral reefs under rapid climate change. *Conservation Letters*, 11(6), e12587. https://doi.org/10.1111/conl.12587

Buerger, P., Alvarez-Roa, C., Coppin, C. W., Pearce, S. L., Chakravarti, L. J., Oakeshott, J. G., Edwards, O. R., & van Oppen, M. (2020). Heat-evolved microalgal symbionts increase coral bleaching tolerance. *Science Advances*, 6(20), eaba2498. https://doi.org/10.1126/sciadv.aba2498

Comeau, S., Cornwall, C. E., DeCarlo, T. M., Doo, S. S., Carpenter, R. C., & McCulloch, M. T. (2019). Resistance to ocean acidification in coral reef taxa is not gained by acclimatization. *Nature Climate Change*, 9(6), 477–483. https://doi.org/10.1038/s41558-019-0486-9

Cooley, S. R., Schoeman, D., Bopp, L., Boyd, P., Donner, S. D., Ito, S.-I., Kiessling, W., Martinetto, P., Ojea, E., Racault, M.-F., Rost, B., & Skern-Mauritzen, M. (2022). *Ocean and coastal ecosystems and their services*. Cambridge University Press.

Cooper, T. F., O'Leary, R. A., & Lough, J. M. (2012). Growth of Western Australian corals in the Anthropocene. *Science*, 335(6068), 593–596. https://doi.org/10.1126/science.1214570

Cornwall, C. E., Comeau, S., DeCarlo, T. M., Larcombe, E., Moore, B., Giltrow, K., Puerzer, F., D'Alexis, Q., & McCulloch, M. T. (2020). A coralline alga gains tolerance to ocean acidification over multiple generations of exposure. *Nature Climate Change*, 10(2), 143–146. https://doi.org/10.1038/s41558-019-0681-8

Cornwall, C. E., Comeau, S., Kornder, N. A., Perry, C. T., van Hooidonk, R., DeCarlo, T. M., Pratchett, M. S., Anderson, K. D., Browne, N.,

Carpenter, R., Diaz-Pulido, G., D'Olivo, J. P., Doo, S. S., Figueiredo, J., Fortunato, S. A. V., Kennedy, E., Lantz, C. A., McCulloch, M. T., González-Rivero, M., … Lowe, R. J. (2021). Global declines in coral reef calcium carbonate production under ocean acidification and warming. *Proceedings of the National Academy of Sciences of the United States of America*, 118(21), e2015265118. https://doi.org/10.1073/pnas.2015265118

Cornwall, C. E., Diaz-Pulido, G., & Comeau, S. (2019). Impacts of ocean warming on coralline algal calcification: Meta-analysis, knowledge gaps, and key recommendations for future research. *Frontiers in Marine Science*, 6, 1–10. https://doi.org/10.3389/fmars.2019.00186

Cunning, R., Gillette, P., Capo, T., Galvez, K., & Baker, A. C. (2015). Growth tradeoffs associated with thermotolerant symbionts in the coral Pocillopora damicornis are lost in warmer oceans. *Coral Reefs*, 34(1), 155–160. https://doi.org/10.1007/s00338-014-1216-4

Darling, E. S., McClanahan, T. R., Maina, J., Gurney, G. G., Graham, N. A. J., Januchowski-Hartley, F., Cinner, J. E., Mora, C., Hicks, C. C., Maire, E., Puotinen, M., Skirving, W. J., Adjeroud, M., Ahmadia, G., Arthur, R., Bauman, A. G., Beger, M., Berumen, M. L., Bigot, L., Bouwmeester, J., … Mouillot, D. (2019). Social–environmental drivers inform strategic management of coral reefs in the Anthropocene. *Nature Ecology & Evolution*, 3(9), 1341–1350. https://doi.org/10.1038/s41559-019-0953-8

DeCarlo, T. M., Cohen, A. L., Barkley, H. C., Shamberger, K. E., Cobban, Q., Young, C., Shamberger, K. E., Brainard, R. E., & Golbuu, Y. (2015). Coral macrobioerosion is accelerated by ocean acidification and nutrients. *Geology*, 43(1), 7–10. https://doi.org/10.1130/G36147.1

DeCarlo, T. M., & Harrison, H. B. (2019). An enigmatic decoupling between heat stress and coral bleaching on the great barrier reef. *PeerJ*, 7, e7473. https://doi.org/10.7717/peerj.7473

Eyre, B. D., Cyronak, T., Drupp, P., De Carlo, E. H., Sachs, J. P., & Andersson, A. J. (2018). Coral reefs will transition to net dissolving before end of century. *Science*, 359(6378), 908–911.

Feely, R. A., Sabine, C. L., Lee, K., Berelson, W., Kleypas, J. A., Fabry, V. J., & Millero, F. J. (2004). Impact of anthropogenic CO_2 on the $CaCO_3$ system in the oceans. *Science*, 305, 362–366.

Frölicher, T. L., Fischer, E. M., & Gruber, N. (2018). Marine heatwaves under global warming. *Nature*, 560(7718), 360–364. https://doi.org/10.1038/s41586-018-0383-9

Gonzalez-Espinosa, P. C., & Donner, S. D. (2021). Cloudiness reduces the bleaching response of coral reefs exposed to heat stress. *Global Change Biology*, 27(15), 3474–3486. https://doi.org/10.1111/gcb.15676

Harrison, H. B., Álvarez-Noriega, M., Baird, A. H., Heron, S. F., MacDonald, C., & Hughes, T. P. (2019). Back-to-back coral bleaching events on isolated atolls in the coral sea. *Coral Reefs*, 38(4), 713–719. https://doi.org/10.1007/s00338-018-01749-6

Hoegh-Guldberg, O. (2012). The adaptation of coral reefs to climate change: Is the red queen being outpaced? *Scientia Marina*, 76(2), 403–408.

Hoegh-Guldberg, O., Kennedy, E. V., Beyer, H. L., McClennen, C., & Possingham, H. P. (2018). Securing a long-term future for coral reefs. *Trends in Ecology & Evolution*, 33(12), 936–944. https://doi.org/10.1016/j.tree.2018.09.006

Howells, E. J., Abrego, D., Liew, Y. J., Burt, J. A., Meyer, E., & Aranda, M. (2021). Enhancing the heat tolerance of reef-building corals to future warming. *Science Advances*, 7(34), eabg6070. https://doi.org/10.1126/sciadv.abg6070

Hughes, T. P., Anderson, K. D., Connolly, S. R., Heron, S. F., Kerry, J. T., Lough, J. M., Baird, A. H., Baum, J. K., Berumen, M. L., Bridge, T. C., Claar, D. C., Eakin, C. M., Gilmour, J. P., Graham, N. A. J., Harrison, H., Hobbs, J. A., Hoey, A. S., Hoogenboom, M., Lowe, R. J., … Wilson, S. K. (2018). Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. *Science*, 359(6371), 80–83. https://doi.org/10.1126/science.aan8048

Hughes, T. P., Kerry, J. T., Álvarez-Noriega, M., Álvarez-Romero, J. G., Anderson, K. D., Baird, A. H., & Wilson, S. K. (2017). Global warming and recurrent mass bleaching of corals. *Nature*, 543, 373–377. https://doi.org/10.1038/nature21707

Hughes, T. P., Kerry, J. T., Baird, A. H., Connolly, S. R., Dietzel, A., Eakin, C. M., Heron, S. F., Hoey, A. S., Hoogenboom, M. O., Liu, G., McWilliam, M., Pears, R. J., Pratchett, M. S., Skirving, W. J., Stella, J. S., & Torda, G. (2018). Global warming transforms coral reef assemblages. *Nature*, 556(7702), 492–496. https://doi.org/10.1038/s41586-018-0041-2

Humanes, A., Lachs, L., Beauchamp, E. A., Bythell, J. C., Edwards, A. J., Golbuu, Y., Martinez, H. M., Palmowski, P., Treumann, A., van der Steeg, E., van Hooidonk, R., & Guest, J. R. (2022). Within-population variability in coral heat tolerance indicates climate adaptation potential. *Proceedings of the Royal Society B: Biological Sciences*, 289(1981), 20220872. https://doi.org/10.1098/rspb.2022.0872

Johnson, M. D., Swaminathan, S. D., Nixon, E. N., Paul, V. J., & Altieri, A. H. (2021). Differential susceptibility of reef-building corals to deoxygenation reveals remarkable hypoxia tolerance. *Scientific Reports*, 11(1), 23168. https://doi.org/10.1038/s41598-021-01078-9

Jones, A., & Berkelmans, R. (2010). Potential costs of acclimatization to a warmer climate: Growth of a reef coral with heat tolerant vs. sensitive symbiont types. *PLoS One*, 5(5), e10437. https://doi.org/10.1371/journal.pone.0010437

Kenkel, C. D., & Matz, M. V. (2016). Gene expression plasticity as a mechanism of coral adaptation to a variable environment. *Nature Ecology & Evolution*, 1(1), 14. https://doi.org/10.1038/s41559-016-0014

Khen, A., Johnson, M. D., Fox, M. D., Clements, S. M., Carter, A. L., & Smith, J. E. (2022). Decadal stability of coral reef benthic communities on Palmyra atoll, Central Pacific, through two bleaching events. *Coral Reefs*, 41(4), 1017–1029. https://doi.org/10.1007/s00338-022-02271-6

Kornder, N. A., Riegl, B. M., & Figueiredo, J. (2018). Thresholds and drivers of coral calcification responses to climate change. *Global Change Biology*, 24(11), 5084–5095. https://doi.org/10.1111/gcb.14431

Lange, I. D., & Perry, C. T. (2019). Bleaching impacts on carbonate production in the Chagos archipelago: Influence of functional coral groups on carbonate budget trajectories. *Coral Reefs*, 38(4), 619–624. https://doi.org/10.1007/s00338-019-01784-x

Lange, I. D., Perry, C. T., & Alvarez-Filip, L. (2020). Carbonate budgets as indicators of functional reef "health": A critical review of data underpinning census-based methods and current knowledge gaps. *Ecological Indicators*, 110, 105857. https://doi.org/10.1016/j.ecolind.2019.105857

Laufkötter, C., Zscheischler, J., & Frölicher, T. L. (2020). High-impact marine heatwaves attributable to human-induced global warming. *Science*, 369(6511), 1621–1625. https://doi.org/10.1126/science.aba0690

Logan, C. A., Dunne, J. P., Eakin, C. M., & Donner, S. D. (2014). Incorporating adaptive responses into future projections of coral bleaching. *Global Change Biology*, 20(1), 125–139. https://doi.org/10.1111/gcb.12390

Logan, C. A., Dunne, J. P., Ryan, J. S., Baskett, M. L., & Donner, S. D. (2021). Quantifying global potential for coral evolutionary response to climate change. *Nature Climate Change*, 11(6), 537–542. https://doi.org/10.1038/s41558-021-01037-2

Matz, M. V., Treml, E. A., Aglyamova, G. V., & Bay, L. K. (2018). Potential and limits for rapid genetic adaptation to warming in a great barrier reef coral. *PLoS Genetics*, 14(4), e1007220. https://doi.org/10.1371/journal.pgen.1007220

Matz, M. V., Treml, E. A., & Haller, B. C. (2020). Estimating the potential for coral adaptation to global warming across the indo-West Pacific. *Global Change Biology*, 26(6), 3473–3481. https://doi.org/10.1111/gcb.15060

McManus, L. C., Forrest, D. L., Tekwa, E. W., Schindler, D. E., Colton, M. A., Webster, M. M., Essington, T. E., Palumbi, S. R., Mumby, P. J., & Pinsky, M. L. (2021). Evolution and connectivity influence the persistence and recovery of coral reefs under climate change in the Caribbean, Southwest Pacific, and coral triangle. *Global Change Biology*, *27*(18), 4307–4321. https://doi.org/10.1111/gcb.15725

National Academies of Sciences, Engineering, & Medicine. (2019). *A research review of interventions to increase the persistence and resilience of coral reefs*. The National Academies Press.

Perry, C. T., & Alvarez-Filip, L. (2019). Changing geo-ecological functions of coral reefs in the Anthropocene. *Functional Ecology*, *33*(6), 976–988. https://doi.org/10.1111/1365-2435.13247

Perry, C. T., Alvarez-Filip, L., Graham, N. A. J., Mumby, P. J., Wilson, S. K., Kench, P. S., Manzello, D. P., Morgan, K. M., Slangen, A. B. A., Thomson, D. P., Januchowski-Hartley, F., Smithers, S. G., Steneck, R. S., Carlton, R., Edinger, E. N., Enochs, I. C., Estrada-Saldívar, N., Haywood, M. D. E., Kolodziej, G., … Macdonald, C. (2018). Loss of coral reef growth capacity to track future increases in sea level. *Nature*, *558*(7710), 396–400.

Pratchett, M. S., McCowan, D., Maynard, J. A., & Heron, S. F. (2013). Changes in bleaching susceptibility among corals subject to ocean warming and recurrent bleaching in Moorea, French Polynesia. *PLoS One*, *8*(7), e70443. https://doi.org/10.1371/journal.pone.0070443

Putnam, H. M., Davidson, J. M., & Gates, R. D. (2016). Ocean acidification influences host DNA methylation and phenotypic plasticity in environmentally susceptible corals. *Evolutionary Applications*, *9*(9), 1165–1178. https://doi.org/10.1111/eva.12408

Putnam, H. M., & Gates, R. D. (2015). Preconditioning in the reef-building coral *Pocillopora damicornis* and the potential for trans-generational acclimatization in coral larvae under future climate change conditions. *Journal of Experimental Biology*, *218*(15), 2365–2372. https://doi.org/10.1242/jeb.123018

Quigley, K. M., & van Oppen, M. J. H. (2022). Predictive models for the selection of thermally tolerant corals based on offspring survival. *Nature Communications*, *13*(1), 1543. https://doi.org/10.1038/s41467-022-28956-8

Quigley, K. M., Willis, B. L., & Kenkel, C. D. (2019). Transgenerational inheritance of shuffled symbiont communities in the coral Montipora digitata. *Scientific Reports*, *9*(1), 13328. https://doi.org/10.1038/s41598-019-50045-y

Rivest, E. B., Comeau, S., & Cornwall, C. E. (2017). The role of natural variability in shaping the response of coral reef organisms to climate change. *Current Climate Change Reports*, *3*(4), 271–281.

Storlazzi, C. D., Cheriton, O. M., van Hooidonk, R., Zhao, Z., & Brainard, R. (2020). Internal tides can provide thermal refugia that will buffer some coral reefs from future global warming. *Scientific Reports*, *10*(1), 13435. https://doi.org/10.1038/s41598-020-70372-9

Torda, G., Donelson, J. M., Aranda, M., Barshis, D. J., Bay, L., Berumen, M. L., Bourne, D. G., Cantin, N., Foret, S., Matz, M., Miller, D. J., Moya, A., Putnam, H. M., Ravasi, T., van Oppen, M. J. H., Thurber, R. V., Vidal-Dupiol, J., Voolstra, C. R., Watson, S.-A., … Munday, P. L. (2017). Rapid adaptive responses to climate change in corals. *Nature Climate Change*, *7*, 627–636. https://doi.org/10.1038/nclimate3374

Tribollet, A., & Golubic, S. (2005). Cross-shelf differences in the pattern and pace of bioerosion of experimental carbonate substrates exposed for 3 years on the northern great barrier reef, Australia. *Coral Reefs*, *24*(3), 422–434. https://doi.org/10.1007/s00338-005-0003-7

van Hooidonk, R., Maynard, J. A., Grimsditch, G., Williams, G. J., Tamelander, J., Gove, J. M., Koldewey, H., Ahmadia, G., Tracey, D., Hum, K., Conklin, E., & Berumen, M. L. (2020). Projections of future coral bleaching conditions using IPCC CMIP6 models: Climate policy implications, management applications, and regional seas summaries. Nairobi, Kenya.

Walsworth, T. E., Schindler, D. E., Colton, M. A., Webster, M. S., Palumbi, S. R., Mumby, P. J., Essington, T. E., & Pinsky, M. L. (2019). Management for network diversity speeds evolutionary adaptation to climate change. *Nature Climate Change*, *9*(8), 632–636. https://doi.org/10.1038/s41558-019-0518-5

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.