Received: 1 September 2017 | Revised: 23 October 2017 | Accepted: 20 December 2017

DOI: 10.1111/gcb.14043

PRIMARY RESEARCH ARTICLE

WILEY Global Change Biology

Vulnerability of the Great Barrier Reef to climate change and local pressures

Nicholas H. Wolff[1,2] | **Peter J. Mumby**[1,3] | **Michelle Devlin**[4,5] | **Kenneth R. N. Anthony**[6]

[1]Marine Spatial Ecology Lab, School of Biological Sciences, The University of Queensland, St Lucia, QLD, Australia

[2]Global Science, The Nature Conservancy, Brunswick, ME, USA

[3]ARC Centre of Excellence for Coral Reef Studies, The University of Queensland, St Lucia, QLD, Australia

[4]Centre for Environment, Fisheries and Aquaculture Science, Lowestoft Laboratory, Lowestoft, Suffolk, UK

[5]Catchment to Reef Research Group, Centre for Tropical Water and Aquatic Ecosystem Research, James Cook University, Douglas, QLD, Australia

[6]Australian Institute of Marine Science, PMB3, Townsville, QLD, Australia

Correspondence

Peter J. Mumby, Marine Spatial Ecology Lab, School of Biological Sciences, The University of Queensland, St Lucia, QLD, Australia.
Email: p.j.mumby@uq.edu.au
and
Kenneth R.N. Anthony, Australian Institute of Marine Science, PMB3, Townsville, QLD, Australia.
Email: k.anthony@aims.gov.au

Funding information

National Environmental Research Programme, Australia

Abstract

Australia's Great Barrier Reef (GBR) is under pressure from a suite of stressors including cyclones, crown-of-thorns starfish (COTS), nutrients from river run-off and warming events that drive mass coral bleaching. Two key questions are: how vulnerable will the GBR be to future environmental scenarios, and to what extent can local management actions lower vulnerability in the face of climate change? To address these questions, we use a simple empirical and mechanistic coral model to explore six scenarios that represent plausible combinations of climate change projections (from four Representative Concentration Pathways, RCPs), cyclones and local stressors. Projections (2017–2050) indicate significant potential for coral recovery in the near-term, relative to current state, followed by climate-driven decline. Under a scenario of unmitigated emissions (RCP8.5) and business-as-usual management of local stressors, mean coral cover on the GBR is predicted to recover over the next decade and then rapidly decline to only 3% by year 2050. In contrast, a scenario of strong carbon mitigation (RCP2.6) and improved water quality, predicts significant coral recovery over the next two decades, followed by a relatively modest climate-driven decline that sustained coral cover above 26% by 2050. In an analysis of the impacts of cumulative stressors on coral cover relative to potential coral cover in the absence of such impacts, we found that GBR-wide reef performance will decline 27%–74% depending on the scenario. Up to 66% of performance loss is attributable to local stressors. The potential for management to reduce vulnerability, measured here as the mean number of years coral cover can be kept above 30%, is spatially variable. Management strategies that alleviate cumulative impacts have the potential to reduce the vulnerability of some midshelf reefs in the central GBR by 83%, but only if combined with strong mitigation of carbon emissions.

KEYWORDS

Acropora, bleaching, coral reefs, cumulative stressors, Paris climate accord, vulnerability, water quality

1 | INTRODUCTION

Coral reefs worldwide are facing impacts from multiple local, regional and global pressures including ocean warming and acidification, pollution, storms, overfishing and invasive pests (Alvarez-Filip, Dulvy, Gill, Côté, & Watkinson, 2009; Bellwood, Hughes, Folke, & Nyström, 2004; Hoegh-Guldberg et al., 2007) (Figure 1). During the 2015/2016 El Niño, Australia's Great Barrier Reef (GBR), the world's largest and most intensively managed coral reef ecosystem, experienced its third and worst coral bleaching event in history, with over 90% of reefs affected (Hughes et al., 2017). Mass bleaching events are projected to increase pan-tropically for all RCP projections, including the most optimistic (Frieler et al., 2013; Ortiz, Bozec, Wolff, Doropoulos, & Mumby, 2014). Furthermore, ocean acidification is projected to lower the scope for coral reefs to calcify and sustain processes that underpin resilience (Anthony et al., 2011; Kleypas et al., 1999). Together, these global stressors contribute uncertainty about the future resilience of the GBR (Hughes, Day, & Brodie, 2015) and the scope for regional management actions to sustain coral reefs.

In response to growing national and international concerns about the GBR (Brodie et al., 2013; Douvere & Badman, 2012), Australia recently released a long-term GBR sustainability plan (Reef 2050, Reef 2050 Long-Term Sustainability Plan 2015) for the years 2016–2050. A central tenet of Reef 2050 is that alleviation of local stressors, mainly through improvements in water quality and effective COTS control, will enhance reef resilience in the face of climate change. Specifically, the plan aims for a minimum of 50% reduction of baseline (2009) riverine nutrient loads by 2018, extending to 80% reduction by 2025. These targets have been informed by scientific syntheses and consensus statements (Brodie et al., 2012, 2013), which in turn have been informed by multiple individual studies reviewed in Brodie et al. (2012). While it is well established that coral reefs are sensitive to nutrient enrichment (Fabricius, 2005), most of the documented impacts of land-based pollutants on the GBR are restricted to inshore reefs (Roff et al., 2012). However, two lines of evidence suggest nutrient run-off may indirectly affect reefs further offshore. First is correlative evidence for a link between nutrient enrichment, phytoplankton blooms, survival of larval COTS and consequent GBR-wide outbreaks (Birkeland, 1982; Fabricius, Okaji, & De'ath, 2010), providing a basis for establishing the 50%–80% targets for nutrients (Brodie et al., 2013; Kroon, Thorburn, Schaffelke, & Whitten, 2016). Second is evidence linking nutrient exposure with greater thermal stress sensitivity (bleaching) through complex physiological processes (Wiedenmann et al., 2013; Wooldridge, 2013) which also indicates a 50%–80% nutrient reduction is necessary (Wooldridge, Brodie, Kroon, & Turner, 2015).

The stated expectation in Reef 2050 is that management efforts will lead to improved coral condition each successive decade through 2050. While improvements in water quality and mitigating COTS outbreaks will benefit GBR ecosystems in general (Brodie & Pearson, 2016), outcomes of Reef 2050 for reef corals are less clear. Two pertinent questions for the GBR are: (1) how vulnerable will the system be to different climate change scenarios? and (2) to what extent can the management of local- and regional-scale pressures compensate for the effects of climate change into the future?

Here, we use a simple model of coral cover dynamics to examine the extent to which water quality improvements and effective COTS control can help sustain or increase coral cover on the GBR in a warming world. Firstly, we evaluate possible GBR futures under six different scenarios capturing plausible combinations of global and

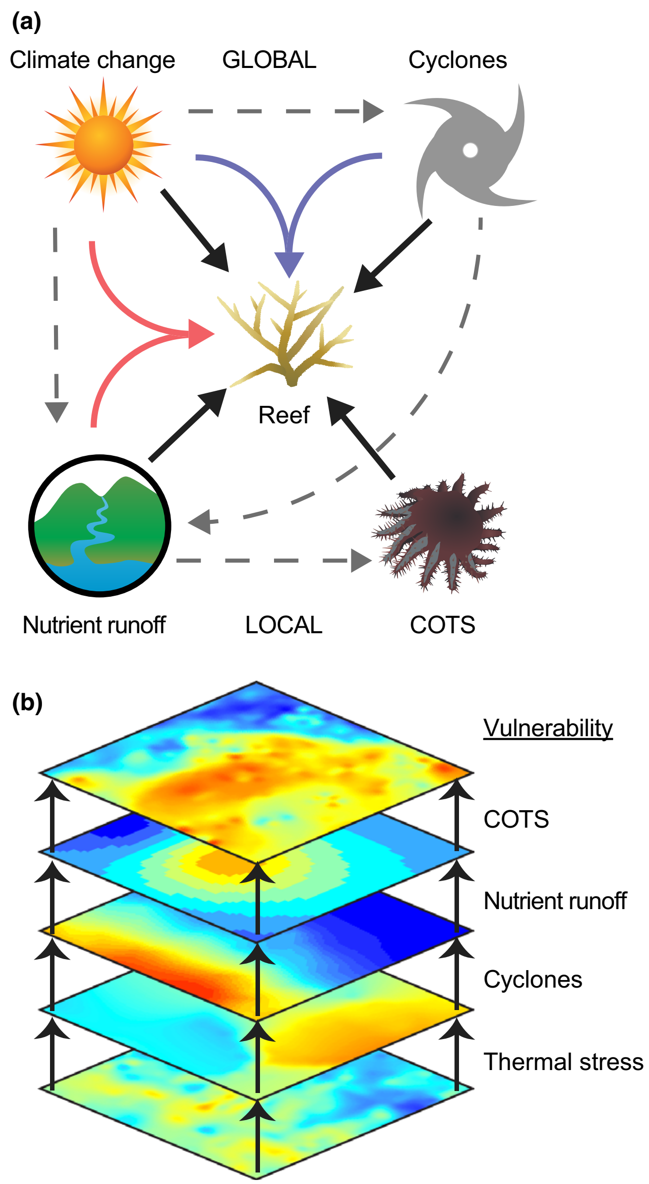

FIGURE 1 (a) Schematic of the primary global (cyclones and climate change) and local (COTS and nutrient run-off) stressors currently affecting GBR coral health. Direct impacts (solid black) include damage from cyclones, bleaching from global warming, reduced thermal tolerance from nutrient run-off and predation from COTS. Interactions between stressors (solid colours) include local reductions in thermal stress due to cyclone induced water cooling (blue), and increased thermal sensitivity to nutrient run-off due to global warming (red). Indirect interactions (dotted grey) include potential climate change influence on cyclone frequency and/or magnitude and on weather patterns (e.g. flooding from more intense rain events). In addition, nutrient run-off is indirectly linked to COTS outbreak frequency due to enhanced larval survival. (b) Dynamic exposure to these stressors is captured using spatially explicit probability layers, which are then integrated using a coral trajectory model. The model is parameterized to represent the impacts of the different disturbances (including interactions) on coral cover (mortality). Multiple simulations are used to capture stochasticity and uncertainty (see Methods for details). Symbols (a) are from Tracey Saxby, Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/imagelibrary/)

local stressors. Secondly, we estimate the relative impacts of these scenarios on patterns of GBR coral vulnerability in space and time. Thirdly, we identify areas where reductions of manageable stressors appear to achieve greater utility in sustaining coral cover. To achieve this, the model integrates spatially explicit exposure layers of thermal stress, cyclones, river run-off (as a proxy for poor water quality inundation) and COTS (Figure 1). We fitted a logistic growth model to historical trajectories of *Acropora* coral cover on the GBR and then parameterized estimates of coral mortality caused by bleaching, cyclone damage and COTS predation. We also include scenarios where the sensitivity of coral to thermal stress is possibly heightened under poor water quality associated with river plumes (Wooldridge, 2009; Wooldridge & Done, 2009; Wooldridge et al., 2017). We note that the model is likely to underestimate cumulative impacts by not accounting for ocean acidification and by disregarding direct impacts of reduced water quality on coral growth and survival. The model is evaluated annually at 1,312 reef locations, between years 2017 and 2050. We then analysed the relative importance of global and local stressors in driving trajectories of coral cover under different climate scenarios and examined to what extent different management regimes can counteract the vulnerability caused by climate change.

2 | MATERIALS AND METHODS

2.1 | Scenario development

We used six environmental scenarios (S1–S6) as input layers for the model to examine a range of possible outcomes for GBR coral cover between 2017 and 2050 (Table 1). Four scenarios (S2–S5) represent business-as-usual levels of management of local stressors across each of the four Representative Concentration Pathways (RCPs) adopted by the IPCC for its Fifth Assessment Report (AR5) (van Vuuren et al., 2011). In addition, we also explored a worst-case scenario (S1) which combined minimal carbon mitigation (RCP 8.5) resulting in accelerated warming, with increased nutrient run-off due to land clearing and suboptimal land-use practices within GBR catchments (Brodie & Pearson, 2016; Kroon et al., 2016). Finally, we used a scenario (S6) that combines a low-emission pathway (RCP 2.6), consistent with the Paris climate accord's ambitions of limiting warming to 1.5°C, with the reduction targets for nutrient run-off set in the Reef 2050 Plan (Table 1). We assume COTS outbreak frequency will increase under S1, driven by increased nutrient run-off and survival of COTS larvae (Brodie, Devlin, & Lewis, 2017; Fabricius et al., 2010). Conversely, under S6 we assume COTS outbreak frequency will decrease due to land-use improvements and lower nutrient exposure (Table 1). Cyclones were treated conservatively as a background disturbance and were thus modelled consistently across all six scenarios using reef-scale impact probabilities based on GBR observations (Wolff et al., 2016).

2.2 | Disturbance probability layers

2.2.1 | Cyclones

Although climate change may explain the recent spate of intense GBR cyclones (Cheal, Macneil, Emslie, & Sweatman, 2017), natural temporal clustering is another plausible explanation for this pattern (Wolff et al., 2016). Observations indicate that cyclone patterns in the South Pacific have not responded to warmer seas, unlike in

TABLE 1 Description of the six different scenarios used here to capture plausible combinations of global and local stressors. Ocean warming projections were based on each of four AR5 RCPs. Each of these RCPs was combined with business-as-usual (BaU) local management which assumed observed nutrient run-off effects on water quality and observed COTS outbreak frequency would remain unchanged (scenarios 2–5). The worst-case scenario (S1) assumes emissions will increase unabated (RCP 8.5) and continued land clearing and catchment development will lead to higher probability of nutrient run-off impacts and more frequent COTS outbreaks. The best-case scenario (S6) assumes both the emissions mitigation ambitions of the Paris climate accord (RCP 2.6) and the management goals of the Reef 2050 plan are successfully implemented, reducing warming impacts, nutrient run-off and COTS outbreak frequency. Cyclone impacts are modelled consistently, based on observed probabilities, across all scenarios. Details of scenario development and implementation can be found in the Materials and Methods

Scenario (name)	Warming (RCP)	Nutrient run-off	COTS frequency (years)	Description
S1 (Worst case)	High (8.5)	Further degraded	10	Business-as-usual emissions and continued land clearing leads to high warming, greater probability of poor water quality impacts and higher frequency of COTS outbreaks
S2 (BaU, RCP8.5)	High (8.5)	Business as usual	15	Business-as-usual emissions and water quality/COTS management
S3 (BaU, RCP6.0)	Moderate high (6.0)	Business as usual	15	Moderate emissions mitigation and business-as-usual water quality/COTS management
S4 (BaU, RCP4.5)	Moderate low (4.5)	Business as usual	15	Moderately strong emissions mitigation and business-as-usual water quality/COTS management
S5 (BaU, RCP2.6)	Low (2.6)	Business as usual	15	Strong emissions mitigation and business-as-usual water quality/COTS management
S6 (Best case)	Low (2.6)	Improved	20	Strong emissions mitigation and successful implementation of Reef 2050 goals results in relatively minor warming and lower probability of water quality/COTS impacts

other ocean basins (Elsner, Kossin, & Jagger, 2008), and that future effects are uncertain (Knutson et al., 2010). Therefore, we here use past cyclone patterns as a surrogate for the future threat. Specifically, we used reef-scale probabilities of cyclone impacts, integrating 100 years of GBR cyclone observations with a library of over 7,000 synthetic cyclone tracks (Emanuel, Sundararajan, & Williams, 2008). Probabilities capture GBR-wide observed distributions in storm intensity, with spatial variability in cyclone frequency and temporal clustering, a previously overlooked characteristic with ecological significance. In general, storms are more frequent and more regularly timed in the central GBR and less frequent and clustered in both the northern and southern GBR (Wolff et al., 2016).

2.2.2 | Thermal stress

Projections of sea surface temperature (SST) were derived from the UK Hadley Centre Global Environmental Model HadGEM2-ES using the four greenhouse gas trajectories adopted by the IPCC for its fifth Assessment Report (IPCC, 2014): RCPs 8.5, 6.0, 4.5 and 2.6 predict global mean temperatures of ~3.7°C, ~2.2°C, ~1.8°C and ~1°C by year 2100 respectively. Coral bleaching events under these RCPs were modelled following the approach of Wolff et al. (2015). Briefly, an observed SST climatology was created using Hadley Centre Sea Ice and Sea Surface Temperature data set (HadISST) for the period 1985–1993 (the climatological period used by NOAA Coral Reef Watch). Future monthly anomalies >1°C above the maximum monthly mean from the climatology were accumulated within a 3 month window to calculate degree heating months (DHMs). Then, for each of the 33 (0.5° resolution) pixels that intersected the GBR, the maximum DHM for each year was extracted.

The IPCC global circulation climate models (GCM), including the HadGEM2-ES used here, are designed to represent broad-scale variability and climate trends and are not meant to capture regional spatial patterns at finer scales (Kwiatkowski, Halloran, Mumby, & Stephenson, 2013). Recent efforts to use statistical downscaling techniques to provide local-scale projections show promise (van Hooidonk et al., 2016), but we were concerned that GCM deviation from observed warming patterns (Kwiatkowski et al., 2013) remains an issue. Here, we use a hybrid approach that relied on fine-scale historical thermal stress patterns to drive spatial distributions, and RCP output to represent the magnitude and variability in future stress. Implicit in this approach is the assumption that spatial patterns of future warming will follow recent observed patterns.

We characterized historical thermal stress patterns (1982–2017) using a degree heating weeks (DHW) metric. Specifically we used version 5 (1982–2012), a 4 km product, of the Coral Reef Temperature Anomaly Database (CoRTAD) (Selig, Casey, & Bruno, 2010) and version 3 (2013–2017) of the NOAA Coral Reef Watch (CRW) 5 km product (Liu et al., 2014). Weekly DHW, similar to DHM, was extracted from each dataset using the methods adopted by NOAA Coral Reef Watch which accumulates any anomaly >1°C over a 12 week window (Strong, Liu, Skirving, & Eakin, 2011). The maximum annual DHW was extracted for each of the 1,312 reef locations (pixels) for the 11 years (1982, 1986, 1987, 1992, 1998, 2002, 2010, 2011, 2015, 2016 and 2017) where significant thermal stress occurred—defined as years with >50% of all reef pixels experiencing DHW >0. For these 11 bleaching years, reef pixels were then ranked, using a standardized scale between 100 (highest DHW) and 0 (lowest DHW). The mean and standard deviation (*SD*) of the percentiles were then calculated for each reef (Figure S2).

Relative percentile rankings were also calculated for the annual future DHM estimates from the four RCP projections. Finally, to distribute future DHM estimates spatially, three steps were used for each year (2017–2050): Firstly, at each reef location, a "random" ranking was generated from a Gaussian distribution using the mean and standard deviation of the CoRTAD/CRW percentile ranking associated with each reef. Secondly, this percentile ranking was used to find the RCP model pixel with the closest matching ranking percentile. The DHM associated with the selected RCP pixel was then used to assign a DHM value for that particular reef and year.

2.2.3 | Water quality

Previous studies have demonstrated strong correlations between wet season river run-off, plume development and water quality gradients (Brodie et al., 2012; Devlin, Schroeder, et al., 2012; Devlin, et al., 2015) which in turn expose coral reefs to nutrients and other contaminants (Fabricius, Logan, Weeks, & Brodie, 2014; Petus, Da Silva, Devlin, Wenger, & Álvarez-Romero, 2014; Petus et al., 2016; Wenger et al., 2016). Although effects of terrestrial run-off on coral biology and ecology are varied (McCook, 1999), we focus here on impacts that extend beyond the nearshore environment and those that correlate with nutrient exposure, specifically coral thermal sensitivity (Wooldridge, 2013) and COTS outbreaks (Fabricius et al., 2010).

Elevated nutrient concentrations, driven primarily by river run-off from altered catchments, has been proposed to reduce the thermal tolerance of corals by 1–2°C, leading to greater bleaching susceptibility (Wiedenmann et al., 2013; Wooldridge, 2009, 2013; Wooldridge & Done, 2009). The potential effect of nutrient exposure on bleaching was captured here by combining the probabilities of exposures to nutrient-rich plume waters with projected thermal anomalies. Probability of exposure to plume waters was calculated for each reef based on 15 years (2000–2014) of remote sensing observations (Devlin, Mckinna, et al., 2012) (Figure S3). Projected DHM in nutrient-enriched plume waters was calculated as above, except anomalies >0°C were used (instead of >1°C), assuming a decreased threshold of 1°C. The acronym NDHM, for degree heating months in nutrient-enriched plume waters is used to distinguish it from the standard DHM estimates.

We recognize there are other river pollution impacts on coral, beyond nutrient exposure effects on thermal sensitivity (and COTS outbreak frequency), that we do not capture here. Coral growth, survival, reproduction and recruitment can be directly affected by various run-off constituents (nutrients, turbidity and light reduction, sedimentation, pollutants) and coral ecology can be indirectly impacted by the influence these constituents have on coral competitors, pests and pathogens (Fabricius, 2005). We focus here on thermal sensitivity to nutrients because of the clear links with climate warming (allowing us to explore variability across scenarios) and the relative ease of parameterizing the relationship between exposure (to plume waters) and effect (increased sensitivity to bleaching).

2.2.4 | Crown-of-thorns starfish (COTS)

The temporal and spatial characteristics of COTS outbreak densities along the GBR was captured using 31 years (1983–2014) of monitoring data from the Australian Institute of Marine Science (AIMS). Outbreaks have occurred at intervals of approximately 15 years and all following flood years (Fabricius et al., 2010). Primary outbreaks form in the northern GBR in an area between Cairns and Cooktown (Figure 4a) and then progress southward at a rate of ~1° of latitude every 3 years (and northward at slower, less consistent rate) via larval dispersal (Pratchett, Caballes, Riveraposada, & Sweatman, 2014). Outbreak density is geographically variable, but particularly persistent (~6–8 years) along the central GBR (Pratchett et al., 2014). Reef-scale outbreak probabilities were modelled here such that they reflect the historical outbreak frequency, regional-scale patterns of outbreak progression and persistence, and regional estimates of annual reef-scale outbreak probability.

2.3 | Ecological model and disturbance impacts

We estimated *Acropora* coral dynamics by fitting a logistic function to observed *Acropora* recovery trajectories of the GBR (Halford, Cheal, Ryan, & Williams, 2004). The Halford et al. (2004) study is particularly well suited for establishing recovery rates because it provides a time series (1984–1996) encompassing a major disturbance (COTS), which reduced coral cover from >80% to <10%, and 13 years of disturbance free recovery. Finding a similar time series from more recent data is difficult due to the frequency of disturbances (De'ath, Fabricius, Sweatman, & Puotinen, 2012; Osborne et al., 2017). Finally, the coral cover information from Halford et al. (2004) consolidates and calibrates data from several studies and methods (manta tow, line intercept and video transect). Although this mix of methods may not be ideal, a meta-analysis of coral cover found that trends were robust across methods (Gardner, Cote, Gill, Grant, & Watkinson, 2003). Details of the model and parameterization are described in Wolff et al. (2016) and in the Supporting Information (Table S1).

We based our model on *Acropora* because it is predicted to play a pivotal role in maintaining GBR resilience under future climate change (Ortiz et al., 2014) and because it currently accounts for most of the hard-coral dynamics on the GBR (Osborne, Dolman, Burgess, & Johns, 2011). Indeed, GBR observations from 1995 to 2009 demonstrated that change in *Acropora* accounted for 68% of the change in total coral cover (Osborne et al., 2011). The important role of *Acropora* in GBR coral dynamics is a function of both its high sensitivity to cyclones, COTS and thermal stress disturbances and its high growth (recovery) rates (Osborne et al., 2011). However, we recognize that GBR coral reef dynamics are far more complex than our model can capture. Therefore, it is important to state up front that our coral trajectories are meant to indicate a relative difference between future scenarios, not an absolute prediction of future coral cover.

The impacts of the four disturbance types were captured within the model through parameterization of observed mortality estimates from several independent GBR studies (Table S1). This included mortality associated with cyclone damage, which varied by cyclone severity (categories 1–5), bleaching mortality during periods of severe thermal stress (DHM >2) and coral mortality from COTS predation during outbreaks. In cases where a reef experienced a cyclone in a given year, it was assumed that the cooling effect of the cyclone was sufficient to negate any thermal stress for that year (Carrigan & Puotinen, 2014). Nutrient-enriched water triggered bleaching mortality when plumes impinged on reefs that were also exposed to thermal stress (NDHM >2). Disturbances affected coral trajectories through the magnitude of mortality and through the frequency with which they occurred.

Reef-scale coral cover was estimated for each of the six environmental scenarios (Table 1) by running the ecological model at 1,312 reefs (Figure S1) across the GBR for the years 2017–2050. For each reef, at each annual time-step, disturbance risks were a function of the disturbance probability of each disturbance type. This was repeated for 100 simulations to introduce stochasticity in outcomes (details in Supporting Information). Each simulation represents a single realization of the different impact probabilities across space and time.

The simple but empirically grounded coral model used here is meant to represent broad ecological impacts of spatially explicit disturbances. Our aim is to contrast the relative effects of different actions and stressors on the overall system to identify possible future trajectories. However, we note that the model is not designed to capture the full range of coral reef dynamics, including interactions with other coral taxa, macroalgae and connectivity among reefs. Furthermore, we assume that the trajectory of recovery for coral cover observed in the 1990s persists through to 2050, which may be optimistic (Albright, Caldeira, et al., 2016; Osborne et al., 2017), and that there is no coral adaptation which may be pessimistic. Estimates of expected adaptation remain a challenge (Mumby & van Woesik, 2014).

2.4 | Reef performance and vulnerability

To evaluate the relative impacts of the four disturbance types, which we explore here, on coral trajectories, we ran the model four separate times for each scenario: (1) The first model run represents natural conditions and includes only cyclone disturbances; (2) The second model run introduces global warming projections and captures bleaching and cyclone impacts; (3) The third model run captures impacts of COTS, bleaching and cyclone impacts; (4) Finally, the fourth run introduces nutrient run-off effects and captures the combined impact of all stressors.

The relative response of GBR coral cover under different disturbances and across scenarios is quantified using a metric of reef performance (Mumby & Anthony, 2015). This metric represents the ratio of mean coral cover (2017–2050) from model runs that include anthropogenic stressors (global warming, COTS, nutrient run-off) to mean coral cover under model runs that represent natural, pristine, conditions (cyclones only). For example, if a reef under only cyclones had a mean coral cover over the time series of 60% and under the addition of global warming had a mean cover of 40% and under all stressors had a mean of 30%, the reef performance under climate change would be 0.67 and under all stressors would be 0.5. In other words, the reef is performing at only 67% of its potential (if climate change was abated) under climate change and at only 50% of its potential if all anthropogenic stressors were abated. In this example, we can calculate that 66% of the reef's performance loss is attributable to climate change and 44% to local stressors. Estimating the GBR-wide performance metrics required two steps. First, the mean ratios (across simulations) are calculated for each reef. Next, the GBR-wide mean and standard deviations are calculated (across reefs). For each scenario, a performance metric is reported for conditions where all stressors are included and for conditions where only global warming (local stressors excluded) is considered.

To explore the spatial variability of disturbance impacts in more detail, we used a metric of vulnerability that measured mean proportion of years (across simulations), relative to the 34 year time series (2017–2050), that coral cover on each reef remained below a 30% threshold. This threshold was chosen because it represents the historical mean coral cover when the GBR was inscribed as a World Heritage Area in 1981 (Great Barrier Reef Marine Park Authority, 2014). Spatially explicit results were mapped for scenarios 2 (business-as-usual management and high [RCP 8.5] emissions) and 5 (business-as-usual management and low [RCP 2.6] emissions). For each scenario, vulnerability results are shown under all stressors and under only global stressors (cyclones and global warming). In addition, management potential, the decrease in vulnerability if local stressors were fully abated, is also shown. Management potential was calculated as the inverse of vulnerability, or the proportion of the total number of years (34) coral cover remained equal to or above the 30% threshold. For reference, a management potential of 0.5 translates to an extra 17 years coral cover could exceed (or equal) 30% if local stressors were fully abated.

To display vulnerability results we used inverse distance weighting interpolation of reef vulnerability results, within ArcGIS 10.2.2. To highlight differences in geographical patterns between the high- and low-emissions scenarios, quintile symbology was used. Quintile classes were determined by pooling results from both scenarios. This approach was used separately for each vulnerability case: all stressors, global stressors and management potential.

Finally, because our model is based on *Acropora* recovery from, and sensitivity to disturbance, our results are applicable only to those GBR reefs where *Acropora* significantly contributes to coral dynamics. Although *Acropora* dominates most of the coral dynamics on the GBR (Osborne et al., 2011), this genus is relatively depauperate on many nearshore reefs, particularly in coastal areas of the Wet Tropics, roughly between Townsville and Cooktown (Clark et al., 2017; Done, 1982; Roff et al., 2012). Whether reduction targets for pollutant run-off set in the Reef 2050 Plan can lead to a return of *Acropora* to the nearshore reefs it once dominated (Clark et al., 2017; Roff et al., 2012) is beyond the scope of this study.

3 | RESULTS

Qualitatively, predicted coral cover followed similar trajectories for all six scenarios, with marked increase during the beginning of the time series followed by a protracted period of decline (Figure 2). The predicted rate of recovery from the estimated GBR-wide mean coral cover in 2016 (13%) was highest for the best-case (Figure 2f) and lowest for the worst-case management scenarios (Figure 2a). Coral cover reached peak values and started declining approximately 8 years earlier for RCP 8.5 (Figure 2a,b) than for RCP 2.6 (Figure 2e, f). Best-case management practices (all local stressors removed) under RCP 2.6 can potentially facilitate a peak coral cover of around 56% by 2030, declining to 33% by year 2050. While a peak of 50% coral cover was predicted to be possible before 2030 for RCP 8.5 under best-case management (top of red trajectory in Figure 2b), the climate-driven decline is much more severe than under RCP 2.6, resulting in 5% coral cover by 2050. As expected, coral trajectories under RCP 6.0 and 4.5 (Figure 2c,d) fell between RCP 8.5 and 2.6 outcomes.

The shapes of the mean trajectories in coral cover are driven primarily by climate change projections (Figure 2); after reaching peaks during the late 2020s to early 2030s, coral trajectories slipped into net decline, with the mean rate of decline determined predominantly by the carbon emission pathway. Under high emissions (RCP 8.5), global warming alone drove declines such that mean GBR performance was only 0.57 of its potential (Figure 2; Table 2). Performance under low emissions (RCP 2.6) was markedly higher at 0.85, representing an improvement relative to RCP 8.5 of nearly 50% (Table 2). Reef performance under moderately low emissions (RCP 4.5) was nearly 18% worse at 0.70 than under RCP 2.6. This difference between RCP 4.5 and 2.6 is worth noting because these two pathways represent Paris climate accord goals (<2°C warming) vs. ambitions (<1.5°C warming) respectively (Schleussner, Rogelj, et al., 2016). Importantly, predicted differences between these two pathways beyond year 2050 are dramatic, with GBR reefs under RCP 4.5 collapsing by 2070 while under RCP 2.6, reefs decline, but do not collapse, and then recover from 2060 to 2100 (Figure S5).

Within the broader envelopes of different RCPs, impacts of nutrient run-off and COTS produced significant variations in outcomes (Figure 2; Table 2). Local stressors contributed as much as 66% of the performance loss under the low emissions, business-as-usual scenario (S5) and as little as 28% under the high emissions, business-as-usual scenario (S2). This variation in attribution across scenarios was primarily driven by the different impacts of climate change, and not by differences in the magnitude of local stressor

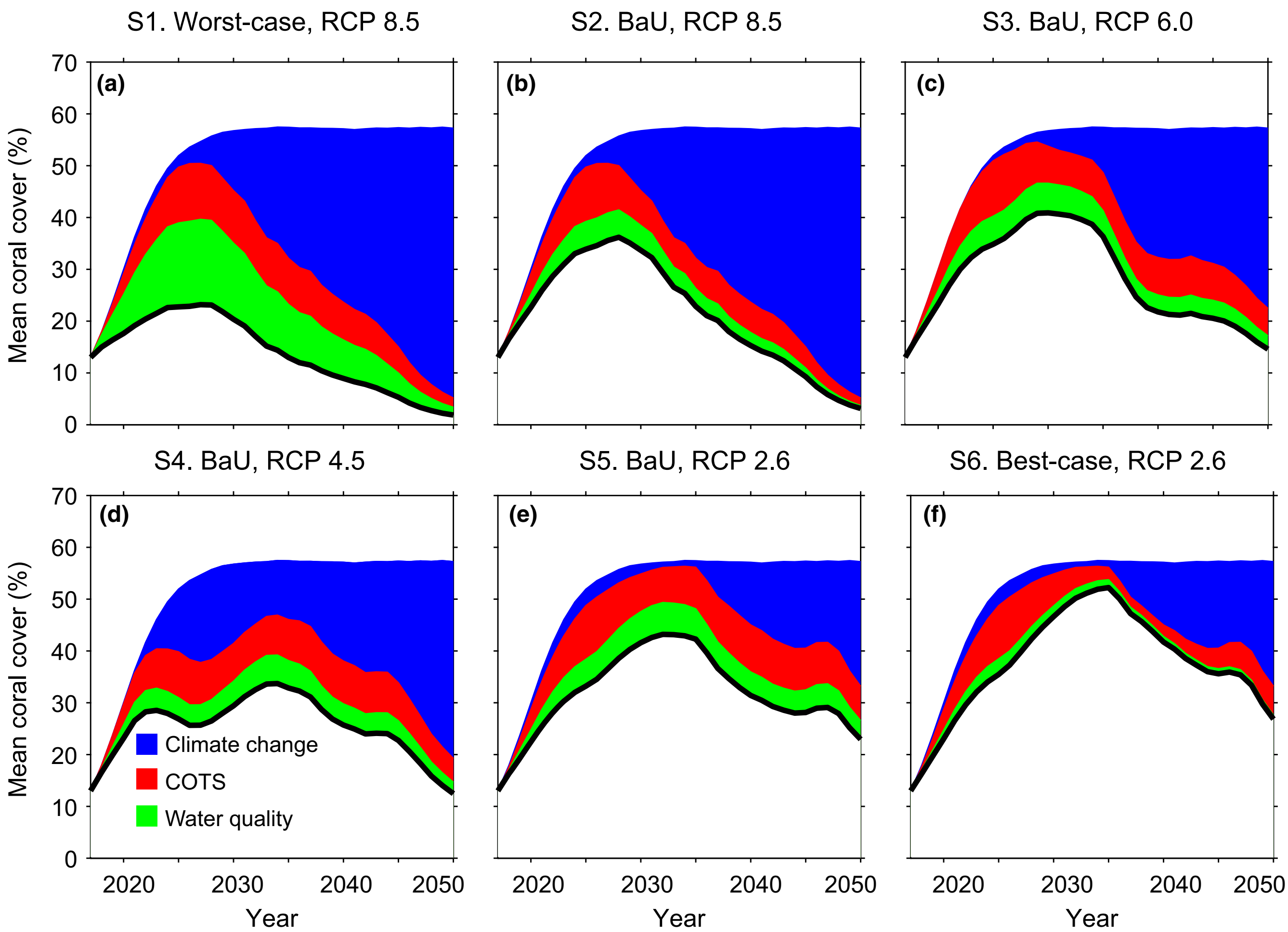

FIGURE 2 Modelled trajectories of mean coral cover on the GBR based on each of the six scenarios (Table 1) encompassing different combinations of local stressors (worst case, business as usual [BaU], best case) with four climate projections (RCPs). Within each scenario, coral trajectories are shown for four model runs: Pristine condition which only includes cyclone disturbance (top of blue trajectory); the addition of climate change impacts (top of red trajectory); the addition of COTS (top of green trajectory); and the addition of nutrient run-off (thick black line). The blue area represents loss due to global warming (bleaching), the red area the loss due to COTS, the green area the loss due to nutrient-induced bleaching and the bottom trajectory represents coral cover when all disturbances are present. The top of the red trajectory represents management potential if all local stressors were removed (best-case management)

TABLE 2 GBR-wide mean (*SD*) reef performance results for each of the six scenarios. Reef performance scores are shown for model runs with all stressors considered, and for just climate change. The causes for the overall total performance loss (climate change vs. local stressors) are shown as per cent attribution. The contribution of COTS vs. river runoff (RR) to the local component of performance loss is also shown. Reef performance metric is calculated as the mean ratio of coral cover under pristine conditions (cyclones only) vs. coral cover under stressor conditions (Mumby & Anthony, 2015)

	Reef performance		Total loss attribution (%)		Local loss attribution (%)	
Scenario	All stressors	Climate change	Climate change	Local stressors	COTS	RR
1. Worst case	0.26 (0.15)	0.57 (0.06)	58	42	44	56
2. BaU, RCP8.5	0.41 (0.13)	0.57 (0.06)	72	28	65	35
3. BaU, RCP6.0	0.54 (0.17)	0.75 (0.06)	54	46	64	36
4. BaU, RCP4.5	0.49 (0.17)	0.70 (0.09)	60	40	65	35
5. BaU, RCP2.6	0.62 (0.20)	0.85 (0.05)	39	66	63	37
6. Best case	0.73 (0.12)	0.85 (0.05)	54	46	76	24
BaU Mean	0.52	0.72	56	44	64	36

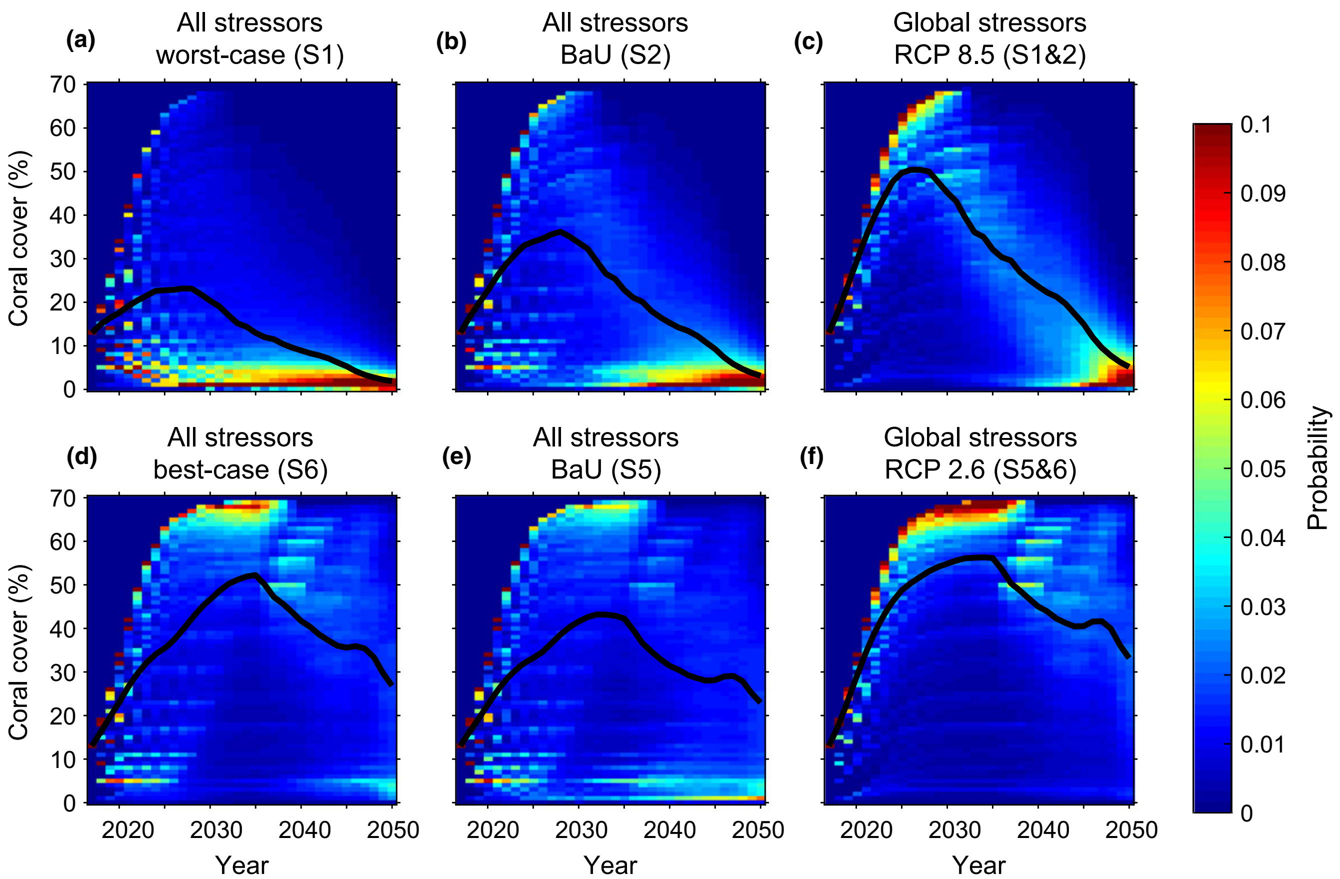

FIGURE 3 Probability matrices of coral cover for all 1,312 reefs across all 100 simulations of coral cover trajectories. Each cell represents the probability that a coral state (*y*-axis) was observed at a given year (*x*-axis). Four scenarios are shown, two from RCP 8.5 (high emission) and two from RCP 2.6 (low emission). The top panels show worst-case scenario (a) and business-as-usual management scenario (b) results for all stressors under RCP 8.5. Panel (c) shows results for just global stressors (local stressors removed). The bottom panels show best-case (d) and a business-as-usual management scenario (e) and results for just global stressors (f) under RCP 2.6. Solid blacklines represent mean of the trajectories

impacts themselves (Figure 2; Table 2). However, for all the scenarios, particularly the RCPs 8.5, 6.0 and 4.5, the relative magnitude of impacts from local stressors declined with time. This can be seen in Figure 2 as a gradual thinning of the relative contribution of local stressors (red and green area) as the relative contribution of climate change (blue area) increases. The reason for this relative decline is twofold. First, as the magnitude of thermal anomalies increases due to global warming, the higher thermal sensitivity of reefs within plume waters matters less. Second, as bleaching mortality drives the coral cover of more reefs to low states, the opportunity for COTS infestation decrease.

The high degree of variability in the trajectories of coral cover (Figure 3) is a function of geographical differences in disturbance probability (Figures S2 and S3) and sheer size (and number of reefs) of the GBR. Yet, embedded within this uncertainty are several interesting differences among management scenarios and stressors that are not revealed by the mean trajectories alone. For example, under RCP 2.6, there is a greater chance that individual reef trajectories will approach carrying capacity (fitted at 68% from the logistic equation) than under RCP 8.5 (Figure 3). Here, analyses of results for RCP 2.6 indicated that approximately one-third of GBR reefs could have coral cover exceeding 60% through 2035 under business-as-usual management regimes (Figure 3e), increasing to nearly one-half of reefs if local stressors are reduced (Figure 3d) and to two-thirds if local stressors are removed (Figure 3f). In contrast, the probability of high cover (>60%) under RCP 8.5 scenarios is much lower. Under the business-as-usual management scenario (Figure 3b), the probability peaks at only 0.2, falling to less than 0.01 by 2036. Under the worst-case scenario, probability of high cover never exceeds 0.09 and falls to less than 0.01 by 2033 (Figure 3a). Even the potential for high cover under RCP 8.5 if local stressors were removed is limited, peaking at 0.44 and dropping to less than 0.01 by 2043 (Figure 3c). This divergence in potential for high coral cover between RCPs further separates as bleaching stress increases. By 2050, none of the reef trajectories exceed 60% coral cover for the RCP 8.5 scenarios, while for RCP 2.6, 4%–9% of reefs still maintain high coral cover, depending on the level of stress from nutrients and/or COTS.

In addition to reducing the probability that reefs will have high cover, local stressors also increase the probability that reefs will be pushed to a degraded state with low cover (Figure 3). Across the

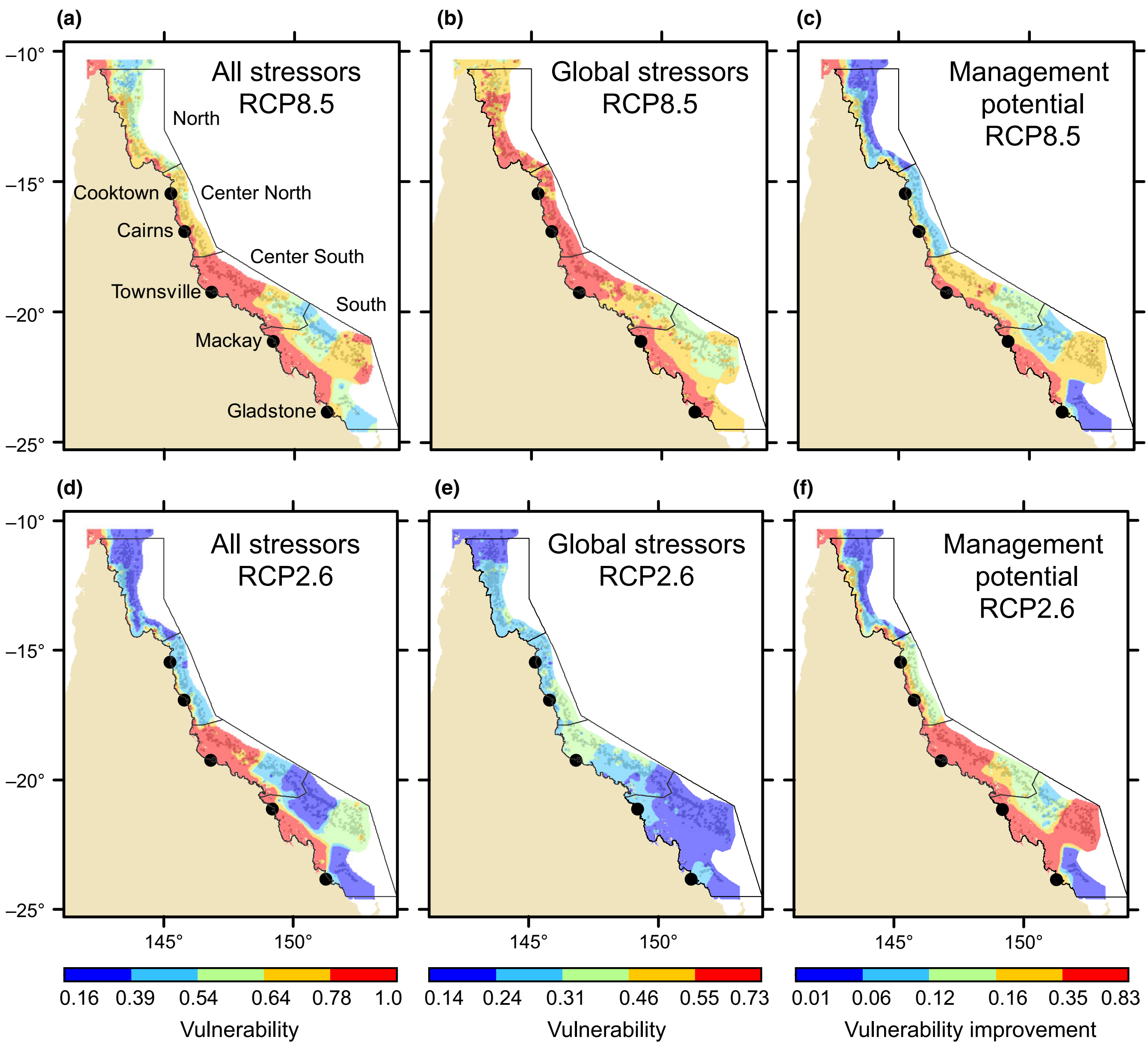

FIGURE 4 Reef-scale vulnerability and management potential to improve vulnerability for business-as-usual scenarios 2 (high emissions, top panels) and 5 (low emissions, bottom panels). Vulnerability (proportion of the 34 years (2017–2050) that reefs are below 30% coral cover threshold) is shown for all stressors (a, d) and for just climate change and cyclones (b, e). Management potential (c, f) represents the vulnerability improvement (net proportion of years above 30% coral cover) that could be gained if local stressors were eliminated. Also shown are geographical boundaries of the four GBR management zones. Note that each column of panels is scaled independently to highlight geographical patterns and differences between RCP outcomes

time series, a mean of 40% of the trajectories in the business-as-usual management scenarios fell below 10% coral cover under RCP 8.5 (Figure 3b). This is nearly two times greater than if local stressors were absent (Figure 3c). Results were similar for RCP 2.6, with a mean of 21% of the trajectories below 10% for business-as-usual management (Figure 3e), compared with 5% of trajectories in the absence of local stressors (Figure 3f). In addition, climate change and local stressors interact, such that the likelihood of a reef being in a low coral state increases with time. As bleaching frequency pushes trajectories towards lower and lower peak cover, seen most clearly as a descending band of higher probability in RCP 8.5, reefs that are also impacted by local stressors spend an increasing amount of time in low coral states.

Contributing to the high variability in GBR-wide reef trajectories (Figure 3) are some important spatial patterns driven by geographical differences in global warming, cyclones, water quality and COTS (Figure 4). We focused here on the business-as-usual management scenarios 2 (RCP 8.5) and 5 (RCP 2.6), contrasting the effects of alternative emission pathways. Analyses indicated that coral vulnerability varied dramatically when all stressors were included (Figure 4a, d), ranging from always vulnerable (100% of the time), to rarely vulnerable (16% of the time). Clear geographical patterns emerged with the northern quarter and parts of the southern GBR less vulnerable than the rest of the GBR. The southern half of the GBR, particularly regions adjacent to Townsville and Mackay, had the highest vulnerability (Figure 4a,d). Under RCP 2.6, over 40% of the reefs were classified as low vulnerability (dark blue) (Figure 4d) while under RCP 8.5 (Figure 4a), no reefs were in this category. Much of the difference in vulnerability between scenarios was driven by climate change (Figure 4b,e). Under RCP 8.5, bleaching stress was sufficient to drive over 42% of the reefs into a highly vulnerable category (red) (Figure 4b), a category that was absent under RCP 2.6 (Figure 4e).

Under both scenario 2 and 5, potential management benefits are geographically variable, with both the southern half, and nearshore reefs most amendable to local and regional interventions (Figure 4c, f). While management potential is significant in both scenarios, nearly 31% of GBR reefs fall within the high improvement category (red) under RCP 2.6 (Figure 4f) compared with only 9% under RCP 8.5 (Figure 4c). The distribution within this category is skewed towards the RCP 2.6 results: 9% of reefs (114) have a management potential exceeding 0.5 under RCP 2.6 compared with less than 1% reefs (7) under RCP 8.5. For context, a vulnerability improvement of 0.5 translates to a potential for management actions to lift coral cover over 30% for an extra 17 years.

4 | DISCUSSION

First, we recognize that our model, based solely on the coral genus *Acropora*, is a coarse simplification of the ecological dynamics of corals on the GBR. Therefore, predictions of future coral cover in this study are indicative only. However, our analyses comparing reef trajectories among scenarios and over time have relative value and offer insights into the GBR's future that is not possible with exposure layers alone. While prior work has examined GBR exposure to disturbances (Maynard et al., 2016), this study captures disturbance impact (sensitivity) and recovery and provides the first reef-scale vulnerability assessment for coral cover on the GBR.

Our results predict that the GBR has substantial scope for coral recovery over the next three decades, but with large spatial variability in the potential for local- and regional-scale management actions to support resilience and sustain moderate to high coral cover. This spatial pattern in management potential is driven by the scope for alleviating the cumulative, and in part interactive, effects of cyclones, warming, COTS and nutrient run-off. Yet, even under the worst-case scenario (S1), with further water quality degradation, more frequent COTS outbreaks, and no global action on emissions, the GBR shows some near-term (one to two decades) capacity to recover from its present and historical lows. This suggests that the recent coral declines on the GBR were driven by an anomalous alignment of disturbance events, including a series of unusually severe cyclones (Puotinen, Maynard, Beeden, Radford, & Williams, 2016) followed by the most intense El Niño ever observed (Hughes et al., 2017; Wolanski, Andutta, Deleersnijder, Li, & Thomas, 2017). The implication is that if near-term conditions return to background impact probabilities, reefs will have time to recover. For example, temporal clustering of storms along the GBR (Wolff et al., 2016) suggests that the period of elevated cyclone activity during the past decade could be followed by relative cyclone quiescence.

On the other hand, any single disturbance, as illustrated by the 2016/2017 bleaching event, can significantly alter GBR outcomes and shorten the opportunity for coral recovery in the coming decades. Furthermore, even our best-case scenario (6), which involves significant restoration of water quality conditions as prescribed by Australia's long-term sustainability plan for the GBR (Reef 2050), halving of the COTS outbreak frequency, and significant reductions in carbon emissions, predicts a 27% decline in reef performance compared with its potential if climate change did not occur. And the least optimistic scenario (S1), which captures the high-emission trajectory (RCP 8.5) the world is currently following (Sanford, Frumhoff, Luers, & Gulledge, 2014), possibly even exceeding (Wagner, Ross, Foster, & Hankamer, 2016), and assumes increases in local stressors due to rampant watershed land clearing (Kroon et al., 2016), predicts that GBR performance will only be at 26% of its potential through 2050. In short, the magnitude and duration of any potential recovery will be constrained by the combined effects of global warming and local stressors.

It is important to reiterate that we only capture two, increased thermal sensitivity and COTS outbreak frequency, of the many mechanisms by which river pollution can impact coral. Other documented effects of river pollution include smothering and rapid mortality from terrestrial mud, reduced growth from less light penetration, lower recruitment and survival due to enhanced substrate competition from macroalgae and greater pathogen-related mortality (Fabricius, 2005). Evidence suggests the cumulative impacts of river pollution has led to the relative lack of coral diversity on inshore reefs (De'ath & Fabricius, 2010), including on some reefs, the near or complete extirpation of *Acropora* from its once historical dominance (Clark et al., 2017; Roff et al., 2012). From a modelling perspective, it remains challenging to parameterize water quality impacts given the paucity of information regarding specific river pollution exposure thresholds that trigger specific negative (or positive) coral response (Brodie, Lewis, Wooldridge, Bainbridge, & Waterhouse, 2014). Furthermore, the impacts we do include are likely more complex than their treatment in this study implies. For example, there remains a need to better quantify how solar irradiance, temperature and nutrient exposure interact to affect coral–algae symbiosis and bleaching risk (Wooldridge, 2013). Also, larval connectivity likely drives greater reef-scale variability in COTS outbreak likelihood than we capture here (Hock, Wolff, Condie, Anthony, & Mumby, 2014; Hock et al., 2017). In summary, future impacts of river pollution, including any management-related improvements, will likely be more temporally and spatially variable than our projections imply.

Our results are consistent with global analyses predicting that the frequency, areal extent and severity of bleaching events will increase for all four RCPs (Logan, Dunne, Eakin, & Donner, 2014; van Hooidonk, Maynard, & Planes, 2013). To date, major global and regional GBR bleaching events have been driven primarily by intense El Niño events (Eakin et al., 2016; Hughes et al., 2017) (although severe GBR bleaching in 2002 was during an ENSO neutral year), with more frequent, but less severe bleaching occurring during less intense El Niño (Eakin, Lough, & Heron, 2009). This general pattern is predicted to hold over the next 10–20 years, but with some uncertainty over the frequency and severity of intense thermal stress events (Ainsworth et al., 2016; Stevenson, 2012; Wang et al., 2017). However, as global sea surface warming is predicted to continue, results suggest that even minor positive temperature deviations will be sufficient to trigger wide-spread bleaching with a frequency that will eventually outpace recovery. Here, we found that a net decline in coral cover is predicted to occur after the late 2030s. This is consistent with several recent studies that predict bleaching frequency will rapidly increase globally during the 2030s and 2040s (Logan et al., 2014; van Hooidonk, Maynard, Liu, & Lee, 2015; van Hooidonk et al., 2013).

Although we show trajectories of coral cover declining under all four RCPs through to 2050, it is important to point out that after 2050, only RCP 2.6 demonstrates the potential to avoid collapse of coral (*Acropora*) assemblages and an opportunity for substantial recovery (Figure S5). The distinction between such collapse under RCP 4.5 vs. recovery under RCP 2.6 has been made before (Ortiz et al., 2014; van Hooidonk et al., 2016) and is particularly important since these two low emissions pathways, respectively, represent the goals (<2.0°C warming) vs. ambitions (<1.5°C) of the Paris climate accord. There is growing evidence that this half-degree difference in warming could represent vastly different outcomes for coral reefs and other ecosystems (Schleussner, Lissner, et al., 2016).

Projections of coral cover in this study are the results of a relatively simple modelling and scenario-development approach in which observed coral bleaching impacts on mortality (Marshall & Baird, 2000) are assumed to be the only consequences of carbon emissions. Recent work has suggested that without significant genetic adaptation, bleaching mortality might increase by 50% as mechanisms of bleaching protection become overwhelmed with future warming (Ainsworth et al., 2016). Furthermore, ocean acidification and warming possibly interact and exacerbate bleaching sensitivity (Anthony, Kline, Diaz-Pulido, Dove, & Hoegh-Guldberg, 2008). Also, ocean acidification is predicted to affect coral calcification negatively, alter competitive interactions with algae and reduce crustose coralline algae which can be important for coral recruitment (Albright, Anthony, et al., 2016; Albright, Caldeira, et al., 2016; Doropoulos, Ward, Diaz-Pulido, Hoegh-Guldberg, & Mumby, 2012). Together, this means slower growth rates, greater susceptibility to storm damage, slower recovery rates between disturbances and overall reduced reef resilience (Anthony, 2016), contributing to more deleterious reef outcomes in the near future (Wolff et al., 2015) than we capture here. There is some evidence that coral recovery rates can decline after bleaching (Osborne et al., 2017). Our results are predicated on the rapid *Acropora* recovery rates (Halford et al., 2004) being sustained in the coming decades. Any factors that either reduce recovery or enhance mortality would likely result in less optimistic reef outcomes than we present here (Figure S6). On the other hand, because our models assume no adaptation our results could also be pessimistic, but by how much is currently uncertain and a major research question (Mumby, 2017).

In conclusion, coral cover on the GBR could recover substantially from its current historical lows, but the path towards long-term sustainability of corals will require a two-pronged strategy including intensive and up-scaled management of water quality and COTS, and meeting the ambitions (<1.5°C warming) of the Paris Climate Agreement. Our results lend some support to the expectation that local and regional management efforts described in Reef 2050, primarily through mitigation of river pollution and COTS control, can potentially lead to improved coral condition each successive decade through 2050. Indeed, we did find that successful management of local stressors can contribute to significant improvements in mean GBR coral cover and large reductions in the vulnerability of certain reefs. However, given that predicted coral cover trajectories are highly sensitive to climate scenarios, the degree to which local management can help sustain coral cover in the medium to long term will be contingent on the carbon emission path.

ACKNOWLEDGEMENTS

This article was made possible by a grant from the National Environmental Research Programme, Australia. We thank Lester Kwiatkowski for providing climate data and Iliana Chollett for helpful discussions.

ORCID

Nicholas H. Wolff http://orcid.org/0000-0003-1162-3556
Peter J. Mumby http://orcid.org/0000-0002-6297-9053
Michelle Devlin http://orcid.org/0000-0003-2194-2534
Kenneth R. N. Anthony http://orcid.org/0000-0002-2383-2729

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

How to cite this article: Wolff NH, Mumby PJ, Devlin M, Anthony KRN. Vulnerability of the Great Barrier Reef to climate change and local pressures. *Glob Change Biol*. 2018;00:1–14. https://doi.org/10.1111/gcb.14043