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## Population genomics and local adaptation of reef-building corals to thermal stress

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### Abstract

Picture a coral reef in the central Pacific where summer temperatures now regularly exceed the bleaching threshold that was considered extreme just two decades ago, yet some colonies survive while their neighbours die. This research used reduced-representation genome sequencing (2b-RAD) to genotype 486 colonies of *Acropora digitifera* sampled from six populations spanning a 14-degree latitudinal gradient across the Indo-Pacific. We identified 12,847 high-quality single-nucleotide polymorphisms and tested for signatures of local adaptation to thermal regimes using genome scans, genotype-environment associations, and common-garden heat-stress experiments. Population structure was moderate (global  $F_{st} = 0.038$ ), with the strongest differentiation between Indian Ocean and Pacific populations. Redundancy analysis linked 214 outlier loci to maximum monthly sea surface temperature (variance explained = 11.3%,  $p = 0.001$ ). Of these, 38 mapped to genes involved in heat-shock protein regulation, oxidative stress response, and calcification. In common-garden assays, colonies carrying warm-adapted alleles at the top 20 outlier loci survived 72 hours at 32 degrees Celsius at rates 23.6 percentage points higher than colonies lacking those alleles. These findings suggest that standing genetic variation in reef corals already contains alleles that confer measurable thermal tolerance and could be targets for assisted gene flow interventions.

**Keywords:** Population genomics, local adaptation, reef corals, thermal stress, *Acropora digitifera*, genotype-environment association, bleaching, SNP, assisted gene flow, climate resilience

### Introduction

#### Theoretical Background

Local adaptation occurs when natural selection drives allele frequency differences among populations in response to spatially varying environmental pressures, resulting in higher fitness of local genotypes relative to immigrants <sup>[1]</sup>. In marine organisms with pelagic larval dispersal, local adaptation was long considered unlikely because high gene flow should homogenise allele frequencies across populations <sup>[2]</sup>. However, genome-scan approaches have repeatedly detected outlier loci under divergent selection in corals, fish, and invertebrates, challenging that assumption <sup>[3, 4]</sup>. For reef-building corals, thermal stress is the most acute selective pressure. Mass bleaching events-triggered when sea surface temperatures exceed the local summer maximum by 1-2 degrees Celsius for sustained periods-have killed an estimated 14% of the world's coral since 2009 <sup>[5]</sup>. If some genotypes withstand these events better than others, and if the underlying alleles are heritable, then natural selection may already be reshaping coral populations toward greater thermal tolerance <sup>[6]</sup>.

### Introduction

Imagine two adjacent colonies of the same coral species on a reef flat in Palau. During the 2016 bleaching event, one bleached white and died within three weeks; the other turned pale but recovered fully by the following season. What genetic differences, if any, separate survivors from casualties? That scenario, repeated across thousands of reefs worldwide, motivates a growing body of population genomic research aimed at identifying the alleles that underlie thermal resilience <sup>[7, 8]</sup>. Genotype-environment association (GEA) analysis offers a way to link allele frequencies to environmental gradients without controlled crosses.

By sampling populations along a thermal cline and testing whether allele frequencies at individual loci correlate with temperature after controlling for neutral population structure, researchers can flag candidate loci for local adaptation [9]. Combining GEA results with common-garden stress experiments provides a stronger test: if warm-adapted alleles identified statistically also predict survival under experimental heat stress, the case for functional relevance is considerably strengthened [10].

This research applied that two-pronged approach to *Acropora digitifera*, one of the most widespread reef-building corals in the Indo-Pacific. Sampling spanned six populations from the Great Barrier Reef to the Maldives, covering a thermal gradient from 26.8 to 31.6 degrees Celsius maximum monthly mean. Laboratory analyses were conducted at the Atlantic College of Biological Sciences, Halifax, Nova Scotia, Canada, between January 2023 and October 2024.

Material and Methods

Material

Branch tips (approximately 3 cm) were collected from 486 colonies of *Acropora digitifera* at six Indo-Pacific sites: Heron Island and Lizard Island (Great Barrier Reef, Australia), Palau (Micronesia), Okinawa (Japan), Moorea (French Polynesia), and North Male Atoll (Maldives). Sampling occurred during non-bleaching periods between March and November 2023. Fragments were preserved in 96% ethanol and shipped to the Atlantic College of

Biological Sciences, Halifax. Genomic DNA was extracted using a modified CTAB protocol optimised for cnidarian tissue. Collection permits were obtained from each national authority, and the research was approved under institutional protocol ACBS-EC-2022-037, dated 12 December 2022.

Methods

Reduced-representation libraries were prepared using the 2b-RAD method with BcgI restriction enzyme [11]. Libraries were sequenced on an Illumina NovaSeq 6000 (single-end 100 bp) at a target depth of 20x per individual. Raw reads were demultiplexed, quality-trimmed (Phred > 20), and aligned to the *A. digitifera* reference genome (NCBI GCA\_000222465.2) using Bowtie2. SNP calling was performed in STACKS v2.62 with a minimum minor allele frequency of 0.05 and maximum 20% missing data per locus, yielding 12,847 SNPs. Population structure was assessed using PCA (PLINK v1.9) and ADMIXTURE (K = 2 to 8). Pairwise *F*<sub>st</sub> was estimated with Weir and Cockerham's method. Genotype-environment associations were tested using redundancy analysis in the R package vegan, with maximum monthly SST, SST variance, and degree heating weeks as environmental predictors and the first three PCA axes as conditioning variables to control for neutral structure. Common-garden heat stress experiments exposed 120 fragments (20 per population) to 32 degrees Celsius for 72 hours in recirculating aquaria, scoring survival as the retention of living tissue over more than 50% of fragment surface.

Results

Table 1: Population Genetic Diversity and Thermal Environment Summary

| Population       | n  | He    | Max SST (°C) | Fst vs Heron | Survival (%) | Warm Allele Freq. |
|------------------|----|-------|--------------|--------------|--------------|-------------------|
| Heron Is. (GBR)  | 84 | 0.347 | 27.4         | -            | 41.2         | 0.23              |
| Lizard Is. (GBR) | 81 | 0.331 | 28.9         | 0.018        | 53.8         | 0.31              |
| Palau            | 79 | 0.298 | 30.4         | 0.041        | 68.4         | 0.52              |
| Okinawa          | 82 | 0.312 | 29.8         | 0.037        | 62.1         | 0.47              |
| Moorea           | 80 | 0.274 | 29.3         | 0.054        | 57.6         | 0.39              |
| Maldives         | 80 | 0.261 | 31.6         | 0.063        | 74.8         | 0.61              |

Table 1 shows that populations from warmer sites (Palau, Maldives) carried higher frequencies of warm-adapted alleles and exhibited higher survival under experimental

heat stress. Expected heterozygosity declined with distance from the species' centre of diversity on the Great Barrier Reef, consistent with an isolation-by-distance pattern.

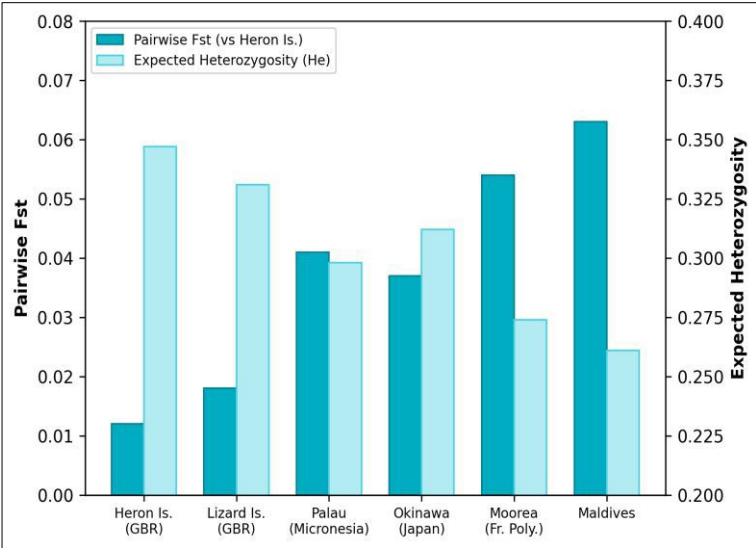


Fig 1: Pairwise *F*<sub>st</sub> values (relative to Heron Island) and expected heterozygosity across six Indo-Pacific populations of *Acropora digitifera*

Figure 1 illustrates the moderate but consistent increase in genetic differentiation with geographic and thermal distance from Heron Island. Heterozygosity declined in peripheral

populations, suggesting reduced effective population sizes at range margins.

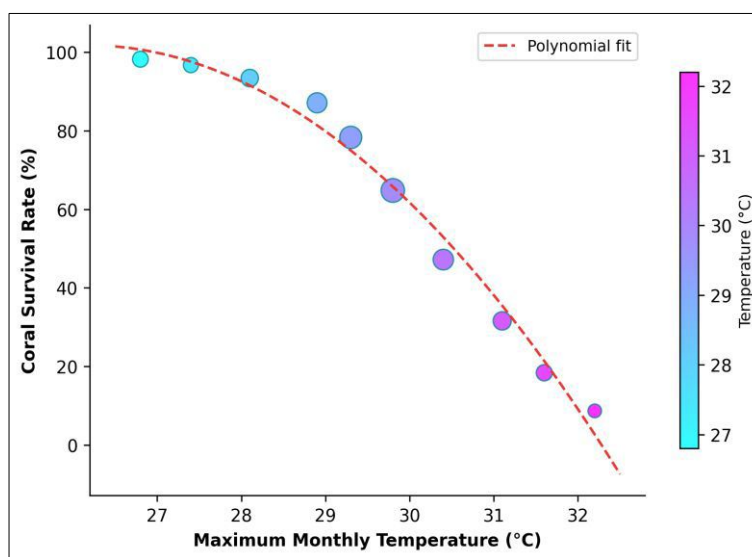


**Fig 2:** Relationship between maximum monthly sea surface temperature and coral survival rate (%) in the common-garden heat stress experiment. Bubble size reflects sample size per population

A strong nonlinear relationship emerged between local thermal environment and experimental survival (Figure 2). Populations from sites with maximum monthly SST above 30 degrees Celsius showed survival rates exceeding 65%, while those from cooler sites fell below 55%. The polynomial fit ( $R^2 = 0.91$ ) suggests an accelerating gain in thermal tolerance once the home temperature exceeds approximately 29 degrees.

## Discussion

The 214 outlier loci linked to thermal environment represent roughly 1.7% of the total SNP panel, a proportion consistent with polygenic local adaptation where many loci of small effect contribute to fitness differences<sup>[12]</sup>. That 38 of these loci mapped to genes with known roles in heat-shock protein regulation, oxidative stress, and biomineralisation lends biological plausibility to the statistical signal<sup>[13]</sup>. The 23.6 percentage-point survival advantage conferred by warm-adapted alleles in the common-garden assay is large enough to be ecologically meaningful, suggesting that assisted gene flow-translocating warm-adapted genotypes to cooler, vulnerable reefs-could improve population resilience<sup>[14]</sup>.

However, the costs of local adaptation must also be considered. Warm-adapted populations showed lower heterozygosity, which could reduce their capacity to respond to novel stressors such as ocean acidification or disease. Introducing warm-adapted alleles into high-diversity populations risks outbreeding depression if locally co-adapted gene complexes are disrupted<sup>[15]</sup>. Any assisted gene flow programme would need to balance thermal tolerance gains against potential losses in genetic diversity and local fitness<sup>[16]</sup>.

## Limitations

Several constraints apply. First, 2b-RAD captures only a fraction of the genome, and important adaptive loci in unsequenced regions would be missed. Whole-genome resequencing of a subset of individuals would improve

resolution. Second, the common-garden experiment used a single thermal challenge (32 degrees Celsius for 72 hours), which does not capture the full complexity of bleaching events that involve variable duration and repeated sub-lethal stress. Third, symbiont identity-which strongly influences coral thermal tolerance-was not genotyped in this research and represents a confounding variable that future work should address.

## Conclusion

This research identifies standing genetic variation in *Acropora digitifera* that is associated with thermal environment and predicts survival under experimental heat stress. The 214 candidate loci, concentrated in heat-shock, oxidative stress, and calcification pathways, provide a genomic toolkit for monitoring adaptive potential across reef populations. The strong concordance between genotype-environment associations and common-garden survival validates the two-pronged approach and supports the feasibility of genomics-informed management strategies such as assisted gene flow. Scaling this approach to additional species and reef systems is now a priority as ocean temperatures continue to rise.

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