Diversity and Distributions

WILEY

Diversity and Distributions

RESEARCH ARTICLE OPEN ACCESS

Seascape Genomics Reveal Contrasting Population Structure in Sympatric and Congeneric Corals Across Thermal Clines

Magena R. Marzonie[1,2,3] | Josephine J. V. Nielsen[2] | Line K. Bay[2,3] | David G. Bourne[1,2] | Matthew R. Nitschke[2,4] | Oliver Selmoni[5,6,7] | Hugo B. Harrison[1,2,3,8]

[1]College of Science and Engineering, James Cook University, Townsville, Queensland, Australia | [2]Australian Institute of Marine Science, Townsville, Queensland, Australia | [3]Aims@JCU, Townsville, Queensland, Australia | [4]School of Biological Sciences, Victoria University of Wellington, Wellington, New Zealand | [5]Department of Plant Biology, Carnegie Institution for Science, Stanford, California, USA | [6]Department of Embryology, Carnegie Institution for Science, Baltimore, Maryland, USA | [7]Department of Integrative Biology, University of California Berkeley, Berkeley, California, USA | [8]School of Biological Sciences, University of Bristol, Bristol, UK

Correspondence: Magena R. Marzonie (magena.marzonie@my.jcu.edu.au)

Received: 22 April 2025 | **Revised:** 1 July 2025 | **Accepted:** 27 July 2025

Editor: Yunwei Dong

Funding: Funding for the collection of samples in the Coral Sea Marine Park was supported by Parks Australia funding to Hugo Harrison, Andrew Hoey, and Morgan Pratchett under Parks Australia permit AU-COM2018-437. Molecular analyses were primarily supported by AIMS@JCU funding to H.B.H., a James Cook University postgraduate scholarship, and American-Australian Association Scholarship to M.R.M., with additional support from the ARC Centre of Excellence for Coral Reef Studies and the Australian Institute of Marine Science (AIMS). Funding for sample collection in the Great Barrier Reef was supported through Agouron and AIMS funding to L.K.B. and J.J.V.N. under GBRMPA Permits G16/38488, G19/43423.1, and G19/43148.1, as well as a James Cook University Postgraduate Research Scholarship to J.J.V.N.

Keywords: connectivity | coral reefs | genetic structure | genotype-by-sequencing | local adaptation | *Pocillopora* | seascape genomics | thermal stress

ABSTRACT

Aim: Understanding local adaptation in species along environmental gradients provides insight for how species can and will adapt to increasing climate-driven marine heatwaves. Here, the population structure of two closely related *Pocillopora* corals was evaluated across environmentally heterogeneous reef gradients to understand spatially variable adaptive potential of vulnerable species.

Location: Australia's Coral Sea and Great Barrier Reef Marine Parks span a ca. 1300 km latitudinal gradient across a 1.6°C range in Maximum Monthly Mean temperatures.

Method: A total of 255 colonies of *Pocillopora verrucosa* and 188 colonies of *Pocillopora* cf. *meandrina* were prepared and genotyped by sequencing using Illumina NovaSeq. Initial filtering and population statistics were conducted for each species. Correlations between genetic structure and environmental variables were assessed using partial redundancy analyses. The specific effects of environmental (including temperature, which was also analysed separately) and spatial variables were quantified to understand the drivers of local adaptation and how this varies across taxa and regions.

Results: Both species exhibited gene flow between the two reef systems (Coral Sea and Great Barrier Reef), indicating connectivity across ~12° of latitude and longitude. Population structure differed between species: *P.* cf. *meandrina* displayed pronounced genetic subdivision with two ancestral lineages partitioned along a north–south axis, while *P. verrucosa* maintained one dominant lineage across most reefs. In both species, population structure was shaped by ancestral lineage and thermal history. Additionally, *P.* cf. *meandrina* showed genetic structure correlated with sea current velocity, whereas *P. verrucosa* correlated with sea surface temperature.

https://doi.org/10.1111/ddi.70065

Main Conclusions: Closely related taxa can exhibit distinct population genetic patterns and environmental responses, reflecting different capacities for local adaptation. These results highlight the importance of incorporating multiple taxa and environmental variables when predicting responses to environmental change. Conservation strategies relying solely on environmental data may suffice for some species but not others.

1 | Introduction

Increasing sea surface temperatures and marine heatwaves are exposing corals to thermal pressures beyond their current limits (McManus et al. 2021). In response to such increasing thermal pressures, phenotypic variation in bleaching responses (i.e., the dissociation of the coral-Symbiodiniaceae relationship (Weis et al. 2008)) can result from either physiological acclimation within a generation (McRae et al. 2021; Yu et al. 2020), evolutionary adaptation of the host across multiple generations (Kenkel et al. 2013), or shifts in the coral's algal symbiont community (Symbiodiniaceae) (Berkelmans and Van Oppen 2006). The adaptive potential of coral reef communities is influenced by local abiotic and biotic factors (Savolainen et al. 2013), evidenced by variable bleaching responses both within and among populations (Dixon et al. 2015; Howells et al. 2016; Humanes et al. 2022), among species (Álvarez-Noriega et al. 2023), and between habitats (Marhoefer et al. 2021). Phenotypic variation occurs spatially across populations spanning vast latitudinal ranges (Ayre and Hughes 2000; Thomas et al. 2017), or highly variable temperature environments (Barshis et al. 2013; Bay and Palumbi 2014; Palumbi et al. 2014; Safaie et al. 2018). Documenting the adaptive potential of coral populations to a rapidly changing environment is crucial for understanding and predicting population trajectories under prolonged climate change.

Corals harbour the capacity to evolve in response to rapid environmental change, reliant on specific demographic traits (e.g., dispersal capacity, mode/rate of reproduction, thermal limits), which can facilitate adaptation to environmental disturbances (Hoffmann and Sgró 2011). The underlying processes that mediate population genetic structure across environmental gradients can also contribute to the adaptive potential of coral populations. For example, genetic drift and migration can alter the neutral and adaptive genetic structure among populations, while abiotic factors can drive divergence between populations, therefore reinforcing the genetic differentiation among populations (Riginos and Liggins 2013). Disentangling the processes of genetic drift and selection is complicated, particularly in broadcast spawning marine organisms with extensive pelagic larval phases (Lowe and Allendorf 2010). Broadcast spawners often have weak population structure due to the ability for larvae to disperse far from natal reefs, which can mask interactions between gene flow and the environment on the genetic structure of populations (Thomas et al. 2020). To separate these two components, it is necessary to investigate corals across large spatial gradients with contrasting environmental conditions or disturbance history. Doing so can elucidate the environmental patterns that shape both neutral and adaptive diversity of coral populations (Holderegger et al. 2006), and subsequently the potential for populations to withstand or recover from the impacts of recurrent disturbances.

The amount and direction of gene flow between coral reefs can shape population replenishment following disturbances (Bernhardt and Leslie 2013). These patterns are mediated by the spatial distance between reefs, sea currents, and physical geographic barriers (Keith et al. 2013; Wood et al. 2014). A range of biotic factors can also influence connectivity, including the development and behaviour of larvae, the duration of larval phases, and post-settlement survivorship of new recruits (Graham et al. 2008; Miller and Mundy 2003). Such abiotic and biotic factors can result in biogeographically isolated reefs with high population structure due to larger geographical distances and a paucity of source reefs for recruitment and population replenishment (Thomas et al. 2017). In contrast, reefs and species with higher connectivity promote the redistribution of standing genetic variation among populations and present an avenue for alleles increasing thermal tolerance to enter a population (Matz et al. 2018). Isolated reefs therefore benefit from stronger local adaptation to present environmental conditions in the absence of extensive dispersal (Borregaard et al. 2017; Santos et al. 2016), but simultaneously face heightened vulnerability to environmental change, due to lower connectivity and therefore lower larval replenishment potential following disturbances.

Coral genetic diversity mirrors taxa-specific reproductive modes and subsequent migration. Species of brooding corals release larvae that often settle close to, or within their natal reef, resulting in stronger genetic differentiation between reefs (Underwood et al. 2009; van der Ven et al. 2021). Broadcast spawning corals differ with a pelagic fertilisation and thus a greater dispersal range of larvae, resulting in higher genetic connectivity and weaker population structure among reefs (Afiq-Rosli et al. 2024; Buitrago-López et al. 2023; Underwood et al. 2020). Other processes may also play a role in shaping taxa-specific patterns of genetic diversity and connectivity, including geographical range margins within a species (Chevin and Bridle 2025; Keith et al. 2013; Schmidt-Roach et al. 2012). Most existing genomic studies of coral populations have targeted a single species to identify the specific extrinsic factors which shape neutral genetic structure (Selmoni, Bay, et al. 2024). Differentiating the amount of genetic variation associated with the environment presents a challenge when using a single study species due to species-specific rates of gene flow. Therefore, the parallel investigation of two or more congeneric species sharing similar life history traits (e.g., mode of reproduction, morphology) and habitats allows for a more comprehensive view of the specific environmental processes which drive genetic variation and whether these predictors are consistent across sympatric taxa.

A seascape genomics approach contextualises both neutral and adaptive genetic structure against environmental gradients and corridors or barriers to gene flow (Manel et al. 2003;

Saenz-Agudelo et al. 2015; Riginos et al. 2016; Selmoni et al. 2020). Using this approach, we assessed population structure and connectivity for two congeneric coral species, *Pocillopora verrucosa* and *Pocillopora* cf. *meandrina*, across the same environmentally heterogenous seascape. We also investigated the predominant abiotic factors that influence genetic variation, including the effects of (1) thermal and (2) non-thermal environmental predictors while controlling for spatial autocorrelation. The study area included two environmentally contrasting seascapes, Australia's Coral Sea Marine Park, which consists of geographically isolated atoll reefs forming distinct habitat patches, and the adjacent Great Barrier Reef, which maintains greater spatial connectivity among reefs via a higher density of reefs per km^2 (Ceccarelli et al. 2013; Hoey et al. 2022). Previous genetic studies that quantified population structure and/or gene flow of marine organisms between the Coral Sea and GBR demonstrated that a brooding coral (van Oppen et al. 2008) and a common coral grouper (Payet et al. 2022) maintained minimal connectivity between the Coral Sea and the GBR. This highlights the paucity of empirical data to determine the existing population structure and connectivity between these important reef systems. Both seascapes have been exposed to five recent mass bleaching events in 2016, 2017, 2020, 2022, and 2024 (Harrison et al. 2019; Hughes, Anderson, et al. 2018; Pratchett and Heron 2021), with bleaching susceptibility varying markedly across reefs and taxa (Burn et al. 2023). The detection of neutral and adaptive population structure in contrasting seascapes and species can provide a baseline to identify reefs which harbour higher genetic resilience amidst rapidly changing environmental conditions.

2 | Methods

2.1 | Coral Collection and Sampling

Two common Pocilloporid coral species, *Pocillopora* cf. *meandrina* and *Pocillopora verrucosa* , were collected, both of which are broadcast spawning corals (Schmidt-Roach et al. 2012) with vertical transmission of algal-symbionts (Hirose et al. 2000). Corals were collected from Australia's Great Barrier Reef (hereafter, GBR) and Coral Sea Marine Park (hereafter, Coral Sea) (Figure 1a). Corals were collected from 16 sites within the GBR and 13 sites within the Coral Sea, with tissue fragments (< 5 cm) from 188 *P.* cf. *meandrina* and 255 *P. verrucosa* coral colonies obtained across both regions and processed for downstream molecular analyses. The samples were collected on SCUBA at an average depth of 6.75 m (±0.28) from the GBR between January 2019 and April 2021 on four separate expeditions, and from the Coral Sea on one expedition between February and March 2020. Reef coordinates and details for all 29 sampling locations are specified in SOM Table S1. Samples were collected from distinct coral colonies > 5 m apart to minimise the likelihood of collecting clonal genotypes, of which none were detected. For each coral individual, photographs were taken at the colony and macro-scales using an Olympus TG-5, and bleaching scores were recorded in situ using a Coral Health Chart (Siebeck et al. 2006). A branch of each coral individual was collected using a hammer and chisel. Each individual fragment was placed into a separate, numbered Ziploc bag while under water and stored in 100% ethanol within 1 h of collection.

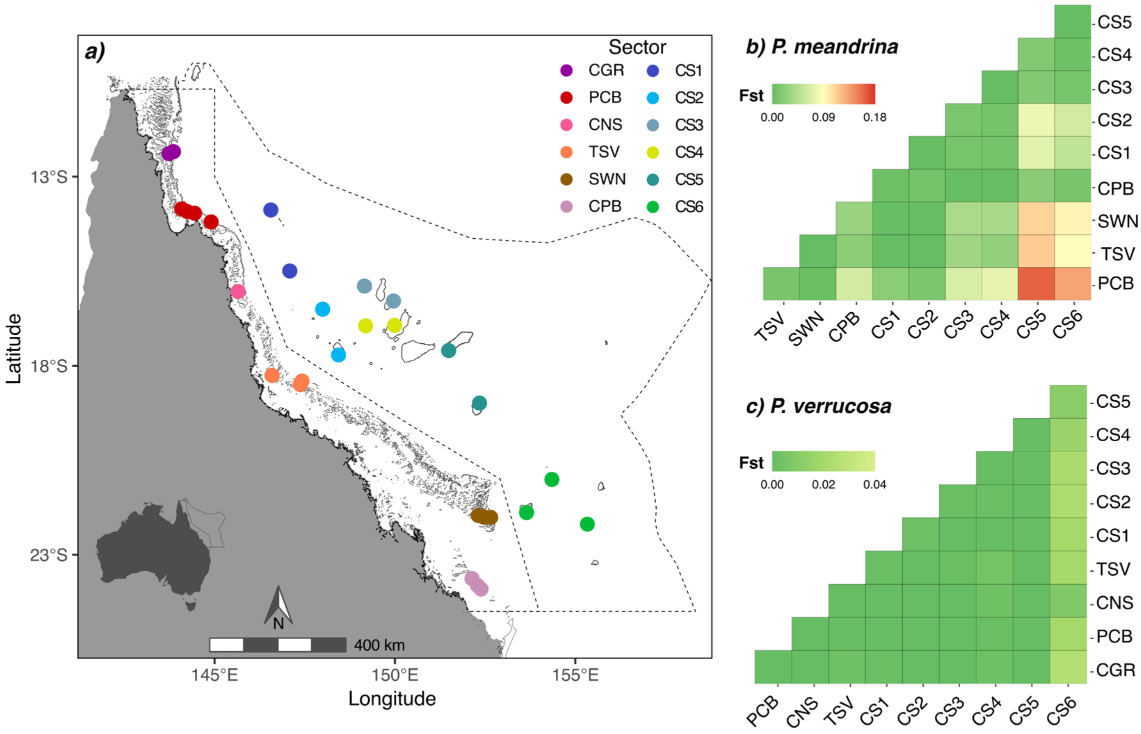

FIGURE 1 | Population structure for *Pocillopora* cf. *meandrina* and *P. verrucosa* across the GBR and Coral Sea. (a) Map of sectors partitioned in Australia's Great Barrier Reef (GBR) and Coral Sea Marine Park. Sectors considered in the analysis of population structure include: Cape Grenville (CGR), Princess Charlotte Bay (PCB), Cairns (CNS), Townsville (TSV), Swains (SWN), Capricorn Bunkers (CPB), Coral Sea sectors 1–6 (CS1-6). Pairwise comparisons of genetic diversity (F_{ST}) between sectors for (b) *Pocillopora* cf. *meandrina* and (c) for *Pocillopora verrucosa*.

2.2 | Species Identification and Sample Selection

Corals were first genetically identified to haplotype level by amplification of the mitochondrial open reading frame (mtORF) marker using two complementary approaches. First, we conducted a Restriction Fragment Length Polymorphism (RFLP) assay modified from Johnston et al. (2018) and detailed in Marzonie et al. (2023). We then used Sanger sequencing of the mtORF region to resolve any unidentified samples and to confirm identification from the RFLP assay with higher resolution. Samples confirmed as either *P. verrucosa* ($n=255$) or *P.* cf. *meandrina* ($n=188$) were selected for a genotype-by-sequencing approach. All samples that could not be identified to species using the RFLP assay or Sanger sequencing were excluded from further analyses. As both *P. meandrina* and *P. grandis* share the same mtORF region (type1/ORF27; Burgess et al. 2024), we cannot explicitly confirm the absence of *P. grandis* in our dataset. However, the morphology and genetic exchange between individuals sampled point to population structure rather than speciation, and we use the convention '*P.* cf. *meandrina*' to refer to this species complex throughout the paper.

2.3 | Genotype-By-Sequencing Approach

Coral tissue samples of *P. verrucosa* and *P.* cf. *meandrina* were sent to Diversity Arrays Technology (DArT, Canberra, Australia), where DNA extractions, library preparation, and sequencing were performed. Briefly, DNA was extracted from *Pocillopora* samples using a NucleoMag kit (Machery-Nagel). Libraries were constructed following a proprietary method of reduced-representation sequencing (DArT-seq; Kilian et al. 2012) following a double digestion with *Pst*I and *Hpa*II to maximise the complementarity of reads between samples (Sansaloni et al. 2011). The two *Pocillopora* species were sequenced on separate Illumina NovaSeq runs using 150 bp paired-end sequencing, each across two lanes. Sequencing reads from both *Pocillopora* species were mapped to the *P. verrucosa* reference genome from Buitrago-López et al. (2020), which is now recognised as the genome of *P. favosa* (Oury et al. 2025). In addition, a DArT species database was developed for each of the two species. Data were initially filtered using proprietary DArT-sequencing pipelines (DArTsoft14). Filtering was then performed on raw sequences using a minimum Phred pass score of 30 for the inline sample barcode region (used for demultiplexing), and a minimum Phred score of 10 for the entire read. Of the 255 samples of *P. verrucosa* , 206 (80.8%) passed initial quality control. Of the 188 samples of *P.* cf. *meandrina* submitted, 115 (61.2%) passed initial quality control and were used in downstream analyses.

2.4 | QC Filtering of SNPS

The initial filtering was conducted using the *dartR* package version 2.9.7 (Gruber et al. 2018) and filtering steps were carried out separately for the two *Pocillopora* species with identical filtering parameters. SNPs were filtered for linkage disequilibrium to retain a single SNP within a fragment when more than one SNP tag was detected. Loci were then filtered by call rate (<0.80) to exclude loci and/or individuals with more than 20% missing data. Further, loci with a mean read depth below 5× were removed from the analysis using the 'gl.filter.rdepth' function (*dartR*). SNPs with minor allele frequencies (MAF) below 0.05 were filtered out to minimise the effects of rare variants. Clone or duplicate samples were identified using the 'mlg.filter' function in *poppr* (Kamvar et al. 2015) and removed from downstream analyses. Missing data were imputed using the 'nearest neighbour' function (*dartR*) in order to run downstream multivariate statistics. Quality filtering resulted in the retention of 200 individuals for *P. verrucosa* and 108 individuals of *P.* cf. *meandrina*. The number of loci retained after each filtering step can be found in SOM Table S2. Multiple call rate filtering scenarios (threshold: 0.90, 0.85, 0.80) were tested for downstream estimates of pairwise genetic comparisons (F_{ST}) and multidimensional analyses to ensure that population estimates of F_{ST} were stable irrespective of filtering (SOM Figures S1–S4). Each filtered dataset was scanned for outlier loci using *PCAdapt* (Luu et al. 2017) and the 'gl.outflank' function in *dartR*. As either no or very few outlier loci were detected with either method (range: 0–11 SNPs), all downstream analyses were conducted using the full SNP datasets.

2.5 | Population Structure Analyses

Reefs were grouped into 'sectors' which were determined based on spatial proximity (Figure 1a) and pairwise comparisons of genetic structure, to balance sample sizes after molecular confirmation of *P. verrucosa* and *P.* cf. *meandrina*. The partitioning into sectors and additional collection metadata can be found in SOM Table S2. Heterozygosity (H_e and H_o) and inbreeding (F_{IS}) statistics for each sector were calculated using the package *hierfstat* (Goudet and Jombart 2022). Pairwise F_{ST} values using the 'WC84' method (*hierfstat*) were computed following Weir and Cockerham (1984). Additionally, five samples were randomly selected and subsampled from each sector and F_{ST} values were computed, where no strong effect of unbalanced sample sizes among sectors was detected (SOM, Figures S5 and S6). An Analysis of Molecular Variance (AMOVA) was run with 999 permutations in *poppr* (Kamvar et al. 2015) to assess the proportion of genetic variance explained within samples, between samples, and between sectors (SOM Tables S3–S4). To explore patterns of isolation-by-distance (IBD) between reefs, the relationship between the linearised genetic distance and the log of geographic distance was measured. Geographic distances were calculated as Euclidean distances between reef centroids using the 'gl.ibd' function (*dartR*), based on the average latitude and longitude of sampled sites at each reef. While these distances do not explicitly avoid landmasses, the open-ocean configuration of reefs in this region minimises potential land barriers. Significance of IBD was assessed using a Mantel test in *vegan* (Oksanen et al. 2022) (SOM Figure S7).

A principal component analysis (PCA) was performed to investigate genetic variation among samples without predictor constraints on population structure (SOM Figure S8). Group membership probabilities were then computed with admixture analysis using the 'snmf' function in *LEA* to define the number of *K*-clusters for each species and membership coefficients per individual (Frichot and François 2015). We selected the optimal number of *K* ancestral populations between 1 and

10 and chose the model with the lowest cross-entropy value (SOM Figure S9). Once the optimal *K* was selected, ten repetitions were performed, and the repetition with the lowest cross entropy was selected. We then extracted membership coefficients for each individual sample under the optimal number of *K*-clusters and plotted admixture coefficients in *ggplot2* (Wickham 2016).

2.6 | Full and Partial Redundancy Analyses

A redundancy analysis (RDA) was used to assess associations between environmental and host population structure, with individual-level SNP genotypes (allele counts per locus) as the response matrix in the *vegan* package (Oksanen et al. 2022). Environmental and spatial variables were extracted at the level of individual sampling location (i.e., reef). We included several predictors related to (1) climate (thermal-related), (2) environment (non-thermal related), and (3) geographic distance between reefs (Table 1). Climatic predictors were acquired from RECIFS (Selmoni et al. 2023). The selected variables included the mean of monthly maxima Degree Heating Weeks (max DHW) from 1985 to 2020, average Sea Surface Temperature (SST) (1985–2020), and Maximum Monthly Mean (MMM) climatology (1986–2012) (NOAA Coral Reef Watch; Liu et al. 2014). The average number of maximum DHW summarises heat stress trends per reef and correlates significantly both with heatwave frequency and maximal intensity of heatwaves (Selmoni, Cleves, and Exposito-Alonso 2024). Environmental predictors were acquired from RECIFS (Selmoni et al. 2023) and from eReefs (Australian Institute of Marine Science). The selected variables included light irradiance (kd490) and sea current velocity (SCV) of each reef (Table 1) (EU Copernicus Marine Service 2022). To account for the geographic and spatial proximity between reefs, distance-based Moran's Eigenvector Maps (db-MEMs) were used to estimate spatial distribution across sites at multiple spatial scales. Db-MEMs were extracted from each reef site using the 'dbMEM' function in *adespatial* (Dray et al. 2023) and used as conditional variables to account for geographic structure in the partial RDA models (SOM Figures S10 and S11).

TABLE 1 | Climatic, environmental, and geographic metrics used in redundancy analyses to determine the significant predictors of genetic variance in *Pocillopora verrucosa* and *P.* cf. *meandrina*.

Type of predictor	Variable	Definition
Climatic	Max DHW	The mean of monthly maxima degree heating weeks from 1985 to 2020
	Mean SST	The average sea surface temperature experienced from 1985 to 2020
	MMM	Maximum Monthly Mean climatology (1986–2012)
Environmental	Kd490	Light irradiance
	SCV	Mean sea current velocity
Geographic	MEM1	Moran eigenvector map (1)
	MEM2	Moran eigenvector map (2)
	MEM3	Moran eigenvector map (3)

After model construction, we checked for correlation among all climate, environment, and geographic predictors to minimise the effects of collinearity and randomly removed one of two variables when $r > |0.8|$ using 'Corrplot' (Wei and Simko 2021) (SOM Figure S12). Variance Inflation Factor (VIF) Scores of selected variables were < 5 and did not exhibit strong collinearity. A backward stepwise model was run with the selected variables using the 'Ordistep' function (*vegan*) which iteratively runs all factors and reduces the model until the highest adjusted R^2 value is reached. The significant factors from the Ordistep model were selected as the final predictors in each partial RDA model (Table 1).

Partial RDA models were then run for each species with identical predictor and response variables to identify the effects of thermal and environmental predictors (Capblancq and Forester 2021). We included two types of models where the dominant admixture coefficient served as (1) a predictor variable and (2) a constraining variable. In both model types, we constrained these for spatial autocorrelation (SOM Table S5). Constraining for the dominant admixture coefficient was used to control for the potential effects of two species and/or strong genetic partitioning present in the *P.* cf. *meandrina* dataset to unmask trends of environmental predictors on within-lineage genetic variance.

3 | Results

3.1 | Library Statistics

The genotype-by-sequencing analysis resulted in the detection of 43,980 single-nucleotide polymorphisms (SNPs) across 108 individuals for *P.* cf. *meandrina*, and 44,310 SNPs across 200 individuals for *P. verrucosa*. After quality filtering, a total of 2075 SNPs for *P.* cf. *meandrina* and 3722 SNPs for *P. verrucosa* were retained. There was no evidence of duplicate samples or clones observed for either species. The observed heterozygosity estimates were significantly higher for *P. verrucosa* (mean $H_o = 0.12 \pm 0.01$, SD) compared to *P.* cf. *meandrina* (mean $H_o = 0.06 \pm 0.01$, SD) across all individuals and sectors (*t*-test; $p < 0.001$, $t = 9.77$, Df $= 18$). Inbreeding coefficients, averaged across all sectors of the GBR and Coral Sea, were positive for both *P.* cf. *meandrina* (mean $F_{IS} = 0.259 \pm 0.03$, SD) and *P. verrucosa* (mean $F_{IS} = 0.209 \pm 0.05$, SD), and genetic diversity appeared higher within *P. verrucosa* populations (Table 2).

3.2 | Genetic Structure Among Regions and Sectors

Pairwise comparisons of global F_{ST} values revealed that *P.* cf. *meandrina* exhibited stronger overall population

TABLE 2 | Genetic diversity metrics for *Pocillopora verrucosa* and *Pocillopora cf. meandrina* across sectors in the GBR and CSMP.

		P. verrucosa					***P.* cf. *meandrina***				
Region	**Sector**	**N**	N_{QC}	H_o	H_e	F_{IS}	**N**	N_{QC}	H_o	H_e	F_{IS}
GBR	Cape Grenville	30	24	0.11	0.13	0.221	—	—	—	—	—
	Princess Charlotte Bay	30	23	0.11	0.13	0.223	19	13	0.07	0.12	0.229
	Cairns	8	5	0.11	0.13	0.192	—	—	—	—	—
	Townsville	30	15	0.11	0.13	0.235	7	4	0.04	0.13	0.229
	Swains	—	—	—	—	—	24	8	0.05	0.13	0.325
	Capricorn Bunkers	6	—	—	—	—	24	14	0.07	0.13	0.26
Coral Sea	CS1	29	29	0.11	0.14	0.239	14	8	0.06	0.13	0.285
	CS2	46	38	0.11	0.14	0.229	12	4	0.08	0.13	0.227
	CS3	24	20	0.11	0.14	0.214	28	18	0.07	0.13	0.283
	CS4	14	10	0.15	0.15	0.082	15	8	0.06	0.13	0.276
	CS5	31	31	0.12	0.14	0.225	17	8	0.07	0.12	0.223
	CS6	8	5	0.12	0.14	0.229	48	23	0.06	0.13	0.257

Note: The number of samples sequenced per species within each sector (N) and the corresponding number of samples passing quality control (N_{QC}). Population statistics calculated include observed heterozygosity (H_o), expected heterozygosity (H_e), and population-level F_{IS} statistics per coral species within each sector.

structure among reef sectors (F_{ST} range: 0–0.146; mean $F_{ST} = 0.030 \pm 0.035$), which were generally higher than pairwise comparisons among sectors for *P. verrucosa* (F_{ST} range: 0–0.024; mean $F_{ST} = 0.004 \pm 0.007$). The analysis of molecular variance (AMOVA) indicated that genetic differences between sectors were small but significant and stronger for *P.* cf. *meandrina* than *P. verrucosa* (*P.* cf. *meandrina* = 0.7%, $p = 0.04$; *P. verrucosa* = 0.1%; $p = 0.02$). AMOVA results also revealed higher genetic variation between colonies within a sector than between sectors alone (*P.* cf. *meandrina* = 36.6%; *P. verrucosa* = 25.9%; $p < 0.001$), supporting high within-population variation in genetic structure.

Pocillopora verrucosa demonstrated overall weaker population structure compared to *P.* cf. *meandrina*. Except for CS6, all sectors and regions displayed extremely low population structure for *P. verrucosa* (F_{ST} range: 0–0.009) (Figure 1c). The strongest genetic differences were detected within reefs of the Coral Sea, between the highest latitude sector (CS6) and the two lowest latitude sectors, CS1 and CS2 (F_{ST} range: 0.021–0.024). Similar levels of genetic differences were also observed between the lowest latitude sectors in the GBR, Cape Grenville and PCB (F_{ST} range: 0.021–0.022), suggesting comparably low rates of genetic structure within and between regions for this species. Stronger sector-level genetic differences for *P.* cf. *meandrina* occurred between spatial extremes in the sampling, namely a low latitude sector of the GBR (Princess Charlotte Bay) and the two highest latitude sectors of the Coral Sea (CS5, CS6). The highest latitude Coral Sea sectors (CS5, CS6) and the GBR were genetically similar in population structure (Capricorn Bunkers; F_{ST} range: 0.007–0.018). Interestingly, there were greater genetic differences between CS5 and CS6 and the geographically closer, offshore Swains reefs (F_{ST} range: 0.084–0.105) (Figure 1b), indicating that geographic distance was not the predominant influence on population structure.

Isolation-by-distance (IBD) models revealed a stronger relationship between geographic and genetic distances for *P. verrucosa* ($R^2 = 0.325$; $p = 0.038$) that was predominantly driven by high latitude reef sectors in the Coral Sea (CS5 and CS6). In comparison, patterns of isolation-by-distance in *P.* cf. *meandrina* were 6-fold weaker ($R^2 = 0.058$; $p = 0.058$) (Figure S3).

3.3 | Model-Based Estimation of Ancestry

Admixture analyses indicated the presence of two distinct genetic clusters for *Pocillopora* cf. *meandrina*, PMCL1 and PMCL2, which were detected across all sectors within the GBR and Coral Sea (Figure 2a,c). Although both genetic lineages were evenly present in the study area (frequency of PMCL1 = 47.0%; PMCL2 = 52.9%), their relative abundance varied markedly by region. The two lineages were unevenly distributed throughout the two regions, where PMCL1 was found in higher prevalence across the GBR (72.6%) compared to the Coral Sea (32.6%). Conversely, PMCL2 was found more commonly in the Coral Sea (67.3%) compared to the GBR (27.3%) (Figure 2a,c). Within regions, PMCL2 was significantly more abundant in high latitude sectors of the Coral Sea (CS5 and CS6) and the southern GBR while PMCL1 was detected in higher abundance in low latitude sectors of the Coral Sea and GBR (Figure 2a,c; *t*-test; $F_1 = 23.34$, $p < 0.001$). The genetic cluster PMCL1 comprised a significantly higher proportion of sampled colonies in Princess Charlotte Bay and Townsville (69.9%), compared to CS5 and CS6 (12.3%) (*t*-test; $F_1 = 37.72$, $p = 0.03$). The detection of PMCL1 increased in the Coral Sea in lower latitude reefs, comprising 70.0% of group membership in CS1 and CS2. The Swains sector of the GBR represented higher group membership to PMCL1 (87.1%) than the Capricorn Bunker region (62.9%), despite the Swains sector being in geographical proximity to the CS5 and CS6 sectors where high PMCL2 group membership occurred (87.7%) (Figure 2a,c).

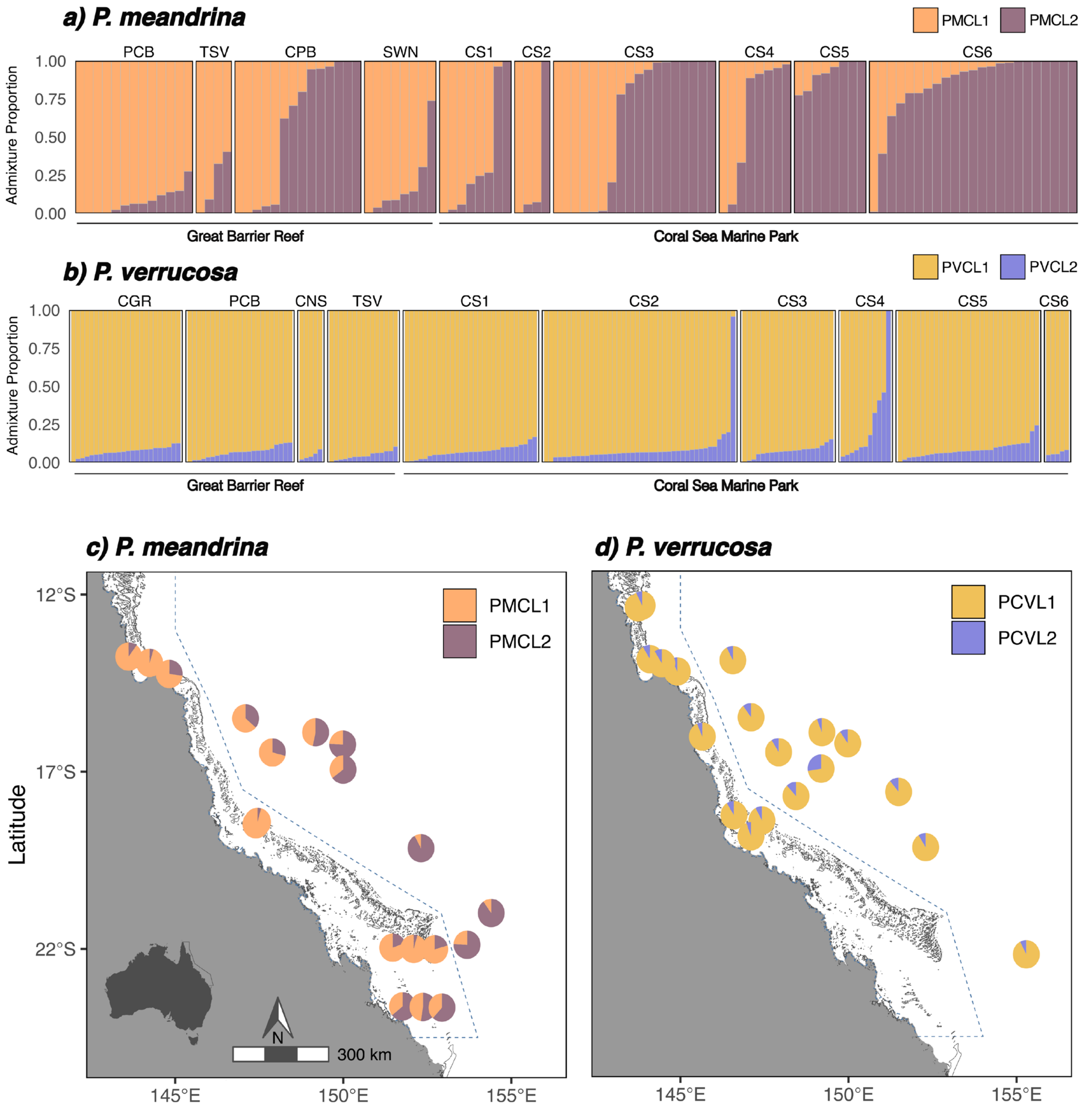

FIGURE 2 | Genetic membership probability and clustering of *Pocillopora* cf. *meandrina* and *P. verrucosa*. Admixture analyses indicated two genetic clusters ($K=2$) for both species, including (a) *P.* cf. *meandrina* (PMCL1 and PMCL2) and (b) *P. verrucosa* (PVCL1 and PVCL2). Each vertical bar depicts one individual and the estimated ancestry coefficient to each cluster. Admixture coefficients in relation to biogeographic patterns of structure for (c) *P.* cf. *meandrina* and (d) *P. verrucosa*.

Two distinct genetic clusters for *P. verrucosa* (PVCL1 and PVCL2) were detected through admixture analysis across the GBR and Coral Sea (Figure 2b,d). There was less defined spatial structuring in *P. verrucosa* compared to *P. meandrina* across both regions. The minimal spatial structuring in *P. verrucosa* was attributed to a dominance of the lineage PVCL1 which accounted for an average membership coefficient of 86.3% per individual across both regions. In contrast, PVCL2 represented 13.6% of membership across all sectors. There were not significant differences in the proportion of PVCL1 and PVCL2 between the GBR and Coral Sea, where PVCL1 made up 92.1% of group membership in samples across the GBR region and 83.5% of samples in the Coral Sea (Figure 2b,d; *t*-test; $F_1=2.01$, $p=0.194$). The proportion of group membership to PVCL2 ranged markedly from 6.2% in the lowest latitude GBR sector (Cape Grenville) to 72.5% in the highest latitude Coral Sea sector (CS6) (Figure 2b,d) and was significantly different between the three highest latitude, offshore reefs (CS4, CS5, and CS6) compared to all other reefs (Figure 2b,d; *t*-test; $F_1=15.78$, $p<0.001$).

3.4 | Environmental Correlations With Individual Genetic Structure

A partial redundancy analysis (pRDA) revealed that genetic differences among individuals were partially attributed to a combination of climatic and environmental gradients throughout the two reef regions, while accounting for spatial autocorrelation. The two main axes of variation explained 5.2% of genetic variation in *P.* cf. *meandrina*, compared to 0.2% of genetic variation in *P. verrucosa* . For *P.* cf. *meandrina*, the first axis alone explained 4.2% of genetic variation among samples and was significantly associated with both thermal history (mean maximum Degree Heating Weeks [DHW]) and sea current velocity (SCV). The second axis had negligible influence from both significant predictors, explaining 1.0% of variation (Figure 3a). The significant predictors of *P.* cf. *meandrina* in the partial RDA model included mean SCV ($F_1 = 2.77$, $p < 0.001$) and max DHW ($F_1 = 1.98$, $p = 0.003$) (Table 2). Individual genetic differences between *P. verrucosa* were associated only with thermal metrics compared to non-thermal predictors. However, the first axis explained only 0.1% of variation and was associated with mean Sea Surface Temperature (SST), while the second axis explained an additional 0.1% of variation and was associated with thermal disturbance history (max DHW) (Figure 3b). For *P. verrucosa*, genetic variation was significantly explained by mean SST ($F_1 = 1.71$, $p < 0.001$) and max DHW ($F_1 = 1.15$, $p < 0.001$) (Table 2).

In parallel, a partial RDA with the additional predictor of admixture coefficients (genetic lineage) indicated that the genetic structure of *P. verrucosa* was still explained by the same thermal predictors including max DHW ($F_1 = 1.08$, $p = 0.024$) and mean SST ($F_1 = 1.08$, $p = 0.038$), as well as by ancestry ($F_1 = 2.03$, $p < 0.001$) (SOM Table S5). In the model with admixture coefficients as an added predictor, the genetic structuring of *P.* cf. *meandrina* was only explained by the dominant ancestry ($F_1 = 12.12$, $p < 0.001$) with no significant thermal or environmental variables when including admixture coefficients as a predictor (SOM Table S5).

3.5 | Spatial Distribution of Environmental Predictors Across the Coral Sea and GBR

Climate history over the past 35 years, including maximum DHW and mean SST (Figure 4a,b) and sea current velocity (Figure 4c), was the strongest predictor of genetic structure across the two regions for both *P.* cf. *meandrina* and *P. verrucosa* when accounting for the conditional effects of geographic distance. Notably, the high latitude reefs of the Coral Sea had

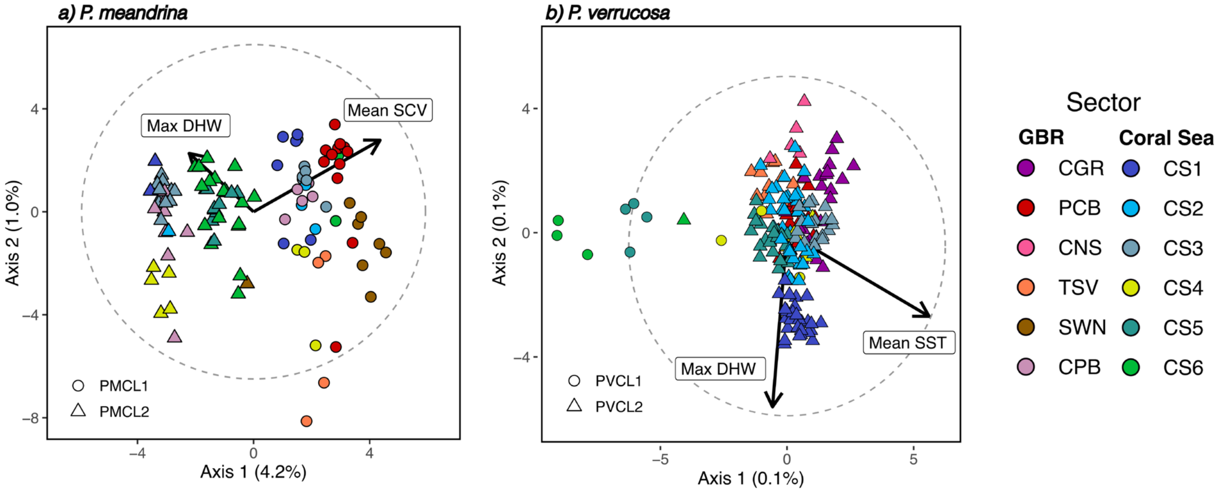

FIGURE 3 | Partial redundancy analysis (pRDA) for the environmental drivers of genetic structure among individuals in (a) *P.* cf. *meandrina* and (b) *P. verrucosa* . Plots are coloured by sectors within the Great Barrier Reef (GBR) and Coral Sea Marine Parks. Vectors indicate environmental predictors which are significant in the partial RDA models (Table 3).

TABLE 3 | Backward stepwise partial redundancy analysis outputs for the environmental predictors of individual genetic structure for *Pocillopora* cf. *meandrina* and *P. verrucosa*.

Species	Variable	Df	Variance	*F*	Pr (> F)
P. cf. *meandrina*	Max DHW	1	11.15	1.9843	0.003
	Mean SCV	1	15.59	2.7738	0.001
	Residual	103	579.01		
P. verrucosa	Max DHW	1	7.96	1.1463	0.001
	Mean SST	1	11.86	1.7088	0.001
	Residual	175	1214.50		

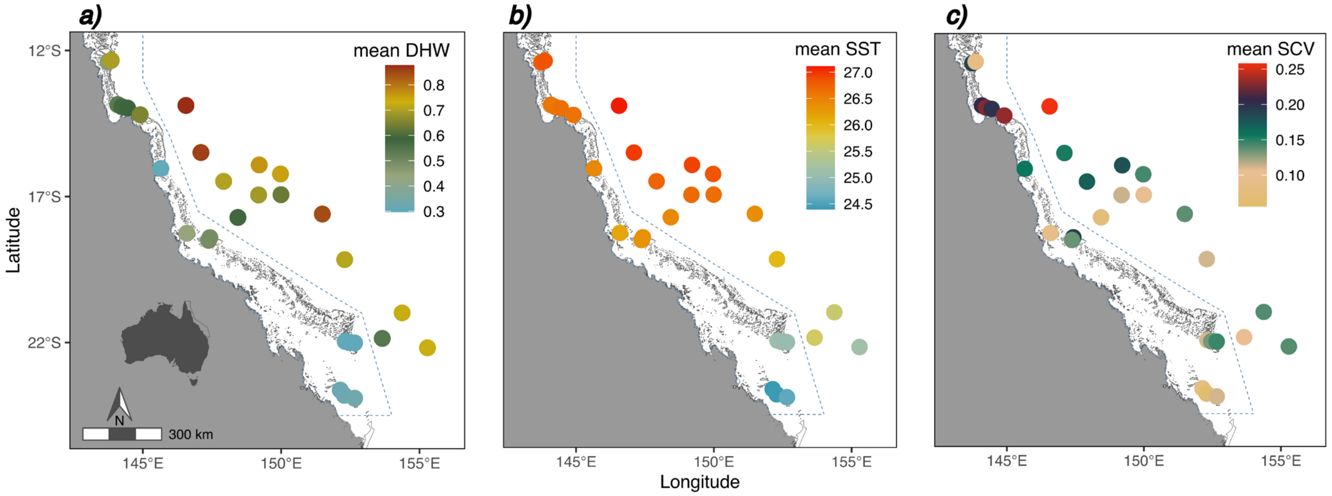

FIGURE 4 | Spatial distribution of significant model predictors for *P.* cf. *meandrina* and *P. verrucosa* across the Great Barrier Reef and Coral Sea Marine Parks. (a) Max DHW refers to the mean of monthly Maximum DHW experienced at each reef. (b) Mean SST refers to the average sea surface temperature at each location. (c) Mean SCV refers to the strength of sea current velocity at each reef. All variables are averaged between 1985 and 2020 using 5 km resolution.

contrasting patterns of thermal and environmental variation compared to adjacent reefs in the GBR (Figure 4a–c). The mean of maximum DHW ranged between 0.30 and 0.69 DHW in the GBR and 0.54–0.88 DHW in the Coral Sea and varied significantly by region (Figure 4a; *t*-test; $F_1 = 37.15$, $p < 0.001$). In contrast, the average SST ranged between 24.39°C and 26.85°C in the GBR and 25.16°C–27.11°C in the Coral Sea and was not significantly variable by region (Figure 4b; *t*-test; $F_1 = 3.00$, $p = 0.09$). Between the two regions, the strength of sea current velocity was not significantly variable between the GBR (0.06–0.23 m/s) and the Coral Sea (0.07–0.26 m/s) (Figure 4c; *t*-test; $F_1 = 0.11$, $p = 0.74$).

The South Equatorial Current bifurcates at ~15° latitude, where currents split in a north and southern trajectory (Ceccarelli et al. 2013; Sun et al. 2024). Grouping across latitude, the northern/central and southern sectors demonstrated significantly variable patterns in average SST (Figure 4b; *t*-test; $F_1 = 6.48$, $p = 0.01$) and the strength of sea current velocity (Figure 4c; *t*-test; $F_1 = 17.62$, $p < 0.001$). However, the mean of maximum DHW did not vary significantly between the northern/central and southern sectors (Figure 4a; *t*-test; $F_1 = 0.86$ $p = 0.36$).

4 | Discussion

Few studies to date have assessed the population structure and connectivity of corals between the Coral Sea and GBR, which are key metrics to quantify the genetic diversity and connectivity of these ecologically important seascapes. Our analyses revealed the genetic structure of Pocilloporids across reefs and regions in the Coral Sea and GBR spanning 12° in both latitude and longitude. The presence of gene flow across large seascapes indicates evidence for gene flow between the GBR and Coral Sea, with important implications for co-management of marine estates in both the GBR and Coral Sea Marine Parks (Roberts et al. 2021). The taxa-specific variability in population structure occurred for two closely related Pocilloporids, where *Pocillopora* cf. *meandrina* maintained higher population structure compared to *P. verrucosa*. These taxa-specific disparities in genetic structure emphasise the importance of quantifying gene–environment trends even in taxa with similar demographic traits. Further, the genetic structure of both species of Pocilloporids correlated with a gradient in thermal history across the GBR and Coral Sea, as well as sea surface temperature for *P. verrucosa* and sea current velocity for *P.* cf. *meandrina*, indicating gene–environment interactions associated with contemporary and historical environmental gradients.

4.1 | High Latitude Reefs Are Genetically Distinct

High latitude, offshore reef populations maintained the strongest genetic separation for both *Pocillopora* species. Specifically, high latitude reefs in the Coral Sea were most genetically distinct from low latitude reefs in the GBR. This genetic structuring indicates potential edge effects of species existing close to their environmental or thermal range limits, with cascading effects on their genetic structure (Ries et al. 2004). The geographic isolation of high latitude reefs may promote greater local adaptation, but also vulnerability, following disturbances (Hughes, Kerry, et al. 2018). High latitude reefs in the Coral Sea and GBR have experienced higher recent thermal disturbance (recent maximum DHW between 2016 and 2020) compared to lower latitude reefs, potentially leading to selection for more heat tolerant species and individuals (Marzonie et al. 2023). The observed genetic differentiation of high latitude reefs may therefore reflect selection for traits associated with heat tolerance. Similar patterns of genetic differentiation have been demonstrated in high latitude reef populations in Western Australia, where strong population structure has been quantified compared to lower latitude and spatially proximate reefs (Thomas et al. 2017). Our study corroborates this evidence in Eastern Australian coral reefs, suggesting local adaptation to environment in isolated, high latitude populations.

4.2 | Population Structure Varies in Sympatric Species

Comparisons across Pocilloporids with similar traits (e.g., broadcast spawners with vertical symbiont transmission) revealed the importance of quantifying population structure and connectivity not only in distinct, but also co-occurring and sympatric taxa. There are several biological and environmental factors that contribute to the patterns observed in the genetic structure of the two Pocilloporid species. First, *Pocillopora verrucosa* has a higher thermal tolerance than *P.* cf. *meandrina*, which has been empirically quantified through controlled heat stress experiments (Marzonie et al. 2023) and is evidenced by variable distribution across warmer and cooler reefs in both the Coral Sea and GBR in this study, as well as across Hawaiian reefs in Johnston et al. (2018). The thermal limits of these species may in part explain the contrasting genetic patterns observed in this study. The stronger population structure observed in *P.* cf. *meandrina* may also be influenced by the presence of additional taxa (e.g., *P. grandis/P. eydouxi*), cryptic speciation (Riginos et al. 2024), or hybridisation, factors which cannot be resolved using the mitochondrial ORF marker alone (Burgess et al. 2024).

The disparities in population structure among the two Pocilloporids are potentially driven by early divergence in the *P.* cf. *meandrina* host and their symbiont communities. The strong division among two symbiont groups residing in the tissue of *P.* cf. *meandrina* (*Cladocopium latusorum* 'north' and 'south') compared to *P. verrucosa* (*Cladocopium pacificum*) across the Coral Sea (Marzonie et al. 2024) is mirrored in trends of host population structure here, indicating that the rapid generation time of symbionts and high-resolution SNP data of the coral host elucidate early signals of genetic subdivision among populations (but not the less rapidly evolving mitochondrial marker of the host). Panmictic populations comprising high gene flow have been observed in *P. verrucosa* across the Western Indian Ocean (Oury et al. 2021; Oury et al. 2023), Eastern African coast (Chiazzari et al. 2019) and Red Sea (Buitrago-López et al. 2023). In contrast, Oury et al. (2021) observed stronger population structure in the *P. meandrina/P. eydouxi* species complex across New Caledonia reefs, reflecting the trends observed in this study. Species-specific population structure has also been observed in two brooding *Pocillopora* species in New Caledonia, where *P. damicornis* comprised higher population structure than *P. acuta* (Selmoni et al. 2021), consistent with the taxa-specific variability observed in this study and highlighting the importance of interspecific studies to identify patterns of local adaptation and connectivity.

4.3 | Potential Climatic, Environmental, and Geographic Drivers of Genetic Structure

Climatic factors were the strongest drivers of the population structure for both species. Maximum Degree Heating Weeks was a stronger predictor compared to non-thermal geographic predictors for both Pocilloporids, highlighting the significant influence of marine heatwaves on population structure across distinct regions and species over a short ecological and evolutionary timeframe (1985–2020). Additionally, the co-dominant clusters of *P.* cf. *meandrina* were influenced by sea current velocity, indicating that non-thermal factors might also play a role in shaping the higher partitioning of population structure observed. Mean current speed has been shown to be a predictor of genetic structure in the brooding coral species, *Stylophora pistillata*, across the GBR (Meziere et al. 2024), corroborating evidence of oceanographic processes in driving population structure. The Southern Equatorial Current bifurcates north and south in the Coral Sea and GBR at between 15° and 17° latitude dependent on depth (Ceccarelli et al. 2013; Sun et al. 2024) and might explain the strong geographic partitioning in the two genetic lineages of *P.* cf. *meandrina* (PMCL1 and PMCL2) and the stronger associations of non-thermal predictors for this species. However, *P. verrucosa* was correlated only with thermal predictors including SST and DHW, where several genetically distinct individuals in the high latitude, Coral Sea reefs strongly influenced this trend. These patterns suggest that local adaptation in these reefs may be driven by their variation in thermal histories (Burn et al. 2023; Harrison et al. 2019; Marzonie et al. 2023). Given samples were genetically confirmed as *P. verrucosa* and *P.* cf. *meandrina* with multiple genetic markers (mtORF marker, SNPs), this trend is likely not an artefact of sampling or sequencing, but potentially a biological signal of adaptation and/or this species reaching the end of their thermal range limits in high latitude reefs.

An important caveat to note with gene–environment associations (i.e., partial RDAs) is that many of the tested variables are likely correlated, and signals of one predictor may also be explained by the influence of other untested predictors that were removed due to high collinearity (Capblancq and Forester 2021). Here, we aimed to reduce the effects of collinearity by accounting for both dominant ancestral lineages (genetic covariate) and spatial autocorrelation when determining the main thermal and environmental predictors driving population genetic structure. *Pocillopora verrucosa* maintained significant genetic variance driven by both maximum DHW and mean SST, indicating that both genetic groups (PVCL1 and PVCL2) are using the same loci and/or gene groups to adapt to environmental variation. In contrast, *P.* cf. *meandrina* had more pronounced patterns of genetic specialisation to differential habitats given the contrasting spatial structuring of the two lineages (PMCL1 and PMCL2). However, the lack of significant environmental predictors when accounting for the dominant ancestral lineage in *P.* cf. *meandrina* indicates difficulties in disentangling the relative influence of predictors (ancestral lineage, environment, geographical partitioning) on the population genetic structure in this species.

5 | Conclusion

This study presented an opportunity to measure the population structure of two common Pocilloporid coral species in the GBR and Coral Sea. The genetic variation of *Pocillopora* cf. *meandrina* and *P. verrucosa* was associated with thermal history, suggesting that population structure in *Pocillopora* spp. may have been influenced by the severity of disturbance history experienced at reefs, as well as the variation in the frequency and magnitude of these disturbances among reefs and regions. Our study provides a strong foundation for aligning the variation of thermal and environmental clines with the genetic structure of corals across large marine seascapes. The detection of environmental trends that shape the genetic structure of coral populations and species can improve our understanding of how reefs are naturally equipped to adapt or respond to the effects of thermal and environmental disturbances.

Author Contributions

M.R.M., H.B.H., J.J.V.N., and L.K.B. designed the experimental collection. M.R.M., H.B.H., J.J.V.N, and L.K.B. conducted the field work. M.R.M. and J.J.V.N. conducted the laboratory work. M.R.M., O.S., M.R.N., and H.B.H. analysed the data. M.R.M. wrote the original draft of the manuscript. All authors provided critical edits to the manuscript.

Acknowledgements

We acknowledge the Meriam Traditional Owners of the Coral Sea Marine Park, and Traditional Owners of the Great Barrier Reef, and their role as the first ecologists and custodians of the land and sea country where we conduct our work. The authors also thank Veronique Mocellin, Kirsty Frith, Darren Anderson, Gina Matthews, Johnston Davidson, Alyssa Budd, the AIMS Long Term Monitoring Program, and the crews of the RV Solander and RV Cape Ferguson for field support on GBR collection trips. We thank Cpt Rob Benn and the Iron Joy crew for support at sea during Coral Sea collection trips. We are grateful for advice from Erika Johnston on molecular assays for Pocilloporid identification and advice from Luke Thomas on sampling protocols for both Pocillopora identification and DArT-sequencing methods. We thank the team at Diversity Arrays Technology for quality control assistance and the development of SNP panels. The findings and views expressed are those of the authors and do not necessarily represent the views of Parks Australia, the Director of National Parks, or the Australian Government. Open access publishing facilitated by James Cook University, as part of the Wiley - James Cook University agreement via the Council of Australian University Librarians.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data and scripts for host population genetic analyses are publicly available at the Github repository https://github.com/magenamarzonie/Pocillopora2020 and as a static Dryad release. https://datadryad.org/share/ua5QxO1KWDuT_Tp6iOhTqqvu-nVznz0rcp4SSoNa9U8. The raw sequence data for both Pocilloporids are available under NCBI BioProject PRJNA1046121. The authors would appreciate being notified if you intend to use these data or analyses in your own work.

Peer Review

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ddi.70065.

References

Afiq-Rosli, L., B. J. Wainwright, J. N. Lee, Z. Waheed, L. M. Chou, and D. Huang. 2024. "Contrasting Patterns of Population Genomic Structure Between Broadcast-Spawning and Brooding Corals in Southeast Asia." *Diversity and Distributions* 30: e13940. https://doi.org/10.1111/ddi.13940.

Álvarez-Noriega, M., I. Marrable, S. H. C. Noonan, D. R. Barneche, and J. C. Ortiz. 2023. "Highly Conserved Thermal Performance Strategies May Limit Adaptive Potential in Corals." *Proceedings of the Royal Society B: Biological Sciences* 290, no. 1990: 20221703. https://doi.org/10.1098/rspb.2022.1703.

Ayre, D. J., and T. P. Hughes. 2000. "Genotypic Diversity and Gene Flow in Brooding and Spawning Corals Along the Great Barrier Reef, Australia." *Evolution* 54, no. 5: 1590–1605. https://doi.org/10.1111/j.0014-3820.2000.tb00704.x.

Barshis, D. J., J. T. Ladner, T. A. Oliver, F. O. Seneca, N. Traylor-Knowles, and S. R. Palumbi. 2013. "Genomic Basis for Coral Resilience to Climate Change." *Proceedings of the National Academy of Sciences of the United States of America* 110, no. 4: 1387–1392. https://doi.org/10.1073/pnas.1210224110.

Bay, R. A., and S. R. Palumbi. 2014. "Multilocus Adaptation Associated With Heat Resistance in Reef-Building Corals." *Current Biology* 24, no. 24: 2952–2956. https://doi.org/10.1016/j.cub.2014.10.044.

Berkelmans, R., and M. J. H. Van Oppen. 2006. "The Role of Zooxanthellae in the Thermal Tolerance of Corals: A "Nugget of Hope" for Coral Reefs in an Era of Climate Change." *Proceedings of the Royal Society B: Biological Sciences* 273: 2305–2312. https://doi.org/10.1098/rspb.2006.3567.

Bernhardt, J. R., and H. M. Leslie. 2013. "Resilience to Climate Change in Coastal Marine Ecosystems." *Annual Review of Marine Science* 5: 371–392. https://doi.org/10.1146/annurev-marine-121211-172411.

Borregaard, M. K., I. R. Amorim, P. A. V. Borges, et al. 2017. "Oceanic Island Biogeography Through the Lens of the General Dynamic Model: Assessment and Prospect." *Biological Reviews* 92, no. 2: 830–853. https://doi.org/10.1111/brv.12256.

Buitrago-López, C., A. Cárdenas, B. C. C. Hume, et al. 2023. "Disparate Population and Holobiont Structure of Pocilloporid Corals Across the Red Sea Gradient Demonstrate Species-Specific Evolutionary Trajectories." *Molecular Ecology* 32: 2151–2173. https://doi.org/10.1111/mec.16871.

Buitrago-López, C., K. G. Mariappan, A. Cárdenas, H. M. Gegner, and C. R. Voolstra. 2020. "The Genome of the Cauliflower Coral *Pocillopora verrucosa*." *Genome Biology and Evolution* 12: 1911–1917. https://doi.org/10.1093/gbe/evaa184.

Burgess, S. C., A. M. Turner, and E. C. Johnston. 2024. "Niche Breadth and Divergence in Sympatric Cryptic Coral Species (*Pocillopora* spp.) Across Habitats Within Reefs and Among Algal Symbionts." *Evolutionary Applications* 17, no. 8: e13762.

Burn, D., A. S. Hoey, S. Matthews, H. B. Harrison, and M. S. Pratchett. 2023. "Differential Bleaching Susceptibility Among Coral Taxa and Colony Sizes, Relative to Bleaching Severity Across Australia's Great Barrier Reef and Coral Sea Marine Parks." *Marine Pollution Bulletin* 191: 114907. https://doi.org/10.1016/j.marpolbul.2023.114907.

Capblancq, T., and B. R. Forester. 2021. "Redundancy Analysis: A Swiss Army Knife for Landscape Genomics." *Methods in Ecology and Evolution* 12, no. 12: 2298–2309. https://doi.org/10.1111/2041-210X.13722.

Ceccarelli, D. M., A. D. McKinnon, S. Andréfouët, et al. 2013. "The Coral Sea. Physical Environment, Ecosystem Status and Biodiversity Assets." In *Advances in Marine Biology*. Academic Press. https://doi.org/10.1016/B978-0-12-408096-6.00004-3.

Chevin, L. M., and J. Bridle. 2025. "Impacts of Limits to Adaptation on Population and Community Persistence in a Changing Environment." *Philosophical Transactions B* 380, no. 1917: 20230322.

Chiazzari, B., H. Magalon, P. Gélin, and A. Macdonald. 2019. "Living on the Edge: Assessing the Diversity of South African *Pocillopora* on the Margins of the Southwestern Indian Ocean." *PLoS One* 14: 220477. https://doi.org/10.1371/journal.pone.0220477.

Dixon, G. B., S. W. Davies, G. A. Aglyamova, E. Meyer, L. K. Bay, and M. V. Matz. 2015. "Genomic Determinants of Coral Heat Tolerance Across Latitudes." *Science* 348, no. 6242: 1460. https://doi.org/10.1126/science.1261224.

Dray, S., D. Bauman, G. Blanchet, et al. 2023. Adespatial: Multivariate Multiscale Spatial Analysis. https://github.com/sdray/adespatial.

EU Copernicus Marine Service. 2022. Global Ocean- In-Situ-Near-Real-Time Observations.

Frichot, E., and O. François. 2015. "LEA: An R Package for Landscape and Ecological Association Studies." *Methods in Ecology and Evolution* 6, no. 8: 925–929. https://doi.org/10.1111/2041-210X.12382.

Goudet, J., and T. Jombart. 2022. Hierfstat: Estimation and Tests of Hierarchical F-Statistics. https://CRAN.R-project.org/package=hierfstat.

Graham, E. M., A. H. Baird, and S. R. Connolly. 2008. "Survival Dynamics of Scleractinian Coral Larvae and Implications for Dispersal." *Coral Reefs* 27, no. 3: 529–539. https://doi.org/10.1007/s00338-008-0361-z.

Gruber, B., P. J. Unmack, O. F. Berry, and A. Georges. 2018. "Dartr: An r Package to Facilitate Analysis of SNP Data Generated From Reduced Representation Genome Sequencing." *Molecular Ecology Resources* 18: 691–699. https://doi.org/10.1111/1755-0998.12745.

Harrison, H. B., M. Álvarez-Noriega, A. H. Baird, S. F. Heron, C. MacDonald, and T. P. Hughes. 2019. "Back-To-Back Coral Bleaching Events on Isolated Atolls in the Coral Sea." *Coral Reefs* 38: 713–719. https://doi.org/10.1007/s00338-018-01749-6.

Hirose, M., R. A. Kinzie, and M. Hidaka. 2000. "Early Development of Zooxanthella-Containing Eggs of the Corals *Pocillopora verrucosa* and *P. Eydouxi* With Special Reference to the Distribution of Zooxanthellae." *Biological Bulletin* 199, no. 1: 68–75. https://doi.org/10.2307/1542708.

Hoey, A., E. McClure, D. Burn, et al. 2022. *Coral Sea Marine Park Coral Reef Health Survey 2022*. Parks Australia.

Hoffmann, A. A., and C. M. Sgró. 2011. "Climate Change and Evolutionary Adaptation." *Nature* 470, no. 7335: 479–485. https://doi.org/10.1038/nature09670.

Holderegger, R., U. Kamm, and F. Gugerli. 2006. "Adaptive vs. Neutral Genetic Diversity: Implications for Landscape Genetics." *Landscape Ecology* 21, no. 6: 797–807. https://doi.org/10.1007/s10980-005-5245-9.

Howells, E. J., D. Abrego, E. Meyer, N. L. Kirk, and J. A. Burt. 2016. "Host Adaptation and Unexpected Symbiont Partners Enable Reef-Building Corals to Tolerate Extreme Temperatures." *Global Change Biology* 22, no. 8: 2702–2714. https://doi.org/10.1111/gcb.13250.

Hughes, T. P., K. D. Anderson, S. R. Connolly, et al. 2018. "Spatial and Temporal Patterns of Mass Bleaching of Corals in the Anthropocene." *Science* 359: 80–83. https://doi.org/10.1126/science.aan8048.

Hughes, T. P., J. T. Kerry, A. H. Baird, et al. 2018. "Global Warming Transforms Coral Reef Assemblages." *Nature* 556, no. 7702: 492–496. https://doi.org/10.1038/s41586-018-0041-2.

Humanes, A., L. Lachs, E. A. Beauchamp, et al. 2022. "Within-Population Variability in Coral Heat Tolerance Indicates Climate Adaptation Potential." *Proceedings of the Royal Society B* 289, no. 1981: 20220872.

Johnston, E. C., Z. H. Forsman, and R. J. Toonen. 2018. "A Simple Molecular Technique for Distinguishing Species Reveals Frequent Misidentification of Hawaiian Corals in the Genus *Pocillopora*." *PeerJ* 2018, no. 2: 1–14. https://doi.org/10.7717/peerj.4355.

Kamvar, Z. N., J. C. Brooks, and N. J. Grünwald. 2015. "Novel R Tools for Analysis of Genome-Wide Population Genetic Data With Emphasis on Clonality." *Frontiers in Genetics* 6: 208. https://doi.org/10.3389/fgene.2015.00208.

Keith, S. A., A. H. Baird, T. P. Hughes, J. S. Madin, and S. R. Connolly. 2013. "Faunal Breaks and Species Composition of Indo-Pacific Corals: The Role of Plate Tectonics, Environment and Habitat Distribution." *Proceedings of the Royal Society B: Biological Sciences* 280, no. 1763: 20130818. https://doi.org/10.1098/rspb.2013.0818.

Kenkel, C. D., G. Goodbody-Gringley, D. Caillaud, S. W. Davies, E. Bartels, and M. V. Matz. 2013. "Evidence for a Host Role in Thermotolerance Divergence Between Populations of the Mustard Hill Coral (*Porites astreoides*) From Different Reef Environments." *Molecular Ecology* 22, no. 16: 4335–4348. https://doi.org/10.1111/mec.12391.

Kilian, A., P. Wenzl, E. Huttner, et al. 2012. "Diversity Arrays Technology: A Generic Genome Profiling Technology on Open Platforms." *Methods in Molecular Biology* 888: 67–89. https://doi.org/10.1007/978-1-61779-870-2_5/COVER.

Liu, G., S. F. Heron, C. M. Eakin, et al. 2014. "Reef-Scale Thermal Stress Monitoring of Coral Ecosystems: New 5-Km Global Products From NOAA Coral Reef Watch." *Remote Sensing* 6, no. 11: 11579–11606. https://doi.org/10.3390/rs61111579.

Lowe, W. H., and F. W. Allendorf. 2010. "What Can Genetics Tell Us About Population Connectivity?" *Molecular Ecology* 19, no. 15: 3038–3051. https://doi.org/10.1111/j.1365-294X.2010.04688.x.

Luu, K., E. Bazin, and M. G. Blum. 2017. "pcadapt: An R Package to Perform Genome Scans for Selection Based on Principal Component Analysis." *Molecular Ecology Resources* 17, no. 1: 67–77.

Manel, S., M. K. Schwartz, G. Luikart, and P. Taberlet. 2003. "Landscape Genetics: Combining Landscape Ecology and Population Genetics." *Trends in Ecology & Evolution* 18, no. 4: 189–197.

Marhoefer, S. R., K. R. Zenger, J. M. Strugnell, et al. 2021. "Signatures of Adaptation and Acclimatization to Reef Flat and Slope Habitats in the Coral *Pocillopora damicornis*." *Frontiers in Marine Science* 8: 704709. https://doi.org/10.3389/fmars.2021.704709.

Marzonie, M. R., L. K. Bay, D. G. Bourne, et al. 2023. "The Effects of Marine Heatwaves on Acute Heat Tolerance in Corals." *Global Change Biology* 29: 1–416. https://doi.org/10.1111/gcb.16473.

Marzonie, M. R., M. R. Nitschke, L. K. Bay, D. G. Bourne, and H. B. Harrison. 2024. "Symbiodiniaceae Diversity Varies by Host and Environment Across Thermally Distinct Reefs." *Molecular Ecology* 33: e17342. https://doi.org/10.1111/mec.17342.

Matz, M. V., E. A. Treml, G. V. Aglyamova, and L. K. Bay. 2018. "Potential and Limits for Rapid Genetic Adaptation to Warming in a Great Barrier Reef Coral." *PLoS Genetics* 14: e1007220. https://doi.org/10.1371/journal.pgen.1007220.

McManus, L. C., D. L. Forrest, E. W. Tekwa, et al. 2021. "Evolution and Connectivity Influence the Persistence and Recovery of Coral Reefs Under Climate Change in the Caribbean, Southwest Pacific, and Coral Triangle." *Global Change Biology* 27, no. 18: 4307–4321. https://doi.org/10.1111/gcb.15725.

McRae, C. J., W. B. Huang, T. Y. Fan, and I. M. Côté. 2021. "Effects of Thermal Conditioning on the Performance of Pocillopora Acuta Adult Coral Colonies and Their Offspring." *Coral Reefs* 40, no. 5: 1491–1503. https://doi.org/10.1007/s00338-021-02123-9.

Meziere, Z., I. Popovic, K. Prata, I. Ryan, J. Pandolfi, and C. Riginos. 2024. "Exploring Coral Speciation: Multiple Sympatric *Stylophora pistillata* Taxa Along a Divergence Continuum on the Great Barrier Reef." *Evolutionary Applications* 17, no. 1: e13644. https://doi.org/10.1111/eva.13644.

Miller, K., and C. Mundy. 2003. "Rapid Settlement in Broadcast Spawning Corals: Implications for Larval Dispersal." *Coral Reefs* 22, no. 2: 99–106. https://doi.org/10.1007/s00338-003-0290-9.

Oksanen, J., G. L. Simpson, F. G. Blanchet, et al. 2022. Vegan: Community Ecology Package. https://CRAN.R-project.org/package=vegan.

Oury, N., M. L. Berumen, G. Paulay, and F. Benzoni. 2025. "One Species to Rule Them All: Genomics Sheds Light on the *Pocillopora* Species Diversity and Distinctiveness Around the Arabian Peninsula." *Coral Reefs* 44: 983–998. https://doi.org/10.1007/s00338-025-02659-0.

Oury, N., P. Gélin, and H. Magalon. 2021. "High Connectivity Within Restricted Distribution Range in *Pocillopora* Corals." *Journal of Biogeography* 48, no. 7: 1679–1692. https://doi.org/10.1111/JBI.14104.

Oury, N., S. Mona, and H. Magalon. 2023. “Same Places, Same Stories? Genomics Reveals Similar Structuring and Demographic Patterns for Four *Pocillopora* Coral Species in the Southwestern Indian Ocean.” *Journal of Biogeography* 51: 754–768. https://doi.org/10.1111/jbi.14788.

Palumbi, S. R., D. J. Barshis, N. Traylor-Knowles, and R. A. Bay. 2014. “Mechanisms of Reef Coral Resistance to Future Climate Change.” *Science* 344, no. 6186: 895–898. https://doi.org/10.1126/science.1251336.

Payet, S. D., M. S. Pratchett, P. Saenz-Agudelo, M. L. Berumen, J. D. DiBattista, and H. B. Harrison. 2022. “Demographic Histories Shape Population Genomics of the Common Coral Grouper (*Plectropomus leopardus*).” *Evolutionary Applications* 15: 1221–1235. https://doi.org/10.1111/eva.13450.

Pratchett, M. S., and S. F. Heron. 2021. “Recurrent Mass-Bleaching and the Potential for Ecosystem Collapse on Australia's Great Barrier Reef.” In *Ecosystem Collapse and Climate Change*, edited by R. B. Canadell Josep and G. Jackson, 265–289. Springer International Publishing. https://doi.org/10.1007/978-3-030-71330-0_10.

Ries, L., R. J. Fletcher, J. Battin, and T. D. Sisk. 2004. “Ecological Responses to Habitat Edges: Mechanisms, Models, and Variability Explained.” *Annual Review of Ecology, Evolution, and Systematics* 35: 491–522. https://www.jstor.org/stable/30034125.

Riginos, C., E. D. Crandall, L. Liggins, P. Bongaerts, and E. A. Treml. 2016. “Navigating the Currents of Seascape Genomics: How Spatial Analyses Can Augment Population Genomic Studies.” *Current Zoology* 62: 581–601. https://doi.org/10.1093/cz/zow067.

Riginos, C., and L. Liggins. 2013. “Seascape Genetics: Populations, Individuals, and Genes Marooned and Adrift.” *Geography Compass* 7, no. 3: 197–216. https://doi.org/10.1111/gec3.12032.

Riginos, C., I. Popovic, Z. Meziere, et al. 2024. “Cryptic Species and Hybridisation in Corals: Challenges and Opportunities for Conservation and Restoration.” *Peer Community Journal* 4: e106.

Roberts, K. E., C. N. Cook, J. Beher, and E. A. Treml. 2021. “Assessing the Current State of Ecological Connectivity in a Large Marine Protected Area System.” *Conservation Biology* 35, no. 2: 699–710. https://doi.org/10.1111/cobi.13580.

Saenz-Agudelo, P., J. D. Dibattista, M. J. Piatek, et al. 2015. “Seascape Genetics Along Environmental Gradients in the Arabian Peninsula: Insights From ddRAD Sequencing of Anemonefishes.” *Molecular Ecology* 24, no. 24: 6241–6255.

Safaie, A., N. J. Silbiger, T. R. McClanahan, et al. 2018. “High Frequency Temperature Variability Reduces the Risk of Coral Bleaching.” *Nature Communications* 9: 1671. https://doi.org/10.1038/s41467-018-04074-2.

Sansaloni, C., C. Petroli, D. Jaccoud, et al. 2011. “Diversity Arrays Technology (DArT) and Next-Generation Sequencing Combined: Genome-Wide, High Throughput, Highly Informative Genotyping for Molecular Breeding of Eucalyptus.” *BMC Proceedings* 5, no. S7: P54. https://doi.org/10.1186/1753-6561-5-s7-p54.

Santos, A. M. C., R. Field, and R. E. Ricklefs. 2016. “New Directions in Island Biogeography.” *Global Ecology and Biogeography* 25, no. 7: 751–768. https://doi.org/10.1111/geb.12477.

Savolainen, O., M. Lascoux, and J. Merilä. 2013. “Ecological Genomics of Local Adaptation.” *Nature Reviews Genetics* 14, no. 11: 807–820. https://doi.org/10.1038/nrg3522.

Schmidt-Roach, S., K. J. Miller, E. Woolsey, G. Gerlach, and A. H. Baird. 2012. “Broadcast Spawning by Pocillopora Species on the Great Barrier Reef.” *PLoS One* 7, no. 12: e50847. https://doi.org/10.1371/journal.pone.0050847.

Selmoni, O., L. K. Bay, M. Exposito-Alonso, and P. A. Cleves. 2024. “Finding Genes and Pathways That Underlie Coral Adaptation.” *Trends in Genetics* 40: 213–227. https://doi.org/10.1016/j.tig.2024.01.003.

Selmoni, O., P. A. Cleves, and M. Exposito-Alonso. 2024. “Global Coral Genomic Vulnerability Explains Recent Reef Losses.” *BioRxiv*. e586253.

Selmoni, O., G. Lecellier, V. Berteaux-Lecellier, and S. Joost. 2023. “The Reef Environment Centralized InFormation System (RECIFS): An Integrated Geo-Environmental Database for Coral Reef Research and Conservation.” *Global Ecology and Biogeography* 32, no. 5: 622–632. https://doi.org/10.1111/geb.13657.

Selmoni, O., G. Lecellier, H. Magalon, et al. 2021. “Seascape Genomics Reveals Candidate Molecular Targets of Heat Stress Adaptation in Three Coral Species.” *Molecular Ecology* 30, no. 8: 1892–1906. https://doi.org/10.1111/mec.15857.

Selmoni, O., E. Rochat, G. Lecellier, V. Berteaux-Lecellier, and S. Joost. 2020. “Seascape Genomics as a New Tool to Empower Coral Reef Conservation Strategies: An Example on North-Western Pacific *Acropora digitifera*.” *Evolutionary Applications* 13: 1923–1938. https://doi.org/10.1111/eva.12944.

Siebeck, U. E., N. J. Marshall, A. Klüter, and O. Hoegh-Guldberg. 2006. “Monitoring Coral Bleaching Using a Colour Reference Card.” *Coral Reefs* 25, no. 3: 453–460. https://doi.org/10.1007/s00338-006-0123-8.

Sun, C., C. Steinberg, E. K. Salas, et al. 2024. “OCEANOGRAPHY Climate Refugia in the Great Barrier Reef May Endure Into the Future.” *Science Advances* 10: eado6884. https://www.science.org.

Thomas, L., W. J. Kennington, R. D. Evans, G. A. Kendrick, and M. Stat. 2017. “Restricted Gene Flow and Local Adaptation Highlight the Vulnerability of High-Latitude Reefs to Rapid Environmental Change.” *Global Change Biology* 23, no. 6: 2197–2205. https://doi.org/10.1111/gcb.13639.

Thomas, L., J. N. Underwood, A. A. S. Adam, et al. 2020. “Contrasting Patterns of Genetic Connectivity in Brooding and Spawning Corals Across a Remote Atoll System in Northwest Australia.” *Coral Reefs* 39, no. 1: 55–60. https://doi.org/10.1007/s00338-019-01884-8.

Underwood, J. N., Z. Richards, O. Berry, D. Oades, A. Howard, and J. P. Gilmour. 2020. “Extreme Seascape Drives Local Recruitment and Genetic Divergence in Brooding and Spawning Corals in Remote North-West Australia.” *Evolutionary Applications* 13, no. 9: 2404–2421. https://doi.org/10.1111/eva.13033.

Underwood, J. N., L. D. Smith, M. J. H. van Oppen, and J. P. Gilmour. 2009. “Ecologically Relevant Dispersal of Corals on Isolated Reefs: Implications for Managing Resilience.” *Ecological Applications* 19, no. 1: 18–29. https://doi.org/10.1890/07-1461.1.

van der Ven, R. M., H. Heyndrickx, and M. Kochzius. 2021. “Differences in Genetic Diversity and Divergence Between Brooding and Broadcast Spawning Corals Across Two Spatial Scales in the Coral Triangle Region.” *Marine Biology* 168, no. 2: 17. https://doi.org/10.1007/s00227-020-03813-8.

van Oppen, M. J. H., A. Lutz, G. De'ath, L. Peplow, and S. Kininmonth. 2008. “Genetic Traces of Recent Long-Distance Dispersal in a Predominantly Self-Recruiting Coral.” *PLoS One* 3, no. 10: 1–12. https://doi.org/10.1371/journal.pone.0003401.

Wei, T., and V. Simko. 2021. R Package “Corrplot”: Visualization of a Correlation Matrix. https://github.com/taiyun/corrplot.

Weir, B. S., and C. C. Cockerham. 1984. “Estimating F-Statistics for the Analysis of Population.” *Structure* 38: 1358.

Weis, V. M., S. K. Davy, O. Hoegh-Guldberg, M. Rodriguez-Lanetty, and J. R. Pringle. 2008. “Cell Biology in Model Systems as the Key to Understanding Corals.” *Trends in Ecology & Evolution* 23, no. 7: 369–376. https://doi.org/10.1016/j.tree.2008.03.004.

Wickham, H. 2016. *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag New York. https://ggplot2.tidyverse.org.

Wood, S., C. B. Paris, A. Ridgwell, and E. J. Hendy. 2014. “Modelling Dispersal and Connectivity of Broadcast Spawning Corals at the Global

Scale." *Global Ecology and Biogeography* 23, no. 1: 1–11. https://doi.org/10.1111/geb.12101.

Yu, X., K. Yu, W. Huang, et al. 2020. "Thermal Acclimation Increases Heat Tolerance of the Scleractinian Coral *Acropora pruinosa*." *Science of the Total Environment* 733: 139319. https://doi.org/10.1016/j.scitotenv.2020.139319.

Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Table S1:** List of sample collection reefs, their assigned sector groupings, latitude, longitude, and Maximum Monthly Mean for each reef. **Table S2:** The number of loci retained after each filtering parameter for *Pocillopora meandrina* and *Pocillopora verrucosa*. **Table S3:** Analysis of Molecular Variance (AMOVA) summary statistics for *P. meandrina* to assess the proportion of genetic variance explained within samples, between samples, and among sectors. **Table S4:** Analysis of Molecular Variance (AMOVA) summary statistics for *P. verrucosa* to assess the proportion of genetic variance explained within samples, between samples, and among sectors. **Table S5:** Backward stepwise partial redundancy analysis outputs for the environmental predictors of individual genetic structure while accounting for the effects of admixture coefficients as a predictor variable. Model results are separate for *Pocillopora meandrina* and *P. verrucosa*. **Figure S1:** Genetic pairwise comparisons (F_{ST}) for *Pocillopora meandrina* using three call rate scenarios (0.90, 0.85, and 0.80) across populations. **Figure S2:** Principal component analyses for *Pocillopora meandrina* using three call rate scenarios (0.90, 0.85, and 0.80). Points are coloured by sector. **Figure S3:** Genetic pairwise comparisons (F_{ST}) for *Pocillopora verrucosa* using three call rate scenarios (0.90, 0.85, and 0.80) across populations. **Figure S4:** Principal component analyses for *Pocillopora verrucosa* using three call rate scenarios (0.90, 0.85, and 0.80). Points are coloured by sector. **Figure S5:** ddi70065-sup-0001-DataS1.docx. *Pocillopora meandrina* genetic pairwise comparisons (F_{ST}) for a subset reduced to $n=5$ randomly subsampled from each sector (left) compared to the full model with all samples present (right). **Figure S6:** ddi70065-sup-0001-DataS1.docx. *Pocillopora verrucosa* genetic pairwise comparisons (F_{ST}) for a subset reduced to $n=5$ randomly subsampled from each sector (left) compared to the full model with all samples present (right). **Figure S7:** Isolation-by-distance models for *P. meandrina* (left) and *P. verrucosa* (right) using the log of geographic distance vs. genetic distance (F_{st}/1-F_{st}), including significance and correlation using a Mantel test. **Figure S8:** A principal component analysis (PCA) illustrates the neutral population structure of *P. meandrina* (left) and *P. verrucosa* (right). Individual genetic distances (points) are coloured by region (top), longitude (middle), and latitude (bottom). **Figure S9:** Cross-entropy criterion showing optimal K-cluster value for *P. meandrina* (left) and *P. verrucosa* (right). **Figure S10:** Distance-based Moran Eigenvector Models (db-MEMs) for *Pocillopora meandrina*. **Figure S11:** Distance-based Moran Eigenvector Models (db-MEMs) for *Pocillopora verrucosa*. **Figure S12:** Correlation plots for climate, environmental, and geographic drivers of host population structure for *P. meandrina* (left) and *P. verrucosa* (right). Only numeric factors are shown.