

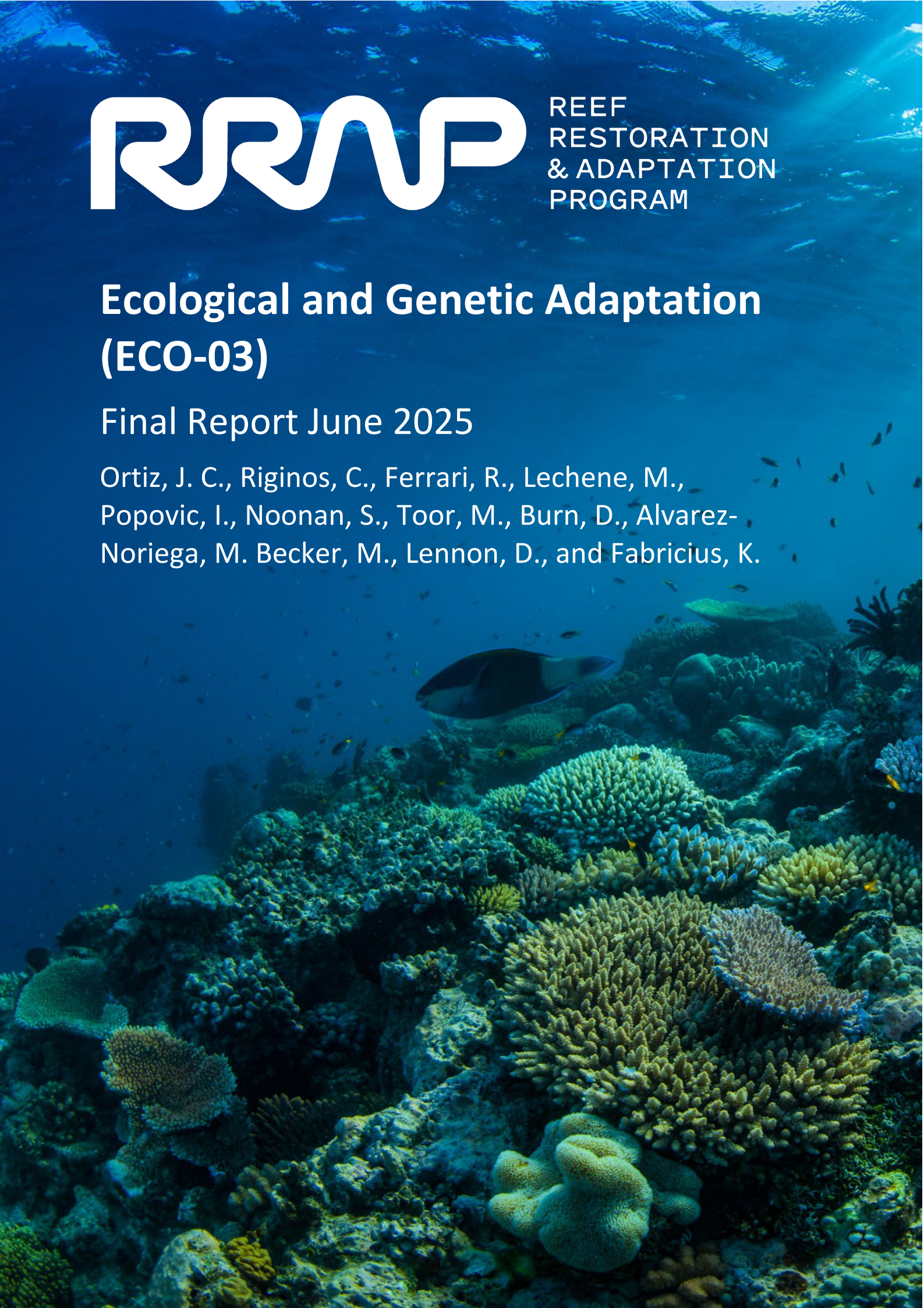


REEF
RESTORATION
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PROGRAM

Ecological and Genetic Adaptation (ECO-03)

Final Report June 2025

Ortiz, J. C., Riginos, C., Ferrari, R., Lechene, M.,
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RRAP Ecological and Genetic Adaptation (ECO-03) Final Report June 2025

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This report summarises work undertaken under *Ecological and Genetic Adaptation (ECO-03)* in accordance with the Reef Restoration and Adaptation Program's *Ecological Intelligence for Reef Restoration (EcoRRAP)* 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.

We specifically acknowledge and thank the following Traditional Owners of sea Country that this report relates to:

Location	Traditional Owner Group
Torres Strait	Masigalgal, Porumalgal, Warraberalgal
Northern GBR	Gunggandji, Ngurruumungu, Dingaal
Central GBR	Manbarra, Bindal
Southern GBR	Woppaburra, Bailai, Gurang, Gooreng Gooreng, Taribelang Bunda

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1 Executive Summary

The Reef Restoration and Adaptation Program (RRAP) is centred around the ambitious goal of developing innovative interventions to mitigate the impact of climate change on the Great Barrier Reef (GBR). Given the biophysical complexity of coral reef ecosystems and the vast size of the GBR, these interventions are inherently innovative, logistically challenging, and designed to harness the natural biophysical properties of coral reef systems in order to scale up their ecological benefits.

Consequently, developing these interventions and evaluating their potential ecological benefits and associated risks requires a thorough understanding of the biological mechanisms targeted by each intervention within an eco-evolutionary context. Likewise, understanding how these interventions may influence coral ecosystems through the intricate web of biological and ecological interactions necessitates a deep knowledge of fundamental biological and ecological processes.

Within this framework, the RRAP Ecological and Genetic Adaptation Project (ECO-03) focused on generating fundamental knowledge in three key areas: coral demographics and their interactions with disturbances, coral thermal performance within and across populations, and the adaptive genetic diversity in coral populations.

The overarching conclusions from the RRAP Ecological and Genetic Adaptation Project (ECO-03) emphasise the complexity of coral reef ecosystems and demonstrate that only by embracing this complexity—and incorporating it into the research, development, and implementation of interventions—can we realistically hope to succeed in mitigating climate change impacts on coral reefs. Within this context, the RRAP EcoRRAP Sub-program has identified three overarching conclusions critical to the continued development of effective interventions to safeguard coral reefs:

- **Coral vital rates (growth, survivorship, and fecundity) are highly variable across species and environmental gradients.** These patterns are complex and will influence the development, spatial and temporal effectiveness, and ecological benefits and risks of various coral reef interventions. The results from this project underscore the importance of understanding how coral vital rates change as individuals grow. Insightful findings reveal that the size of a coral colony at the time of a disturbance or intervention deployment has a significant impact on the ecological consequences of both disturbances and interventions.
- **Thermal performance strategies in corals of the Great Barrier Reef vary among taxa and are highly adapted to local thermal environments.** However, evidence suggests that natural selection has favoured thermal strategies that maximise colony growth rates rather than minimise thermal risk during marine heatwaves.

Thus, thermal performance as a trait is poorly correlated with marine heatwave tolerance and should not be used to identify species or individuals that are particularly resistant to thermal stress. These species-specific strategies can support the development of assisted evolution methods by identifying taxa with plastic thermal performance strategies that enhance the success of assisted gene flow. Conversely, they may limit the effectiveness of such interventions if they target corals with narrow thermal breadth, which are likely to suffer trade-offs when exposed to novel thermal environments.

- **Genetic diversity in the Great Barrier Reef is high and variable across taxa.** Cumulative evidence produced by this project indicates that this genetic diversity provides significant potential for adaptation—both naturally and through assisted evolution. However, complexities must be addressed to realise this potential. One critical challenge identified by this project is the high frequency of cryptic taxa. Overlooking this taxonomic complexity could hinder efforts to mitigate climate change impacts through interventions that foster natural adaptation or involve assisted evolution.

RRAP Ecological and Genetic Adaptation (ECO-03) – focuses on region- and habitat-specific rates, trajectories, and drivers of adaptation. The methodologies employed in this project include coral community observations using cutting-edge photogrammetry imaging (in collaboration with another EcoRRAP Project, Integrated Field-testing and Sub-program Management (ECO-01)), aquarium-based experiments using the world-class National Sea Simulator (SeaSim) system at AIMS, and population genomic surveys. conducted at unprecedented scope and resolution. Key outcomes from this project that are particularly relevant to the overall RRAP goals include:

- **Largest Coral Vital Rates Dataset:**

The RRAP Ecological and Genetic Adaptation Project (ECO-03) has produced the largest published dataset of coral vital rates to date, covering over 20,000 coral colonies across two-three years. This dataset has informed multiple activities across intervention sub-programs and the design of the Pilot Deployments Program (PDP). Critically, the data have been incorporated into one of the ecosystem models (C~scape) developed in the RRAP Modelling and Decision Support (M&DS) Sub-program, making it the only coral reef metacommunity model capable of exploring coral community dynamics at the reef scale (200 metres) across diverse environments in the GBR.

- **Bleaching Dataset from the 2022 Event:**

The RRAP Ecological and Genetic Adaptation Project (ECO-03) has also delivered a unique, spatially detailed dataset on coral bleaching extent and severity during the 2022 mass bleaching event in the Central GBR. This dataset can be used to track survivors of heat stress and assess their future susceptibility to bleaching, thereby improving understanding of thermal tolerance in corals exposed to repeated heat stress. Importantly, the relatively mild nature of the 2022 event allowed for rare insights into the sub-lethal effects of bleaching, such as changes in growth rates and partial mortality—factors that are critical to coral population dynamics and reef function.

- **Deployment Prioritisation Tools:**

The RRAP Ecological and Genetic Adaptation Project (ECO-03) has developed heuristic rules to guide deployment prioritisation for restoration practitioners and the PDP. The program’s methodological advancements have matured into globally leading, state-of-the-art technologies, with published Standard Operating Procedures (SOPs) now routinely applied within EcoRRAP and adopted by the Enhanced Corals and Treatments Sub-Program of RRAP, AIMS, and internationally.

- **Thermal Performance Characterisation Across the GBR:**

The RRAP Ecological and Genetic Adaptation Project (ECO-03) has generated the first comprehensive thermal performance profiles for multiple coral taxa (five species) across the full latitudinal gradient of the GBR. The resulting reef- and taxon-specific temperature-growth curves revealed critical spatial patterns in coral performance that were previously unknown. These findings have been incorporated into the RRAP Modelling and Decision Support (M&DS) Sub-program ecosystem models to assess the impacts of chronic temperature increases on coral population dynamics. Moreover, species-specific insights have informed taxon selection for RRAP’s assisted evolution initiatives and revealed important limitations in current approaches to thermal phenotyping and broodstock selection for selective breeding.

- **Genetic Diversity and Dispersion patterns:**

The RRAP Ecological and Genetic Adaptation Project (ECO-03) has delivered multispecies datasets capturing spatial patterns of genetic diversity and connectivity across the largest extent of coral genetic research to date, spanning from the Capricorn-Bunker group to the Torres Strait. These datasets have informed models of adaptive potential in GBR corals, highlighted critical challenges for the continued development of assisted evolution methods (e.g. the high frequency of cryptic species), and provided essential data for parameterising models that aim to predict the spread of adaptive traits over generations.

2 Background and Justification for the Research

Problem and Rationale

The Reef Restoration and Adaptation Program (RRAP) is a collaboration of Australia’s leading experts to create a suite of innovative and targeted measures to help preserve and restore the coral reefs globally. These interventions must have strong potential for positive impact, be socially and culturally acceptable, ecologically sound, ethical and financially responsible.

Key knowledge gaps were identified in 2020, which needed to be filled to ensure the success and cost-effectiveness of reef restoration interventions. For example, key knowledge gaps existed on coral population dynamics, e.g. in understanding how fast coral colonies and populations can grow and persist under disturbances in different environments, how their growth responds to local temperature conditions, and which reefs or species are best suited where for restoration or will recover on their own. Studies lacked detailed, region-specific background data on coral life histories, let alone on coral performance after repeated or extreme climatic disturbance events. Also, there was previously only one study in Australia investigating the effect of sea temperature on coral growth, and that was run over only three days.

This led to the creation of the RRAP Sub-program **EcoRRAP**. It was designed to advise on the ‘what, where and when’ of interventions, and filling these crucial gaps in ecological knowledge for the GBR. Figure 1 provides a diagram depicting the interconnectedness of EcoRRAP with the other RRAP programs.

Under this umbrella, the RRAP Ecological and Genetic Adaptation Project (ECO-03) investigates how coral communities adapt to environmental change through both ecological and genetic mechanisms, enhancing their climate resilience.



Figure 1: Diagram showing how EcoRRAP (red box) provides input across all RRAP programs.

Research Questions

One core focus of the RRAP Ecological and Genetic Adaptation Project (ECO-03) is to understand how different coral species survive and grow at various temperatures, which helps define their thermal "comfort zones." Through the project’s research on corals from different parts of the Great Barrier Reef, we learn how heat stress affects their growth and how this varies by location and species. These findings are being used to improve models that predict how reefs respond to climate change and guide decisions about which coral populations are best suited for restoration efforts or to provide broodstock. This research also looks at coral

survival and growth on the reef across different environments, and at the impact of heatwaves on these vital rates, helping to inform strategies that boost reef resilience under future warming.

The goal is to ensure that restored reefs can keep providing essential benefits—like habitat for important fish and coastal protection—even in the face of future climate impacts. The findings will also support the development of models that guide where interventions will be most effective, taking into account natural variation and coral communities' ability to adapt.

3 Research Objectives and Key Findings

A current list of project outputs are listed on the [RRAP website](https://gbrrestoration.org): gbrrestoration.org. Key research objectives and findings are detailed below.

Table 1: Key findings of the Project aligned to the overarching and specific research questions for each sub-project.

Objective	Key Findings and/or Outcomes
1. Ecosystems and communities	
<p>1 (a) How does ongoing natural ecological adaptation affect the effectiveness of different RRAP interventions?</p> <p>Phenotypes – term used in genetics for the observable characteristics of an organism.</p>	<p>Understanding how quickly corals can adapt to the various pressures driven by climate change is essential for evaluating the need to develop innovative interventions to mitigate the impacts of climate change on reefs. Furthermore, to determine the effective size required for these interventions to be successful, it is critical to understand how the dynamics of population thermal tolerance may be affected by such actions.</p> <p>However, there is significant uncertainty regarding the mechanisms that influence natural adaptation rates in corals, as well as the characteristics and performance of individuals generated through assisted evolution and deployed on reefs. As part of the RRAP EcoRRAP Sub-program, In collaboration with other RRAP Sub-programs, Enhanced Corals and Treatments (ECT) and Modelling and Decision Support (M&DS), significant progress has been made to inform our understanding of natural coral thermal adaptation rates.</p> <p>While substantial uncertainty remains, we have used information generated by RRAP to model natural adaptation—primarily the selection component—in the model called C~scape (Cresswell et al. 2024, Bozec et al. 2025). Although a module has also been developed in C~scape to account for the emergence of new phenotypes (beyond selection from existing variability), we have not used this module in a meaningful way due to the lack of basic data needed to parameterise it. Additionally, our approach does not track allele frequencies or the polygenic nature of thermal tolerance but instead focuses solely on modelling phenotypic dynamics.</p> <p>Using this approach, we modelled the expected dynamics of thermal tolerance for different coral types in C~scape.</p> <p>We found that population thermal tolerance is likely to increase due to natural selection by between 2.5 and 6 Degree Heating Weeks (DHWs) over the next 75 years, depending on the taxa and climate change scenario considered (Figure 2). Importantly, these rates are emergent properties of the model simulations, resulting from the interaction between selection events and taxa-specific demographic factors.</p>

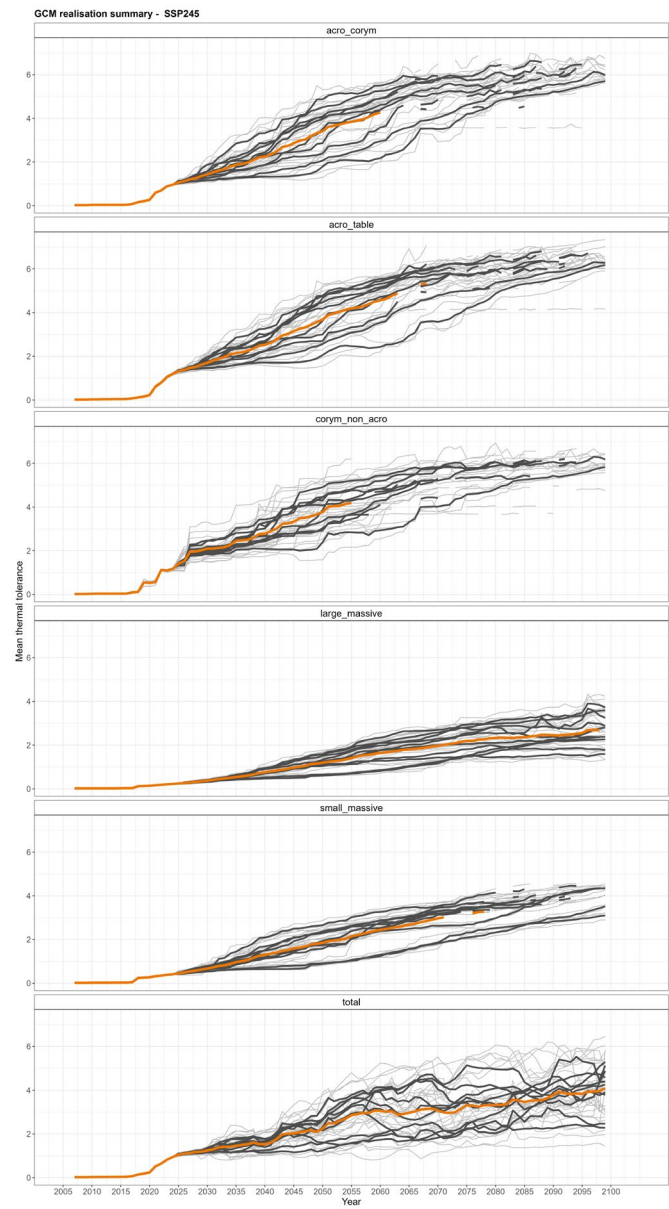


Figure 2: Population thermal tolerance for different coral groups based on C~scape parametrisation of natural selection for SSP 245 based on information from EcoRRAP

In collaboration with M&DS (including the **C~scape** and Adaptive Dynamic Reef Intervention Algorithms (ADRIA) teams), we also modelled how assisted evolution interventions could accelerate the increase in population thermal tolerance under different intervention intensities (Figure 3). These simulations showed that the rate of increase in population thermal tolerance could be significantly enhanced if sufficient thermal enhancement is achieved. These findings have been pivotal in establishing enhancement-level targets for planned assisted evolution research and development.

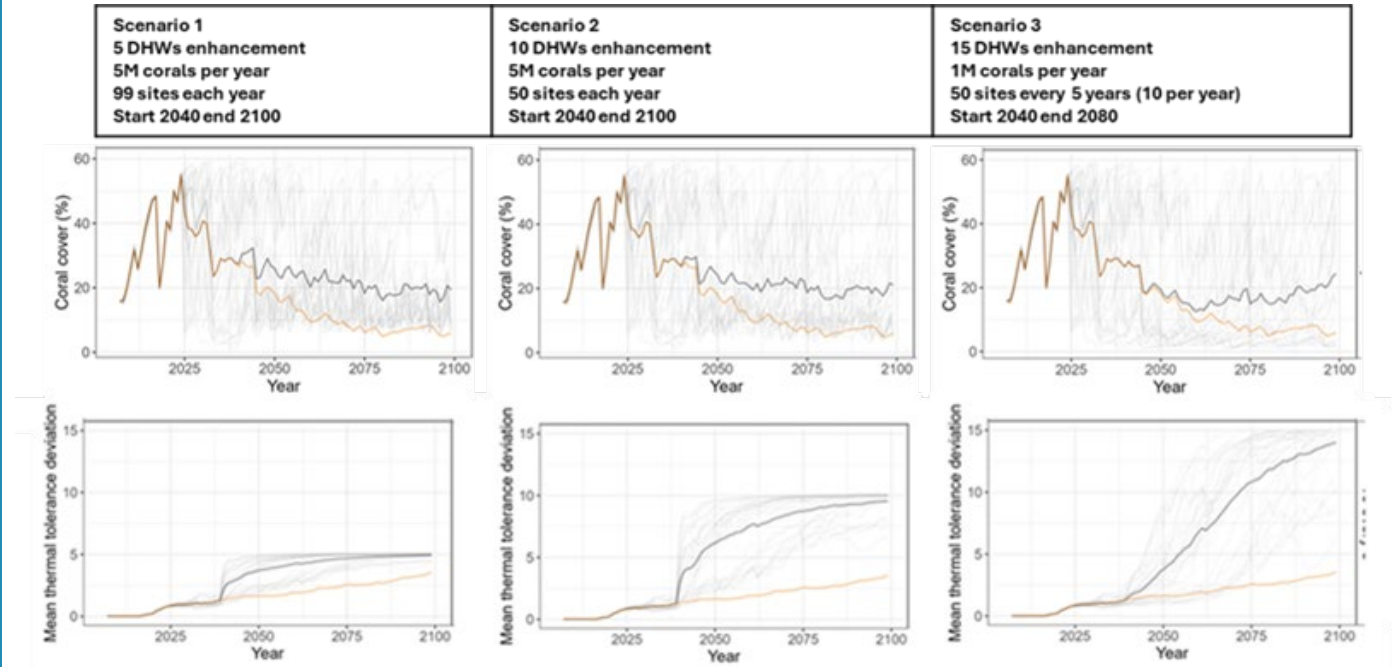


Figure 3: Approximate intervention intensity required to achieve an increase in overall average cluster coral cover from the expected counterfactual average cover of ~4% to ~20% at the end of the century.

Text on top of graphs describes the intervention intensity in each scenario. Intervention intensity is defined as the interaction between the amount of thermal enhancement in the deployed corals (in Degree Heating Weeks (DHW) increase in tolerance relative to the receiving population), the number of corals deployed, the number of sites targeted and the frequency of deployment.

Top panels: Coral cover for the whole cluster average across all sites for the counterfactual (orange line) and the intervened scenario (black line). Grey lines represent the average coral cover for the whole cluster in each intervened simulation (different climate models).

Bottom panels: black lines represent the spread of thermal enhancement from deployed corals over time shown as average coral thermal tolerance (DHWs increase from the initial distribution of thermal tolerance) in comparison with the increase expected to

Objective	Key Findings and/or Outcomes
	naturally occur due to natural adaptation in the counterfactual runs (orange lines). Grey lines represent average thermal tolerance for the cluster in each simulated climate future.
1 (b) What is the optimal coral community composition to optimise recovery, biodiversity and ecosystem functions?	<p>Community composition and structure includes biodiversity, relative abundance and functional structure. These can influence the trajectory of an ecosystem and its likelihood and speed to recover after acute disturbances. Diverse and well-structured communities can enhance resilience, speed up recovery post-disturbances and support a broad range of ecosystem functions. For instance, a reef dominated by fast growing corals (e.g. <i>Acropora spp.</i>) that also have higher likelihood of mortality from heat-stress is expected to have a larger decrease in coral cover after massive bleaching compared to a reef dominated by more heat tolerant, but slower growing, corals (e.g. massive <i>Porites spp.</i>). However, a reef dominated by slow growing corals will take longer to return to the pre-disturbance coral cover.</p> <p>Communities with high diversity have higher capacity to adapt to changing conditions, making them more resilient to disturbance and increasing their recovery probabilities and speed post-disturbance. Different taxa within a community are likely to use resources and respond to disturbance in different ways, in turn this enhances ecosystem function and resource utilisation efficiency, leading to higher productivity and stability (McWilliam, Chase, and Hoogenboom 2018; Clements and Hay 2021). A diverse and well-balanced community is likely more functionally redundant than a less diverse or less balanced (mostly dominated by one taxon) community. Functional redundancy increases the likelihood of a community to maintain stability and resistance to disturbances. In short, a well-balanced and diverse community is essential to optimise reef recovery, maintain biodiversity and provide a myriad of ecosystem functions. We used large-area-imaging and artificial intelligence (AI) to map large areas of reef (~1200 - 5000 m²) at each EcoRRAP reef, to measure community composition and structure. We found that reefs in the GBR and the Torres Strait (TS) have diverse, but not always well-balanced, community composition and structure. Community composition and structure varied from north to south, as well as inshore to offshore (Figure 4). Community composition and structure also varied across habitats and within reefs (Figure 5).</p>

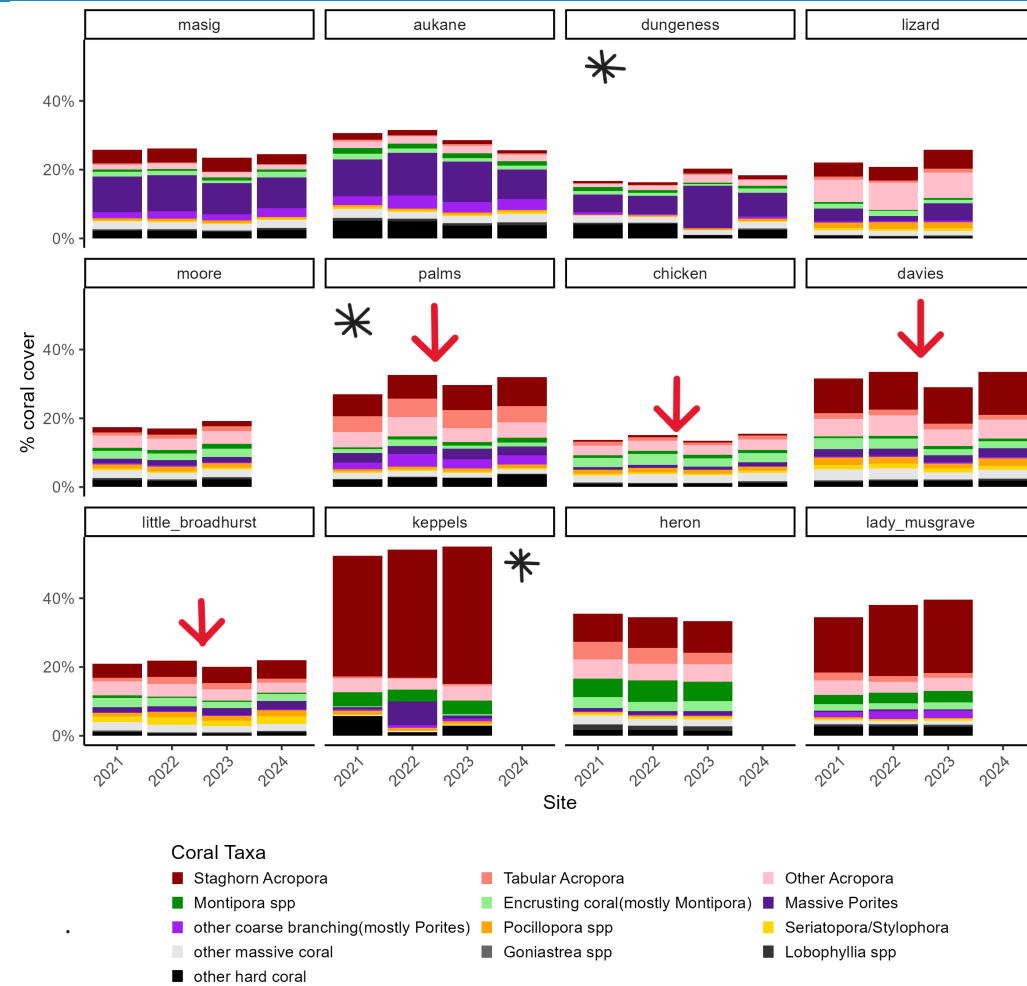


Figure 4: Community composition and structure shown as relative abundance (as percent cover) of the 13 dominant coral morphotaxa on EcoRRAP reefs between 2021 and 2024. Reefs are ordered from north to south (TS: Masig, Aukane, *Dungeness; North GBR: Lizard and Moore; Central GBR: *Palms, Chicken, Davies and Little Broadhurst; South GBR: *Keppels, Heron, Lady Musgrave). Asterisks denote turbid/inshore reefs, and red arrows show the 2022 mass bleaching event. Porites spp. and Lobophyllia spp. dominate the reefs in the Torres Strait, while Acropora spp. dominate the reefs in the GBR. Staghorn Acropora spp. monocultures are common on reefs around the Keppel Islands, and Montipora spp. are more common in the southern GBR.

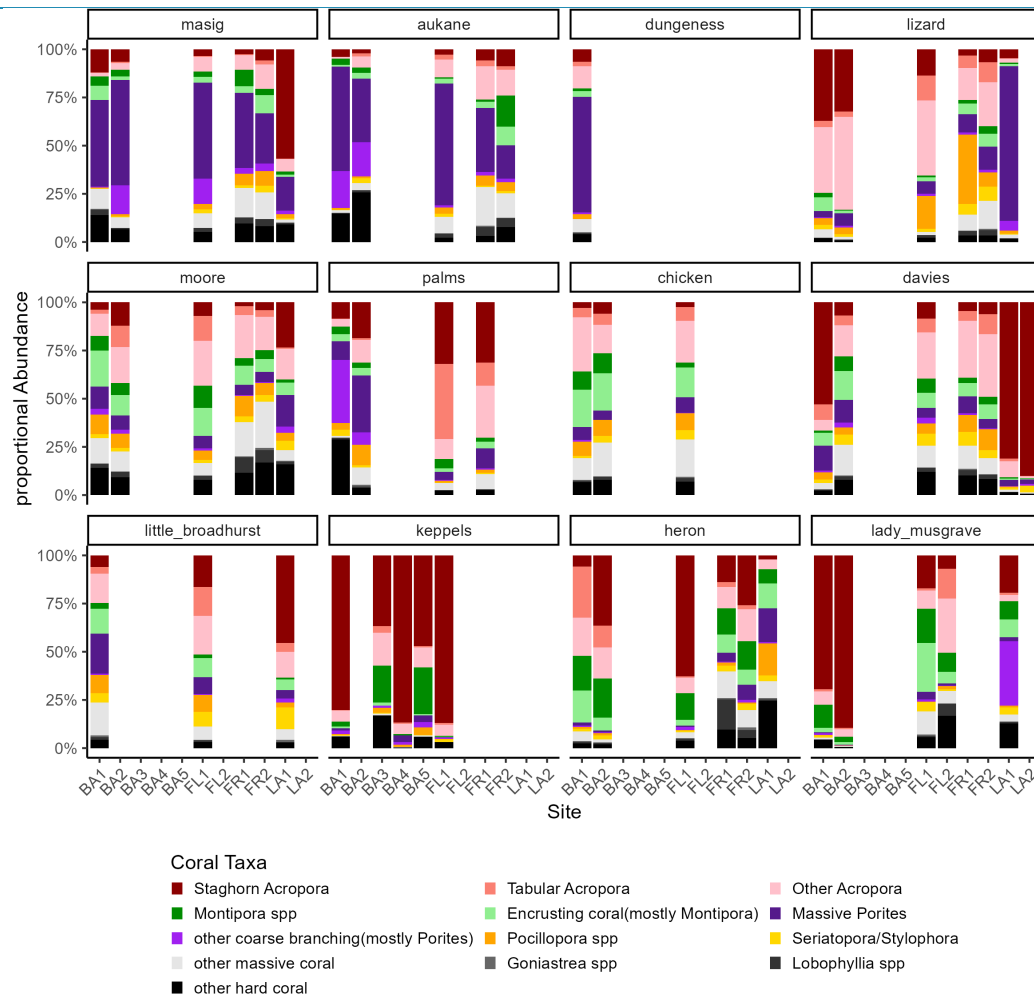


Figure 5: Community composition and structure shown as relative abundance (as percent cover) of the 13 dominant coral morphotaxa on EcoRRAP habitats and within reefs in 2023. Reefs are ordered from north to south (TS: Masig, Aukane, *Dungeness; North GBR: Lizard and Moore; Central GBR: *Palms, Chicken, Davies and Little Broadhurst; South GBR: *Keppels, Heron, Lady Musgrave). The Asterisk denotes inshore reefs and x-axis acronyms reflect different habitats within a reef (BA = sheltered slope, FL = flank or moderately exposed slope, FR = front or exposed slope, LA = lagoon). North to south patterns seen in Figure 5 remain, but community composition does vary across habitats and within reefs, with lagoons standing out for being the most different, and while there are some exceptions (e.g. Moore reef) flanks being the worst-balanced communities.

Objective	Key Findings and/or Outcomes
<p>1 (c) How variable are vital rates of key species across environments, and how do they contribute to reef recovery?</p>	<p>Understanding variability in vital rates (i.e. growth, survival, and recruitment) of corals is fundamental for understanding their relative contributions to population maintenance and recovery following disturbance. We quantified size-dependent growth and survival from nine dominant morpho-taxa across 88 sites spanning the Great Barrier Reef (GBR) and Torres Strait (TS), alongside complementary surveys of coral recruitment (using recruitment tiles).</p> <p>Growth and survival varied markedly among taxa and were strongly size-dependent: across all taxa, small (~5 cm diameter) colonies exhibited ~85% annual survival compared to ~93% for medium (10–20 cm) and ~96% for large (>80 cm) colonies. Smaller colonies showed faster relative growth compared to larger colonies. Taxa with slower growth (i.e. massive <i>Porites</i>, <i>Goniastrea</i>, <i>Platygyra</i>) had higher survival than fast-growing branching taxa (e.g. tabular and corymbose <i>Acropora</i>).</p> <p>While growth and survival were remarkably consistent across environmental gradients for most taxa, two of the nine taxa investigated (<i>Acropora</i> and <i>Pocillopora</i>) were affected by turbidity, temperature, or current velocity (Aston et al. in review).</p> <p>In contrast, recruitment was driven primarily by environmental gradients. Current velocity, sedimentation, and depth negatively affected recruitment, with offshore, clear-water reefs exhibiting three-fold higher densities than inshore turbid reefs, highlighting the role of water quality and current flow as bottlenecks to early life-stage success (Drake et al. 2025).</p>
<p>1 (d) Are there trade-offs between community resistance and ecosystem functions, and how can we “set ecologically relevant restoration targets</p>	<p>Taxa with slower growth (i.e. massive <i>Porites</i>, <i>Goniastrea</i>, <i>Platygyra</i>) had higher survival (97–99%) than fast-growing branching taxa (e.g. 89-92% annual survival for tabular and corymbose <i>Acropora</i>), consistent with well-established life-history trade-offs (Aston et al. in review). Thus, corals that provide the reef with higher resistance are likely the slowest growers.</p> <p>EcoRRAP vital rate research findings can be brought together to infer the relative contributions of vital rates to population maintenance or recovery potential at regional and local scales in the GBR and TS (Figure 6, Burn et al. in prep).</p> <p>Understanding which vital rates are critical or limiting in population maintenance (and recovery potential), and how this differs spatially, is critical to inform which coral restoration techniques may be best implemented to assist recovery where is it most needed.</p> <p>To do this, we predicted size-based growth and survival, and recruitment of <i>Acropora</i> (a taxon important for recovery) across latitudinal regions, shelf positions, and habitats within reefs. For <i>Acropora</i>, recruitment was notably higher offshore, particularly on reef backs and flanks, suggesting these low-flow habitats may serve as important sources of replenishment (Figure 6).</p> <p>In contrast, inshore reefs, and especially reef fronts, appear recruitment limited. However, there was evidence that <i>Acropora</i> exhibited higher survival inshore versus offshore (odds ratio = 0.58, 95% HPD: 0.40–0.79), and on reef backs versus fronts (odds ratio = 1.49, 95% HPD: 1.04–2.01).</p> <p>Colony growth was also higher inshore versus offshore across all size classes, but didn’t differ among habitats (Figure 6).</p>

Objective

Key Findings and/or Outcomes

Higher growth and survival of *Acropora* inshore suggests growth and persistence of remnant colonies may be important for recovery in these environments, compensating for low recruitment.

There was strong evidence that *Acropora* grew quickest in the TS compared with the central (Torres Strait – Central GBR: estimate = 0.21, 95% HPD: 0.12–0.31) and southern (Torres Strait – Southern GBR: estimate = 0.21, 95% HPD: 0.11–0.32) regions for both inshore and offshore reefs, averaged across colony sizes and habitats (Figure 6). There was also evidence that growth was higher in the Northern GBR compared with the Southern GBR (Northern GBR – Southern GBR: estimate = 0.11, 95% HPD: 0.01–0.22).

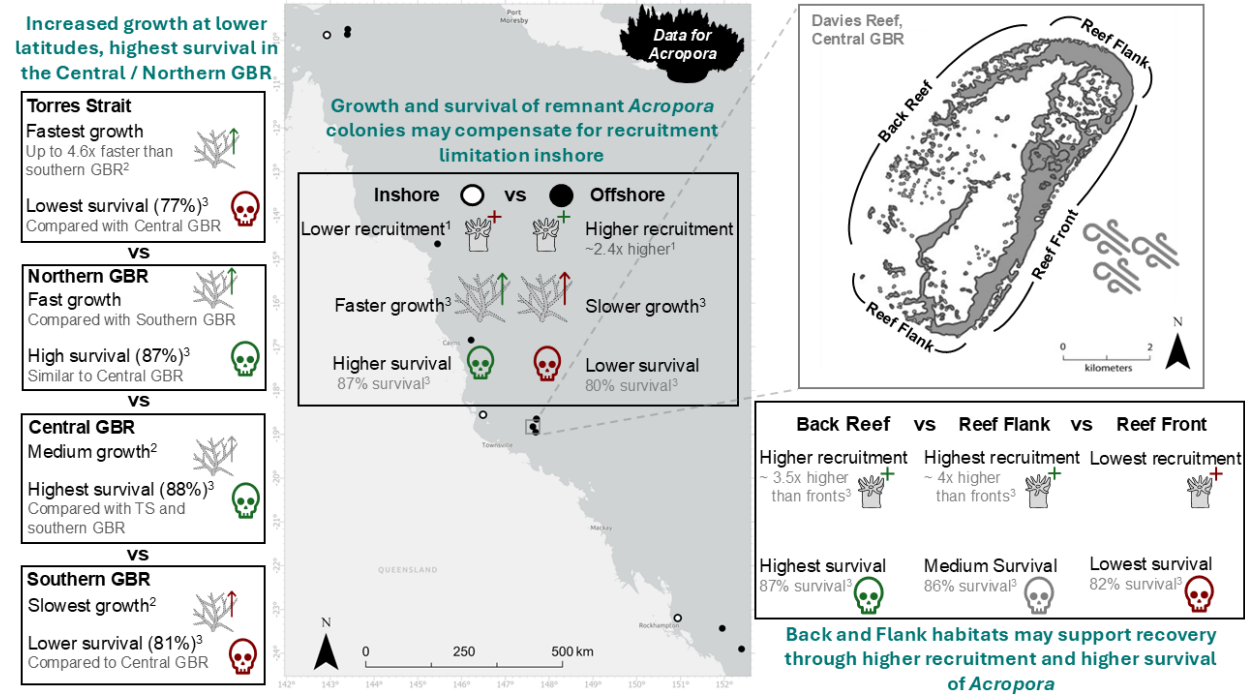


Figure 6: Summary of growth, survival, and recruitment rates of *Acropora* compared across (a) regions, (b) shelf positions, and (c) habitats, based on extensive in situ data collected from 88 sites at 12 reefs spanning the GBR and Torres Strait. Reefs are displayed on the map inset of Queensland (centre) by circles (white = inshore, black = offshore), and habitats are labelled on the map inset of Davies Reef, Central GBR (right). Red icons indicate a negative effect, green icons indicate a positive effect, and grey icons indicate no difference in mechanisms of recovery (growth, survival, recruitment) compared with other regions, shelf positions, or habitats. Data is taken from 1 (Aston et al. in review), 2 (Drake et al. 2025), and 3 (unpublished analysis- Burn et al. in prep). Survival values represent posterior mean survival probabilities. Associated 95% Highest Posterior Density (HPD) intervals are as follows—Regions:

Objective	Key Findings and/or Outcomes
	<p><i>Central GBR (0.833–0.912), Northern GBR (0.817–0.923), Southern GBR (0.758–0.862), Torres Strait (0.702–0.833); Habitats: Back (0.834–0.900), Flank (0.790–0.913), Front (0.762–0.862); Shelf: Offshore (0.754–0.840), Inshore (0.825–0.912). HPD intervals indicate the range within which the true value lies with 95% probability, given the data.</i></p>
<p>1 (e) What are key predictors for reef recovery potential across different reef environments?</p>	<p>Research findings suggest different reef environments likely support recovery of <i>Acropora</i> populations through different mechanisms—broadly; offshore reefs via recruitment, whilst the survival and regrowth of existing colonies may be more important on inshore reefs, with fastest growth in the TS. More specifically, back reefs may provide conditions conducive for recovery of <i>Acropora</i>, with higher recruitment and survival compared with reef fronts (Figure 7).</p> <p>These insights offer practical implications for restoration, whereby interventions may be most effective when tailored to complement the dominant recovery process in each environment. However, it should be noted that whilst the extensive empirical data presented here provide a new benchmark for understanding coral population dynamics, our findings suggest that recovery will heavily depend on post-disturbance size structure, subsequent recruitment dynamics, and species composition and structure within these taxonomic groups (Figure 7).</p> <p>During the 2022 bleaching event on the GBR, EcoRRAP central sites were monitored to understand how bleaching severity varies across space and taxa, and predict changes in community composition and structure due to climate change impacts. Using photogrammetry, we measured colony size and scored bleaching severity of > 5000 colonies of 13 taxa across 26 sites (> 7400 m² of reef). We quantified the relationship between bleaching severity and key biological and environmental factors: colony size, taxonomic identity, degree- heating weeks (DHWs), water velocity, various measures of reef three-dimensional (3D) structural complexity, depth, and distance to coast.</p> <p>Our results show that bleaching probability decreased with increasing colony size for most taxa, contradicting the current understanding of size- dependent bleaching. Counter to conventional thinking, tabular <i>Acropora</i> spp. presented very low levels of bleaching in 2022 despite being among the most severely bleached taxa during the bleaching event in 1998, suggesting possible adaptation in the last two decades. Our results show a high level of idiosyncrasy in environmental gradients of bleaching severity. For instance, the effect of depth on was taxon- dependent and the effect of wave velocity differed between inshore and offshore reefs (Alvarez-Noriega et al. 2025).</p> <p>We also compared the survival and growth of corals between the year before bleaching (2021 – 2022), and during bleaching (2022 – 2023) and found that both coral survival and growth decreased in the latter year. Colony size and bleaching severity were the two major predictors of bleaching legacy effect, with larger colonies showing more capacity to survive and grow during heat</p>

stress compared to smaller colonies. Environmental effects were taxa dependent and only secondary to the effect of size and bleaching severity (Lechene et al. in review).

Our results challenge prevailing paradigms around the role of colony size and environment in regulating bleaching susceptibility, suggesting that refugia are not universal but instead depend on specific environment- taxonomic combinations and taxon- specific colony sizes (Alvarez-Noriega et al. 2025).

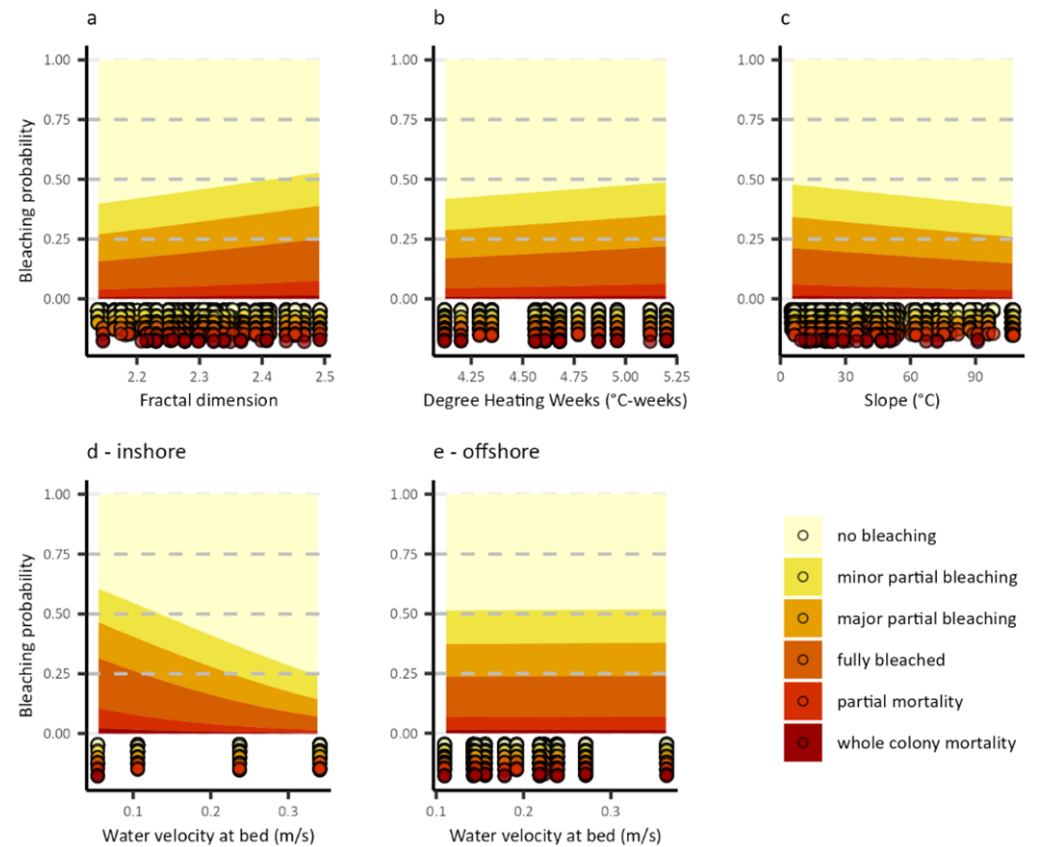


Figure 7: Fitted model predictions of the probability of a colony presenting different levels of bleaching severity as a function of fractal dimension (a) degree heating weeks (DHWs) (b) slope of the reef (c) and water velocity at bed in inshore (d) and offshore reefs (e) in shallow sites. The coloured surfaces indicate the bleaching score predicted by the Cumulative Link Mixed Model (CLMM) model for the given variables, and the points underneath the plot show the raw data ($n = 3559$). Each colour represents a bleaching score, reflecting different levels of bleaching severity. Reproduced from Alvarez-Noriega et al. 2025.

Objective	Key Findings and/or Outcomes
<p>1 (f) What is the relationship between reef recovery and reef 3D complexity, biodiversity, reef accretion rates?</p>	<p>Coral recovery will vary across environments, a key difference across reef types is the maximum coral cover that a community can sustain, hereafter referred to as its “upper limit”. The EcoRRAP Project Ecological and Genetic Adaptation (ECO-03) used 32 years of data from the GBR to quantify the relationship between estimated upper limits and key environmental factors (hard substrate, temperature and water clarity) on the GBR to inform restoration goals. For instance, what is the coral cover at which a reef has reached its upper limit?</p> <p>We found varying upper limits across the GBR, with a median of 33% coral cover and only 17% of the estimated upper limits exceeded 50% coral cover. Upper limits increased with hard substrate availability, which is the dominant contributor to large scale 3D structural complexity on coral reefs. Upper limits increased towards the southern reefs, decreased with temperature and, to a lesser extent, with water clarity (Figure 8) (Alvarez-Noriega et al. 2024).</p> <div data-bbox="638 603 1585 1197"> <p>Figure 8 consists of two panels. Panel a, titled 'a- Among reef variation', is a map of the Great Barrier Reef coastline from 10°S to 25°S and 144°E to 153°E. It shows the estimated upper limit values for each reef, represented by colored circles. The color of the circles indicates the upper limit estimate, ranging from high (yellow) to low (black) as shown in the legend. The size of the circles indicates the number of sites per reef, with sizes corresponding to 1, 2, 3, and 4 sites. Panel b, titled 'b - Within reef variation', is a box plot showing the estimated upper limit for sites within reefs, categorized by wave exposure: Sheltered, Intermediate, and Exposed. The y-axis represents the upper limit percentage, ranging from 0 to 80. The plot shows individual data points overlaid on the box plots, indicating the distribution of upper limits within each exposure zone.</p> </div> <p><i>Figure 8: Spatial variation of upper limits among and within reefs. Panel a: The estimated upper limit values across the Great Barrier Reef averaged by reef. The colour of the points shows the upper limit estimates from high (yellow) to low (black) for each reef (averaged across all sites within reef). The size of the points shows the number of sites that had upper limits and were averaged for each reef (with a maximum of four sites per reef, one for each wave exposure zone). Panel b: The estimated upper limit for sites within reefs (sheltered or back reefs, intermediate or flank reefs, and exposed or front reefs). The points show upper</i></p>

Objective	Key Findings and/or Outcomes
	<p><i>limit values, and the boxplots show their distribution (horizontal bar shows the median, the box shows the upper and lower quartiles, and whiskers show the range of values). Reproduced from Alvarez-Noriega et al. 2024.</i></p> <p>The upper limits estimated in this study are much lower than what is commonly assumed when modelling ecological dynamics, most likely resulting in expected recovery rates being inappropriately optimistic. This means it is critical to use before-after-control-impact study designs to evaluate the impact of restoration interventions if the upper limits are not known for a specific reef. Although hard substrate ultimately restricted upper limits, there are mechanisms constraining the proportion of hard substrate that is covered by hard corals. The negative relationship between temperature and upper limits may be related to changes in community composition.</p> <p>The quantitative relationships between the upper limits of coral cover and environmental variables will provide critical information to prioritise sites for management interventions. For example, our findings highlight that sites with similar coral cover may be in very different states if we account for hard substrate availability. Recovery rates are affected by the assumptions made on the upper limit of communities because, as communities approach their upper limit, competition is expected to intensify, slowing down community growth. For example, it would take a reef dominated by slow growing corals approximately seven more years to increase their coral cover from 1 – 30% if the upper limit of that reef was 33%, compared to 70%.</p> <p>For a reef dominated by fast growing corals, the same difference is three years slower (Figure 9). Thus, when deploying a restoration intervention on a reef with an upper limit of 33%, it would take 4.3 years to detect an increase of 5% coral cover (assuming perfect monitoring), while on a neighbouring reef with an upper limit of 70%, the same change could be detected within 3 years (Alvarez-Noriega et al. 2024).</p>

Objective

Key Findings and/or Outcomes

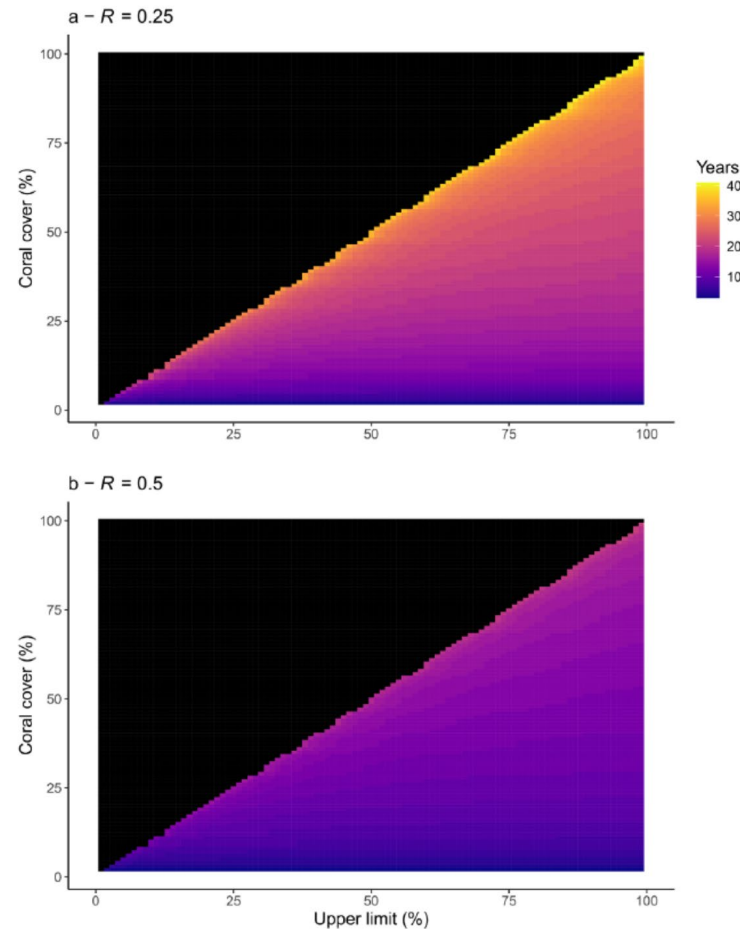


Figure 9: Differences in coral cover recovery trajectories across hypothetical communities with different upper limits.

The panels show the expected number of years (denoted by colour gradient) that it takes a community to grow from 1% coral cover to a range of coral covers (in the y- axis), given an upper limit (in the x- axis) when the maximum rate of growth, R , is 0.25 (panel a), typical for a reef dominated by slow-growing massive corals, and 0.5 (panel b), typical for a reef dominated by fast growing *Acropora* spp. corals. Areas in black indicate that target coral cover > upper limit and is therefore never reached. Reproduced from Alvarez-Noriega et al. 2024.

Objective	Key Findings and/or Outcomes
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2. Reef- and species-specific thermal niches of GBR corals

2 (a) How does chronic and acute temperature patterns affect coral colony growth?

Growth Temperature Curve (GTC) – the curve generated from our coral aquarium growth studies measuring growth at different seawater temperatures.

This project explored the impact of temperature on coral colony growth through multiple approaches. A large, multi-year temperature-growth experiment conducted at the AIMS National Sea Simulator (SeaSim) over three years characterised how temperature affects coral growth, both through chronic exposure (year-round increases in sea surface temperature driven by climate change) and the legacy effects of acute thermal stress (both hot and cold) across multiple coral species.

We found that temperature has a significant and differential effect on colony growth for all studied coral taxa. Coral growth is slow at low temperatures, increases gradually with rising temperature, reaches a thermal optimum where growth is maximised, and then quickly declines as temperatures continue to rise. Notably, the rate of decline after the optimum is steeper than the rate of growth before the optimum for all coral types (Figure 10).

While this general pattern was consistent, there were clear differences in both the thermal optimum and the slopes of pre-optimum increase and post-optimum decline among coral species as shown in Figure 10.

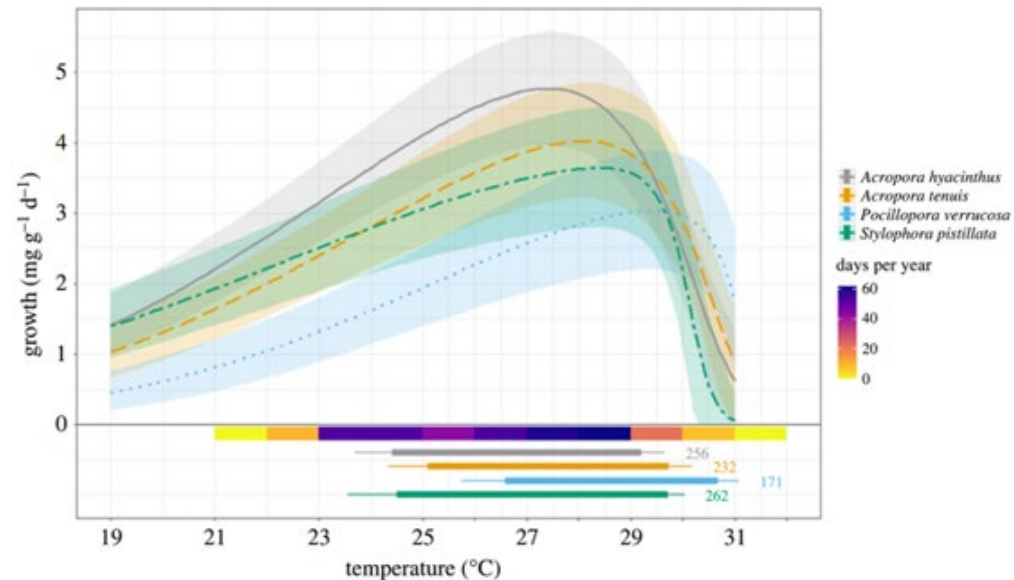
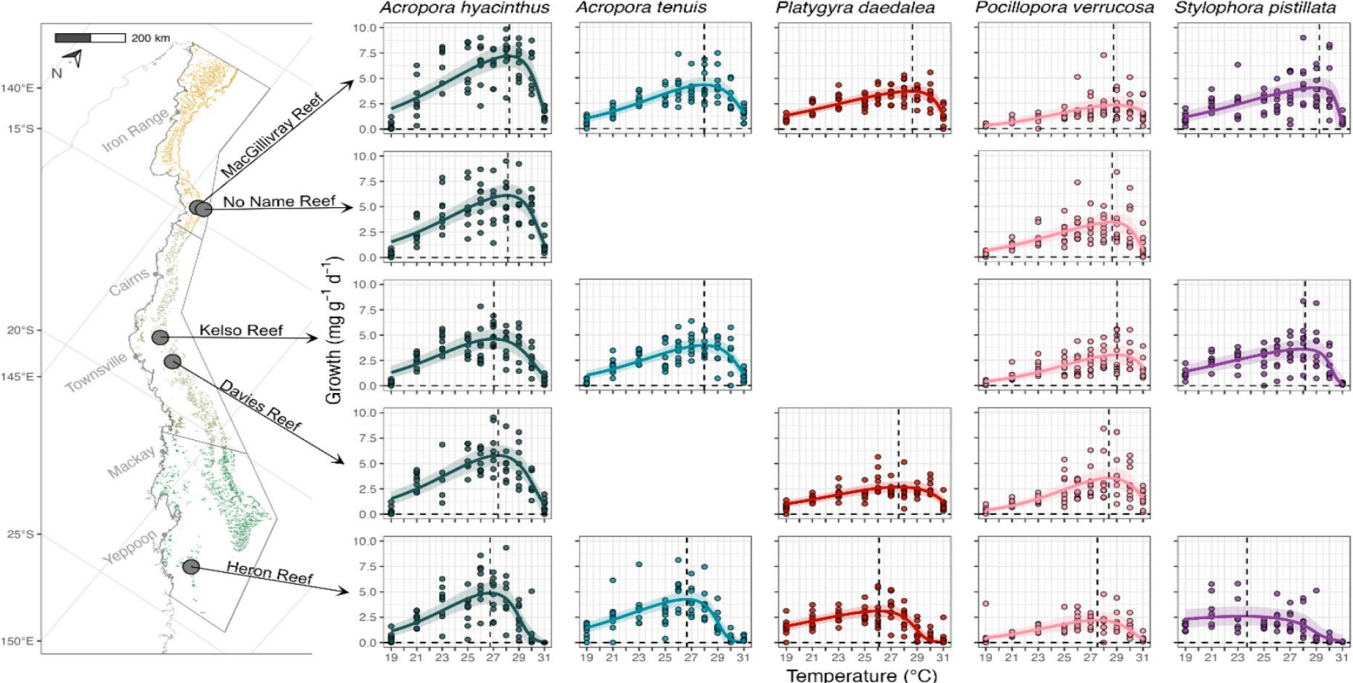


Figure 10: Growth temperature curves for four coral taxa from Kelso Reef in the central GBR. Colour bars in the bottom of the plot show number of days per year each taxa grows at above 80% of its maximum growth (Alvarez Noriega et al. 2023).

Objective	Key Findings and/or Outcomes
	<p>These interspecific differences, combined with consistent thermal performance strategies across individuals of the same coral type within a given reef, suggest that corals in the GBR have adapted to their local thermal environments. These adaptations likely optimise colony growth across seasonal temperature fluctuations.</p> <p>Consequently, chronic temperature increases under climate change are expected to affect coral growth rates in different ways—both in magnitude and direction—depending on species and region. Moreover, as the frequency and intensity of acute thermal disturbances are predicted to increase, changes in growth rate may become critical for determining population recovery rates between disturbance events.</p> <p>As part of the same multi-year experiment, we also examined the effects of acute thermal stress—both hot and cold—on the subsequent growth of surviving coral colonies (Figure 11).</p>

Objective	Key Findings and/or Outcomes
	<p>Surprisingly, <i>Platygyra daedalea</i>, a boulder shaped coral species previously identified as the most heat-tolerant in terms of mortality among the five species studied, exhibited some of the largest reductions in growth after both hot and cold stress.</p> <p>These findings are critical for understanding how coral populations may recover following future marine heatwaves. They also have important implications for restoration strategies, such as assisted gene flow. Corals that are collected and moved from warmer (e.g. northern GBR) to cooler southern sections of the GBR in order to enhance thermal tolerance in recipient coral populations may suffer reduced performance due to cold stress during winter.</p>
<p>2 (b) How do Growth Temperature Curves (GTCs) vary between taxa and across the GBR?</p>	<p>Clear and distinctive temperature-growth relationships were observed among taxa across the broad temperature gradient of the Great Barrier Reef (Figure 12). While all coral taxa exhibited a reduction in thermal optimum from north to south, the shape of the temperature-growth curves varied between taxa. These differences suggest that the impact of chronic temperature increases will differ among taxa across the GBR and are likely to influence coral community composition over time.</p>  <p>Figure 12: Growth as a function of temperature for five coral taxa across the GBR latitudinal gradient (Crossman et al. 2025 under review).</p>

Objective

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In collaboration with the C~scape team within RRAP M&DS Sub-program, the temperature-growth relationships for each taxon have been incorporated into C~scape—an ecosystem model focused on within-reef coral community dynamics developed for RRAP. Preliminary explorations of the impact of chronic temperature increases on coral community composition suggest that, under certain climate change scenarios and in specific GBR regions, corals such as *Pocillopora verrucosa* may increase in dominance by mid-century (Figure 13). Incorporating this modelling capability is essential for accurately evaluating the potential impacts of assisted evolution methods on the GBR.

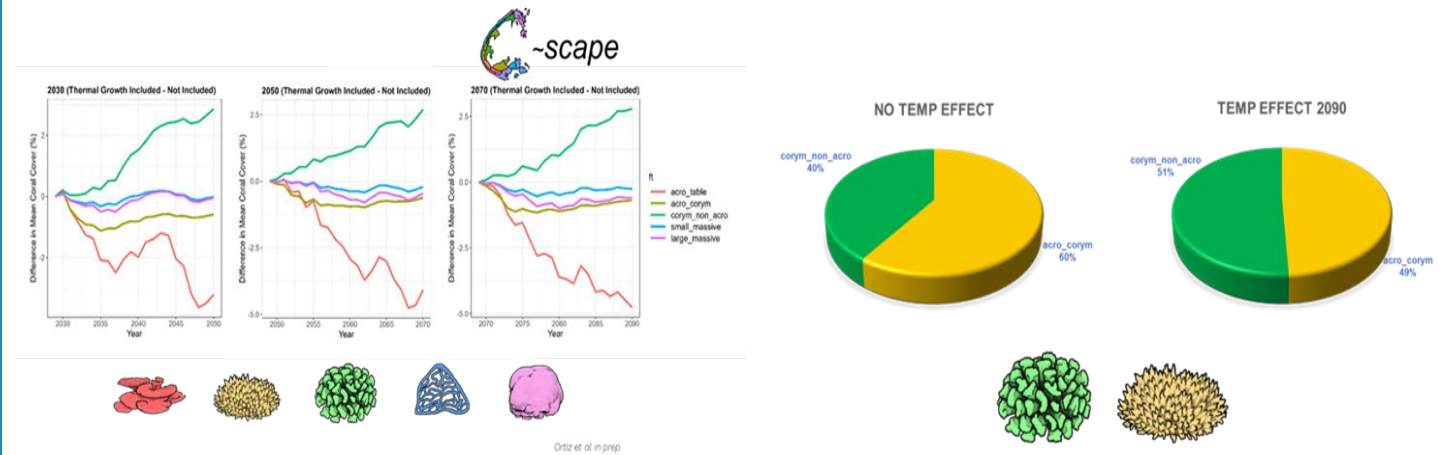
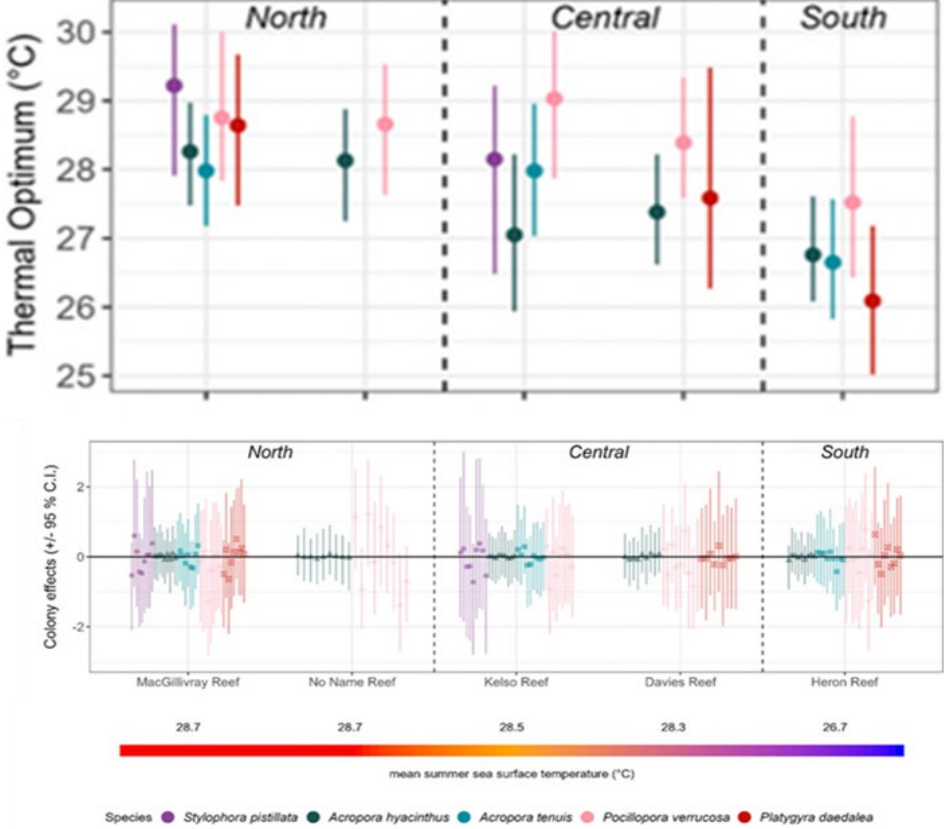


Figure 13: Difference in predicted coral cover for each coral type when comparing scenarios with and without incorporating temperature-growth relationships for the Moore Reef cluster (left). A shift in dominance from corymbose Acroporids to corymbose non-Acporids is projected by 2090, due to the chronic impacts of increased temperature.

Objective	Key Findings and/or Outcomes
<p>2 (c) What is the relationship between local historic temperature patterns and local Growth Temperature Curves (GTCs)?</p> <p>Thermal optima – the optimum temperature for maximum growth rate of a species of coral. This rate varies from species to species.</p>	<p>Growth performance curves—and particularly thermal optima—showed a strong positive relationship with local (reef-level) historic summer temperatures (Figure 14, top panel). This pattern was further supported by the high consistency in thermal optima among individual colonies of the same taxon from a given reef (Figure 14, bottom panel). Together, these results provide strong evidence of local thermal adaptation across all coral taxa studied.</p>  <p>Figure 14 consists of two panels. The top panel is a dot plot with error bars showing Thermal Optimum (°C) for five coral taxa across three reefs: North, Central, and South. The y-axis ranges from 25 to 30. The taxa are Stylophora pistillata (purple), Acropora hyacinthus (dark teal), Acropora tenuis (light teal), Pocillopora verrucosa (pink), and Platygyra daedalea (red). The bottom panel is a dot plot showing Colony effects (+/- 95% C.I.) for the same taxa and reefs. The y-axis ranges from -2 to 2. A color scale at the bottom indicates mean summer sea surface temperature (°C) from 28.7 to 26.7. The reefs are MacGillivray Reef (28.7), No Name Reef (28.7), Kelso Reef (28.5), Davies Reef (28.3), and Heron Reef (26.7). The legend identifies the species: Stylophora pistillata (purple), Acropora hyacinthus (dark teal), Acropora tenuis (light teal), Pocillopora verrucosa (pink), and Platygyra daedalea (red).</p> <p>Figure 14: Relationship between historic thermal regime and thermal optimum for five coral taxa in the GBR (Crossman et al. 2025 under review) (top); and within taxa variability in thermal optimum in each reef (individual colony departure from population level thermal optimum) (bottom).</p>

Objective	Key Findings and/or Outcomes
	<p>Notably, the surprisingly limited variability in thermal optima within species at each thermal environment may suggest a constrained adaptive potential for this trait. While overall variability was low across all taxa, it was significantly higher in Pocilloporids compared to Acroporids. This, coupled with the observation that <i>Pocillopora verrucosa</i> consistently exhibited the highest—or second highest—thermal optimum across all reefs, supports the idea that this species may be a promising candidate for assisted evolution initiatives.</p>
<p>2 (d) What elements of historical thermal exposure best explain local thermal optima (T_{opt}) and thermal maxima for coral colonies and populations?</p> <p>Thermal maxima – the maximum temperature at which a species of coral still manages to grow. Above this temperature, growth rapidly declines and can actually stop.</p>	<p>While thermal optimum represents the temperature at which performance is maximised (in this case, growth), thermal critical maximum is a metric derived from thermal performance curves that indicates the temperature at which performance collapses — here defined as 20% of maximum growth. This metric is commonly used as a proxy for thermal tolerance.</p> <p>For GBR corals, thermal optimum (Figure 15, top panel) appears to be more closely aligned with local summer temperatures than the thermal critical maximum (Figure 15, bottom panel).</p> <p>While the far southern reefs exhibited a lower critical maximum temperature, reefs across the remainder of the thermal gradient showed relatively similar values.</p> <p>These patterns suggest that, from an evolutionary standpoint, a thermal optimum finely tuned to the local thermal environment may have a greater influence on fitness than a finely tuned critical maximum.</p> <p>Interestingly, variability in critical maximum temperature was greater among taxa within a reef than among reefs themselves. This implies that other taxon-specific traits may influence which thermal strategy is optimal within a given environment.</p>

Objective

Key Findings and/or Outcomes

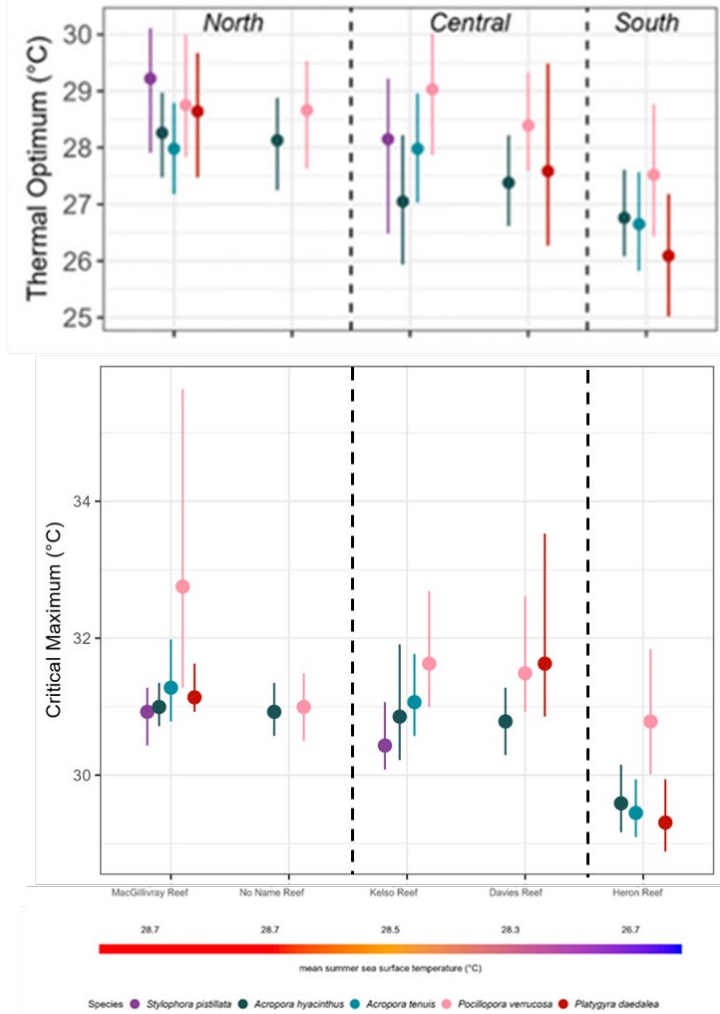


Figure 15: Relationship between local summer temperature and thermal optimum (top panel) and thermal critical maximum (bottom panel) for the five coral taxa.

Objective	Key Findings and/or Outcomes
2 (e) How does coral colony growth shift across populations and communities following bleaching in different regions?	<p>Understanding the impacts of bleaching on coral growth across different populations and communities requires both <i>ex-situ</i> experimental approaches and <i>in-situ</i> observational methods. Experimental approaches allow for the exploration of a wide range of thermal disturbance intensities under controlled conditions, with the added advantage of being planned. In contrast, empirical exploration of the legacy effects of marine heatwaves—while offering greater ecological realism—is limited by the unpredictable nature of such events in both occurrence and intensity. To address this, the RRAP EcoRRAP Sub-program employs both approaches to investigate the long-term effects of marine heatwaves on coral growth.</p> <p>Experimental Exploration of Acute Thermal Disturbances on Coral Growth</p> <p>As described in the response to Question 2a, we monitored the growth of coral fragments that had been exposed to one month of acute thermal stress—both hot (marine heatwave-like) and cold—at two reef locations with contrasting thermal histories: MacGillivray Reef in the northern GBR and Heron Island in the southern GBR.</p> <p>Results showed significant reductions in growth across all coral taxa for at least one month following both cold and hot disturbances, with decreases ranging from 10% to 110%. (Figure 16). Notably, corals from the warmer northern reef exhibited</p>

significantly greater growth reductions after cold stress, whereas corals from the cooler southern reef showed greater reductions following heat stress.

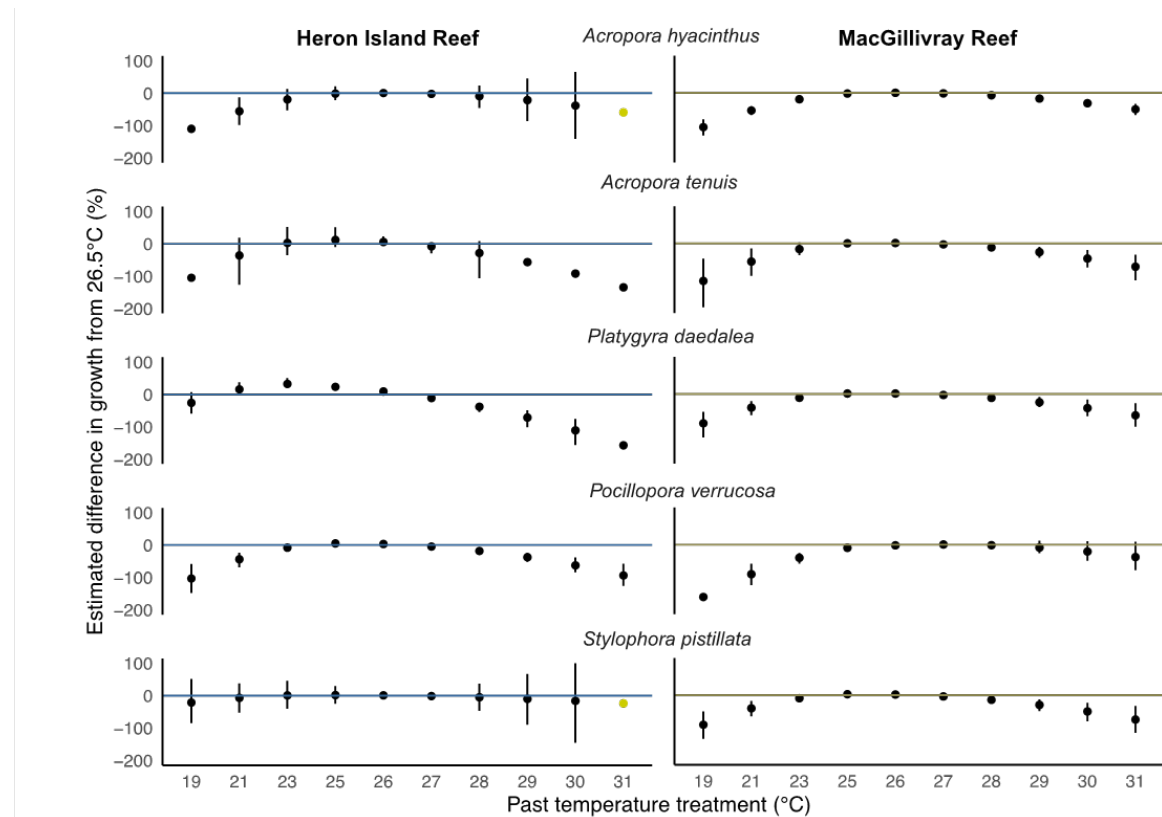
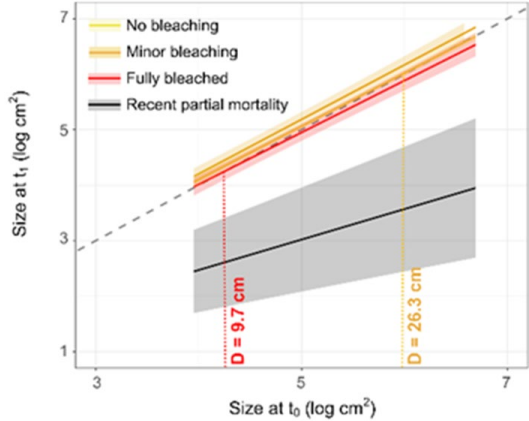


Figure 16: Legacy effect magnitude (estimated difference in growth) of coral fragments contrasted to estimated growth at 26.5°C (intercept) after one-month. Considering five reef-forming species – *Acropora hyacinthus*, *Acropora tenuis*, *Pocillopora verrucosa*, *Stylophora pistillata* and *Platygyra daedalea* – collected from Heron Island Reef in 2022 and MacGillivray Reef in 2023. The black points and black lines show the median and 95% Bayesian credibility intervals (CI) of the model, respectively. The intercept is shown.

These findings have critical implications for assisted evolution strategies, particularly those involving assisted gene flow. Specifically, they suggest that northern corals transplanted to southern environments could suffer prolonged reductions in growth during cold winters. Such reductions could jeopardise their reproductive output and given that growth suppression lasted for at least six months (see results in Question 2a), they may also undermine the anticipated benefits of enhanced thermal tolerance during subsequent marine heatwaves following cold seasons in the south.

Objective	Key Findings and/or Outcomes
	<p>Empirical characterisation of the legacy effect of marine heatwaves</p> <p>During the first five years of EcoRRAP research, the reef suffered two mass bleaching events: a mild one in 2022 and a severe one in 2024. The mild mass bleaching event impacted the Central GBR, while the severe one in 2024 impacted the southern and a few reefs in the northern GBR.</p> <p>The mild mass bleaching event of 2022 provided the project team with the unique opportunity to investigate the legacy effects of bleaching and the impact of the 2022 bleaching event on both survival and growth of corals. Understanding the lethal and sublethal effects of bleaching on coral demographics is vital for predicting reef responses to climate change.</p> <p>This study examined the effects of a mild but spatially extensive bleaching event on corals of the central GBR in summer 2022. We assessed how bleaching severity influenced the growth of dominant coral taxa, accounting for biological and environmental factors such as taxonomic identity, colony size, water clarity, sea surface temperature, and water velocity.</p> <p>By using large-area orthomosaics, we were able to virtually tag colonies and track them before, during, and after bleaching to accurately quantify coral responses, including bleaching-induced partial mortality.</p> <p>Results showed that colony size and bleaching severity were the most important drivers of reduction in growth and survival probabilities during the year following the mild mass bleaching event, with only marginal effects from environmental conditions (Figure 17).</p>  <p>Figure 17: Growth model outputs for <i>P. verrucosa</i>. (a) Survival probability as a response of bleaching severity, error bars correspond to 95% confidence intervals. (b) Survival probability as a response of initial size, ribbon represents 95% confidence intervals. (Modified from Lechene et al. 2025, Thesis, Chapter 4). Size at t_1 as a function of size at t_0 and (c) bleaching severity and (d) The ribbons correspond to 95% confidence intervals. The dashed line represents the stasis line. Initial size or size at t_0 is size in</p>

Objective		Key Findings and/or Outcomes
		<p><i>January 2022, size at t1 is size in January 2023. The vertical dotted lines represent the approximate diameter at which growth curves cross the stasis line.</i></p> <p>These findings offer critical insights for coral informing assisted evolution interventions by identifying coral individuals that show lower legacy effect of marine heatwaves. Furthermore, it provides valuable information to inform ecosystem models on the impact of marine heatwave legacy effect on post disturbance population and community dynamics (Lechene et al. 2025 in review doctoral thesis, Chapter 4).</p>
2 (f)	How do bleaching responses of coral colonies and populations scale with various T_{opt} ?	<p>Some metrics have been derived from thermal performance curves (TPC) to infer relative heat tolerance. For example, organisms with either high post-optimum sensitivity (steep post-optimum slope), negative thermal safety margin (the difference between the thermal optimum and the ambient temperature) or low critical maximum (maximum temperature below which performance is positive) would be expected to have low tolerance to marine heatwaves while organisms with low post-optimum sensitivity, positive thermal safety margin or high critical maximum would be expected to have high heat tolerance to marine heatwaves (Figure 18 A).</p> <p>From the posteriors of the TPC Bayesian models, we used a bootstrapping analysis to calculate the probability that each TPC-based heat tolerance metric would correctly predict the field observations-based marine heatwave tolerance ranking of each species). The latter is supported by multiple independent field-based studies of tolerance to marine heatwaves. We found poor</p>

accuracy of the coral growth TPC-based heat tolerance metrics to predict species tolerance to marine heatwaves (Figure 18, B-F), compared to our theoretical expectation (Figure 18 A).

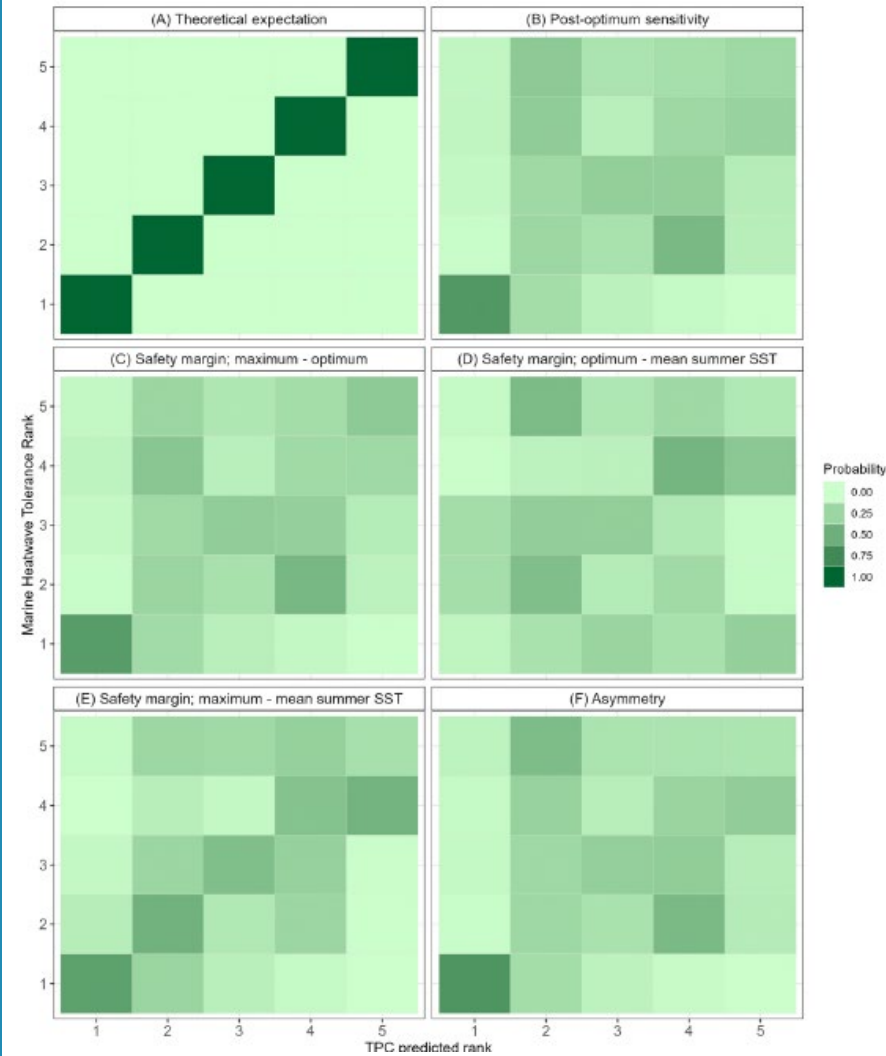


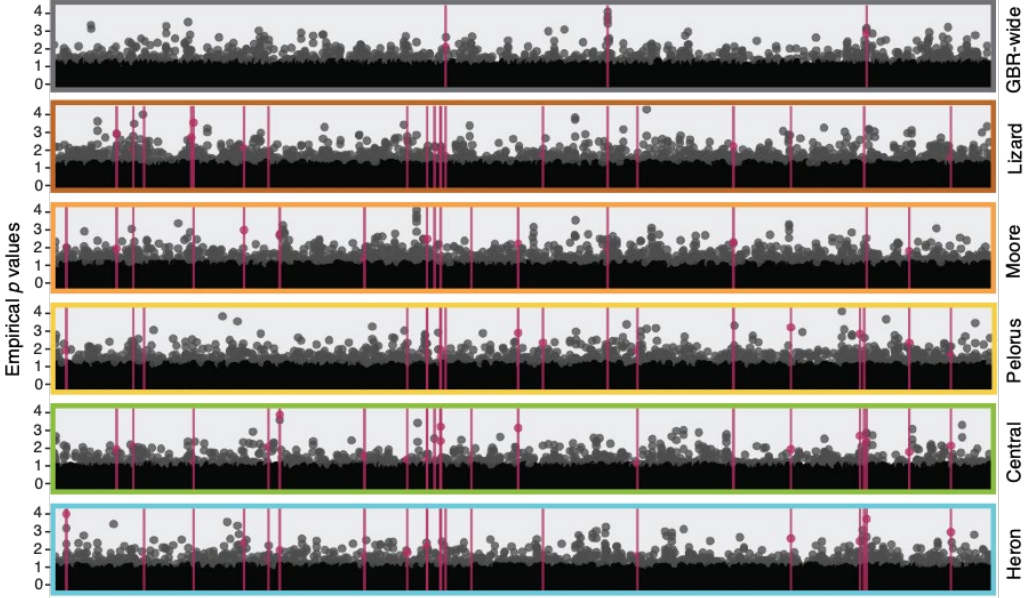
Figure 18: Relationship between thermal performance curve predictors of thermal tolerance and empirical tolerance to marine heatwaves (bleaching impacts) based on field observations (Crossman et al. 2025 under review).

Objective	Key Findings and/or Outcomes
	<p>Panel A shows the expected probability map if the two variables are perfectly correlated. Panels B to F show relationships between empirical tolerance and the five most commonly used proxies of thermal tolerance based on thermal performance curves parameters.</p> <p>Eleven of the 15 predictions (diagonal cells in Figure 18) give equal or lower probability of the correct ranking than any other ranking. Furthermore, only one of the 15 had a probability greater than 50% of predicting the correct marine heatwave tolerance ranking (post-optimum sensitivity of <i>S. pistillata</i>, Figure 18 D). However, even for <i>S. pistillata</i>, one of the three metrics (thermal safety margin) predicted a ranking at the opposite end of the tolerance spectrum (high tolerance rank of 4, Figure 18 E). Another two cases (both for <i>P. verrucosa</i>) predicted the ranking erroneously but showed the gradient (Figure 18 E and F, predicted rank 5). In four cases, there was a higher probability of being at the opposite end of the gradient than the observed marine heatwave tolerance ranking.</p> <p>One of the potential reasons why the TPC-based metrics were not good predictors of tolerance to marine heatwaves might be because they are focused on different metabolic pathways.</p> <p>The temperature-dependence of growth may be closely associated with whole-organism metabolic rates, whereas marine heatwave conditions instigate the breakdown of the symbiosis between the coral host and algal symbiont leading to organismal death, a mechanism that is influenced by a variety of interacting, often time-dependent factors including the abundance/density of Reactive Oxygen Species (ROS), host tissue thickness, thylakoid membrane fluidity, the photoprotective response of both the symbionts and the host coral, the environmental setting and the heterotrophic capacity of the coral. Critically, these factors and their interactions can vary among species and individuals to influence their relative heatwave tolerance.</p> <p>From an evolutionary perspective, growth temperature dependence may be poorly linked with marine heatwave tolerance because the selective pressure of maximising growth has been stronger than the selective pressure of surviving marine heatwaves, until recently. The coral coring record from the GBR and the Coral Sea shows that marine heatwaves have been extremely infrequent in the last 400 years (with an increase in frequency in the last two decades).</p> <p>(Modified form Crossman et al. under review).</p>
2 (g)	<p>How rapidly does coral colony and population T_{opt} shift due to bleaching events?</p> <p>Based on the poor correlation between tolerance to marine heatwaves and growth temperature strategies explained in the previous question, our results suggest that marine heatwaves are unlikely to significantly change the thermal optimum of coral populations rapidly.</p> <p>Importantly, marine heatwaves are clearly becoming a strong and increasingly frequent selective pressure, and over evolutionary time new thermal performance strategies that maximise fitness under high frequency of marine heatwaves are likely to arise.</p> <p>However, what the shape of the growth temperature curves will be in these new thermal strategies cannot be predicted based on the current relationships due to the low correlation between thermal performance and tolerance to marine heatwaves.</p>
3(f)	<p>How does thermal tolerance differ among species and align with ecological traits (reproductive</p> <p>Patterns of TPC metrics for growth across the five species studied in the previous objective appear to fit species-specific strategies that maximise growth across the year, given the combination of the different species' traits (Table 2).</p>

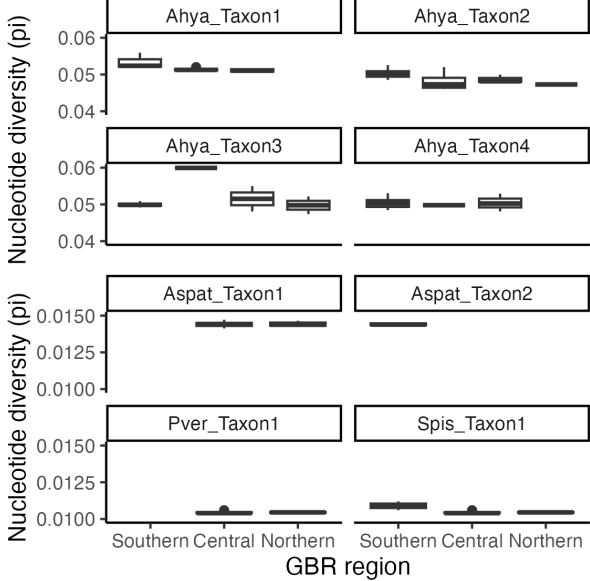
Objective	Key Findings and/or Outcomes																																				
<p>modes, growth forms, abundance, etc.)?</p>	<p>At one end of the spectrum, the thermally sensitive tabular coral <i>Acropora hyacinthus</i> has evolved a low thermal optimum (lower than the mean summer Sea Surface Temperature (SST) for four of the five reefs studied) and grows above 80% of its maximum growth for >70% of the year at most locations.</p> <p>We speculate that the high tissue/skeleton ratio of tabular corals maximises light harvesting and provides a surplus of energy that compensates for the reduced growth in summer. This hypothesis is supported by the fact that populations of tabular <i>A. hyacinthus</i> from the southern reef—where temperatures are significantly lower—did not have a thermal optimum lower than the mean summer SST, potentially indicating a physiological thermal boundary to lowering the thermal optimum.</p> <p><i>Table 2: Relationship between thermal tolerance and other traits for five coral taxa in the GBR (modified from Crossman et al. under review).</i></p> <table border="1" data-bbox="618 587 1720 884"> <thead> <tr> <th>Species</th> <th>Filed-base thermal tolerance</th> <th>Maximum growth</th> <th>Local thermal efficiency</th> <th>Thermal breadth</th> <th>Thermal optimum</th> </tr> </thead> <tbody> <tr> <td><i>Stylophorapistillata</i></td> <td>L</td> <td>M</td> <td>M</td> <td>M</td> <td>H</td> </tr> <tr> <td><i>Acropora hyacinthus</i></td> <td>L</td> <td>H</td> <td>H</td> <td>M</td> <td>L</td> </tr> <tr> <td><i>Acropora tenuis</i></td> <td>M</td> <td>M</td> <td>M</td> <td>M</td> <td>M</td> </tr> <tr> <td><i>Pocillopora verrucosa</i></td> <td>H</td> <td>L</td> <td>L</td> <td>L</td> <td>H</td> </tr> <tr> <td><i>Platygyra daedalea</i></td> <td>H</td> <td>L</td> <td>H</td> <td>H</td> <td>M</td> </tr> </tbody> </table> <p>At the other end of the spectrum <i>P. daedalea</i>, a thermally tolerant slow growing species, maximised growth with the largest thermal breadth (spanning over 5.5°C in some reefs) at an intermediate thermal optimum (Table 2).</p> <p>With this thermal strategy, less growth is sacrificed in summer and the species can also grow at 80% of its maximum growth rate for >70% of the year, including in the coolest months.</p> <p><i>P. verrucosa</i>, the other species with high thermal tolerance and a low growth rate, had the highest thermal optimum but the lowest proportion of days (45–65%) growing above 80% of its maximum growth.</p> <p>Similarly to <i>P. daedalea</i>, <i>P. verrucosa</i> cannot afford to sacrifice growth during summer due to its low growth rate, but it was also limited in its thermal breadth due to its very low growth at low temperatures (almost 0 growth at 19 degrees in all reefs).</p> <p>Consequently, <i>P. verrucosa</i> can only maximise growth by taking advantage of the warm temperatures in summer (highest thermal optimum). The other two species with intermediate growth rate and low to medium thermal tolerance exhibited a strategy where the thermal optimum was greater than tabular <i>A. hyacinthus</i>, and thermal breadth narrower than <i>P. daedalea</i>, with a corresponding intermediate proportion of the year growing close to the maximum growth rate</p>	Species	Filed-base thermal tolerance	Maximum growth	Local thermal efficiency	Thermal breadth	Thermal optimum	<i>Stylophorapistillata</i>	L	M	M	M	H	<i>Acropora hyacinthus</i>	L	H	H	M	L	<i>Acropora tenuis</i>	M	M	M	M	M	<i>Pocillopora verrucosa</i>	H	L	L	L	H	<i>Platygyra daedalea</i>	H	L	H	H	M
Species	Filed-base thermal tolerance	Maximum growth	Local thermal efficiency	Thermal breadth	Thermal optimum																																
<i>Stylophorapistillata</i>	L	M	M	M	H																																
<i>Acropora hyacinthus</i>	L	H	H	M	L																																
<i>Acropora tenuis</i>	M	M	M	M	M																																
<i>Pocillopora verrucosa</i>	H	L	L	L	H																																
<i>Platygyra daedalea</i>	H	L	H	H	M																																

3. Adaptive genetic diversity in natural populations

Objective	Key Findings and/or Outcomes
<p>3 (a) How is naturally occurring adaptive genetic diversity, especially that associated with thermal tolerance, distributed within and among reefs of the GBR?</p> <p>Adaptive genetic diversity – genetic diversity that allows a species to adapt to changing conditions.</p> <p>Genomic – studies focusing on all aspects of an organisms genes (structure, function, evolution, mapping and editing), whereas genetics focuses on single genes.</p>	<p>Adaptive genomic diversity for temperature adaptation, and its geographic partitioning across the Great Barrier Reef, has been most extensively investigated in the coral <i>Stylophora pistillata</i>.</p> <p>Our research across the EcoRRAP study sites found that <i>S. pistillata</i> populations at each reef are genetically distinct, with low levels of genetic mixing between populations. These findings are consistent with low dispersal ability in this brooding species (a coral that internally fertilises and nurtures larvae) and suggest that each reef is evolving separately from the others.</p> <p>These characteristics make <i>S. pistillata</i> an ideal system to study how adaptive genetic diversity varies across reefs in the Great Barrier Reef.</p> <p>Consistent with low levels of genetic mixing between populations, we found that <i>S. pistillata</i> populations have adapted to specific environmental conditions within each regional reef group. This finding suggests that genetic differences related to thermal adaptation are mostly unique to each region and can vary over the extent of the GBR.</p> <p>In contrast, adaptive diversity (including that associated with temperature adaptation) is geographically widespread in the high dispersal coral, <i>Pocillopora verrucosa</i>.</p>
<p>3 (b) Which genomic loci are candidates for thermal tolerance based on their associations with GBR seascape features (e.g. microhabitats within reefs, depth, latitude, and past bleaching events)? (this is a <i>genotype-by-environment approach</i>)</p> <p>Genomic loci – physical location of a gene or DNA sequence on a chromosome.</p>	<p>We studied how corals of the species <i>Stylophora pistillata</i> have adapted to temperature changes by examining genetic variation strongly linked to temperature variation across different reefs.</p> <p>We found that thermal adaptation involves many parts of the genome, with hundreds of candidate genetic markers identified. Most of the genetic markers involved in adaptation differed between reefs, but we also identified 29 genomic regions that consistently showed an association with temperature variation in multiple populations (Figure 19).</p> <p>These regions could be a key to understanding how corals adapt to heat stress on the Great Barrier Reef.</p> <p>Future research will focus on confirming how these genetic markers affect coral traits, including thermal tolerance. By developing this workflow for <i>S. pistillata</i>, we will be able to study the genetic basis of thermal adaptation in other coral species.</p>

Objective	Key Findings and/or Outcomes
<p>Genotype – the entire genetic makeup of an organism.</p>	 <p><i>Figure 19: Signatures of within-reef thermal adaptation and repeatability across <i>Stylophora pistillata</i> coral populations.</i></p> <p>Results from genomic analyses (based on genotype-by-environment associations) provide evidence that <i>Stylophora pistillata</i> corals are adapting to temperature changes within individual reefs, and that some of these genetic adaptations appear repeatedly in different populations.</p> <p>The y-axis represents the significance of the association between genomic regions and temperature variation. For each population, genomic regions significantly linked to temperature variation (panels two to five from top to bottom) are shown as grey dots ($p < 0.05$). Twenty-nine regions showing consistent associations to temperature variation are putatively adaptive in multiple populations (red dots and bars; $p < 0.05$).</p>
<p>3 (c) Is the geography of natural adaptive variation consistent among coral species or idiosyncratic (where knowledge regarding candidate loci for adaptive variation derives from knowledge obtained from both</p>	<p>By studying over 800 colonies of the coral <i>Acropora hyacinthus</i> (sampled under both RRAP Projects – Ecological and Genetic Adaptation (ECO-03) and Genetic Basis of Key Traits (ECT-01)), we examined how natural adaptive variation is distributed across different regions in the GBR.</p> <p>Unexpectedly, we found that hybridisation – genetic mixing between closely related species – enables the sharing of adaptive variation among three of the four cryptic <i>A. hyacinthus</i> coral species studied in southern reefs, namely of the Capricorn Bunker region. However, hybridisation is much less common in the northern reefs, likely due to lower hybrid fitness (relative to parental colonies).</p>

Objective	Key Findings and/or Outcomes
<p>RRAP Projects – Ecological and Genetic Adaptation (ECO-03) and Genetic Basis of Key Traits (ECT-01))</p> <p>Cryptic species – in relation to RRAP, they are corals that share the same physical characteristics and therefore look similar but are genetically distinct.</p>	<p>In the southern reefs, in contrast, genomic data revealed extensive genetic mixing among the three species, leading to genetic differences between northern and southern populations.</p> <p>Interestingly, we found that certain genetic patterns associated with adaptation were consistent among different coral species in the south, suggesting that hybridisation may enable these populations to co-adapt to changing conditions.</p> <p>Future work should investigate whether hybridisation can speed up adaptive evolution in corals, potentially informing new intervention strategies to help reefs cope with environmental stress.</p>
<p>3 (d) Can reef-level adaptive genetic diversity be predicted by the seascape’s environmental or geographical attributes?</p>	<p>Genetic diversity is a fundamental part of biodiversity, because it provides the raw material for species to adapt to changing conditions. Generally, higher genetic diversity means a greater potential for adaptation and evolutionary resilience.</p> <p>We conducted one of the most comprehensive surveys of coral genomic diversity in the GBR to date, focusing on four coral species complexes: <i>Stylophora pistillata</i>, <i>Pocillopora verrucosa</i>, <i>Acropora spathulata</i> and <i>Acropora hyacinthus</i>.</p> <p>For each taxon, we examined differences in genome-wide diversity across three different regions. Surprisingly, most species showed similar levels of genomic diversity across regions. However, for <i>A. hyacinthus</i>, there was a small but significant difference between northern and southern populations (Figure 20).</p> <p>These findings suggest that while overall genetic diversity is similar, different populations may still carry unique genetic variation that may underly local adaptation. We are now conducting further analyses to better understand how levels of genetic variation are linked to different environmental conditions and adaptation in these coral taxa.</p>

Objective	Key Findings and/or Outcomes
	 <p data-bbox="613 927 1995 986"><i>Figure 20: Mean genetic diversity, estimated by nucleotide diversity, for eight coral taxa (cryptic taxa separated) sampled across the GBR. Genetic diversity was calculated per reef and averaged across three main regions.</i></p> <p data-bbox="613 1010 2022 1066">Genetic diversity did not vary spatially across reefs or regions, with the exception of <i>A. hyacinthus</i> taxa which showed a significant difference in mean genetic diversity between southern and northern regions.</p>
3 (e) Over what spatial and time scales is natural gene flow sufficient to spread adaptive variants?	<p data-bbox="613 1098 1995 1222">Understanding how far coral larvae travel or ‘disperse’ is crucial for reef conservation. The scale of larval dispersal determines whether reefs can repopulate each other after disturbances and how far and fast adaptive genetic variants can spread via gene flow. To study this, we used methods proven to work well in plants and fish to estimate how far coral larvae disperse in natural populations.</p> <p data-bbox="613 1249 2011 1374">We analysed data for seven coral species on the GBR. We used genomic datasets collected from RRAP Projects Ecological and Genetic Adaptation (ECO-03) (<i>Stylophora pistillata</i> and <i>Pocillopora verrucosa</i>) and Genetic Basis of Key Traits (ECT-01) (<i>Acropora spathulata</i>), alongside previously published literature (<i>Pocillopora damicornis</i>, <i>Acropora millepora</i>, <i>Acropora kenti</i> and <i>Pachyseris speciosa</i>).</p> <p data-bbox="613 1401 1211 1428">For each species, we measured two scales of dispersal:</p>

Objective	Key Findings and/or Outcomes
	<ul style="list-style-type: none"> • Demographic replenishment scale (2σ): This area represents the genetic neighbourhood – how far larvae regularly move and settle within a single generation. • Rare dispersal event scale: This measures how far a small number of larvae can travel (1% probability dispersal distance) and spread beneficial genetic variants, even if they do not significantly contribute to population numbers until the next generation (see Panels B-D, Figure 21). <p>For most of the studied corals, the genetic neighbourhood was relatively small, just tens to hundreds of meters. In the brooding species <i>Stylophora pistillata</i> ($2\sigma = 202$ m) and <i>Pocillopora damicornis</i> (alpha; $2\sigma = 94$ m) with mixed reproductive mode, gene flow is very limited.</p> <p>These findings suggest that larvae from brooded species rarely travel greater than 1 km (see Top Left Panel, Figure 21) and that corals within habitats in different parts of the reef could evolve somewhat independently.</p> <p>However, for spawning species with higher dispersal potential, gene flow can extend across entire reefs, potentially connecting nearby reefs and spreading genetic variants more widely.</p> <p>We are now undertaking a global synthesis of coral dispersal across the world.</p>

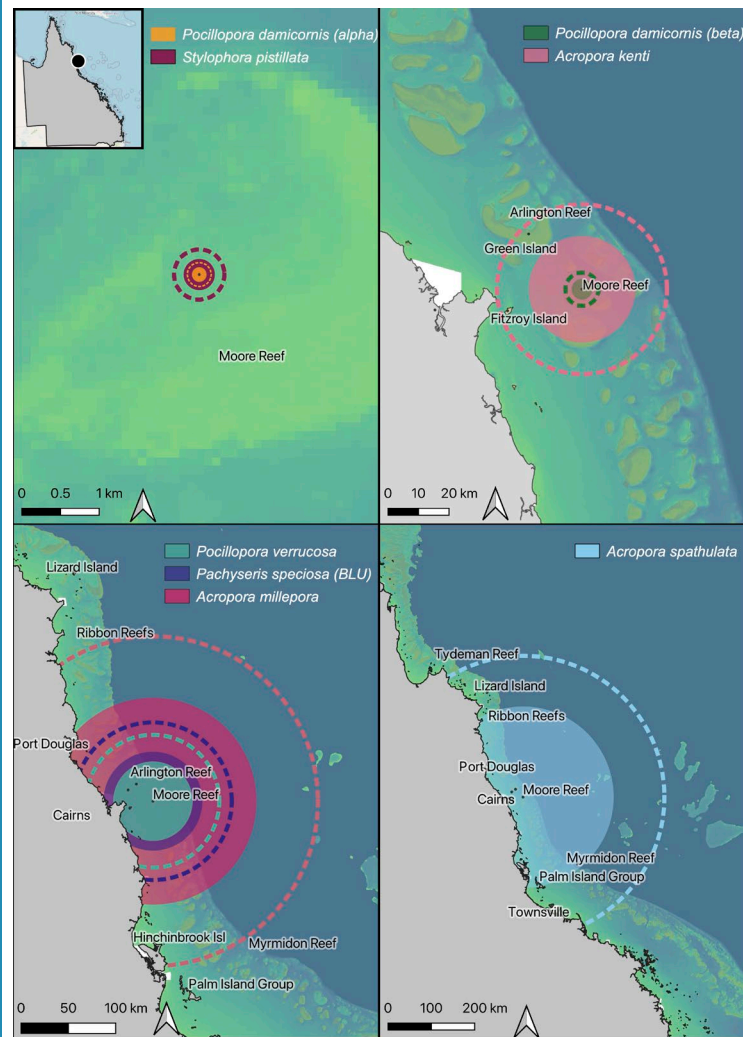


Figure 21: Variable spatial scales of effective coral larval dispersal for seven coral species on the GBR.

A centre point was arbitrarily chosen at Moore Reef to represent the parent's spatial position.

Shaded circles represent a population neighbourhood where larvae frequently travel from the centre point and the dotted outside circle is where rare dispersal occurs (1% probability).

Objective	Key Findings and/or Outcomes
	Different coloured circles represent different coral species, and each panel shows increasing spatial scales to best represent the different dispersal distances for each species.

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
No adjustments to report	

4 Genetic work in progress

Genomic work under RRAP Projects Ecological and Genetic Adaptation (ECO-03) has focused on identifying spatial patterns of genetic diversity, understanding dispersal and adaptation across a cross-section of GBR coral species.

This work contributes to understanding how and why coral species differ in their genetic diversity and how these patterns vary across different regions of the GBR.

This fundamental knowledge is crucial for intervention planning and more targeted and effective reef restoration strategies. For instance, determining what locations and spatial scales are appropriate to source broodstock, identifying colonies already adapted to future conditions, and projecting how quickly coral populations might adapt to new conditions.

Current projects and key findings:

- **Genotype-environment association (GEA) analyses**

This approach relies on identifying genetic markers showing strong correlations with environmental variables.

These analyses provide two important pieces of information: they (i) find which environmental variables shape spatial genetic patterns and can therefore be used to predict which populations and individuals are naturally pre-adapted to future conditions, and (ii) yield candidate genetic markers for adaptation to environmental conditions (such as temperature).

Undertaking GEA's was a focal goal for this project and results for several coral species are underway.

Results for *Stylophora pistillata* have already identified several temperature-related genetic markers, which could guide selective breeding and restoration efforts (led by University of Queensland (UQ) PhD student Zoe Meziere). Preliminary analyses have been completed for *Acropora hyacinthus*, and *Pocillopora verrucosa*. We have genomic data in hand for upcoming GEA analyses in several other coral species, including *Acropora humulis*, *Pocillopora spp.*, *Isopora spp.*, and *Montipora spp.*, in the Coral Sea and Lord Howe Island and *Seriatopora hystrix*, focusing on responses to environmental stressors in various regions of the GBR.

- **Adaptive hybridisation in *Acropora hyacinthus***

Unexpectedly, hybridisation has been found to be extensive in some *A. hyacinthus* populations, with beneficial genes crossing species boundaries through a process called adaptive introgression. The three-way adaptive introgression (involving three *A. hyacinthus* taxa) that we have found is highly unusual (across the tree of life) and therefore we anticipate presenting these data in a high impact publication.

The discovery of widespread adaptive introgression points to hybridisation as an important mechanism for adaptive change in corals.

- ***How far do corals disperse each generation?***

How far coral larvae travel is critical for understanding genetic connectivity between reefs.

Dispersal distances form key parameters in modelling natural and intervention scenarios and yet there is virtually no empirical data on this. For example, hydrodynamic models *predict* distances but do not measure realised dispersal.

Adopting methods from plant genetics, our reanalysis of coral genetic data sets shows that dispersal distances can range from just centimetres to tens of kilometres. These findings will inform models of coral connectivity and resilience under climate change, with potential implications for designing restoration strategies that account for species-specific dispersal capabilities.

- ***Multi-species symbiont diversity and environmental reservoirs***

Hundreds of coral genomes collected under RRAP Projects Ecological and Genetic Adaptation (ECO-03) and Genetic Basis of Key Traits (ECT-01) have enabled the development of scalable computational approaches to characterise symbiont diversity.

These approaches are being applied to identify symbiont diversity in several co-distributed coral genera across the GBR..

Outcomes of this work also include refining and recovering the genomes for vertically transmitted symbionts for the first time using population genomic data from wild populations. Additionally, data are in hand for examining sediment microbes to assess potential environmental reservoirs of symbionts, which could play a role in post-bleaching coral recovery and serve as indicators of coral health.

These results will help validate whether data from other environmental microbial databases (e.g. Australia's Integrated Marine Observing System (IMOS)) can be used towards such monitoring.

5 Future Research Recommendations

5.1 Coral demographics, thermal performance strategies and their interactions with disturbances (ecological adaptation)

- ***Continue monitoring to understand coral population size frequency distribution and its interactions with vital rates.***

Given the identified critical importance of size-specific variation in coral vital rates it is fundamental that additional monitoring at colony level is continued to be able to develop more robust predictions of the impact of size frequency distribution on coral communities' recovery and response to interventions. Future work would include additional dominant taxa and the legacy effect of the 2024 bleaching event.

- ***Coral fecundity characterisation.***

While this project made important contributions to our understanding of coral survivorship, colony growth and coral recruitment and their potential influence on intervention outcomes, coral fecundity continues to be understudied. Given the fact that the spread of desirable traits through coral generations is one of the main mechanisms proposed to catalyse the upscale of intervention benefits, empirical and experimental work on coral fecundity is fundamental for the successful evaluation of intervention potential and success.

- ***Explore the role of light and nutrients in the thermal performance strategies of coral populations across the GBR environmental gradients.***

The characterisation of thermal performance strategies produced by this project has provided an avenue to explore the impact of chronic increases of temperature in coral community dynamics, however, it is limited as it assumes that light and nutrients that also vary significantly across the environmental gradient studied in the GBR are constant.

It is possible that predicted increases in coral colony growth during the cooler months due to chronic warming may not eventuate if light and or nutrients are a limiting factor under these conditions. As a consequence, we recommend that a combination of experimental and field-based explorations are prioritised characterising the effect of light and nutrients on thermal performance strategies in the GBR.

- ***Systemic synthesis of observed ecological patterns.***

While data analysis and synthesis were one of the main focuses of this project in the past year, the amount of data generated, and the complexity of big picture interpretation of information across multiple ecological mechanisms requires ongoing synthesis and the application of creative qualitative approaches to integrate information and generate actionable knowledge.

Future research would include, but not be limited to, cryptic species and functional groups distribution models, demographic population and community models to identify the demographic drivers of recovery and how they vary across environments, the further exploration of structural complexity metrics as surrogates of biodiversity and adaptation to climate change (i.e. does higher structural complexity provide higher level of shading and thermal protection during bleaching?)

5.2 Adaptive genetic diversity in coral populations

-

Plan for cryptic coral species

Across our published work (e.g. Meziere et al. 2024; Riginos et al. 2024; Naugle et al. 2024) we find that at least 60% of coral species thought to be a single species comprise two or more cryptic species.

This can complicate restoration efforts because it implies that most species targeted for interventions are not single species. Cryptic species may not interbreed successfully in captivity, and they may have different environmental tolerances, which may lead to mismatches between the species that are out planted and the receiving environment, diminishing intervention success.

We encourage any work with corals to consider how cryptic species could affect their plans. See Riginos et al. 2024 (Figure 5 and Table 1) in the published paper for details. Establishing genetic baselines to identify these cryptic species will be key to planning effective interventions.

- ***Expand GBR genetic surveys to additional species with contrasting biology***

Although we have aggregated comprehensive records of spatial genetic patterns for six GBR coral species, many important species and life histories are not represented. Species such as *Pocillopora* spp. (a complex of species) and *Porites* spp. (massive body form, generally considered as being less sensitive to high temperatures) could provide critical insights into coral adaptation. We have extensive tissue collections for these species in hand but have not had time (or funding) to genotype and analyse.

- ***Explore fine-scale environmental variation to find heat-tolerant colonies***

Large-scale environmental datasets (e.g. eReefs) provide a wealth of environmental information for the GBR (mostly at 1 km spatial scale), but coral dispersal and adaptation processes occur at much smaller scales.

AIMS visiting postdoctoral fellow Annie Guillaume and Katherine Prata from AIMS will be using topographic and photogrammetry-derived predictors of meter-scale environmental attributes to evaluate their influences on coral adaptation and thermal tolerance.

- ***Develop and maintain a long-term genomic database within photogrammetry plots***

The photogrammetry plots created in EcoRRAP that support demographic analyses and include geotagged genotyped corals is unique worldwide.

These data offer a unique opportunity to pair genomics with demography data such as growth, survival, and reproduction over time providing valuable insights into how genetic variation influences coral resilience.

Specifically, we can develop a genomic scoring method for corals and examine long-term trade-offs between heat tolerance and growth, fecundity, and survivorship to other stressors.

Additionally, we can fit more complex quantitative genetic models to demographic data for brooding species where we recover close kin. This kind of a dataset combining demography and 'omics would be one-of-a-kind and its usefulness for understanding coral adaptation would extend well beyond RRAP.

- ***Characterising maladaptive diversity in corals***

While much of the focus has been on identifying adaptive genetic diversity, the RRAP Project Ecological and Genetic Adaptation (ECO-03) is also examining the distribution of harmful genetic variants (genetic load) in coral populations. Large populations can carry high genetic loads that can have an impact on fitness when population sizes become small.

Understanding levels of genetic load in natural coral populations can help predict how coral populations might respond to future stressors, guide broodstock selection for restoration efforts and help anticipate the impacts of captive breeding (by tracking genetic load in lab-reared versus wild populations).

- ***Investigating hybridisation as an intervention strategy***

The discovery of adaptive introgression in *A. hyacinthus* opens up new avenues for developing interventions based on using natural hybrids to enhance coral resilience.

Hybridisation could speed up adaptive phenotypic change, especially naturally occurring hybrids are used as parents rather than laboratory crosses to make the first filial generation (F1's).

However, future work needs to test whether natural hybrid corals differ in phenotypes, such as thermal tolerance, from their parental species.

- ***Synthesising across species to identify multi-species evolutionary resilience***

While we have been amassing information on genotype-environment associations and spatial genetic diversity patterns for individual species, by combining findings across multiple co-distributed species we can predict:

- (i) reef locations consistently harbouring populations that are pre-adapted to future conditions (GEAs) or have high general evolutionary resilience (inferred from genetic diversity patterns) and;
- (ii) candidate genomic regions consistently involved in local adaptation among diverse coral taxa. These patterns focused on co-distributed coral hosts should also be compared to spatial diversity in symbionts.

5.3 Shared recommendations across RRAP Projects Ecological and Genetic Adaptation (ECO-03) and Genetic Basis of Key Traits (ECT-01)

- ***Validation of candidate adaptive loci through experiments, gene manipulation, and evolutionary modelling***

While the genomic work under RRAP Projects Ecological and Genetic Adaptation (ECO-03) and Genetic Basis of Key Traits (ECT-01) has identified candidate genetic regions associated with thermal adaptation and other fitness aspects, experimental validation is needed.

Using common garden or reciprocal transplant experiments, ribonucleic acid (RNA) sequencing, and gene manipulation techniques will help confirm the relationship between these candidate markers, phenotypes and fitness.

RNA sequencing data are already in hand to validate results from Genome-wide Associations Study (GWAS) analysis from *Acropora hyacinthus* colonies with extreme thermal tolerance phenotypes (led by SCU PhD student Melissa Naugle).

These experiments may be combined with future field-based validation of acute phenotypes and gene manipulation can also be used to check the effects of specific genetic markers on coral traits.

The results could be used to determine the genetic architecture of thermal adaptation, inform evolutionary modelling on the rate of natural adaptation and guide assisted evolution interventions to enhance coral resilience to climate change.

- ***Integrating 'omic approaches and other technologies to strengthen inferences***

Genotyping under RRAP has focused on whole genome sequencing, some reduced representation sequencing, and symbiont characterisation with ITS2 (internal transcribed spacer) metabarcoding and whole-genome k-mer analysis.

Integrating other RNA sequencing for gene expression analysis and other 'omics techniques could provide deeper insights into the molecular pathways associated with thermal tolerance and other adaptive traits, including metabolites and non-dinoflagellate microbial partners. This could help identify key genes or structural variants that confer resilience to stressors.

An emerging result across the field of ecological genetics is that large structural variants in genomes are important for adaptation. Uncovering the role of structural variants in GBR corals would require improving genomic resources for target species, such as creating chromosomal level reference genome assemblies and using long range sequencing.

- ***Future directions for genomics harnessing parent-offspring resources***

Knowledge on recombination rate and mutation rate variation in corals will provide critical information for evaluating the impacts of captive breeding on genetic diversity.

Accounting for these two intrinsic genetic processes will also help identify adaptive variation and its ecological drivers. Furthermore, parent-offspring phenotyping and genotyping would allow trait additive genetic covariances to be estimated and thus inform us of pleiotropy and/or phenotypic correlations

- ***Improving communication of genetic findings***

Knowledge gained from genomic data can be difficult to communicate to broader audiences.

During the first phase of RRAP, we focused on generating results and largely overlooked outreach and communication. Future efforts will focus on making these insights accessible to Traditional Owners, managers, and other stakeholders to facilitate informed decision-making.

- ***Unite RRAP Projects Ecological and Genetic Adaptation (ECO-03) and Genetic Basis of Key Traits (ECT-01) genomic work***

Linkages and collaborations between the two projects have been very productive and we recommend uniting this work more cohesively in the future to enhance benefits from shared genomic resources and procedures.

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