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RESTORATION
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PROGRAM

ReefMod R&D (M&DS-04)

Final Report June 2025

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This report summarises work undertaken under *ReefMod R&D (M&DS-04)* in accordance with the Reef Restoration and Adaptation Program's *Modelling and Decision Support Project Agreements*. It provides a summarised, point-in-time synopsis of activities, methods, findings and outcomes completed in accordance with the approved project scope up to 30 June 2025.

All information reflects project scope and outcomes as of May-June 2025. Subsequent updates, analyses, or scientific developments are not included. This report should be read alongside any associated and publicly available technical reports, datasets, and publications for full detail. This report does not provide scientific inferences, policy guidance or operational instructions beyond the project's defined scope and duration.

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The RRAP partners acknowledge Aboriginal and Torres Strait Islander Peoples as the first marine scientists and carers of Country. We acknowledge the Traditional Owners of the places where RRAP works, both on land and in sea Country. We pay our respects to elders; past, present, and future; and their continuing culture, knowledge, beliefs, and spiritual connections to land and sea Country.

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1 Executive Summary

Projecting the future of coral reefs requires ecosystem models that not only integrate the complex mechanisms of coral demography and evolution under global warming, but also reliably simulate the impacts of various stressors on coral populations and the effectiveness of management interventions. These models must also account for the inherent uncertainties in environmental and ecological forecasting. Furthermore, for such models to be truly effective, they need to be accessible to a broad range of users, from scientists to reef practitioners, ensuring that these tools can inform decision-making at multiple levels.

For the initial phase of RRAP, we worked on enhancing the credibility of ReefMod simulations that project potential coral futures for the Great Barrier Reef (GBR), by incorporating plausible scenarios of future heat stress events and their associated uncertainties, more accurately representing the adaptive capacity of corals through natural selection by bleaching, and simulating multiple management interventions with greater realism, including the control of Crown-of-thorns starfish (COTS) outbreaks and innovative approaches relying on the deployment of coral out-plants. Significant effort was also devoted to developing fast, user-friendly simulation tools and interfaces that enhance the accessibility and usability of our modelling capacities to a wide range of users, including reef practitioners.

We have significantly improved the bleaching model of ReefMod by adjusting at depth the mortality function of heat stress (degree heating weeks (DHW)) and letting resistance to bleaching vary among coral individuals. This resulted in accurate predictions of the 2016 bleaching impacts validated by monitoring data. Moreover, variations of heat tolerance among individuals is key for the simulation of coral evolution under warming, as it enables emergence of natural hardening in populations through the successive elimination of heat-sensitive phenotypes.

Building on the enhanced capacity to simulate impacts of bleaching, we have consolidated the ability of ReefMod to reconstruct past trends of GBR coral cover by revising the hindcast (2008-2024) using updated environmental forcing (bleaching and cyclones up to 2024) and GBR1 coral connectivity. This new hindcast provides a simulation-based assessment of coral health that is currently guiding reef management (reef prioritisation for COTS control).

A new model of coral adaptation to warming was developed in ReefMod to produce more robust projections of future coral resilience and adaptive capacity under climate change. The evolutionary model was simplified to a single thermal trait (survival to heat stress) and parameterised with novel data on among-colony variability of heat tolerance and partial inheritance from coral parents to offspring. In simulations, adaptation to warming emerges from the natural selection of heat tolerant phenotypes and their transmission across multiple generations.

We used this new model of coral adaptation to project possible futures for GBR corals across multiple (counterfactual) scenarios of warming. Each emission scenario was supported by a multi-model ensemble of heat-stress projections derived from the last generation (Climate Model Intercomparison Project Phase 6 (CMIP6)) of climate models, downscaled at 10 km resolution. Our simulations show that limiting global warming to no more than +2 °C above pre-industrial levels is critical for maintaining coral populations at levels necessary to sustain viable reef ecosystems on the GBR.

In parallel, we have created an eco-evolutionary genetic simulation model of a single reef experiencing projected climate change under various assisted evolution interventions: coral fragmentation, selective breeding, assisted gene flow (AGF), and gene editing. Initial analyses on a hypothetical reef suggest that interventions such as gene editing, selective breeding, and AGF would greatly enhance the reef relative to the counterfactual. Gene editing has the most beneficial effect, while selective breeding and AGF have intermediately positive effects without compromising genetic diversity.

To facilitate access to ReefMod to a broader range of users, including RRAP Modelling and Decision Support (M&DS) Sub-program collaborators, we have created a fast version embedded in an Application Programming Interface (API) (the ReefMod Engine (RME)) that replicates the code while also providing all the

necessary flexibility to control the parameterisation and access the variety of model outputs. As a result, the RME considerably increases our simulation capacity and promote interoperability with other decision-support tools (e.g. Adaptive Dynamic Reef Intervention Algorithms (ADRIA)).

In addition, we have created user-friendly interfaces that do not require any coding skill, enabling broader access to ReefMod, particularly to reef practitioners. These interfaces allow users to set-up, run and visualise specific scenarios of interventions across the GBR. They are embedded into a new software, the Reef Resilience Management Tool (RMT), available online (<https://gbrrestoration.org/rmt/index.html>).

Workshops with reef practitioners were conducted to demonstrate the capabilities of the RMT. This provided an opportunity to showcase the functionalities and performance of the tool, test its usability across a diverse group of participants and needs, and gather valuable feedback for future improvements.

Overall, this project has followed the guiding principles of the RRAP Modelling and Decision Support (M&DS) Sub-program, providing transparent, credible and validated modelling. Model insights and capabilities were developed in close collaboration with the Reef stakeholders.

2 Background and Justification for the Research

The RRAP Concept Feasibility Phase explored existing model capabilities for evaluating the efficacy of restoration interventions across the GBR. ReefMod is the most comprehensive ecological model being used by RRAP. It is already linked to eReef's water quality and connectivity and simulates individual corals of six functional groups along with Crown-of-thorns starfish (COTS) and seaweed. The model includes GBR parameterisations for sedimentation, anchor damage, coral bleaching, cyclones, and COTS control as well as pilot model of coral adaptation to warming. Despite ReefMod's sophistication of being able to simulate the full range of restoration interventions so that their efficacy can be evaluated at the scale of multiple reefs up to entire GBR, there were several background processes that could improve model credibility and build confidence in assessing the efficacy of restoration interventions. This included a more credible modelling of genetic adaption but also integration of critical ecosystem services into the valuation of restoration benefits. Moreover, a robust assessment of intervention efficacy required exploration of a large spectrum of intervention designs; this would be essential in identifying locations that are genuinely more amenable to restoration in the context of multiple disturbances and existing management actions. Developmental research was required to enable a fast and accurate emulation of ReefMod while improving its interoperability with the other RRAP Modelling and Decision Support (M&DS) projects and end-users beyond RRAP. The RRAP ReefMod Research and Development (R&D) Project (M&DS-04), therefore had four areas of focus:

Sub-project 1: Model credibility: Plug critical gaps in ReefMod parameterisation and functionality

The gaps that were planned to be filled included nutrient runoff impacts on algae, ocean acidification, and a more appropriate model of coral genetic adaptation. The influence of water quality will be updated in ReefMod-GBR by integrating the effects of sedimentation on coral recruitment (Wakwella et al. 2020) in relation to eReefs predictions of sediment deposition and resuspension rates. We planned to develop a parameterisation for turbid-tolerant coral species as a new coral group, allowing for greater credibility in modelling coral demographics on inshore reef environments. The capacity of ReefMod-GBR to simulate realistic inshore reef dynamics with seven coral groups will be tested against the Australian Institute of Science (AIMS) Marine Monitoring Program (MMP) dataset.

It also integrates the model with thousands of simulated cyclone tracks, particularly important to determine how predictable cyclone refugia are across the GBR. This provides guidance on how to reduce the risk to interventions from cyclone damage (i.e. to avoid losses of significant infrastructure from the same or multiple cyclones). We had planned to revisit the parameterisation of coral mortality with cyclone strengths using species- and size-specific relationships between water velocity and the mechanical vulnerability of coral colonies (Madin et al. 2014). Combined with high-resolution (100 metre) predictions of wave-generated velocity metrics available for each cyclone track (Callaghan et al. 2020), this new parameterisation improves our ability to predict cyclone impacts in time and space.

Sub-project 2: Extend ReefMod to include an important reef value: carbonate budgets

Carbonate budgets have been added to the list of key metrics of reef health for reporting on the state of the GBR by the Great Barrier Reef Marine Park Authority (GBRMPA) and the Queensland Government. A Caribbean carbonate budget was linked directly to ReefMod previously (Kennedy et al. 2013) but this has not been attempted for Indo-Pacific coral reefs. We have created calibrations of coral calcification and morphology to annual rates of carbonate production but this can be improved with empirical data.

The plan was to integrate the recent calibrations of carbonate accretion and erosion and fill some key data gaps in allowing us to translate outputs of ReefMod-GBR (which includes eReefs and climate models) into projections of restoration impacts on carbonate budgets. It comprises limited field work needed to parameterise models of coral carbonate production and carbonate loss as a function of habitat type. A link is yet to be established between carbonate budgets and relevant biogeochemical variables predicted by

eReefs, so that the current and future dynamics of carbonate chemistry under ocean acidification can be incorporated into ReefMod-GBR. We had proposed to integrate mechanistic predictions of coral calcification developed by Matthew Adams (QUT) in response to light, temperature, salinity, dissolved inorganic carbon and total alkalinity. This model can be linked to eReefs to infer the calcification rate of different coral species across the GBR. It will allow capturing spatial and temporal variations of coral calcification and their integration into carbonate budgets predicted by ReefMod-GBR under different scenarios of reef restoration. Ultimately, carbonate budget outputs were to be coupled to the RRAP Restoration Explorer to project the impacts of restoration on future functioning of coral reefs, with carbonate budgets as a key proxy of a diversity of functions.

Sub-project 3: Create and integrate a model of genetic adaptation in corals

The [RRAP Investment Case](#) integrated a theoretical model of coral adaptation (Matz et al. 2017) into ReefMod which has the necessary individual-based design to implement genetic models (Bozec and Mumby 2019), but it has several limitations. This includes its scale (not currently parameterised for entire coral population sizes), structure (non-overlapping generations), and lack of empirical data to support assumptions (thermal tolerance, trait heritability). Yet the sensitivity of the reef outputs was high making the process of natural adaptation a key uncertainty that will affect assessments of the counterfactual and efficacy of restoration.

Including genetic adaptation is to help us get a handle on future genetic diversity in corals. Two genetic models that were available focus on the cnidarian and have not yet incorporated adaptive contributions of symbionts. The project will revisit which model strategy is most appropriate for which questions and spatial scales in RRAP. Findings from parallel examinations of small-scale models will be used to parameterise large scale models that incorporate reefs of different sizes and various migration rates. Updated parameter information on thermal traits (coral growth, mortality, fecundity), and a literature review will be incorporated into models to allow exploration of trade-offs and their impacts on coral's evolution under a warming climate. Single-reef and large-scale models will be used to explore the parameter space of thermal adaptation and evaluate the scope for coral evolution under standard Representative Concentration Pathways (RCP) projections. We will then explore the conditions (introduction number, heritability, genomic architectures of coral out-plants) under which assisted introductions may benefit thermal trait adaptation over what time horizons. GBR-scale simulations will also assess the degree to which restoration methods (including Solar Radiation Management (SRM)) can enhance or compromise future genetic diversity.

Sub-project 4: Building the RRAP Restoration Explorer (RE)

One of the ultimate aims was building a prototype for the RRAP Restoration Explorer to extend the capabilities of ReefMod-GBR in simulating restoration interventions and develop the accessibility of model outputs. Improving the accessibility of model outputs required (1) faster simulations of the model enabling the extensive exploration of restoration strategies with optimisation methods and (2) an effective model interoperability by building an Application Programming Interface (API) into the RRAP-RE enabling Decision Support (DS) scientists to interact directly with the model from another platform. Essentially, the API provides a direct portal into the fast version of ReefMod-GBR, allowing the fast exploration of restoration interventions.

One straightforward approach will be adapted from the previously developed Resilience-Based Management (RBM) tool in which the outcomes of the linked eReefs Water Quality (WQ)/connectivity/climate models were run through the emulation of ReefMod-GBR and offered as a menu of management interventions to the user including COTS control, WQ improvement and prevention of anchoring. We propose to undertake a similar approach for developing an effective, flexible and user-friendly interface for the RRAP-RE where the menu proposes a range of restoration tools. This will allow the user to specify a bespoke set of interventions and evaluate the improvement of reef metrics relative to a counterfactual. The RRAP-RE will be designed to allow multiple users (sub-program researchers in RRAP and managers) to specify a region of interest, time scale, counterfactual of climate change, background management interventions and a bespoke set of

restorations in time and space. Decision-Support users will be able to interact directly with the emulated output via the API.

3 Research Objectives and Key Findings

A current list of project outputs are listed on the RRAP website: gbrrestoration.org. Key research objectives and findings are detailed below.

3.1. Model credibility: Plug critical gaps in ReefMod parameterisation and functionality

While we had general confidence in our ecological model – as tested against the Australian Institute of Marine Science’s Long Term Monitoring Program (LTMP) (Bozec et al. 2022) – some concerns have been raised about the implemented relationship between heat stress (DHW exposure) and coral mortality, given it was parameterised using field data collected at shallow depths (approximately 2 metre depth). The concern was that excessive mortality may have been inferred as the model simulates coral demographics representative of mid-depth reef environments. Moreover, there were concerns that the bleaching model does not accurately represent the natural selection of thermally-tolerant corals, potentially underestimating the progressive hardening of coral communities expected to occur across multiple marine heatwaves. Overall, this pointed towards a lack of validation of the bleaching model with observations of coral loss following recent major bleaching events on the GBR.

Without an increase in resourcing, we did reconsider our objectives to prioritise key improvements to the modelling of multiple coral futures across the GBR (counterfactuals). Essentially, R&D activities that aimed to improve the counterfactuals in inshore environments were postponed in favour of improving the model efficacy in those areas farther offshore where restoration is actively being designed and implemented. The revised focus was to improve the simulation of bleaching impacts – with a proper validation of the reconstructed impacts of recent events of mass bleaching, and the simulation of evolutionary mechanisms underlying the adaptation of corals to warming. We also planned to incorporate heat stress projections downscaled from the last generation of Global Circulation Models (GCMs) based on the work performed by collaborators from the University of Exeter under subcontract. Finally, we had planned to integrate higher-resolution (one kilometre) larval connectivity for corals and COTS if available from CSIRO, and a proper implementation of connectivity and vital rates for coral brooders. The latter objective was postponed allowing for more in-depth work on implementing a robust model of coral adaptation and enhancing the credibility of counterfactual projections under multiple warming scenarios.

Improvements of the bleaching model

Originally, bleaching mortality in ReefMod was based on data collected during the 2016 bleaching event (Hughes et al. 2018), resulting in mortality curves for each coral group (Bozec et al. 2022) as a function of cumulative heat stress (Degree Heating Weeks (DHW)). Being typical of shallow reef environments, we adjusted these curves to reflect bleaching conditions at approximately seven metres (in line with ReefMod’s representative depth) using bleaching mortality data collected along a depth profile in the Northern GBR (Baird et al. 2018).

Previously in ReefMod, all coral colonies within a community group had the same heat tolerance, leading to uniform bleaching responses. However, heat tolerance varies among individuals of the same species, with some colonies surviving better than others. Ignoring this variability can overestimate mortality when projecting future warming. Using experimental data from Palau (Humanes et al. 2022), we introduced inter-individual variations in heat tolerance, allowing for more realistic bleaching responses within a coral group (Fig. 1), and enabling natural selection of heat-tolerant variants to occur.

Community-level responses to bleaching predicted by ReefMod were then tested against an independent dataset – AIMS LTMP and MMP data before and after the 2016 marine heatwave (Fig. 1). The model provides a fairly accurate reproduction of the observed relative coral cover changes, highlighting the capacity of ReefMod to simulate realistic responses to marine heatwaves.

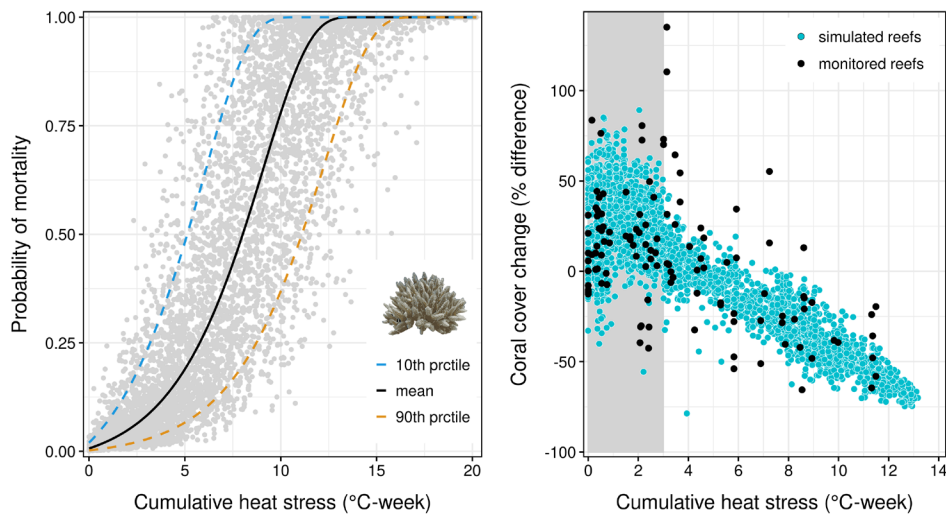


Figure 1: Left: bleaching-induced coral mortality resulting from accumulated heat stress (Degree Heating Week, DHW, in °C-week) at model initialisation (i.e. naive response to heat stress). Corals of a given group (here, corymbose acroporids) follow an average dose-response (black curve) modelled from depth-adjusted mortality. Variability in heat tolerance (\pm HT; °C-week) among coral individuals (grey dots) is simulated by shifting the dose-response curve along the DHW axis, reflecting individual deviations from the group mean response at initialisation. The blue and orange mortality curves indicate, respectively, the bleaching response of the 10th and 90th percentiles of the HT distribution within the group based on data on *Acropora digitifera* (Humanes et al. 2022). Right: impacts of the 2016 mass bleaching on total coral cover (relative change) recorded at 5–10 m depth by AIMS monitoring surveys (black dots, N=117 reefs) and predicted by the model (blue dots, N=3,806 reefs), versus reef-level DHW exposure recorded by NOAA. Bleaching at DHW < 3°C-week was ignored. Extracted from Bozec et al. (2025).

Consolidated hindcast reconstruction of coral cover trends across the GBR

Along with the refinement of the bleaching model, we extended the historical environmental forcing with the last available datasets to update our hindcast reconstruction of GBR coral cover trajectories. We integrated National Oceanic and Atmospheric Administration (NOAA) satellite data on heat stress (DHW) until 2024 (inclusive) and estimated past cyclone exposure by combining historical cyclone tracks provided by the Bureau of Meteorology with a wind-field model, allowing to estimate wind speed at each individual reef along every cyclone track between 2008 and 2024. Finally, we integrated eReefs GBR1 connectivity data for coral larvae, increasing the resolution of larval dispersal (1 km versus 4 km previously) for more accurate coral connectivity simulations.

With these model improvements, the latest hindcast of coral cover trajectories closely aligns with observed trends in GBR-wide coral cover from 2008 to 2024 (Fig. 2). At the individual reef scale, modelled trajectories also showed good agreement with monitoring data. The model estimates current coral cover at 32% overall (North: 33%, Central: 36%, South: 28%), with the 2024 mass bleaching event causing particularly severe losses in the Southern region. Overall, these new developments help consolidate the credibility of ReefMod in simulating GBR coral dynamics under multiple stressors. They also provide a simulation-based assessment of coral health that can inform reef management (e.g. prioritising reefs for COTS control).

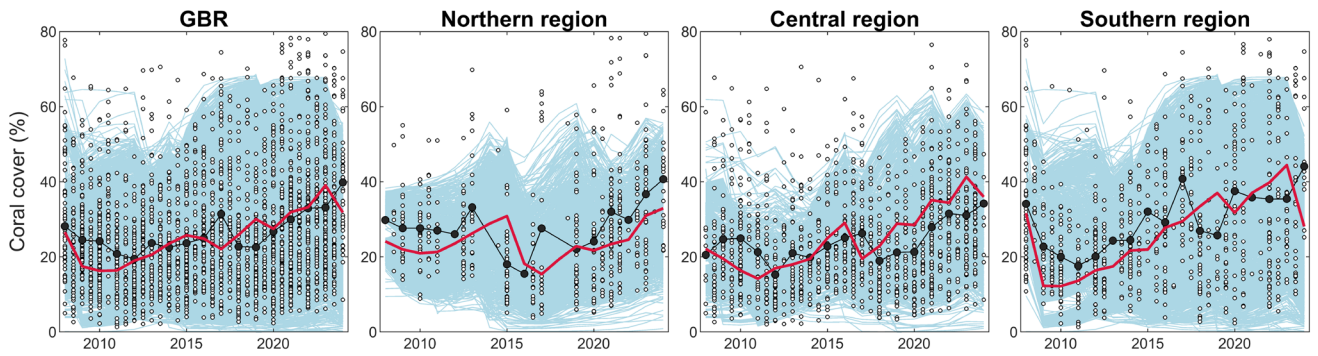


Figure 2: Hindcast (2008–2024) reconstruction of trajectories of total coral cover (blue lines: individual reef trajectories averaged over 20 simulations; red line: regional average) for the entire Great Barrier Reef (GBR, $n = 3,806$ reefs) and for the northern ($n = 1,201$ reefs), central ($n = 957$ reefs) and southern ($n = 1,648$ reefs) regions. Data points represent coral coverage observations from AIMS LTMP (photo-transect and transformed manta tow estimates following Bozec et al. 2022), where open dots correspond to individual reef surveys conducted during a specific season and filled dots indicate the annual average across all surveys. Average coral cover was not calculated for years with fewer than five reef surveys.

Integration of downscaled CMIP6 projections of heat stress

Previously we used temperature projections from Coupled Model Intercomparison Project Phase 5 (CMIP5) climate models to forecast coral futures for the GBR (Mason et al. 2023) under four emission pathways (Representative Concentration Pathways, RCPs). Temperature projections were provided at the spatial resolution of each climate model, which was often coarse. A new generation of climate models (CMIP6) became available, with a key improvement: the mechanistic downscaling of temperature projections, enabling estimation of future heat stress events (annual maximum DHW) at a finer 10-km resolution (McWhorter et al. 2022), under five alternative emission pathways (Shared Socioeconomic Pathway, SSP).

A first step resulted in the integration of DHW projections derived from five CMIP6 models (McWhorter et al. 2022). We then realised that many CMIP6 models are biased towards warmer projections, compared to the previous model generation (Hausfather et al. 2022). A measure of the sensitivity of climate models to warming processes is provided by their equilibrium climate sensitivity (ECS), which is defined as the increase in global temperature for a sustained doubling of atmospheric carbon dioxide (CO_2) concentrations (Tokarska et al. 2020). Given their climate sensitivity, four out of the five climate models we were using can be considered being “too hot” due to a high ECS value (Fig. 3). To obtain a more balanced representation of future warming, the downscaled temperatures projections of five additional CMIP6 models were provided (Paul Halloran, University of Exeter), extending to 47 warming scenarios the set of possible futures for the GBR. In total, the 10 GCMs span the range of ECS values currently represented in the global CMIP6 model ensemble.

These differences in the sensitivities of climate models to carbon emissions prompted us to revise our multi-model ensemble approach for future warming projections. Instead of treating all climate models as equally probable, we weighted their contributions based on a probability distribution of equilibrium climate sensitivity available from the climate literature (Fig. 3). This approach reduces the influence of warm-biased models in the final ensemble of warming projections.

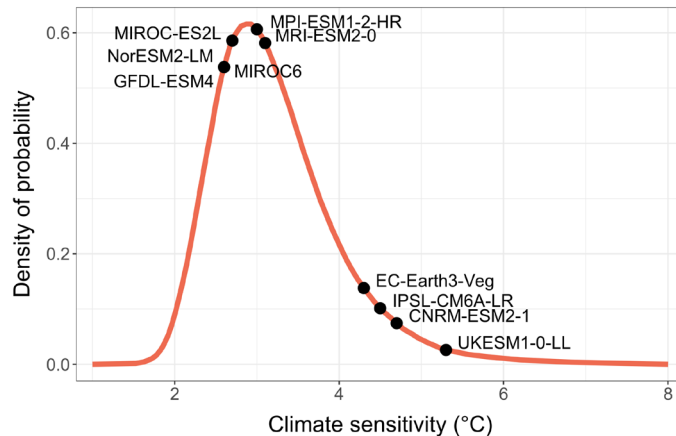


Figure 3: Probability density of Earth's climate sensitivity (extracted from Sherwood et al. 2020) and equilibrium climate sensitivity (ECS) values of the ten CMIP6 climate models (Tokarska et al. 2020). Extracted from Bozec et al. (2025).

3.2. Extend ReefMod to include an important reef value: carbonate budgets

While the methodology has been previously developed for estimating the coral production and calcification part of the carbonate budget, a key element was missing for an operational integration into ReefMod: the estimation of parrotfish bioerosion that needs to be subtracted from the amount of carbonate construction by corals and algae. Modelling parrotfish bioerosion requires knowledge on how many bites parrotfish take (bite rate), the volume of resulting bite scars, the density of excavated calcium carbonate, and any interactions existing between these parameters. Currently, parrotfish bite rate data relevant to the GBR are largely limited to shallow reef environments in northern regions, and substratum density is usually based on an average skeletal density of live coral taxa despite parrotfish primarily feeding on dead substrata. Utilising data from AIMS LTMP to inform carbonate budgets models could provide estimates of net carbonate production. Given that LTMP data is collected at six to nine metres depth, we first needed to establish if bite rates of parrotfish individuals changed with depth to determine if extensive bite rate data reported in shallow water environments were appropriate for estimating bioerosion on reef slopes. Furthermore, we also needed to test if substratum density based on live corals was an appropriate substitute for dead substratum density in bioerosion models.

Hannah Allan's PhD thesis (submitted in April 2025) sought to explicitly quantify relationships between parrotfish foraging and bioerosion and depth with the goal of providing information vital to estimating bioerosion accurately across different depths. Her work found that Individual-level bite rates of parrotfish did not change with depth in the studied species (five species). Assuming this is representative of all parrotfish, the implications for bioerosion models is that parameterisation of bite rates can remain consistent for all site depths. However, when bioerosion models were informed by bite rate data relevant to Lizard Island, northern GBR, bioerosion at Heron Island was overestimated by ~50%, highlighting the importance of using region- or site-specific bite rates. If carbonate budgets are to be applied across vast spatial scales, such as LTMP locations spread widely across the GBR, bite rates should be established intermittently across latitudes, prioritising excavating species which are the primary contributors to bioerosion.

Substratum density along a depth gradient is particularly understudied as research on skeletal density has historically focussed on the density of living corals, not dead substrata where parrotfish feed. A high-resolution method (computed tomography (CT)-scanning) was used to measure the density of different dead substratum morphologies along a depth gradient. With every metre increase in depth, the density of any dead substrata decreased by 2.5% (Fig. 4). Dead branching corals were at least 20% denser than any other substrata. Dead massive coral was the least dense substratum and was approximately half the density of dead branches at any given depth.

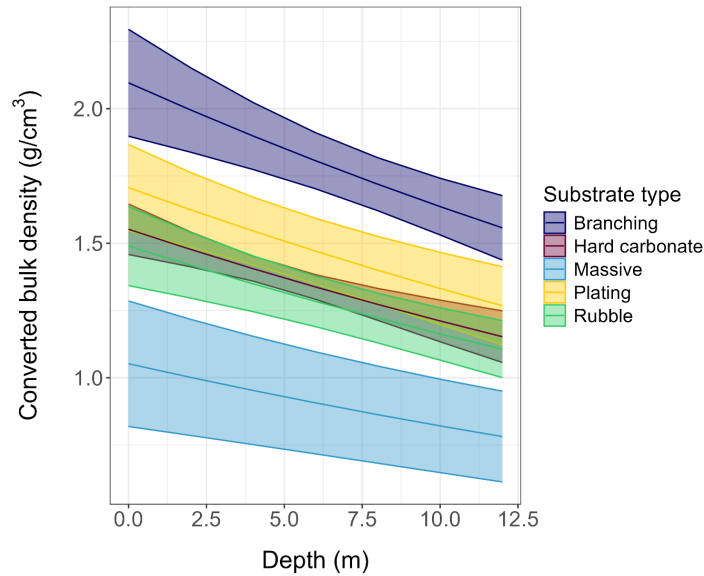


Figure 4: Predicted decline in bulk density (g/cm^3) with depth of different dead substratum types. Density was converted from Archimedes' principal values to equivalent of the upper 0.1 mm portion of CT scanned values. Substratum-level regressions shown \pm SE.

Based on findings, the skeletal density of feeding substrata down a reef slope is dependent both on depth and the relative availability of each type of dead substratum. This was incorporated into bioerosion modelling at Heron Island by determining the weighted skeletal density based on percent cover of each dead substratum type and depth-specific density, as well as accounting for the relationship between substratum density and bite volume (larger bites in low density substratum). Bioerosion estimates using site- and depth-specific density were not significantly different from estimates based on a generalised density value from live coral. However, at sites with large excavators (*C. microrhinos*), generalised substratum density parameterisation led to the overestimation of bioerosion by up to ~20%. Hence, the non-significant difference between erosion estimates was likely driven by the low abundance of large excavators at Heron Island, and bioerosion models for sites with high abundances of large excavators such as *C. microrhinos* and *Bolbometopon muricatum* (most abundant in central and northern GBR), should be informed by depth- and site-specific substratum density values.

LTMP benthic survey methods would need to be modified to capture dead substrata morphology to determine site-specific density values. Alternatively, future work could extract site-specific density from any photographic data collected along the GBR. Overall, for carbonate budgets to be more precisely estimated for the GBR, additional research is required to determine latitudinal parrotfish bite rates and site-specific substratum density. While this delay has prevented us to properly implement carbonate budgets into ReefMod, we now have a robust and realistic framework for future integration.

3.3. Create and integrate a model of genetic adaptation in corals

- Implementation in ReefMod of a new model of coral adaptation to warming

The original genetic model implemented in ReefMod (Bozec and Mumby 2019) was built on the approach developed by Matz et al. (2017), which used SLiM (an open-source evolutionary simulation framework) (Haller and Messer 2023) to simulate genetic variation and adaptation of coral fitness to chronic temperature change. We had applied the same key principles for modelling genetic adaptation to both acute and chronic thermal stress, focusing on coral survival and growth/reproduction, respectively. However, due to limited empirical data for a robust parameterisation, we shifted our focus to a single thermal trait: coral survival under acute heat stress.

This shift was facilitated by new empirical data (Humanes et al. 2022) capturing the variability in bleaching response among individuals of a specific coral population (i.e. heat tolerance, as shown in Fig. 1). Characterising the inter-individual variability of a trait under selection is critical, as natural selection acts on trait variation to eliminate the individuals that are less fit. Figure 5 illustrates this process, with the simulation of the 2016 mass bleaching. In thermally-sensitive groups (acroporids and pocilloporids), the mean heat tolerance of modelled individuals increased after the bleaching. This shift was proportional to the severity of heat stress (DHW), as more intense stress led to greater mortality among individuals with the lowest heat tolerance, thereby increasing the mean tolerance of the surviving population.

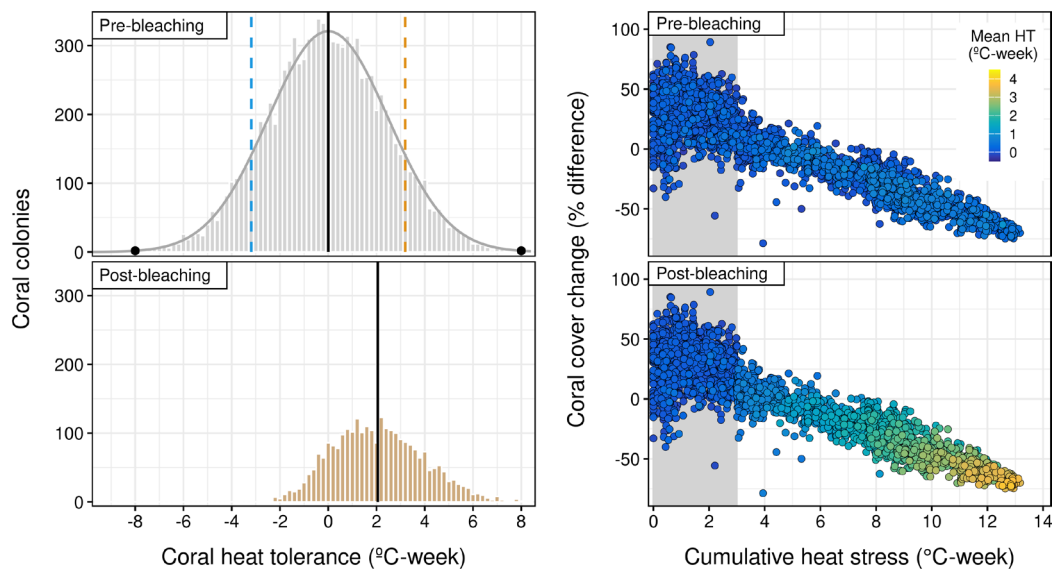


Figure 5: Left: simulated heat tolerance (HT) distributions before and after a hypothetical heat stress of 10°C-week, illustrating the natural selection of heat-tolerant corals. At initialisation, the distribution is truncated normal, with mean 0°C-week (black line), the 10th and 90th percentiles as in Fig. 1, and HT limits set to ± 8 °C-week (black dots). Right: simulated 2016 bleaching impacts as in Fig. 1, showing changes in the mean tolerance of heat-sensitive coral groups (acroporids and pocilloporids) following selection by bleaching. Extracted from Bozec et al. (2025).

Equally important was the publication of recent findings on the heritability of thermal traits in corals (Bairos-Novak et al. 2021, Humanes et al. 2024). The extent to which a trait is heritable is critical to a population’s capacity to adapt to a changing environment, as it determines how effectively beneficial traits can be passed from one generation to the next (Fig. 5). Using the reported heritability value for heat tolerance, we were able to simulate the progressive transmission of heat tolerance, selected by successive bleaching events, across multiple generations with the breeder’s equation (Falconer and Mackay 1996).

By combining our enhanced capacity to simulate bleaching response at individual levels and the partial inheritance of heat tolerance from parents to offspring, we ran eco-evolutionary coral simulations for each of the 3,806 reefs of the GBR across the multi-model ensemble of warming scenarios (Fig. 6a). We assessed coral projections based on the “likely” distributions of the average coral cover across the Great Barrier Reef, derived annually from the CMIP6 weighted ensemble of climate forecasts. ReefMod projected a sharp coral decline over the next 15 years for all emission scenarios (Fig. 6b), with mean coral cover dropping to 17% in 2040 (mean of the likely distribution across all SSPs). We found that keeping global warming below 2°C (SSP1-2.6) would promote coral recovery in the second half of the century as temperatures cease to rise, though retrieving the contemporary levels of coral cover would require a more stringent mitigation of emissions. Under a more likely global warming of ~ 2.7 °C (SSP2-4.5), coral populations would decline throughout the century, with projections of mean coral cover dropping to 16% by 2050 and to 8% by 2100. Unmitigated emissions (SSP3-7.0) would drive the GBR to a precipitous decline over the century, achieving a near total loss of coral cover by 2080–2100.

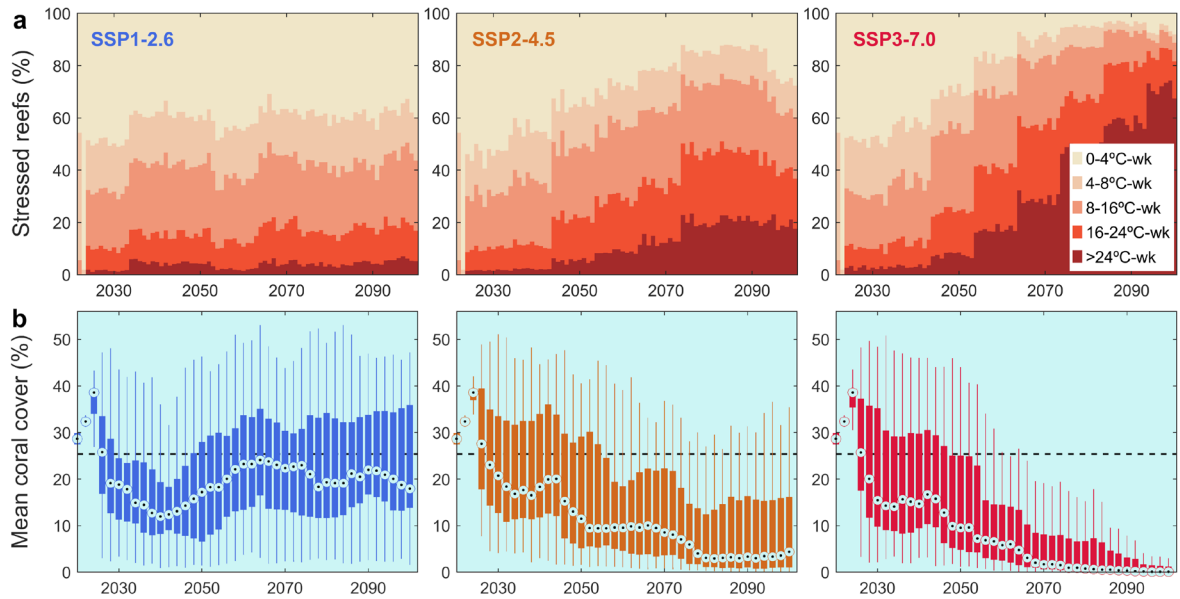


Figure 6: Ensemble projections of Australia's Great Barrier Reef during 21st century under three climate futures. From left to right, projections are shown for three emission pathways (Shared Socioeconomic Pathways, SSPs), SSP1-2.6, SSP2-4.5 and SSP3-7.0, leading to a global warming by 2100 of +1.8°C, +2.7°C and +3.6°C, respectively. (a) Percentage of reefs ($n=3,806$) under different categories of heat stress (Degree Heat Weeks, DHW) across all climate model projections ($n=200$). DHW events within each downscaled climate projection were shuffled per decade to generate stochastic fluctuations in the occurrence of bleaching. (b) Likely biennial distributions of the predicted GBR mean total coral cover among 1,000 bootstrap samples, each consisting of 20 individual runs of the eco-evolutionary model drawn at random using the likelihood of the underlying climate projection as weight. Boxes represent the interquartile range (IQR), showing the spread of mean total coral cover predictions between the 25th (Q1) and 75th percentiles (Q3) of the likely distributions. The central point mark is the median.

- Development of an eco-evolutionary genetic model to simulate assisted evolution interventions

We developed a genetic simulation of coral evolution specific to a coral population at Moore Reef using SLiM (Haller and Messer 2023). SLiM allows gene-level dynamics by simulating and tracking individual genes and loci across the population and through time (Fig. 7) – and therefore is more suitable to modelling the varying effects of assisted evolution interventions in enhancing natural adaptation. This modelling framework also allows us to model very specific genetic architectures and assisted evolution interventions. This includes the effect of adding a single gene of large effect on thermal tolerance (i.e. gene editing) versus many genes of small effect (as with assisted gene flow) or selecting the top 10% of thermally-tolerant individuals and reproducing them (selective breeding) or fragmenting them and replanting them (clonal fragmentation). We explicitly track individual genotypes by simulating 100 quantitative trait loci (QTLs) controlling the genetic component of individual phenotype, and thus fitness. In addition, we incorporated similar biological realism to ReefMod by incorporating strong size-dependent demography of corals, which was missing in the original SLiM models of Haller and Messer (2023). The SLiM model is structured to ingest temperature data and therefore can run simulations for any RCP or SSP (shared socio-economic pathway) scenario – though currently we use 'middle-of-the-road' SSP–2.45.

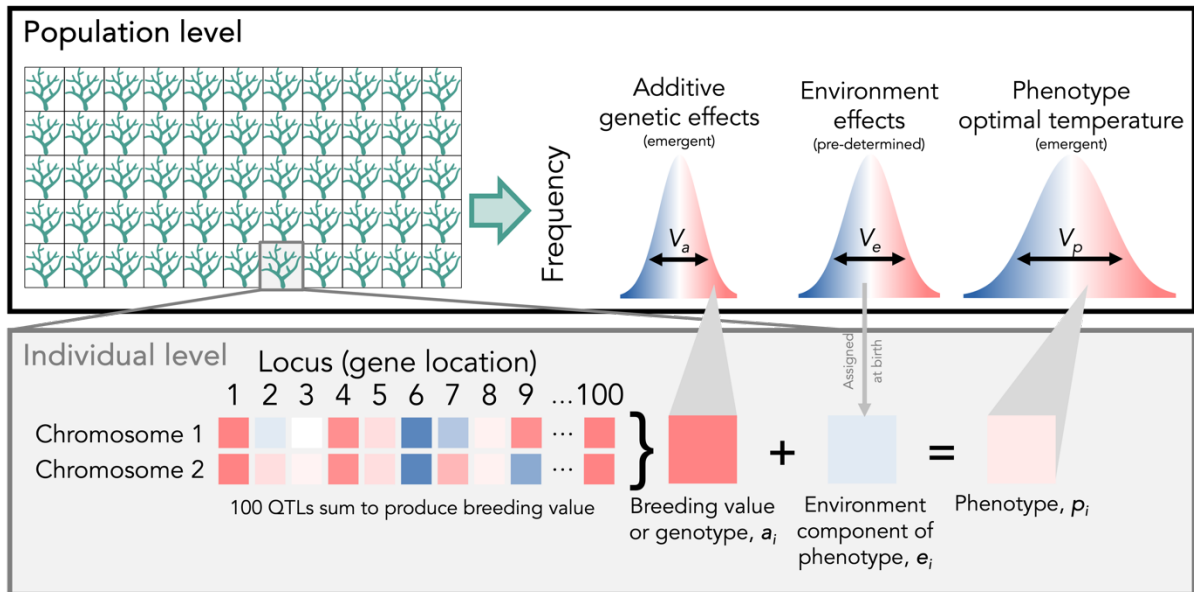


Figure 7: Representation of simulated genetics of a population within our SLiM model, allowing more realistic evolutionary dynamics in response to proposed assisted evolution interventions.

We use the mismatch between the mean maximum temperature observed for each year and an individual's thermal optimum to determine their probability of survival, with a maximum of 100% survival when there was a perfect match of an individual's phenotype to their environment and declining fitness based on a Gaussian stabilising selection function (Bürger and Lande 1994). Using this Gaussian fitness function to determine survival, individuals that more closely match their annual mean temperature across time are more likely to survive and pass on their genes (QTLs) to future generations individuals. QTL mutations are randomly drawn during a burn-in period, with their effect size proportional to a heritability of 30% of the total phenotypic variance, with the remainder (70%) being assigned to individuals as non-heritable environmental 'noise' effects. Since heritability is largely an emergent phenomena, our model simulates additive genetic variance as such, and therefore is not overly sensitive to differing heritability.

We then simulate predicted population sizes across time and compare our counterfactual simulation (i.e. no intervention) with three different genetic interventions:

1. Assisted gene flow (AGF) – 10% of natural recruitment on the reef is replaced by individuals from a reef that is either: +0.25°C, +0.5°C, +0.75°C, +1.0°C, +1.25°C, +1.5°C, +1.75°C, or +2°C above the mean temperature of the focal reef.
2. Selective breeding – 10% of natural recruitment is replaced by larvae created via breeding the top 25 coral colonies in terms of additive genetic effects (i.e. based on polygenic scoring of thermal tolerance).
3. Gene editing – 10% of natural recruiting larvae receive a single gene (i.e. QTL) that significantly increases thermal tolerance via CRISPR-Cas9 (Clustered Regularly Interspaced Short Palindromic Repeats), conferring either a: +0.25°C, +0.5°C, +0.75°C, +1.0°C, +1.25°C, +1.5°C, +1.75°C, or +2°C increase in thermal tolerance.

All interventions begin in the year 2025, and we tested for the effect of longer consecutive years of intervention: either using a single year (2025), over three consecutive years (2025-2027), or intervention over five years (2025-2029) for each of the intervention types. We present only the five-year case for simplicity here, with 10% of natural recruitment being replaced across models (Table 1). Each intervention model is directly compared to an otherwise identical counterfactual simulation to determine the effect of the intervention on population resilience relative to the counterfactual using the percentage difference method

([intervened – counterfactual] / counterfactual). We used 50 different simulations or ‘seeds’ with entirely different genetic backgrounds to ensure results are robust across recent genetic histories.

Table 1: Mean number of individuals intervened upon per year for assisted evolution interventions, based on 10% replacement of natural recruitment.

Year \ Intervention	Selective Breeding	Assisted Gene Flow	Gene Editing
2025	90450	90450	90450
2026	83702	83848	83904
2027	86187	86351	86265
2028	85831	85910	85889
2029	83406	83185	83096

All assisted evolution interventions were able to enhance adaptation, with gene editing having the strongest effect (Fig. 8). AGF using highly adapted populations (+1.5°C) was only marginally better than selective breeding, highlighting the power of selective breeding using only 25 individuals to improve population outcomes. The effects of very high levels of phenotype increase (+1°C and above) saw increased then declining effects on thermal tolerance with individuals that were highly enhanced (+2°C) being maladaptive in earlier years (2030-2050), and generally purged from the population prior to the expected increase of temperatures with climate change in later years (2050 onwards).

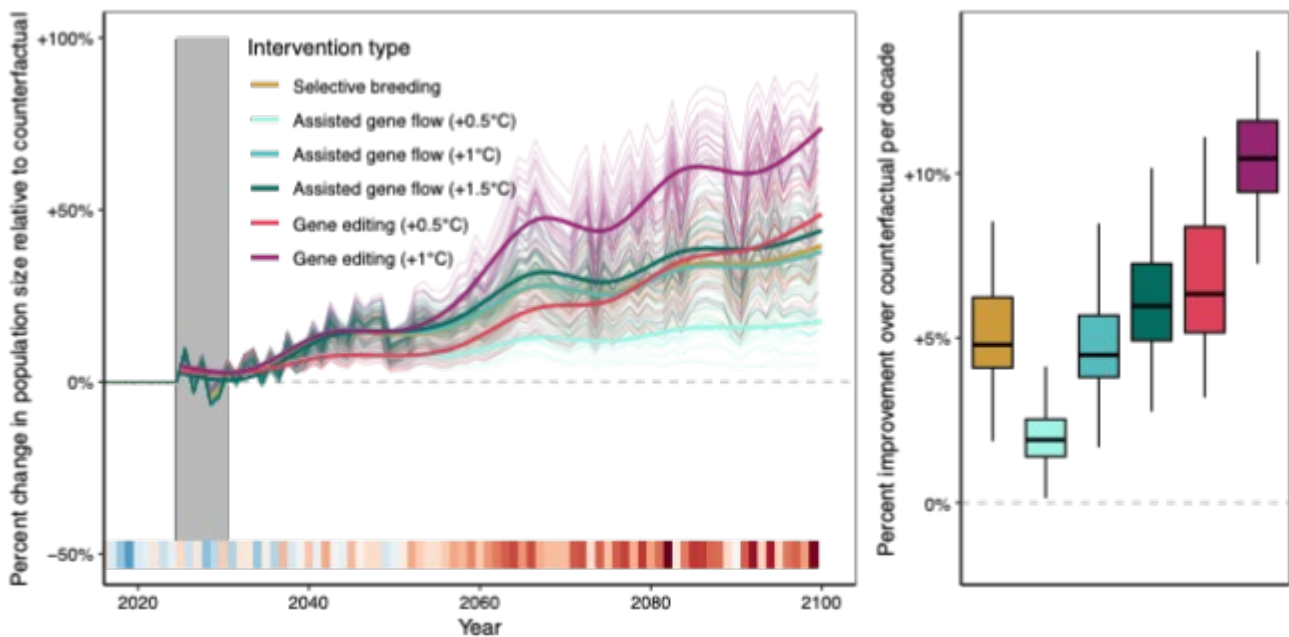


Figure 8: (a) Improvement in population size attributable to each intervention (relative to an identical counterfactual simulation but with no assisted evolution intervention). Multiple lines for each intervention represent $n=50$ unique genetic simulations in response to forecasted temperatures using SSP2-4.5 (2025–2100; colour gradient bar at bottom). Grey vertical rectangle represents the intervention period across 5 years. Not all interventions are displayed in order to maintain plot readability. (b) Boxplots of each model’s percent improvement per decade, assuming a linear increase of each intervention from 2031–2100.

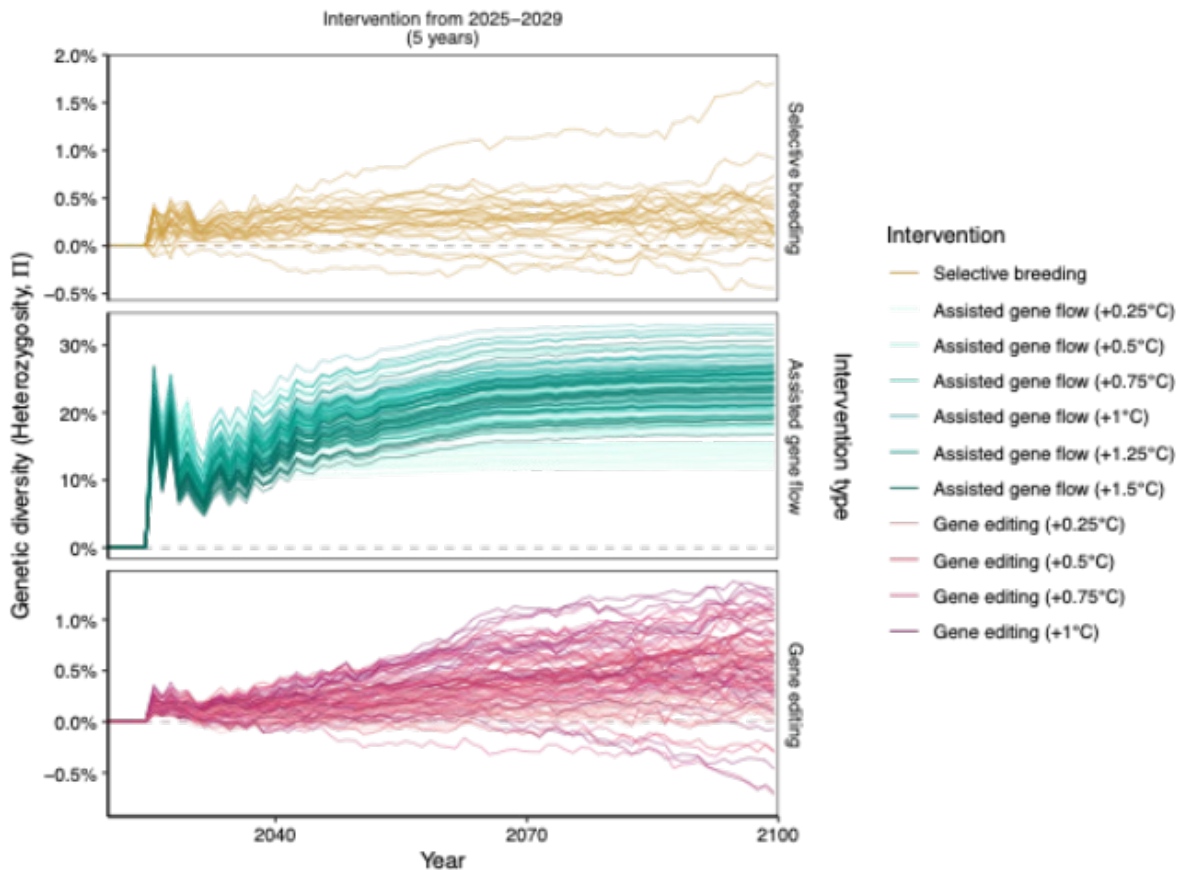


Figure 9: Effects of various assisted evolution interventions on percent change in genetic diversity (expected heterozygosity) relative to the counterfactual simulation. Note that the y-scale varies across panels, highlighting differences in the magnitude of effects of each simulation on genetic diversity.

We also examined the resulting genetic and functional diversity of coral communities in response to future temperatures projected for Moore Reef, including:

- Heterozygosity – a commonly calculated measure of overall genetic diversity, calculated based on the number of heterozygous versus homozygous alleles found within the population;
- Proportion of all sites that are polymorphic – a similar measure of neutral genetic diversity commonly used in population genetic analyses;
- Additive genetic variance – a measure of the relative genetic diversity that translates to phenotypic trait variation and thus related to both genetic diversity and evolvability.

All measures for genetic diversity were not adversely affected by assisted evolution interventions (selective breeding and gene editing) or significantly positively affected (i.e. greater genetic diversity) in the case of assisted gene flow; therefore, we present only heterozygosity here (Fig. 9). This suggests negligible downsides in terms of genetic diversity if populations are selected based on only a single trait of thermal optimum. However, with increased local adaptation or negative trade-offs among traits, genetic diversity could still be reduced by these interventions. Further simulations and genomic analyses will aim to quantify the amount of local adaptation and genetic covariance among multiple traits.

In the next phase of SLiM models, we plan to incorporate and examine a number of effects that likely impact the effectiveness of assisted evolution interventions, namely: (1) multi-reef gene flow and effects of local adaptation; (2) effects of temperature stochasticity at the time of intervention and varying SSP projections of temperature; (3) multi-trait selection models with genetic trade-offs (pleiotropy) and phenotypic (e.g. energetic) trade-offs; and (4) coral-symbiont co-evolutionary models and host-specificity.

3.4. Building the RRAP Restoration Explorer

- Developing a fast, operational version of ReefMod-GBR

Previous efforts to develop a faster version of ReefMod-GBR have relied on various approaches that emulate the functionality of the source code written in MATLAB (Matrix Laboratory) (Bozec et al. 2022), ultimately leading to the Resilience-Based Management tool released in 2020 (Mason et al. 2020). However, due to the persistence of a divergent behaviour of the emulated simulations, we finally decided to entirely implement the source code in C++, based on the expectation that a C++ version of the model would offer significantly improved performance over MATLAB. This has resulted into the ReefMod Engine (RME) created by John Hedley (Numerical Optics Ltd.). The RME replicates the MATLAB code with much faster computation times, with end-century simulations lasting only few minutes while it takes about 2 hours to run them using the source code. In addition, the RME simplifies the set-up of management interventions (conventional COTS control, coral out-planting, larval enhancement, rubble stabilisation) which can be applied to any of the 3,806 reefs of the GBR. In addition, the RME can be used to simulate interventions on a virtual reef customised with a specified environmental forcing, coral community composition and heat tolerance, larval supply and disturbance regime.

The RME has been used in multiple operational deliverable studies. First, an intervention efficacy study was conducted using the virtual reef concept to investigate how restoration benefits, which is the added increase in coral cover in this case provided through restoration are impacted by the context of the intervention. Main findings of this study show that external larval supply and number of larvae retained on the reef impact restoration success the most. More specifically, out-planting corals on a reef with low larval supply under low disturbance pressure could result in a four-fold increase in coral cover benefit compared to doubling the restoration area or number of corals out-planted per m² on the target reef (Fig. 10).

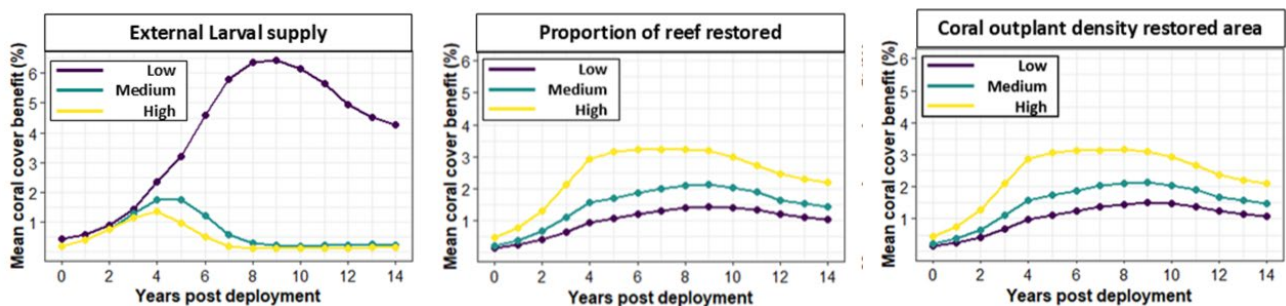


Figure 10: Mean coral cover benefits predicted on a virtual reef subject to variable larval supply, outplanting area and density of outplants. The impact of each individual factor on predicted mean coral cover benefit (%) is plotted while keeping remaining variables constant in partial dependency plots. Individual lines represent a single parameter setting while points represent progressive timepoints post deployment when variable data was predicted. Y-axis represents the predicted mean coral cover benefit. On the x-axis 0 years represent the timepoint of coral out-planting.

Our exploration of coral out-planting interventions also show that benefits can persist if an acute disturbance, such as mass bleaching, impacts after deployment. The timing of a bleaching event after restoration influences the benefits of out-planting (Fig. 11), with greater benefits observed when bleaching occurs later. These benefits peak sooner on reefs with limited external larval supply but strong larval retention. Moreover, out-planting corals with enhanced thermal tolerance (+ 3 DHW) can double these benefits.

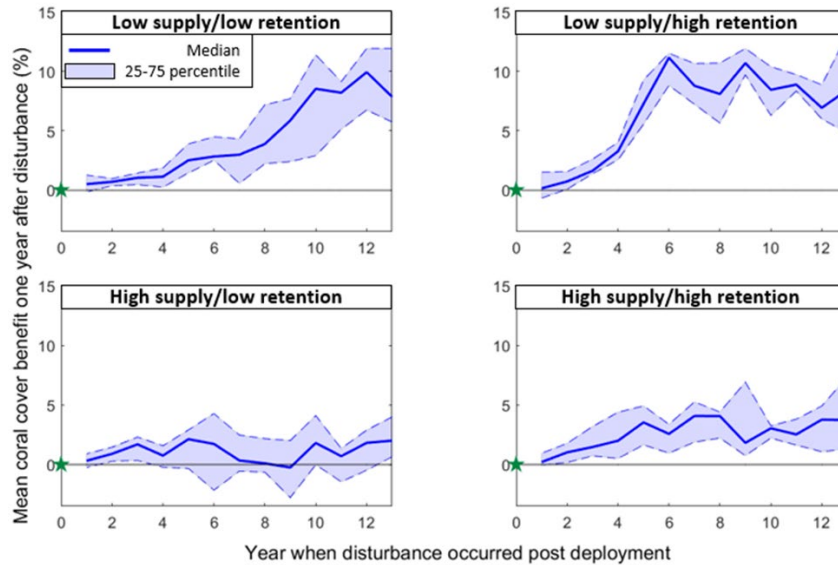


Figure 11: Simulated coral cover benefit of coral out-planting one year after a hypothetical bleaching event under different conditions of external larval supply and self-retention. In all scenarios, we assumed that thermal tolerance in the out-planted corals was enhanced by +3 DHW compared to native corals). The green star shows when the intervention took place.

The RME was also used to explore specific intervention scenarios on real reefs for the investment case. We investigated the potential of thermally-enhanced coral out-plants to produce ecological benefits across the Moore Reef cluster. Assuming deployment will start in 2030, we simulated the impacts of this intervention throughout the century (Fig. 12) under the SSP2 4.5 climate scenario. Overall, we found that increasing the area of restoration could result in higher benefits in coral cover, ranging from 5-10% depending on the number of corals out-planted. Furthermore, we observed a 1-4-fold increase in coral cover benefit when the out-planted corals were enhanced with +5 DHW of heat tolerance, compared to non-enhanced coral out-plants. Similar results can be observed when comparing benefits under +5 and +10 DHW enhanced corals, assuming such levels of thermal enhancement could be achieved in aquaculture.

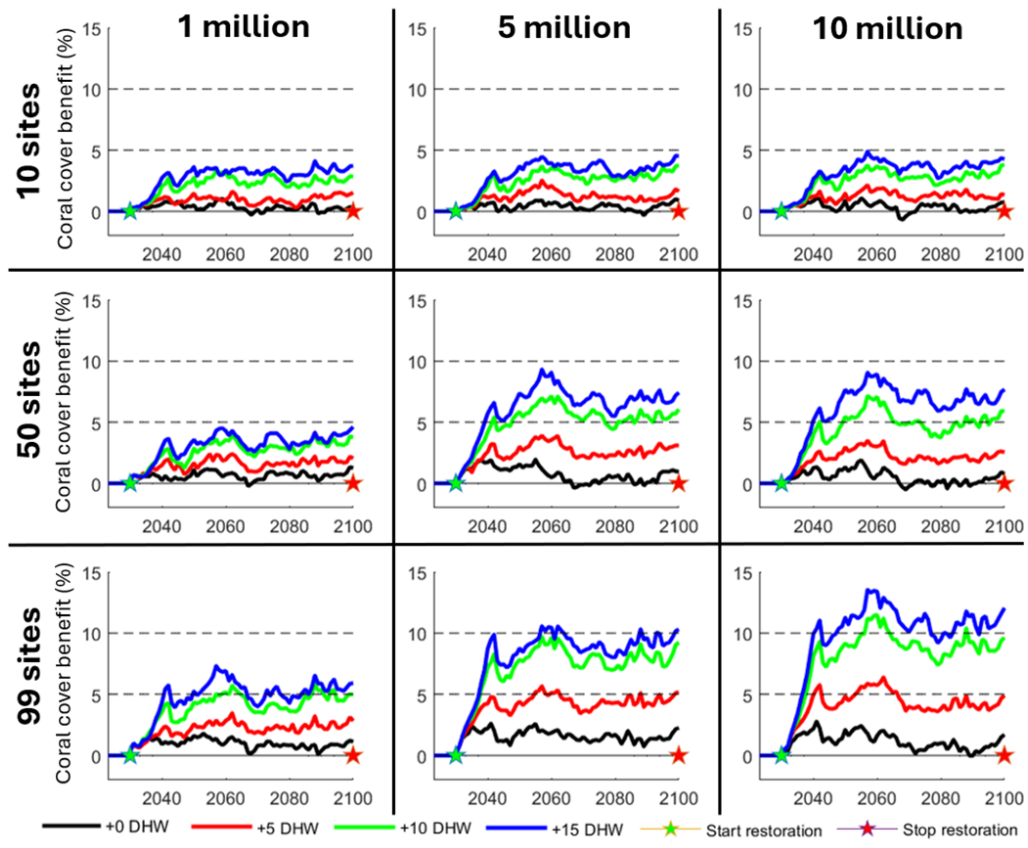


Figure 12: Total coral cover benefits (%) across the Moore Reef cluster when out-planting corals with different levels of thermal enhancement (+0, +5, +10, +15 DHW) at a yearly frequency, starting in 2030 until 2100 (averaged across 120 scenarios). From top to bottom, the same number of out-plants is deployed over an increasing area (number of sites). From left to right, an increasing number of out-plants is deployed over the same area. Stars correspond to start (green) and stop (red) of restoration effort.

- Developing a flexible and user-friendly interface

The RME is compatible with both Windows and Linux operating systems and can be easily deployed on high-performance computing (HPC) systems. Its interoperability allows seamless integration with existing decision-support modelling platforms (Fig. 13), including the ADRIA decision-support capabilities developed at AIMS. The integration with ADRIA has proven effective, facilitating numerous explorations of management intervention scenarios.

To facilitate the use of ReefMod, and promote its access to multiple users, a separate software, the Resilience Management Tool (RMT), was created to interface with the RME. A web interface (<https://gbrrestoration.org/rmt/index.html>) was also developed to facilitate access to the RMT and allow multiple users to explore online their own intervention scenarios and visualise the results of their simulations.

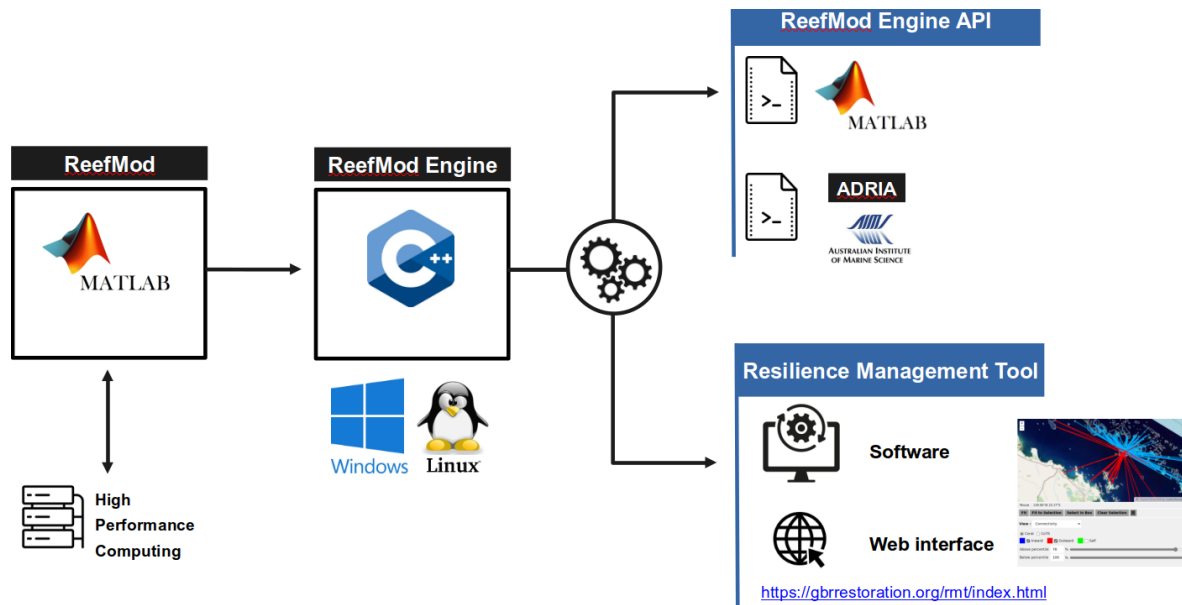


Figure 13: The ReefMod tool suite. The source code of ReefMod, written in MATLAB, has been reimplemented in C++ to create the ReefMod Engine (RME). The RME is an Application Programming Interface (API) that provides a faster version of ReefMod and facilitates interoperability with other decision-support tools, such as ADRIA. A separate software, the Resilience Management Tool (RMT), was created to interface with the RME and allow stakeholders to simulate ReefMod. The RME and RMT are both compatible with Windows and Linux. A web interface was also developed to promote access to multiple users.

The online version of the RMT is a user-friendly interface (Fig. 14) designed to streamline the setup and execution of intervention scenarios. Users can define custom timeframes, configure specific warming trajectories (five SSPs supported by 10 climate models) and select target reefs for intervention. Integrated visualisation tools include an interactive map that allows users to explore the GBR and select individual reefs for targeted analysis of intervention benefits, and a graphical output window to plot and review the simulation of the specified intervention combined with its counterfactual (warming scenario without intervention). The network of coral connectivity can also be visualised across the GBR map.

The capabilities of the RMT were demonstrated during two dedicated workshops organised with reef practitioners at the Reef Resilience Symposium in Cairns in April 2024 and at the Reef Futures Symposium in Mexico in December 2024. Workshop participants had the opportunity to engage in hands-on exercises and practice using the tool in real-time scenario planning. Feedback from reef practitioners is being integrated to prioritise future developments of the RMT functionalities and visualisations. Although a stand-alone version of the software exists, it is not yet publicly available for installation. This is due to ongoing efforts to implement appropriate safeguards regarding access, which will require further consultation with the government.

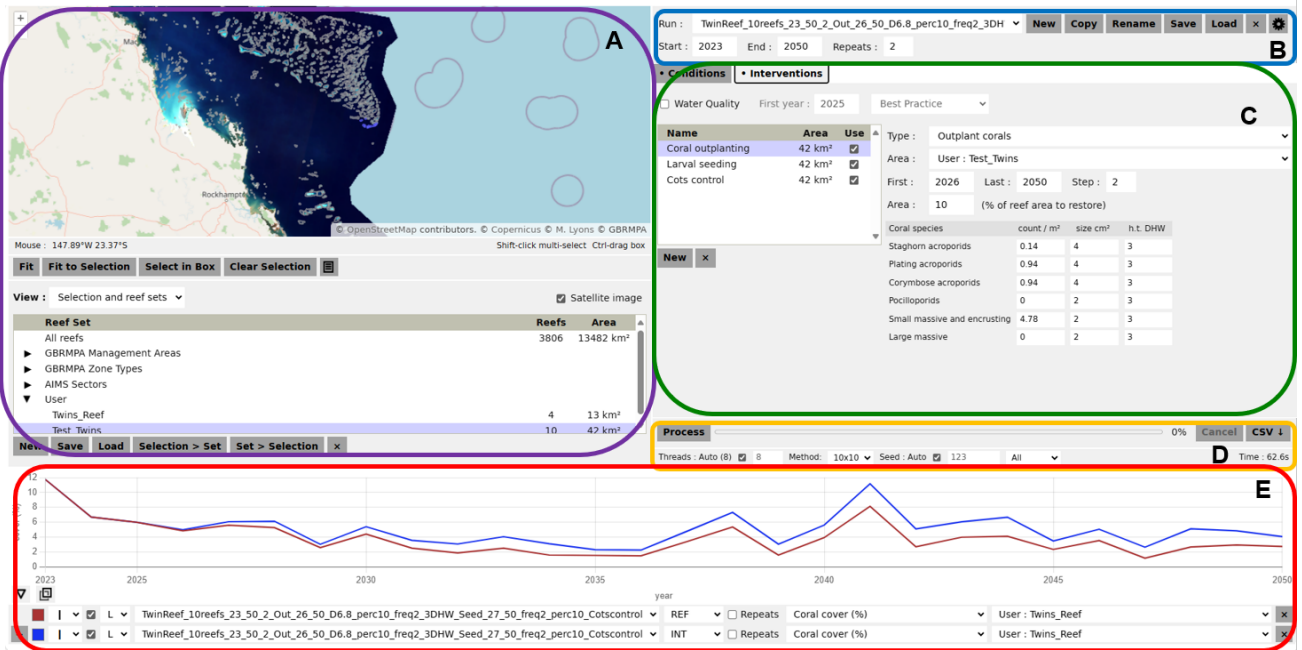


Figure 14: Screenshot of the web-based Reef Resilience Management Tool using the ReefMod Engine backend. Panels give access to different components of a model run. A) Reef map for setting reefsets, environmental conditions and connectivity across reefs and rank reefs based on output variables at timepoint X. B) Create model run, set timeframe and model replication. This section of the RMT can also be used to save and load previously saved model runs. C) Parameterise environmental conditions and intervention settings. D) Process model run, E) plot counterfactual (REF), intervention (INT) or INT minus REF model outcomes over time for a given reefset.

Table 2: Key findings of the Project aligned to the overarching and specific research questions for each sub-project.

Objective	Key Findings and/or Outcomes
1.	<p data-bbox="219 316 790 379">Model credibility: Plug critical gaps in ReefMod parameterisation and functionality</p> <p data-bbox="813 316 2011 451">We have improved ReefMod’s ability to simulate realistic impacts of coral bleaching, making the bleaching model empirically-based (Hughes et al. 2018), depth adjusted (~ 7 m) (Baird et al. 2018) and variable at colony level (Humanes et al. 2022). The model was validated by comparing community-level predictions with observations (AIMS monitoring data) of bleaching impacts during the 2016 mass bleaching.</p> <p data-bbox="813 467 2011 563">We have consolidated ReefMod’s ability to reconstruct past trends of GBR coral cover by revising the hindcast (2008-2024) using updated environmental forcing (bleaching and cyclones up to 2024) and GBR1 coral connectivity.</p> <p data-bbox="813 579 2011 643">ReefMod’s hindcast of past coral cover trends provides a simulation-based assessment of coral health that is currently guiding reef management (reef prioritisation for COTS control).</p> <p data-bbox="813 659 2011 778">We have implemented multiple scenarios of future heat stress informed by the last generation (CMIP6) of climate models, downscaled at 10 km resolution. We have created a multi-model ensemble of warming scenarios that accounts for the sensitivity of each climate model to future emissions, avoiding a warm bias in future heat stress for more reliable warming projections.</p>
2.	<p data-bbox="219 810 790 874">Extend ReefMod to include an important reef value: carbonate budgets</p> <p data-bbox="813 810 2011 842">We have already created the methodology for estimating carbonate production and erosion.</p> <p data-bbox="813 858 2011 922">We have developed relationships for estimating parrotfish bioerosion across different depths, accounting for bite rates, volumes of carbonate removed per bite and the skeletal density of feeding substrata.</p> <p data-bbox="813 938 2011 962">What we are lacking for a full integration of carbonate budgets is specific information about parrotfish species.</p>
3.	<p data-bbox="219 986 790 1050">Create and integrate a model of genetic adaptation in corals</p> <p data-bbox="813 986 2011 1177">We have refined the model of coral adaptation to warming in ReefMod to produce more robust projections of future coral resilience and adaptive capacity under climate change. The model has been simplified to a single thermal trait (survival to heat stress) and uses novel data to parameterise the variability of tolerance to heat stress among coral individuals, and its partial inheritance from coral parents to offspring. The model allows for the simulation of the evolution of heat tolerance resulting from natural selection caused by successive bleaching, and the transmission of heat tolerant phenotypes across multiple generations.</p> <p data-bbox="813 1193 2011 1329">We used this new model of coral adaptation to project possible futures for GBR corals across multiple (counterfactual) scenarios of warming, informed by our multi-model ensemble of heat-stress projections. Our simulations show that limiting global warming to no more than +2°C above pre-industrial levels is critical for maintaining coral populations at levels necessary to sustain viable reef ecosystems on the GBR.</p> <p data-bbox="813 1345 2011 1441">In parallel, we have created an eco-evolutionary genetic simulation of a single reef experiencing projected climate change under various assisted evolution interventions (coral fragmentation, selective breeding, assisted gene flow – AGF, and gene editing). Initial results suggest that interventions such as gene editing, selective</p>

Objective	Key Findings and/or Outcomes
	<p>breeding, and AGF would greatly enhance the reef relative to the counterfactual. Gene editing has the most beneficial effect, while selective breeding and AGF have intermediately positive effects without compromising genetic diversity. Selective breeding of larvae using the top 10% of adults (via genotyping) could provide the greatest 'bang for buck' and use local genetic diversity to enhance the reef. The resulting model will provide the basis for future developments in ReefMod, allowing the simulation of assisted evolution interventions across the GBR.</p>
<p>4. Build the RRAP Restoration Explorer</p>	<p>We have created a fast version of ReefMod embedded in an API (the ReefMod Engine) that considerably increases our simulation capacity while promoting interoperability with other decision-support tools (e.g. ADRIA).</p> <p>We have created user-friendly interfaces that do not require any coding skill, enabling broader access to ReefMod, particularly for reef practitioners. These interfaces allow users to set-up, run and visualise specific scenarios of interventions across the GBR.</p> <p>We conducted workshops with reef practitioners to demonstrate the capabilities of the software and associated web-based interface. This provided an opportunity to showcase its functionalities and performance, test its usability across a diverse group of participants and needs, and gather valuable feedback for future improvements.</p>

Adjustments to key research objectives

Table 3: Variation in the Project over time.

Initial Research Question	Explain when, how and why the research question changed
<p>Improve model credibility in simulating inshore reef dynamics (algal dynamics, nutrient effects on coral-algal competition, effects of sedimentation on coral recruitment)</p>	<p>We change our R&D priorities mid-2022 to increase focus on model credibility, which required (1) greater realism in simulating interventions, (2) more accurate (and validated) simulations of coral bleaching, and (3) a robust and defensible model of coral adaptation to warming. A greater focus on improving the modelling of mid-shelf and outer-shelf reefs was justified considering this is where restoration is actively being designed and implemented.</p>
<p>Integrate the effects of ocean acidification</p>	<p>Changed to increase focus on the modelling of coral evolution under increasing heat stress</p>
<p>Implement a new coral group to represent brooders with connectivity</p>	<p>Same as above, although this will likely be one of the primary questions addressed in the next development priorities</p>
<p>Limitations within the theoretical model of coral adaptation included in the pre-RRAP version of ReefMod including its scale (not currently parameterised for entire coral population sizes), structure (non-overlapping generations), and lack of empirical data to support assumptions (thermal tolerance, trait heritability).</p>	<p>This limitation can be overcome with the new SLiM model (available for a single reef) which can directly calculate metrics of future genetic diversity, but ReefMod doesn't, since it now relies on a simple model of phenotypic transmission, which does not explicitly simulate genetics. There are plans to use the new SLiM model to explore relationships between genetic diversity and reef characteristics (reef area, larval supply). These relationships can be later integrated into ReefMod, allowing the model to estimate genetic diversity across the GBR for different scenarios of warming and intervention.</p> <p>We shifted our focus and replaced the SLiM-based implemented in ReefMod during the RRAP Feasibility Phase by a simple model of phenotype transmission. ReefMod now simulates the evolutionary dynamics of a single thermal trait: coral survival under acute heat stress. This was facilitated by new empirical data (Humanes et al. 2022) capturing the variability in bleaching response among individuals of a specific coral population (see Fig. 1) and empirical estimates on the heritability of these traits (Bairros-Novak et al. 2021, Humanes et al. 2024).</p>
<p>Comparing ecological and evolutionary modelling frameworks at the small scale (single reef), while simultaneously building up a large scale (but simpler) GBR-wide evolutionary model. Several novel features are suggested: reproduction via cloning, trade-offs among thermal traits, overlapping coral generations, evolutionary dynamics of symbionts, variable genomic architectures.</p>	<p>The new SLiM model includes cloning specific to an assisted evolution intervention, a trade-off in terms of cold-water survival/bleaching for highly evolved corals, overlapping coral generations, and evaluates differing genomic architectures in terms of the number of loci, but is missing any symbiont-specific dynamics or multi-trait selection (e.g. growth-thermal tolerance tradeoffs). In the next phase of our SLiM modelling, we plan to expand to multiple reefs, yet expanding to all reefs will not be computationally feasible. We would need to extrapolate the smaller-scale findings of the SLiM model for specific interventions into future iterations of ReefMod. Trade-offs with multiple traits are also currently considered as an extension of the SLiM model. We have attempted to develop a very simple model of genetic 'pleiotropy' (genetically-constrained trade-offs, where evolution to one trait causes maladaptation or co-evolution in another), but we lack estimates of how much of currently identified trade-offs are genetically based. This is typically assessed using the animal model of quantitative genetics and examining the genetic covariance matrix for positive versus negative covariances among traits – and is going to be estimated by</p>

	Holland Elder from the RRAP EcoRRAP Sub-program in the near future and then can be incorporated into the model.
Improved modelling of genetic adaptation to allow us to predict future changes in genetic diversity, and the impacts of interventions on that diversity.	The SLiM model can directly calculate metrics of future genetic diversity and discussions have been undertaken to use the model developed by Kevin Bairos-Novak to simulate future genetic diversity and thermal tolerances of a single reef given assisted evolution interventions and use these relationships to parameterise ReefMod genetic diversity changes in future implementations but due to time and job change constraints, this was not completed.
Updated parameter information on thermal traits (coral growth, mortality, fecundity) from the RRAP EcoRRAP Sub-program and the literature review will be incorporated into models to allow exploration of trade-offs and their impacts on coral's evolution under a warming climate.	Thermal tolerance as a function of DHW is integrated into ReefMod, but the new SLiM model tracks the evolution of optimum temperature on coral fitness. Therefore, there are structural differences between the two modelling approaches that prevent a formal quantitative comparison. Yet, we can compare how the two models behave qualitatively. We haven't updated yet our models with data from the RRAP EcoRRAP Sub-program but plan to do it in the future. We haven't done this for ReefMod as this will likely require an extensive re-calibration of the larval stock-recruitment function and new validation exercises.

4 Future Research Recommendations

Model functionality

An explicit decision was taken not to invest in extending the model to represent inshore reefs of the GBR because restoration was considered to be more likely in mid- to outer-shelf reefs and we also needed to prioritise the inclusion of evolutionary adaptation. However, it continues to be important to expand the model inshore, which will involve capturing the effects of poor water quality on macroalgal dynamics, coral-macroalgal interactions, and patterns of herbivory. We have previously modelled these processes in the Caribbean but they will need a complete overhaul to capture the species and conditions in Australia.

Another omission from the model is ocean acidification but this remains both difficult to parameterise – particularly the link to coral growth rate – and is of dubious relevance, though it will impact carbonate budgets through bioerosion rates on inshore reefs in particular. This is not yet a high priority to address.

We have incorporated Allee effects based on data from *Acropora* but have not had time to complete exploring its impact. This is a priority for the next set of models but it will need to be coupled with future RRAP EcoRRAP Sub-program studies that explore the likelihood of Allee effects in non-acroporid corals. This is a pretty challenging task experimentally and is not part of the current EcoRRAP plan.

In terms of model functionality we intend to delve more deeply into the ecology of brooders, now that new data from the RRAP EcoRRAP Sub-program suggests extremely limited dispersal. We also plan to integrate the more recent demographic data on broadcast spawners from the EcoRRAP Sub-program, though care must be taken to distinguish latitudinal gradients associated with recent stress from long-term underlying patterns.

Lastly, while we are currently using the GBR1 coral connectivity and moving towards an even higher resolution for COTS connectivity, there continues to be a need to agree a new set of coral reef polygons for operational management. The community still uses the GBRMPA Indicative Boundaries even though individual polygons can comprise multiple separate reefs. Although the models currently use the new reef boundaries for scaling purposes (e.g. larval output), a revised set of polygons will need to be agreed and then connectivity matrices recalculated to the more realistic reef boundaries. A project is exploring this under the National Environmental Science Program (NESP) but it remains a hurdle for all working in the GBR modelling space.

Use of models and working with end users

It is particularly important to revisit the efficacy of interventions in light of the great diversity of data being generated by the RRAP interventions teams. A stronger link with RRAP logistics teams is also advisable so that costings can be compared.

As a team, our opportunity to extract useful ‘rules’ for intervention design has been limited and we plan to invest heavily in this work. There are two components to this. First is to break down the silos among management levers and take a holistic approach that considers restoration alongside other management actions, including COTS control, zoning, and anchor damage. Note that this may well require us to add new functionality to the models. Second, we need to explore effective site selection strategies that could be operationalised in practice, often with imperfect knowledge. This will require us to design plausible criteria and explore their efficacy. Partnership with the Reef Authority is essential for these tasks, as well as engagement with Crown-of-thorns starfish (COTS) Control Innovation Program (CCIP) and National Environmental Science Program (NESP) activities including Citizen Science.

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