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RESEARCH ARTICLE

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Demographic resilience may sustain significant coral populations in a 2°C-warmer world

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Abstract

Projections of coral reefs under climate change have important policy implications, but most analyses have focused on the intensification of climate-related physical stress rather than explicitly modelling how coral populations respond to stressors. Here, we analyse the future of the Great Barrier Reef (GBR) under multiple, spatially realistic drivers which allows less impacted sites to facilitate recovery. Under a Representative Concentration Pathway (RCP) 2.6 CMIP5 climate ensemble, where warming is capped at ~2°C, GBR mean coral cover declined mid-century but approached present-day levels towards 2100. This is considerably more optimistic than most analyses. However, under RCP4.5, mean coral cover declined by >80% by late-century, and reached near zero under RCP ≥6.0. While these models do not allow for adaptation, they significantly extend past studies by revealing demographic resilience of coral populations to low levels of additional warming, though more pessimistic outcomes might be expected under CMIP6. Substantive coral populations under RCP2.6 would facilitate long-term genetic adaptation, adding value to ambitious greenhouse emissions mitigation.

KEYWORDS

benthic community composition, coral cover, coral reef, demography, ecological model, individual-based model, multi-model ensemble, ocean warming, Representative Concentration Pathway, resilience

1 | INTRODUCTION

Globally, coral reefs are indicator systems for the environmental impact of marine-linked human activities and global climate change—for instance, coral cover is a key performance metric under the Aichi biodiversity targets (Tittensor et al., 2014). The Great Barrier Reef (GBR) is recognised as a 'global commons' possessing outstanding universal value (Day et al., 2012) and acts as a key case study of climate impacts on a linked social–ecological system (Bohensky et al., 2011; Cumming et al., 2017; Marshall et al., 2019). The strong governance and management arrangements surrounding the GBR are increasingly reliant on strategic planning with multi-decadal horizons (Costa et al., 2020). Therefore, achieving accurate projections of reef trajectories is of substantive importance to human stewardship of the GBR.

Several important studies of the consequences of climate change on coral reefs have focused on the increased frequency of coral bleaching events (Frieler et al., 2013; McWhorter et al., 2022; Schleussner et al., 2016; UNEP, 2020; van Hooidonk et al., 2013, 2016) and established a threshold beyond which net reef recovery is unlikely, of 1.5–2°C of warming. However, it is now possible to model the dynamics of corals explicitly and at spatially realistic scales (Bozec et al., 2022). This is important because not all reefs experience climate change in the same way; for example, only a subset of reefs bleach during any given event (Hughes, Kerry, & Simpson, 2018). Moreover, individual reefs exist within networks of connected coral populations and are subjected to a variety of disturbances that are spatially uneven in their intensity (Graham et al., 2006; McManus et al., 2021). The overall response of reef corals will be impacted by this spatial heterogeneity with temporary refugia helping more heavily impacted reefs to recover. Here, we explore GBR reef futures using a field-tested coral reef model that encompasses spatially realistic water quality, larval dispersal, cyclones, thermal stress and crown-of-thorns starfish outbreaks (Bozec et al., 2022). We examine the temporal and spatial trends across 3806 connected reefs between 2021 and 2099, under an ensemble of climate models.

2 | METHODS

2.1 | Climate data

We used climate projections from the Coupled Model Intercomparison Project phase 5 (CMIP5) as the ability of these models to adequately simulate El Niño conditions has been assessed (Cai et al., 2018), and the El Niño-Southern Oscillation is an important driver of bleaching conditions on the GBR. Five climate models that demonstrate excellent performance in resolving the oceanic heating patterns associated with eastern Pacific versus central Pacific El Niño events were chosen: GISS-E2-R, GFDL-ESM2M, CCSM4, CESM1-WACCM and MIROC5. A sixth model, HadGEM2-ES, was selected for comparative purposes as the HadGEM family of models has been used frequently in future projections of bleaching under climate change (Donner et al., 2007; Edwards et al., 2011; Wolff et al., 2018). We obtained daily historical sea-surface temperature (SST) projections of these models over 1985–2005 and Representative Concentration Pathways (RCPs) 2.6, 4.5, 6.0 and 8.5 (as available). Daily observed SST data were obtained for the 1 January 1985–28 February 2021 period from the CoralTemp v3.1 product of Coral Reef Watch (Skirving et al., 2020). Data from the first 2 months of 2021 covered the expected period of annual maximum observed Degree Heating Weeks (DHW), as cooling was observed over the GBR from 1 March 2021 onwards. Reefs were matched to a climate model grid cell and an observational data grid cell by the position of the centroid of the reef. To compensate for the difference between observed and projected SST that could be due to model structure and parameterisation, we subtracted from each month of the projected data the difference between climatological monthly means (over 1985–2005) of the observational data versus the historical projection, at each reef.

2.2 | Heat stress calculation

We calculated DHW for each day of our model hindcast/burn-in period (2008–2020) and model forecast period (2021–2099), using the DHW equation of Coral Reef Watch (Liu et al., 2014). For application of this algorithm, the maximum monthly mean was calculated from the observational data over the period of 1985–2012 (Liu et al., 2014). DHW calculations for each day summed SST anomalies over the retrospective 84 day period, for example, the DHW on 1 January 2021 summed over the final 84 days of 2020. As DHW is a method for assessing the dose–response of corals to heat stress and therefore integrates heat stress through a season, for application in ecosystem modelling we simply took the maximum DHW value per year.

2.3 | Ecosystem modelling

Modelling of coral cover in response to climate change was performed using ReefMod-GBR (Bozec et al., 2022; Ortiz et al., 2014). This is a coral reef ecosystem model that uses an individual-based modelling approach. A patch of reef 20 × 20 m in size is represented as a grid, with each grid cell containing colonies of six coral types: branching *Acropora*, tabular *Acropora*, corymbose *Acropora*, pocilloporids, a mix of encrusting plus small massive corals and large massives; and several algal types. The size and identity of each individual colony of each coral type is tracked through time. The size structure and density of coral colonies and algal patches are initialised according to coral cover surveys from the GBR performed under the Australian Institute of Marine Science (AIMS) Long-Term Monitoring Program (Sweatman et al., 2008). Coral colonies and algal patches are updated at 6 month intervals to account for recruitment, growth, reproduction, partial and whole-colony (background) mortality, and mortality due to heat stress or tropical storms, the rates of which are parameterised from experimentally measured values. The modelled reef experiences bleaching driven by SST anomalies, and cyclone damage, which cause full or partial colony mortality. Impacts of water quality (suspended sediment level) upon coral reproductive success, recruit survival and juvenile growth are modelled, though not reduction in bleaching due to suspended sediments lowering irradiance (Fisher et al., 2019). Sufficient grazing by reef herbivores is assumed to eliminate ecologically detrimental levels of macroalgae. Rubble is generated from the skeletons of corals killed through bleaching and cyclones, and impacts upon juvenile coral survival. The model has been verified over time against 60 AIMS Long-Term Monitoring Program sites. A detailed description of, and access to, the canonical version of the ReefMod-GBR model is provided in Bozec et al. (2022).

For the forecast projections, initial (2020) cover for the six coral types was estimated using the model hindcast/burn-in (2008–2020) that used realistic forcing of water quality, heat stress and cyclones in space and time (Bozec et al., 2022). Cyclone damage between 2021 and 2099 was driven using timeseries of synthetic cyclone tracks (Wolff et al., 2016), where a different timeseries was used for each of 10 future projections of ReefMod-GBR that were then averaged. Spatial layers of suspended sediments from the eReefs biogeochemical model (2011–2018: Baird et al., 2020) were applied in recursive sequences until the end of the century.

Bleaching-induced mortality was estimated on a per reef basis from the maximum DHW value per year per reef (when max DHW exceeded 3) following the model developed in Bozec et al. (2022). First, a probability of initial coral mortality was estimated by applying DHW/mortality relationships fitted to observations performed on shallow (2m depth) reefs of the GBR at the peak of the 2016 mass-bleaching event (Hughes, Kerry, Baird, et al., 2018):

$$\text{Initial\_mortality} = \exp(0.167 + 0.347 \times \text{DHW}) - 1.$$

The resulting estimate of initial mortality was bound between 0 and 1 and extended to include subsequent mortality likely to occur in the weeks or months following a heatwave:

$$\text{Total\_mortality} = \left(1 - (1 - \text{sensitivity\_bleaching} \times \text{Initial\_Mortality})^{x}\right),$$

where sensitivity_bleaching are sensitivity coefficients that adjust mortality to each modelled coral group based on reported species-specific mortalities (Hughes, Kerry, Baird, et al., 2018) and x is a coefficient determined by model calibration with longer-term (8 months) observations of coral cover losses at 2m depth following the 2016 mass bleaching (Hughes, Kerry, Baird, et al., 2018). A value of $x=6$ was found to reproduce the observed cover losses (see detailed analysis and parameters in Bozec et al., 2022).

The output of the equations relating DHW to bleaching mortality was halved to transfer the bleaching mortality from 2 to 7m depth according to Baird et al. (2018), as ReefMod-GBR is parameterised to represent reef slope (~5–10m depth) coral communities. To simulate cyclone-induced cooling of water, bleaching was not applied to a reef if it had been impacted by a cyclone during the same year.

Analysis of coral bleaching surveys through time has revealed that locations that have previously bleached suffer from less bleaching during subsequent warming events (Guest et al., 2012, but see Hughes, Kerry, & Simpson, 2018). In some locations, this is because thermally susceptible taxa have been replaced by thermally tolerant taxa (Lafratta et al., 2017; McClanahan & Muthiga, 2014). Thermal physiological plasticity has been observed in wild corals (Brown, Downs, et al., 2002; Brown, Dunne, et al., 2002; Kenkel & Matz, 2017), but its ability to increase long-term thermal thresholds in response to repeated bleaching events remains uncertain. Microevolutionary thermal adaptation is theoretically possible (Matz et al., 2018), though it is yet to be explicitly demonstrated in the field. Our model allowed for 'adaptation' of reefs to occur through species assemblage shifts involving replacement of thermally susceptible with thermally tolerant taxa, but not adaptation through microevolution or physiological acclimation.

2.4 | Output variables

In each climate model, we assessed the trajectory of the GBR over time using a mean timeseries of total coral cover, over 3806 reefs and 10 simulations (where the cyclone trajectory was varied per simulation). A multi-model ensemble trajectory was determined by taking the average of total coral cover under each climate model, at each reef, and then averaging over all reefs, at each timepoint.

Change in benthic community composition was compared among decades and among climate models within each RCP. Cover of each of the coral types and algal types was standardised to the amount of pavement available per reef, and one average was taken for each cover type over the entire reef and over the 10 simulations per decade. A metric multi-dimensional scaling analysis was then performed across all models, decades and RCPs.

2.5 | Robustness of climate models under revised equilibrium climate sensitivity

Equilibrium climate sensitivity (ECS), the globally averaged warming under 2×preindustrial atmospheric CO_2, has been revised to a likely range of 2.3–4.5°C (up from 1.5–4.5°C) as a result of verification of climate models using palaeo- and historical climatic constraints (Inglis et al., 2020; Nijsse et al., 2020; Sherwood et al., 2020). The members of our multi-model ensemble at RCP2.6 were distributed throughout this updated ECS range or its boundary: 4.6°C (HadGEM2-ES; Andrews et al., 2012), 2.73°C (CESM1-WACCM; Marsh et al., 2016), 2.9–3.2°C (CCSM4; Bitz et al., 2012; Meehl et al., 2020), 2.6°C (MIROC5; Watanabe et al., 2010) and 2.44–3.3°C (GFDL-ESM2M; Andrews et al., 2012; Paynter et al., 2018). GISS-E2-R, with an ECS of 2.1–2.3°C (Marvel et al., 2016; Meehl et al., 2020), was only a part of the multi-model ensemble for RCP4.5 and RCP8.5. The relatively wide spread of these ECSs suggests that our warming-driven reef trajectories at RCP2.6 are not overly 'warm' nor 'cold' biased.

3 | RESULTS

Six climate models were selected on the grounds of their maturity, and their prowess at capturing El Niño events (Cai et al., 2018), which are an important driver of coral bleaching events (Eakin, 2022; Eakin et al., 2014). Ensemble coral trajectories declined under all RCPs (Figure S1). Under focused global action to reduce emissions and keep within a 2°C warming envelope, RCP2.6, the GBR declined from an average coral cover of 25% in 2021 to 12% by mid-century, a 52% decline in relative terms (Figure S1a). However, this was followed by an increase in coral cover to ca. 19%–22% by the century's end. Under moderate abatement in which global emissions peak in 2040 then decline, RCP4.5 (Meinshausen et al., 2011), average coral cover declined from 25% in 2021 to ca. 5% by the 2060s, an 80% decline in relative terms (Figure S1b). Average coral cover was maintained at 2%–6% through to the century's end. Under unambitious mitigation that achieves peak emissions by 2080, RCP6.0, average coral cover declined from 25% in 2021 to ca. 3% by the 2060s (Figure S1c). This trajectory was qualitatively different from RCP4.5 in two respects: firstly, coral cover was maintained at slightly higher levels in the lead up to the 2060s, and secondly, coral cover continued to decline from that decade onwards, reaching virtually zero by the century's end. Under intensification of emissions, RCP8.5, average coral cover declined from 25% in 2021 to 1% by 2060, and then continued to decline to the end of the century (Figure S1d). Importantly, there was considerable variability among our climate models, particularly for the lower emission trajectories RCP2.6 and 4.5 with the ranking (from most pessimistic to most optimistic) being HadGEM2-ES, CCSM4, MIROC5, CESM1-WACCM, GFDL-ESM2M and GISS-E2-R (Figure 1a,b).

Benthic community composition analysis indicated that severe climate trajectories (manifested as either higher RCPs or more pessimism in climate models) generate significant, near-term impacts to benthic cover. Our modelled benthic community consisted of six coral types representing common categories of coral on the GBR that have distinct life-history characteristics. Under each climate model, the community compositions in each succeeding decade of this century were explored using metric multi-dimensional scaling. Changes in benthic composition under warming occur, and are largely completed, within the first decades of the 2020–2099 period in some models of moderate or high pessimism under RCP2.6 (Figure 2a) and in all models under RCP6.0 and RCP8.5 (Figure 2c,d). The more optimistic models display some resilience in their benthic

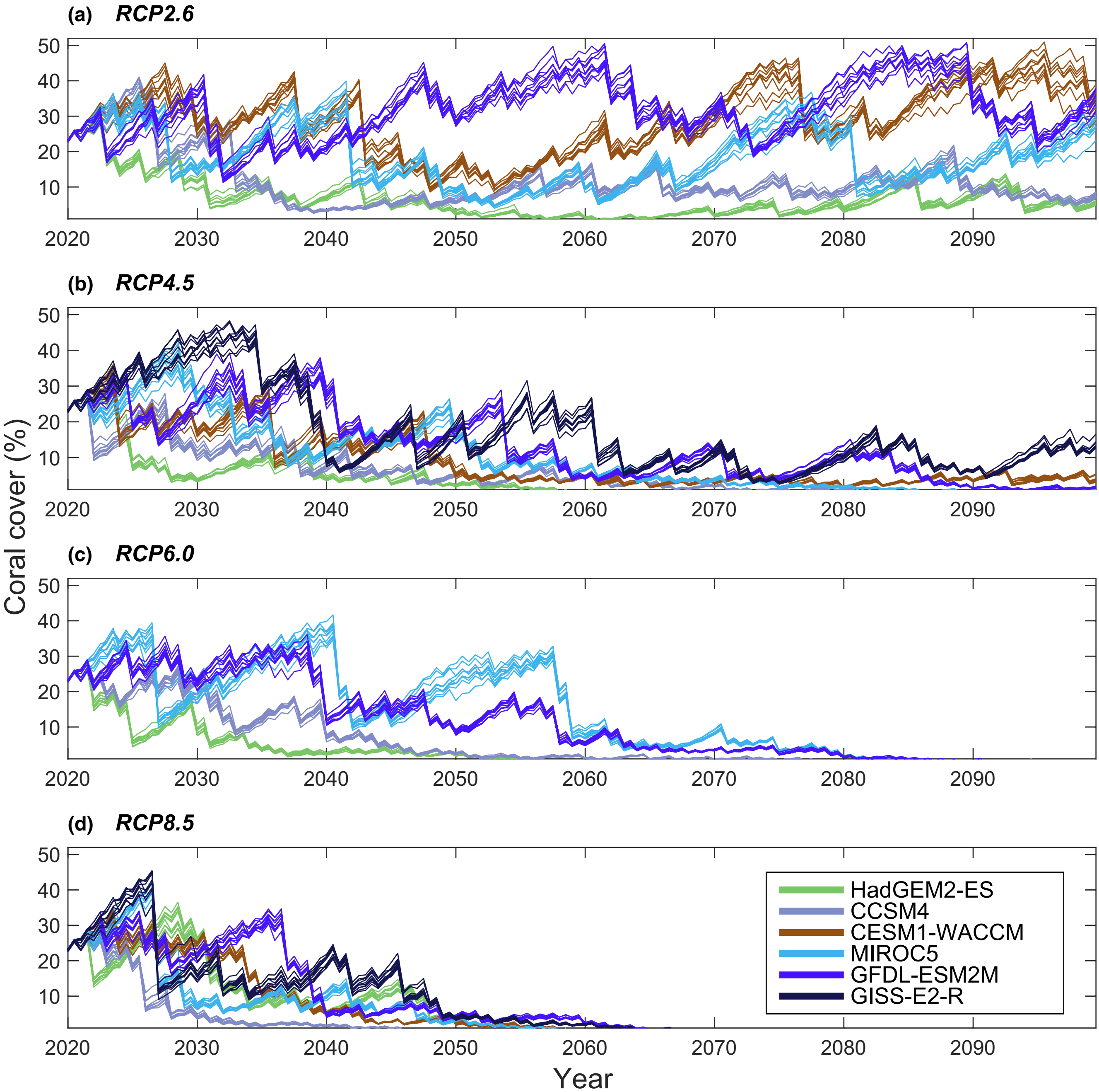

FIGURE 1 Mean coral cover on the Great Barrier Reef (GBR) under (a) RCP2.6, (b) RCP4.5, (c) RCP6.0 and (d) RCP8.5, in each of 10 ReefMod-GBR model runs (individual lines) per climate model. RCP, Representative Concentration Pathway.

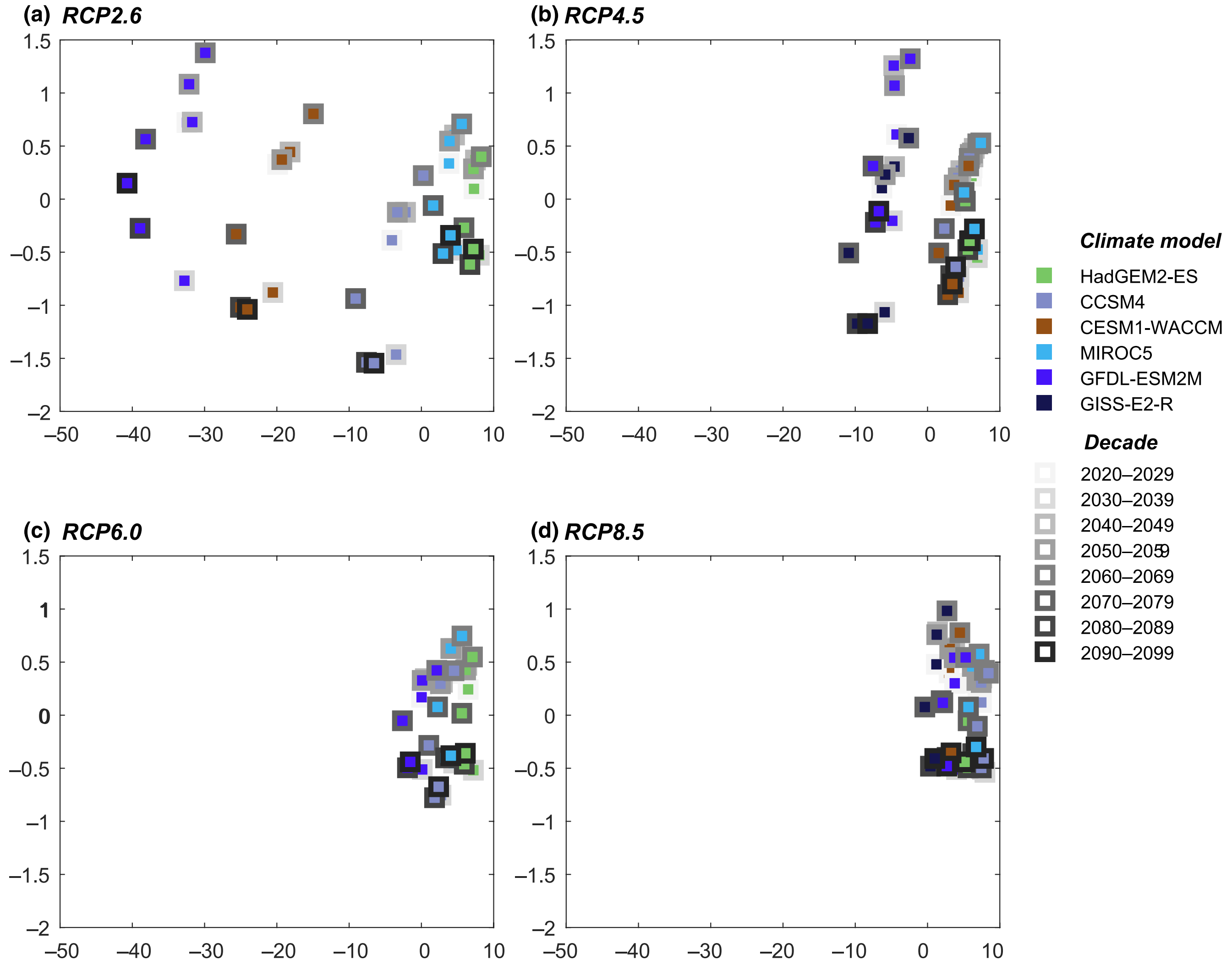

FIGURE 2 Benthic community composition (represented in metric multidimensional scaling plots) under GFDL-ESM2M, CESM1-WACCM, CCSM4 and GISS-E2-R becomes increasingly similar to that under MIROC5 and HadGEM2-ES under progressively more severe climate trajectories, whilst composition under MIROC5 and HadGEM2-ES remains mostly constant across the four climate trajectories. In RCP6.0 and RCP8.5, benthic community composition of all models and all decades was clustered together in a small region of 'highly disturbed' benthos in the plots (c, d). In RCP4.5, benthic composition of CCSM4, MIROC5, CESM1-WACCM and HadGEM2-ES clustered within the 'highly disturbed' region (b). GFDL-ESM2M and GISS-E2-R benthic compositions were mildly distant from this region. Under RCP2.6, MIROC5 and HadGEM2-ES clustered in the 'highly disturbed' region, whereas CCSM4, CESM1-WACCM and GFDL-ESM2M were increasingly separated from this region in the same order as their increasing levels of optimism (a). Average community composition is calculated from decadal averages of percent cover of six coral types and several algal types.

cover under RCP2.6, with the 2020s timepoint situated relatively close to the 2090s timepoint in these models, despite change in the intervening decades. However, under RCP4.5, benthic community composition in optimistic models demonstrates decay towards a highly disturbed benthic state (Figure 2b), and this decay is completed fully in RCP6.0 (Figure 2c).

4 | DISCUSSION

Our projections of GBR outcomes under climate change differ from past assessments at RCP2.6, which stabilises global temperatures at 2°C of warming. A recent assessment of coral reef responses to climate change, in the Intergovernmental Panel on Climate Change 1.5°C report, has concluded that 70%–90% of reefs globally will be lost at 1.5°C, and 99% at 2°C (Hoegh-Guldberg et al., 2018; Schleussner et al., 2016). We found a 52% decline in coral cover across the GBR at RCP2.6. Our focus on the GBR is unlikely to be the cause of the apparent difference between these assessments, as the intensification of warming on Australian reefs is not substantively different from that at other major reef systems in an ensemble of CMIP5 climate models (van Hooidonk et al., 2016). Realised warming on the GBR may even exceed that at most other reef regions due to its particular oceanographic setting (Wolanski et al., 2017).

Differences between our analysis and other recent assessments likely stem from differences in methodology, particularly the choice of heat stress metric and the way that heat stress is propagated into ecological impacts. Past assessments have used Degree Heating Months (DHM; now known to overestimate heat stress), have applied a simple mass-mortality threshold of >2 DHM and have applied thresholds-based heuristic methods to convert mortality frequency into projections of reef outcomes. We replaced DHM with the well-validated DHW algorithm. Empirical relationships of coral mortality versus heating dose are now available for the GBR and other reefs, so we replaced the binary mortality threshold with a continuous, empirically derived equation (Bozec et al., 2022; Hughes, Kerry, Baird, et al., 2018). Heuristic thresholds for reef decline (e.g. 10 back-to-back bleaching events: UNEP, 2020, van Hooidonk et al., 2013, 2016) were superseded in our study through individual-based ecological modelling.

The explicit articulation of the impact of coral vital rates and spatial connectivity on coral cover change in our modelling revealed resilience to mild additional warming missed by previous works. Robustly parameterised rates of coral recruitment (explicitly tied to existing adult stock and population connectivity), survival, growth and mortality at different coral life stages—with calibration against long-term field datasets—produces realistic coral demography and responses to stressors in our model (Bozec et al., 2022). Moderate coral cover persistence under RCP2.6 warming therefore indicates that realistic coral demographic processes provide some inbuilt resilience of coral cover to the anticipated regimes of bleaching-induced coral loss.

Our outcome under RCP2.6 of a decline in mid-century coral cover followed by end-of-century recovery could reflect natural variability or may be a signature of the temperature overshoot that is anticipated by the RCP2.6 scenario. The modelled socio-economic pathway within RCP2.6 involves a mid-century peak in atmospheric greenhouse gases, during which radiative forcing reaches ca. 3 watts m^{-2}, followed by a rapid decline to 2.6 watts m^{-2} by the end of this century (van Vuuren et al., 2011). The individual trajectories for four out of five climate models display mid-century dips (Figure 1a), though the timings of these dips are not identical among models. Natural variability unrelated to the global radiative forcing and temperature trends, or internal model variability superimposed on these trends, are possible explanations for the mid-century nadir in coral cover. Were the radiative forcing peak to be the cause, the sensitivity of the reef trajectory to an additional 0.4 watts m^{-2} would indicate the existence of a non-linear ecosystem threshold just above 2.6 watts m^{-2}.

Our results demonstrate the high sensitivity of ecosystem projections to the choice of climate model, especially under the lower emissions scenario RCP2.6. Two models projected coral cover below 10% by century's end, whereas three models projected cover between 20 and 40% (Figure 1a). Indeed, both the current generation of climate models, CMIP6, and the previous generation, CMIP5, display a wide range of sensitivities to greenhouse forcing (Meehl et al., 2020). CMIP6 models are (on average) more sensitive to emissions than CMIP5 models, but whether this higher sensitivity is accurate or not is still a matter of debate (Nijsse et al., 2020; Tebaldi et al., 2021; Tokarska et al., 2020). Whilst our subset of CMIP5 models fall within or bound the equilibrium climate sensitivity range updated following CMIP6 (see Section 2), as more CMIP6 models display higher ECS values, we anticipate that many CMIP6 multi-model ensembles may paint a more pessimistic future of the GBR than presented here.

The identification of resilience to mild warming provided by coral demography and population interconnections highlights the importance of including individual-based modelling in climate model-derived reef projections. Substantive coral populations under RCP2.6 would facilitate long-term genetic adaptation; hence, the expected demographic resilience may facilitate improvements in reef resilience through microevolution. The exclusion of adaptation from our model was in fact useful in revealing that resilience through demographic processes alone is important under RCP2.6. At RCP4.5 and above, this source of resilience no longer supported substantive coral cover long term. Despite a more hopeful outlook under mild additional warming, our analysis supports that avoiding overshoot of 2°C warming remains necessary to avoid the wholesale degradation of the GBR. Application of coral demographic modelling to CMIP6's Shared Socioeconomic Pathway 1–1.9 model outputs will reveal whether the lower heat stress expected under a 1.5°C cap on warming (McWhorter, Halloran, Roff, Skirving, & Mumby, 2022; McWhorter, Halloran, Roff, Skirving, Perry, et al., 2022) avoids the mid-century dip in GBR coral cover that we have projected at 2°C of warming.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

MATLAB code, modelling results and associated data used in this analysis are available at https://doi.org/10.5281/zenodo.7725355 (Mason et al., 2023).

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SUPPORTING INFORMATION

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