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Genetic divergence and range expansion in a western North Pacific coral

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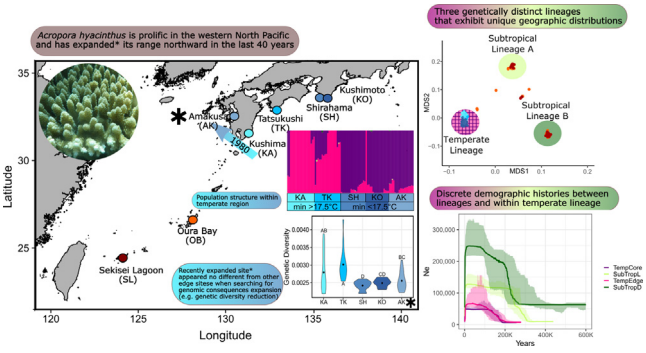
HIGHLIGHTS

- Three cryptic *Acropora hyacinthus* lineages with distinct contemporary and historical distributions
- Temperate lineage is genetically differentiated between range edge and core populations
- Genomic signatures of potential local adaptation reflecting different environmental conditions at the range edge

GRAPHICAL ABSTRACT



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ABSTRACT

Coral poleward range expansions have recently been observed in response to warming oceans. Range expansion can lead to reduced genetic diversity and increased frequency of deleterious mutations that were rare in core populations, potentially limiting the ability for adaptation and persistence in novel environments. Successful expansions that overcome these founder effects and colonize new habitat have been attributed to multiple introductions from different sources, hybridization with native populations, or rapid adaptive evolution. Here, we investigate population genomic patterns of the reef-building coral *Acropora hyacinthus* along a latitudinal cline that includes a well-established range expansion front in Japan using 2b-RAD sequencing. A total of 184 coral samples were collected across seven sites spanning from ~24°N to near its northern range front at ~33°N. We uncover the presence of three cryptic lineages of *A. hyacinthus*, which occupy discrete reefs within this region. Only one lineage is present along the expansion front and we find evidence for its historical occupation of marginal habitats. Within this lineage we also find evidence of bottleneck pressures associated with expansion events including higher clonality, increased linkage disequilibrium, and lower genetic diversity in range edge populations compared to core populations. Asymmetric migration between populations was also detected with lower migration from edge sites. Lastly, we describe genomic signatures of local adaptation potentially attributed to lower winter temperatures experienced at the more recently expanded northern populations. Together these data illuminate the genomic consequences of range expansion in a coral and highlight how adaptation to discrete environments along expansion fronts may facilitate further range expansion in this temperate coral lineage.

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1. Introduction

Populations are often adapted to local environmental conditions (i.e. local adaptation) that allow them to thrive. Large-scale environment changes influence these niche conditions and can result in expansion, contraction, or extinction of populations or entire species (Travis, 2003). Poleward expansions in response to warming oceans are a recent trend, with some species increasingly found in higher latitudes (also referred to as tropicalization), specifically in regions where habitats are degraded or altered (Hickling et al., 2006).

An expanding population can experience strong neutral and non-neutral processes that leave signatures in the genome. Neutral founder effects can randomly change allele frequencies (Hallatschek et al., 2007; Excoffier and Ray, 2008) and low frequency alleles can thereby 'surf' on the wave of expansion leading to high frequencies at the range front (Klopfstein et al., 2006a; Hallatschek and Nelson, 2008). These neutral processes can lead to reductions in genetic diversity (Watts et al., 2010; Garroway et al., 2011; Swaegers et al., 2015), higher mutational load if deleterious alleles surf (Peischl et al., 2013), and false signatures of selection (Excoffier and Ray, 2008; Klopfstein et al., 2006a; Edmonds et al., 2004). In contrast, non-neutral effects associated with range expansion can produce strong selective pressures through spatial sorting (Shine et al., 2011), where colonizers of new edge populations have high dispersal abilities (Swaegers et al., 2015; Hill et al., 2011) and/or natural selection when there is some fitness benefit to being an early colonizer (Travis and Dytham, 2002). Additionally, expansion into new environments implies that populations are exposed to novel (i.e. not experienced at their natal habitat) selection pressures; for poleward expansion, this entails selection pressures imposed by different temperature regimes (i.e. increased seasonality) (Lancaster et al., 2015; Dudaniec et al., 2018).

Understanding how an organism's range responds to environmental change is particularly important for species that are biological pillars for essential ecosystems, as corals are to coral reefs. Corals are some of the world's most important habitat-forming marine organisms, however their recent declines are global in scale (Hughes et al., 2017). Their sensitivity to temperature (Hughes et al., 2017) and rapid dispersal capabilities (routinely >10 km/year; reviewed in Jones et al., 2009) mark corals as candidates for range expansion under predicted future warming (IPCC, 2014). The survival of coral species under a changing climate might depend on their ability to successfully shift their ranges; however, studies examining coral range expansion often focus on survey data (Yamano et al., 2011a; Baird et al., 2012; de Oliveira Soares et al., 2018; Nakabayashi et al., 2017) with fewer taking a population genetics approach to range expansion (Leydet et al., 2018; Nakabayashi et al., 2019).

In Japan, the coral *Acropora hyacinthus* has been observed to expand its range (Yamano et al., 2011), which has been correlated with rising temperatures in the region, with temperature increases of 0.5 °C/decade between 1982 and 2010 (Lima and Wethey, 2012). These increases are likely mediated by the nearby Kuroshio Current's high sea surface temperature (SST) warming rate (two to three times faster than the global mean SST warming rate) (Wu et al., 2012). This ocean warming has promoted macroalgal-to-coral phase shifts both directly, by increased competition from the expansion of tropical corals into the contracting temperate macroalgae range, and indirectly, via deforestation by the expansion of tropical herbivorous fish (Kumagai et al., 2018). However, historically (~5000 years ago) corals existed even further north than their current range limits when temperatures were 2–4 °C higher than today (Veron, 1992a), suggesting that, like other organisms in this region (Han et al., 2020), corals may contract and expand along coastal Japan in response to glacial cycles.

Recent studies focusing on *A. hyacinthus* in Japan have provoked intriguing questions related to their population genetic patterns. Using nuclear and mitochondrial markers, (Suzuki et al., 2016) found that recently expanded populations showed reduced genetic diversity, which is expected along an expansion front (Excoffier et al., 2009). Additionally, they discovered the presence of four genetically distinct *A. hyacinthus* lineages in the region. Only one of these lineages (HyaD) existed within the temperate region, while all four were found in the southern Ryukyus with HyaD becoming progressively rarer in southern islands. Nakabayashi et al. (2019) found three genetically distinct lineages of *A. hyacinthus* using microsatellite markers and confirmed the presence of only one lineage within the temperate region. This divergence between mainland Japan and the Ryukyus has also been observed for a number of terrestrial (reviewed in Komaki and Igawa, 2017) and marine species (Mukai et al., 2004; Liu et al., 2008; Kojima et al., 2006; Yasuda et al., 2009; Albinsky et al., 2018; Tsang et al., 2008; Xu et al., 2009; Kuriiwa et al., 2014; He et al., 2015; Chang et al., 2017; Yasuda et al., 2021) between the terrestrial biogeographical barrier called the Watase line (also referred to as the Tokara gap). This temperate-subtropical genetic separation has been attributed to allopatric speciation during glacial maximums (Xu et al., 2009; He et al., 2015; Chang et al., 2017; Yamazaki et al., 2017), the opening and closing of oceanographical barriers facilitated by shifts in the Kuroshio current during glacial maximums (Liu et al., 2008; Kojima et al., 2006; Kuriiwa et al., 2014; Yamazaki et al., 2017), and divergent environmental selection pressures (Yasuda et al., 2009; Albinsky et al., 2018; Takeuchi et al., 2020).

Here, we examine populations of the coral *A. hyacinthus* near their range edge surrounding mainland Japan, which includes a recently colonized site (~40 years; Yamano et al., 2011), and nearby populations in the subtropical Ryukyus islands (Fig. 1). We expand on previous studies in this region that used limited markers by leveraging 2b-RAD-seq to examine 1000 s of loci. These additional loci allow us to employ demographic and outlier analyses as well as elucidate finer scale population structure that may have previously been overlooked due to limited marker resolution. Using population genomics, we 1) identify *A. hyacinthus* cryptic lineages and their associated distributions and demography, 2) further explore the recent range expansion and core-edge population genomic dynamics within the temperate region, and 3) investigate potential loci under selection on the range expansion front that might confer local adaptation to differential environmental conditions experienced across the temperate range.

2. Methods

2.1. Sample collection, sequencing and pre-processing

2.1.1. Coral colony sampling and 2b-RAD-seq library preparations

Fragments of *A. hyacinthus* colonies (33–50 colonies/site between 5 and 300 cm in diameter) were collected from seven sites in Japan between 2009 and 2016 via SCUBA (Supp. Table 1; Fig. 1) under prefectural permit 21–18, 24–36, 25–44 and with agreement from local fishermen's unions. Samples were identified as *A. hyacinthus* using gross morphology from descriptions by Veron (1992b). Samples were photographed and a subsample of five cm skeletal voucher fragments were stored at the University of Miyazaki (MUFS-Acr371–428, 500–531). Samples were immediately preserved in 99% ethanol, stored at −20 °C, and transferred to the United States under CITES permit (13JP002699/TE, 14JP000665/TE, T-WA-12-001588, T-WA-13-002421, T-WA-14-00589). DNA was isolated using a modified phenol-chloroform extraction method (Davies et al., 2013), cleaned with ZYMO-DNA-clean-and-concentrator kits, and resulting extracts were prepared for 2b-RAD-sequencing following Wang et al. (2012) to sequence a subset of the approximately 1.2×10^8 bp *A. hyacinthus* genome (López-Nandam et al., n.d.). Eight replicate samples were prepared to assist with clone identification. A total of 188 samples (19–40 samples per site; Supp. Table 1) were successfully barcoded and sequenced across four lanes of Illumina HiSeq 2500, High Output v4 using single-end 50 bp at Tufts University Core Facility (TUCF) (library sizes, coverage and mapping rates are available in Supp. File 1).

2.1.2. Genotype calling

Raw reads were trimmed, deduplicated and quality filtered with FASTX TOOLKIT (http://hannonlab. cshl.edu/fastx_toolkit) and only reads with Phred scores >20 were maintained (-q 20 -p 100). Quality-filtered reads were mapped to the *Acropora millepora* genome (Fuller et al., 2019) via bowtie2 (Langmead and Salzberg L, 2013). *Acropora millepora* and

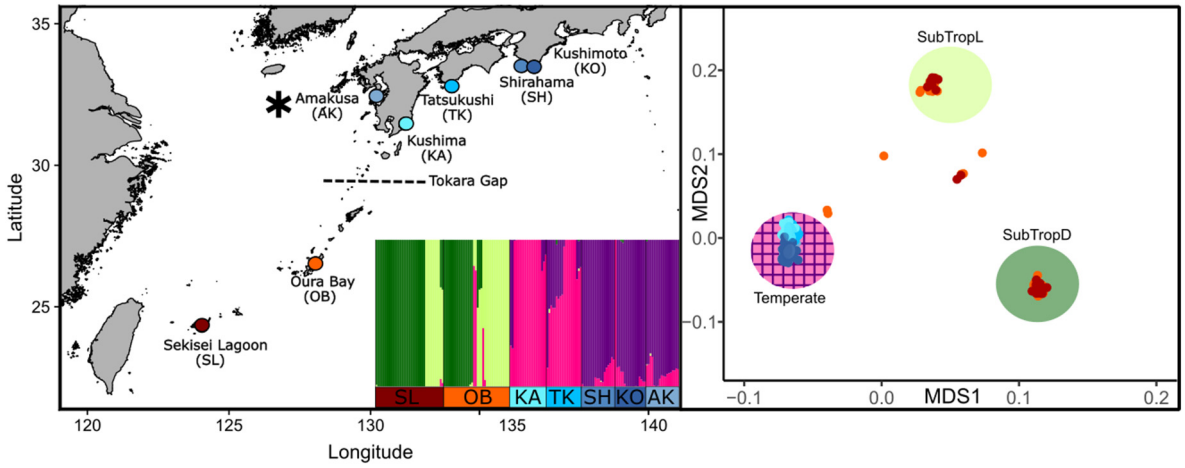

Fig. 1. Left panel: Map of all *Acropora hyacinthus* collection sites in Japan including site names (abbreviation). Asterisk denotes recently expanded site (in the last 40 years), Amakusa. Inset: Results from ADMIXTURE analysis where each bar represents an individual coral colony and the color of the bar denotes its inferred membership to each of the 4 putative ancestral populations. The pink and purple ancestral populations make up the temperate lineage on the right panel. Right panel: Multidimensional scaling (MDS) plot based on genetic covariance matrices of all samples, which highlights the presence of three major cryptic lineages (SubTropL, SubTropD, and Temperate). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

A. hyacinthus exhibit a low level of evolutionary divergence (Rose et al., 2021) allowing for the genome of this species to serve as a reference for our *A. hyacinthus* data. Genotyping and identification of single nucleotide polymorphisms (SNPs) was performed using ANGSD v0.921 (Korneliussen et al., 2014). Standard filtering that was used across all analyses included loci present in at least 80% of individuals, minimum mapping quality score of 20, minimum quality score of 25 (unless no minimum allele frequency (MAF) filter was used in which case quality scores of 25 and 30 were used), strand bias p-value > 0.05, heterozygosity bias >0.05, removing all triallelic sites, removing reads having multiple best hits and lumped paralogs filter (see Supp. Table 2 for number of loci for each analysis and Supp. File 1 for proportion of missing data for each analysis). All analysis pipelines are open source and can be found at https://github.com/jamesfifer/JapanRE.

2.1.3. Clone identification

Additional filtering was performed to detect clonemates, which included only sites with MAF > 0.05, depth of coverage > 5 reads, and SNP p-value > 0.05. Clones were detected using hierarchical clustering of samples based on pairwise identity by state (IBS) distances calculated in ANGSD. Technical replicates were used to identify appropriate height cutoff (Supp. Fig. 1). Only one clonemate was retained for all downstream analyses (Supp. Table 1).

2.2. Acropora hyacinthus between lineage analyses

2.2.1. Lineage assignments

Additional site filtering was performed prior to downstream analyses, which included only sites with MAF > 0.05 and linked loci were filtered out using ngsLD (Fox et al., 2019) and the provided prune_graph.pl script (max distance 5 kb, minimum weight 0.2) to ensure population structure was not driven by linkage. To detect admixture in corals from all seven sites, the program ADMIXTURE (v. 1.3.0; Alexander and Novembre, 2015) was used to find the optimal number of clusters (K) with the least cross validation error. Single Nucleotide Polymorphisms (SNPs) were hard called using genotype likelihoods estimated by SAMtools with a SNP p-value < 0.05. Principal Component Analyses (PCAs) were performed using a covariance matrix based on single-read resampling calculated in ANGSD and admixture results were visualized using the K with the least cross validation error reported from ADMIXTURE. If a sample had an ADMIXTURE assignment proportion >75% to a single cluster (i.e. bar color), it was assigned to that lineage. All other samples were removed from downstream lineage specific analyses (4 samples removed; Supp. Table 1). This threshold was chosen to remove individuals who were admixed from recent inter-lineage hybridization events to avoid confounding demographic analyses.

Individual lineage assignments were based on ancestral population assignments from ADMIXTURE results, where ancestral populations were only considered lineages if separation was shown on the first axis of the PCA. Separation of the 2b-RAD-seq data set into three lineages was confirmed via phylogenetic analyses using RAxML (Stamatakis, 2014). First, we explored a range of thresholds for loci coverage between samples (50, 60, 70, 80 and 90% of individuals), MAF filter (none, <0.001, <0.01, <0.05), and minimum depth of coverage (1×, 2×, 4×, 6×, 8×, 10×). All RAxML analyses were completed with linked sites removed. RAxML, with a GTRGAMMA model and 100 rapid bootstraps, was used to explore the resulting concatenated sequence matrices and filters were chosen that produced the most reliable trees (based on node resolution and support). All trees agreed in terms of separation of the three lineages and we used the standard filtering from other analyses (80% of individuals, minimum 1× depth of coverage, minimum mapping quality score of 25, minimum quality score of 30) plus a MAF filter <0.05 because this maximized bootstrap support.

2.2.2. Analyses of genetic divergence and demographics between lineages

To determine genetic differentiation between lineages, ANGSD was used to calculate the site allele frequency (SAF) for each lineage and then realSFS calculated the site frequency spectrum (SFS) for all possible pairwise comparisons. These SFSs were used as priors with the SAF to calculate global F_{ST}. Here, only weighted global F_{ST} values between lineages are reported. Heterozygosity was then calculated using genotype likelihoods generated by ANGSD and an expectation maximization algorithm (EM) used by realSFS in a custom script (git@github.com:sbarfield/Yap_Ahyacinthus-.git/heterozygosity_beagle.r). Differences in heterozygosity between lineages was calculated via a Welch two sample *t*-test.

The only additional filtering for demographic analyses consisted of removing linked sites using ngsLD and the provided prune_graph.pl script (max distance 5 kb, minimum weight 0.2). ANGSD was used to obtain 100 series of 5 block-bootstrapped SFS replicates, which were averaged to create 100 bootstrapped SFS for each lineage. SFS was polarized using the *A. millepora* genome as an ancestral reference. Using an outgroup reference that separated over a million years ago is the preferred method for discriminating between ancestral and derived SNPs (Matz, 2017) as SNP states in the *A. millepora* genome can be assumed to be ancestral to our *A. hyacinthus* dataset (Gojobori et al., 2007). Multimodel inference in moments (Jouganous et al., 2017) was used to fit two-population models

(https://github.com/z0on/AFS-analysis-with-moments) and all unfolded models were run on 10 bootstrapped SFS and replicated six times. The best fit model was then selected based on lowest AIC value. Parameters (i.e. migration, epoch times, and effective population sizes (N_e)) for the best fit model were obtained by running the best fit model on 100 bootstrapped SFS and replicated six times. Additionally, we ran the unsupervised analysis StairwayPlot v2 (Liu and Fu, 2020) to one dimensional SFS as a second effort to reconstruct effective population sizes. For all demographic analyses we used a mutation rate of $4e^{-9}$ per base per year and generation time of 5 years from estimates for the *Acropora* genus (Richards et al., 2013) and *A. millepora* (Matz et al., 2018), respectively.

2.2.3. Identifying loci under selection across lineages

Additional filtering of loci was conducted prior to outlier analyses, which included SNP p-value e^{-5} (SNPs were hard called for this analysis) and MAF < 0.05. Two outlier detection programs were used and our data were subsetted to include only two pairs of lineages for each comparison. The aim of this approach was to isolate outlier loci between the temperate versus both subtropical lineages. First, PCAdapt (v. 4.3.3 (Luu et al., 2017)) was used to determine the optimal K for all pairwise comparisons using a score plot displaying population structure. After filtering out two outlier individuals that skewed clustering, a K of 2 was selected for all pairwise comparisons between all lineage pairs and p-values were extracted from PC1 which separated each lineage pair. We performed an FDR correction on these p-values and a q-value of 0.05 was used as a cutoff for determining outlier loci. BayeScan (v. 2.1 (Foll, 2012)) was then used as a second approach to identify outlier loci. The same two outlier individuals were removed and the F_{ST} outlier method implemented in BayeScan identified outlier loci for each pairwise lineage comparison using 5000 iterations, 20 pilot runs with length 5000, and burn-in length of 50,000. We employed the default prior odds of neutrality (10) and a q-value cut-off of 0.05 after FDR correction. Given that we are already reducing false positives by only accepting loci that overlap between BayeScan and PCAdapt, we employed no additional FDR correction to account for our multiple pairwise comparisons. If the same locus was identified across both analyses, the locus was considered a true outlier and the annotated genes 1 kb upstream or downstream of this outlier locus were reported. These genes were then compared with the module of genes previously associated with the environmental stress response (ESR) in Pacific *Acropora* corals (Dixon et al., 2020). A Fisher's exact test was performed to test if the proportion of ESR genes for outlier loci was significantly different from the proportion of ESR genes for non-outlier loci.

2.3. Analyses within the recently expanded temperate Acropora hyacinthus lineage

Only samples from the northern sites surrounding mainland Japan (Amakusa, Kushima, Kochi, Kushimoto, and Shirahama; Fig. 1), which were all assigned to the temperate lineage (N = 93; Supp. Table 1), were used for the following analyses.

2.3.1. Population genetic structure, expansion direction, testing theoretical expansion consequences and demographics

To investigate basic population genetic structure within the temperate lineage, we implemented PCAs and admixture analyses, and calculated global weighted F_{ST} for all pairwise comparisons and expected and observed heterozygosities for each population. All analyses were conducted as described within Section 2: *Acropora hyacinthus* lineage analyses. The PERMANOVA function *Adonis* (from the R package vegan (Oksanen et al., 2020)) was used to determine if clustering was significant. To test for differences in the number of clone pairs between populations, a Pearson's chi-squared test was used.

Next, Slatkin's directionality index Ψ (Peter and Slatkin, 2013) was calculated to confirm the direction of expansion. Loci with fixed ancestral alleles were removed using SAMtools (Li et al., 2009) and the directionality index Ψ was calculated using the script devtools::install_github ("BenjaminPeter/rangeExpansion", ref = "package") and the function get.all.psi. Linkage disequilibrium (LD) was estimated independently for each population using ngsLD (Fox et al., 2019), and r^2 was plotted for each population using fit_LDdecay.R (max 200 kb).

Purifying selection was assessed to estimate the degree of mutational load. To calculate purifying selection, sites with synonymous and missense mutations were identified using Variant Effect (McLaren et al., 2016). Global Watterson's theta was calculated for each site using the thetaStat tool in ANGSD from the maximum likelihood estimate of the SFS. Watterson's theta was estimated at this subset of sites for all temperate populations. We then correlated the ratio of missense to synonymous site diversity with the site's distance from Kushima using Pearson's correlation coefficient. Lastly, demographic analyses in moments were run as described for the coral lineage analyses between all five temperate populations surrounding mainland Japan.

2.3.2. Identifying selection pressures and loci under selection

Patterns of isolation-by-distance (IBD) were evaluated among the temperate populations using a Mantel test with 10,000 random permutations between the F_{ST} matrix and pairwise oceanographic distance. A Mantel test was also performed between the F_{ST} matrix and pairwise differences in mean, maximum and minimum SST (i.e. the absolute lowest temperature experienced over the entire date range), mean chlorophyl *a* and Photosynthetically Available Radiation (PAR). These SST data were extracted from the Modis Satellite (https://oceancolor.gsfc.nasa.gov/) at 4 km resolution from 2005 to 2013.

Outlier analyses were conducted as described previously between the two ancestral populations within the temperate region identified using ADMIXTURE.

3. Results

3.1. Presence of cryptic Acropora hyacinthus lineages with distinct evolutionary histories

Analyses of population structure with ADMIXTURE using samples from all sites show the presence of four (K = 4) ancestral populations with the majority of individuals assigning with high proportion (>0.75) to a single population (Fig. 1). PCAs demonstrate that these populations can be separated into three distinct clusters on PC1 and PC2 (referred to as lineages here) (Fig. 1). We refer to these lineages as cryptics as they cannot be differentiated via gross morphological assessments and all fall under the species description for *Acropora hyacinthus* in Veron (1992b). We follow semantic precedent established by previous studies (Han et al., 2020; Peter and Slatkin, 2013; Li et al., 2009; McLaren et al., 2016; Ladner & Palumbi, 2012) that describe this species complex as a group of genetically distinct cryptic lineages, but acknowledge no study to date has employed in-depth skeletal morphometrics to determine if these lineages are truly "cryptics". All three lineages are found in Oura Bay, two are present in Sekisei lagoon and only one is present in the temperate region surrounding mainland Japan. Hereafter these are referred to as subtropical light green (SubTropL) subtropical dark green (SubTropD) and temperate lineages. Pairwise F_{ST} indicated high genetic differentiation (0.1770–0.236) between all lineages (Supp. Fig. 2A) and phylogenetic analyses confirmed the presence of three phylogenetically distinct clusters with bootstrap support (79–90; Supp. Fig. 2B; Supp. Fig. 3). Expected heterozygosity was lower in the temperate lineage compared to the other two lineages ($p < 0.05$) (Supp. Fig. 2C). There is genetic substructuring within the temperate lineage as shown by the K = 4, PC3 using all data (Supp. Fig. 4) and PC1 using only the temperate lineage samples (Fig. 4). This genetic substructuring corresponds to the two geographic regions around mainland Japan- edge (Amakusa, Shirahama and Kushimoto) and more central locations hereafter referred to as "core" (Kushima and Kochi). Demographic analyses were done a) between all four genetic clusters, splitting the temperate lineage into "TempCore" and "TempEdge" and b) between the three main lineages. Pairwise F_{ST} was lower between the temperate and subtropical lineages

when the temperate lineage was split into substructures (0.102–0.114) (Supp. Fig. 5A) and heterozygosity of both temperate clusters maintained lower levels compared to subtropical lineages (Supp. Fig. 5B).

3.1.1. Three lineage comparisons

Demographic analyses for all three pairwise comparisons showed best fit models included a scenario supporting the presence of genomic islands (Supp. Fig. 6; Supp. Fig. 9; Supp. Table 3). These genomic islands were all regions of the genome that exhibited reduced gene flow compared to the rest of the genome (Fig. 2). All analyses between all three pairwise lineage comparisons showed support for a split roughly 200 kya (Supp. Fig. 7). Both subtropical lineages (SubTropL, SubTropD) showed asymmetrical migration with the temperate lineage with higher gene flow from subtropical lineages to the temperate lineage (Supp. Fig. 7). Migration between subtropical lineages was symmetrical for the first epoch and asymmetrical for the second epoch (Supp. Fig. 8) with higher gene flow in the SubTropL-SubTropD direction (Fig. 2). Effective population sizes were estimated to be consistently lower in the temperate lineage when compared to the two subtropical lineages, both subtropical lineages showed an increase in N_e following divergence while the temperate lineage decreased (Supp. Figs. 7–8). Effective population sizes from the stairway plot analysis were consistent with the moments analysis, with the exception of the appearance of recent N_e contractions in the past few thousand years and N_e increases starting roughly 50 kyr earlier for all three lineages (Fig. 3). It is noteworthy that the temperate lineage was the first lineage to exhibit this contraction.

3.1.2. Demographic analyses splitting temperate lineage into substructures

While the models showed support for asymmetrical migration between the temperate lineage and the two subtropical lineages as explained above, the direction of migration changed depending on the genetic cluster within the temperate lineage. The TempCore cluster showed higher gene flow going out while the TempEdge cluster showed higher gene flow coming in (Fig. 2). Divergence time and presence of an epoch of symmetrical migration became highly variable between runs once the temperate lineage was split this way likely due to reduced sample size, so those results are not considered further. Effective population sizes were consistent with the three lineage comparisons, with both TempCore and TempEdge maintaining reduced effective population size compared to the subtropical lineages (Fig. 3; Supp. Fig. 8). However, splitting data into substructures revealed an interesting pattern in the stairway plot with the TempEdge cluster showing a brief increase in N_e while the TempCore cluster shows a stasis of N_e immediately prior to the aforementioned contraction (Fig. 3).

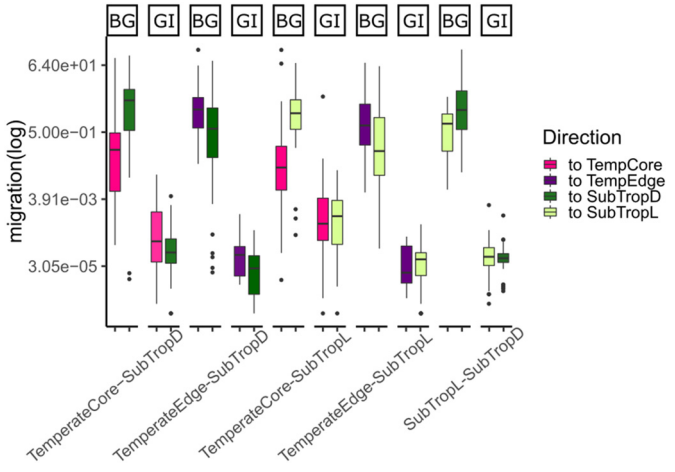

Fig. 2. Moments migration parameter output for pairwise analyses showing both genetic background and (BG) genomic islands (GI). Boxplots display mean log (migration) with the box representing the interquartile range (IQR) between the upper and lower quartile. The whiskers extend from the hinge to the highest value that is within 1.5 * IQR of the hinge.

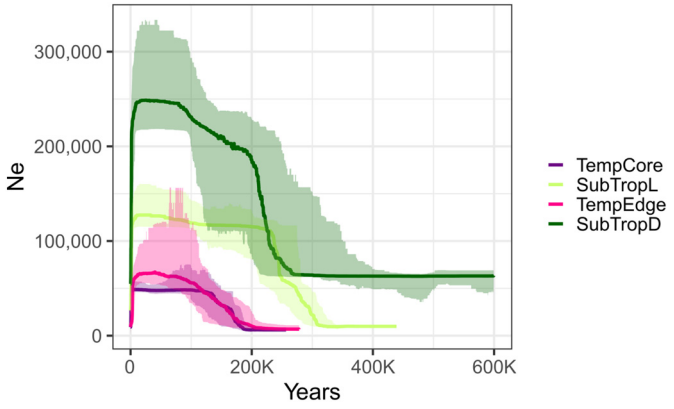

Fig. 3. Stairway Plot showing effective population sizes (N_e) through time for each *Acropora hyacinthus* lineage with the temperate lineage split up into the substructured genetic groups (TempCore and TempEdge). Lines show median N_e, ribbons represent 95% confidence intervals.

In the SubTropL-temperate lineage comparison we identified outlier loci near 34 genes – 17 of which were in the top three environmental stress response (ESR) gene modules (1264 genes) from Dixon et al. (2020). In the SubTropD-temperate comparison we found outlier loci near 16 genes, 10 of which were ESR candidates. Five outlier genes overlapped in both temperate-subtropical lineage comparisons, three of which were ESR candidates (centrosomal protein 290kDA, elongation of very long chain fatty acids protein 4 (EVOL4) and one unannotated gene). In the SubTropD-SubTropL comparison we found 35 outlier genes, 17 of which were ESR candidates (Supp. File 1; Supp. Fig. 12). Proportion of ESR candidates for outlier loci was not significantly different from the proportion of ESR candidates for non-outlier loci ($p > 0.05$; Fisher's exact test), for all comparisons.

3.2. Genetic signature of range expansion and demographics within the temperate lineage

Analysis of population structure with ADMIXTURE and PCAs demonstrated separation of genetic variation ($p < 0.001$) between the three edge sites compared to the two core sites (Fig. 4A, B). Weighted F_{ST} estimates demonstrate low levels of differentiation among edge populations (0.017–0.024) and among core populations (0.017) and higher levels of differentiation between edge and core (0.036–0.045) (Fig. 4C). The directionality index Ψ for range expansions (Peter and Slatkin, 2013) supported the more southern sites (Kushima/Kochi) as the ancestral origin for Amakusa, Shirahama and Kushimoto (Fig. 5). Expected heterozygosity was higher in core populations compared to edge populations for all pairwise comparison ($p < 0.05$) (Fig. 6B). Nucleotide diversity at synonymous and missense sites followed the same trend; however, edge sites showed a greater decrease in nucleotide diversity at missense sites, which resulted in a decreasing thetaN/thetaS ratio as populations were further from the proposed origin site Kushima (Fig. 6C). This result suggests that purifying selection is stronger as distance from Kushima increases (Fig. 6C). While LD was similar across all temperate populations, edge populations did show a trend of higher LD (Fig. 6A). Edge populations also contained significantly more clone pairs when compared to core populations (Pearson chi-squared = 23.969, df = 1, p = 9.789e−07; Fig. 6B).

Demographic analyses revealed asymmetrical gene flow between all core and edge populations, with lower migration out of edge sites (Fig. 7; Supp. Fig. 10). Migration within edge and within core sites both show symmetrical gene flow (Fig. 7; Supp. Fig. 10) and estimated N_e was consistently lower at edge sites compared to core sites (Fig. 7).

Mantel tests showed genetic variation does not seem to follow isolation by distance (IBD) expectations, nor is it associated with sea surface temperature (SST) minimums, maximums, and means, mean chlorophyl *a* or mean PAR ($p > 0.05$). However, minimum SST did show an association trend

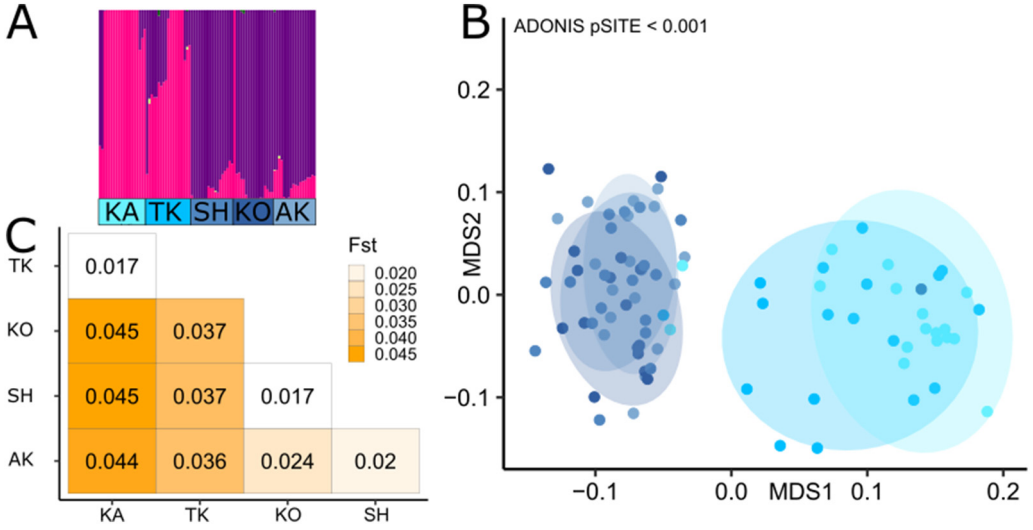

Fig. 4. Population genetic structure within the temperate *Acropora hyacinthus* lineage. A) ADMIXTURE results where each bar represents a coral individual and the color of the bar represents its inferred membership in each of the 2 potential ancestral populations within the temperate region (Pink: TempCore, Purple:TempEdge). B) Multidimensional scaling (MDS) plot based on genetic covariance matrices demonstrating significant clustering between samples from the core sites (light blue) and the edge sites (dark blue). C) Pairwise global F_{ST} between all temperate region sites. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

($p < 0.10$) and had a higher correlation with F_{ST} ($r = 0.7$) compared to any other metric (Supp. Fig. 11). When comparing edge vs core sites, we detected six genes that were near outlier loci, three of which were ESR candidates (Supp. File 1). Association of an outlier loci with an ESR candidate was not significantly different from association of a non-outlier loci with an ESR candidate ($p > 0.05$; Fisher's exact test).

4. Discussion

4.1. Presence of Acropora hyacinthus lineages that vary in their spatial distributions

Consistent with previous work using different loci (microsatellites (Nakabayashi et al., 2019); mitochondrial and nuclear markers (Suzuki et al., 2016)), our 2b-RAD-seq data suggest the presence of three morphologically cryptic *A. hyacinthus* lineages across our sampled sites in Japan. This species is well known for its cryptic lineages with two or more lineages previously identified in Palau, American Samoa, Australia, Pohnpei, Palmyra (Ladner & Palumbi, 2012), Fiji, Philippines, Tonga, Tuvalu, Cook Islands (Sheets et al., 2018), the island of Yap in Micronesia (Barfield et al., n.d.), and Taiwan (Suzuki et al., 2016). However, the presence of sympatrically occurring cryptic *A. hyacinthus* lineages is not always observed. For example, Davies et al. (2015) found no evidence of sympatrically occurring cryptic lineages across the entire expanse of Micronesia, using multilocus SSR data. In addition, only one lineage has been reported in the islands of Moorea and Tahiti in French Polynesia (Kriefall et al., 2020), which used the same 2b-RAD-seq approach leveraged here. In our project we find only the temperate lineage surrounding mainland Japan whereas all three lineages are present in the two southern Ryukyus sites, consistent with Nakabayashi et al. (2019) and Suzuki et al. (2016).

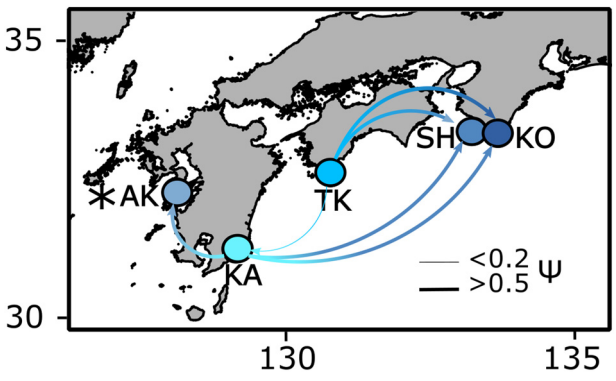

Fig. 5. Genetic signature of range expansion between each temperate lineage *Acropora hyacinthus* population sampled in mainland of Japan. Direction of arrow denotes direction of expansion determined by positive or negative psi value. Thickness of arrow, denoting strength of signal of expansion shows absolute value of psi. Asterix indicates the most recently expanded site sampled here, Amakusa (AK).

Although this study did not investigate the physiological differences between *A. hyacinthus* lineages, coral cryptic lineages are known to exhibit differences in thermal tolerance (Rose et al., 2021; Gómez-Corrales and Prada, 2020; Boulay et al., 2013) as well as differences in spawning times (Rosser, 2015; Furukawa et al., 2020; Ohki et al., 2015). Interestingly, the temperate and one of the subtropical lineages have previously been shown to spawn at the same time (June) in the Ryukyus (Suzuki et al., 2016). Crosses between subtropical and temperate lineages exhibited low fertilization rates but they were semi-compatible (Suzuki et al., 2016), suggesting that these lineages maintain some capacity for hybridization – consistent with our admixture and PCA results. Taken together, our findings of cryptic lineages reiterate the importance of first exploring the potential for divergent lineages before investigating population connectivity, calculating speciation rates, and predicting species distributions.

4.2. Demographic history of Acropora hyacinthus lineages

We observed increases in effective population size following divergence for the two subtropical lineages, but not the temperate lineage. This pattern could be due to population expansion or introgression with another species/lineage. In the scenario of possible population expansion we were interested if this tracked well with evidence for *A. hyacinthus*'s expansion into the Ryukyus as this would align with previous genomic work suggesting that rapid adaptation within *Acropora* has been facilitated by colonization of new habitats (Mao et al., 2018). Our divergence times should be interpreted with caution as these numbers are based on an estimated mutation rate for the *Acropora* genus (Richards et al., 2013). Additionally, even if we had confidence in the mutation rate, our analyses suggested divergence and increase in population size occurred during the Pleistocene, which fails to align with the fossil records for the lower and upper Ryukyus that

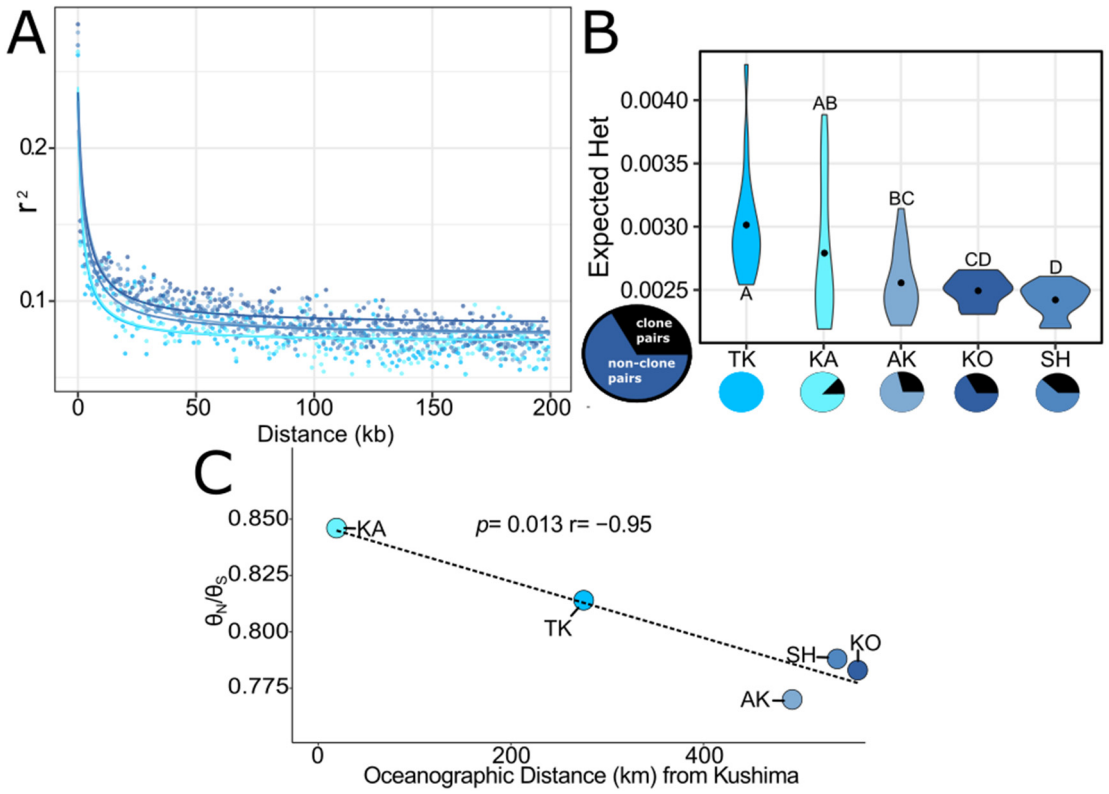

Fig. 6. Genetic signatures of range expansion in the temperate *Acropora hyacinthus* lineage. A) Estimated linkage disequilibrium (LD) for 0–200 kb in each populations with line showing best fit decay. B) Mean expected heterozygosity (H_e) estimates for each population. Letters in common denote non-significant differences ($p > 0.05$) of H_e between sites. Circles below represent the proportion of samples that made of clone pairs (black) relative to unique genotypes (shades of blue). C) Estimated θ_N/θ_S ratios for each population plotted against oceanographic distance from Kushima (km) with the dotted line representing the linear model fit for purifying selection as distance increases. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

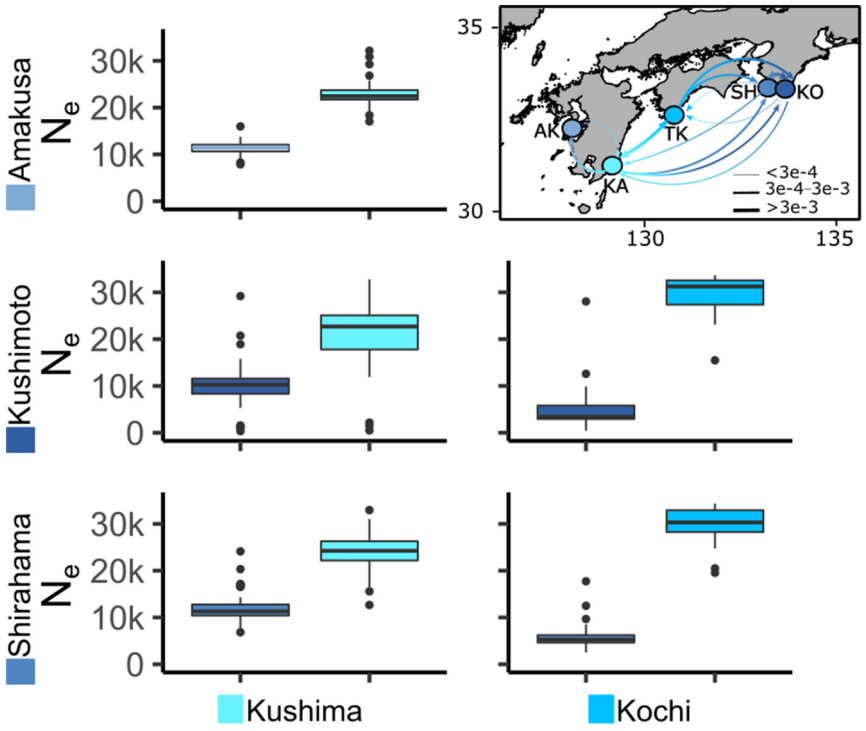

Fig. 7. Pairwise moments parameter outputs for the temperate populations of *Acropora hyacinthus* demonstrating mean effective population estimates (N_e) and mean pairwise migration rates (the fraction of the total population that are new immigrants in each generation) between sites (shown via relative thickness of arrows, double sided arrows represent symmetrical migration).

demonstrate the presence of *A. hyacinthus* in the mid-Pleistocene (~400 kya) (Humblet et al., 2009). An alternative explanation for the increase in population size is if divergence was mediated by introgression into the subtropical lineages. Future work focusing on elucidating if this introgression occurred from another lineage of *A. hyacinthus* or a different species of Acroporid is warranted.

An increase in effective population size during the last interglacial period (100 kya) was observed for all three lineages, which aligns with the pattern of major reef development in the Ryukyus that responded to 100 kyr cycles starting in the mid-Pleistocene (Sagawa et al., 2001) and is consistent with data from *Acropora tenuis* in Japan showing increasing N_e during the last interglacial period (Mao et al., 2018). While we acknowledge once again that the time scale reported here is based on an estimated mutation rate and should be treated with caution, the referenced *A. tenuis* study also used a similar mutation rate and thus can be compared in relation to our results. This result is particularly interesting as *A. tenuis*'s range overlaps with *A. hyacinthus,* while other Acroporids not found as far north as these two species show a decrease in effective population sizes during this time period (Mao et al., 2018). Reduced frequencies of Acroporids in the fossil record have been observed during the last interglacial period, potentially suggesting that this group of corals experienced large die-offs during this time, especially in the tropics of the Northern Hemisphere due to increasing temperatures (Kiessling et al., 2012). Given that several Acroporids sympatrically distributed with *A. hyacinthus* exhibited decreasing N_e during this time period (Nakamori, 1986), it is possible that these dieoffs led to niche availability, which *A. hyacinthus* subsequently filled. Additionally, according to limited Pleistocene coral fossil records in the Ryukyus, *A. palifera* (which like *A. hyacinthus* inhabits the shallow upper reef slope) had higher abundances during the mid-Pleistocene than modern day (Humblet et al., 2009). These patterns are consistent with patterns observed in Caribbean corals where increases in N_e during the last interglacial period have also aligned with simultaneous loss of spatially co-occurring species (Prada et al., 2016).

Demographic analyses reveal genomic islands of restricted gene flow and opposite directions of introgression migration within the two distinct genetic subclusters that make up the temperate lineage (TempCore and TempEdge). Restricted introgression spread throughout a large portion of the genome has also been observed between lineages of the Caribbean octocoral, *Eunicea flexuosa* (Prada and Hellberg, 2021), and the Caribbean scleractinians *Montastraea cavernosa* and *Siderastrea siderea* (Rippe et al., 2021). Heterogeneous divergence across a substantial portion of genome between coral lineages has been hypothesized to be due to intragenomic incompatibility among alleles (Dobzhansky–Muller or DM incompatibilities; Orr, 1996), where maladaptive combinations of alleles from lineage mixing are selected against when a first-generation hybrid backcrosses to one of the parental lineages (Rippe et al., 2021). These DM incompatibilities can explain the preservation of these discrete *A. hyacinthus* lineages even though they occur sympatrically and introgress. When the temperate lineage was split into TempCore and TempEdge substructures, the regions of the genome that *do* show introgression exhibited an interesting pattern of asymmetrical gene flow. The TempCore cluster shows higher introgression in the temperate-subtropical direction for both subtropical lineages. This pattern follows the geographic distribution of these lineages where individuals assigned to the temperate core cluster were found in the subtropical region, but corals assigned to the subtropical lineages were not found in the temperate region. In contrast the TempEdge exhibited the opposite pattern of introgression, where gene flow was higher in the subtropical-temperate direction. This reversal can be explained by the pattern of introgression, between the edge and core genetic clusters which occurs in the TempCore-TempEdge direction. Given that the geographic distribution of TempEdge does not overlap with the subtropical lineages, introgression between TempEdge and subtropical lineages is likely mediated by the TempCore cluster.

Demographic analyses revealed evidence for historical occupation of marginal habitats by the temperate lineage. We use the term “marginal” to include populations that are not necessarily at the edge, but are still isolated from much of the global distribution of *A. hyacinthus*. Acroporids occupied present-day marginal habitats such as Taiwan in the mid-Pleistocene (Gong et al., 1998) and mainland Japan in the Holocene (~5–6 kya) (Veron, 1992a), but no information is available specifically showing the presence of *A. hyacinthus* in either of these regions during the Pleistocene. The temperate lineage shows lower heterozygosity, but while the central-marginal theory predicts lower heterozygosity in marginal habitats, there are exceptions (Eckert et al., 2008) and these patterns can be influenced by either historical or more contemporary demographics (Yang et al., 2016). However, central-marginal theory also predicts effective population sizes should be lower at margins (Sagawa et al., 2001) and we observe lower effective population size in the temperate lineage throughout this lineage's history compared to the subtropical lineages. Additionally, contractions shown in the Stairway Plot analyses during the last thousand years could be due to global cooling, which started 8–10 kya in the western North Pacific (Meyer et al., 2016), or sudden changes in temperature during the mid-Holocene due to higher variation in temperature anomalies (Asami et al., 2020). Fossil evidence shows 5–6 kya, when SST was ~2 °C higher than present day, reefs were prolific along the coast of Japan and found at higher latitudes (Veron, 1992a). This range contraction aligns well with the modeled N_e decline observed here. Cold temperate kelp species – the major competitors for substrate space around mainland Japan – have shifted their range under interglacial/glacial cycles (Assis et al., 2016), suggesting the mechanism of modern range expansion in this region could have facilitated historical range expansion of *A. hyacinthus* as well. The temperate lineage's earlier contraction relative to the two other lineages may suggest that it historically occupied higher latitude reefs than the other two lineages and thus was more susceptible to cooling. Additionally, when the temperate lineage is split according to the substructuring, the TempEdge genetic cluster shows an increase in N_e prior to the contraction while the TempCore cluster does not. It is possible that this pattern reflects differential abilities of the two clusters to expand their range further northward.

4.3. Outlier Loci detected between Acropora hyacinthus lineages suggest adaptation to different environmental conditions

It is important to note that with any reduced representation sequencing approach many genes potentially important to adaptation are likely to be missed. Nevertheless, in our outlier analyses we report potential candidate genes that could facilitate occupation of different environmental conditions between the temperate lineage relative to the two subtropical lineages. Five overlapping outlier genes were detected in both temperate-subtropical comparisons and three of these genes (two of which were annotated) have previously been implicated in the coral's environmental stress response (ESR) (Dixon et al., 2020). These genes included centrosomal protein 290kDA and elongation of very long chain fatty acids protein 4 (EVOL4). Centrosomal protein 290kDA is involved in early and late steps in cilia formation (Avidor-Reiss and Leroux, 2015) and EVOL4 is a lipid biosynthesis enzyme, which has previously been shown to exhibit differential expression between coral hosts infected with a homologous or heterologous algal symbiont strain (Matthews et al., 2017). One of the non-ESR outlier genes was helicase senataxin which is involved in DNA damage response generated by oxidative stress (Suraweera et al., 2007). Variants of helicases have also previously been found in heat resistant populations of *A. digitifera* in the Ryukyus and were theorized to convey resistance against light-stress associated with heat waves (Selmoni et al., 2020).

Several other outlier genes were present in only one of the two temperate-subtropical lineage comparisons. Between the temperate lineage and SubTropL lineage, ESR outlier genes included Mucin-like protein and collagen alpha-5 (VI), which have both been previously reported in the mineralizing matrices of mollusks (Marin et al., 2000; Suzuki et al., 2009; Joubert et al., 2010). Peroxidase was found to be an ESR outlier gene between the temperate lineage and SubTropD lineage and several studies have linked coral peroxidase activity with anti-oxidant potential (Hawkridge et al., 2000; Olano and Bigger, 2000). Non-ESR outlier genes included Fibrillin-2, which is associated with wound healing and responds

to stress in *Nematostella* (Reitzel et al., 2008) and other invertebrates (Riesgo et al., 2012) and was also identified as an outlier gene between *A. tenuis* lineages (Cooke et al., 2020). Hemicentin-1 – another stress response wound healing gene – was found to be an ESR outlier gene between the temperate lineage and SubTropD lineage. This gene was also identified as an outlier between *A. tenuis* lineages (Cooke et al., 2020). Lastly, a ubiquitin-protein ligase gene, HERC2, was an outlier between the temperate and SubTropL lineage. Another ubiquitin-protein ligase fell within a region of strong genetic divergence between the heat resistant and susceptible lineages of *A. hyacinthus* in American Samoa (Rose et al., 2021). Taken together, these results suggest that the temperate lineage might exhibit higher frequencies of alleles that allow for adaptation to different environmental conditions, possibly facilitating this lineage's occupation of temperate habitats, which experience increased seasonal temperature fluctuations.

4.4. Edge and core dynamics manifested in genomic signatures

Our genomic analyses within the temperate lineage confirm previous survey predictions (Yamano et al., 2011), suggesting that the direction of expansion occurred from South to North within the temperate region – although we were unable to pinpoint which site was the most likely origin out of the two core sites. Interestingly, when exploring the assumptions of genetic consequences of range expansion we were unable to detect separation between the recently expanded Amakusa population and the range edge sites Kushimoto and Shirahama. Edge populations can share many of the same characteristics as recently expanded populations including low genetic diversity (Hoffman and Blows, 1994), increased LD (Jorgensen et al., 2002), increased selfing (Barrett, 2010) and increased clonality (Baums et al., 2006). The high degree of similarity we observed between these site types might be because the Amakusa population expanded several coral generations ago (~40 years) and continued gene flow over this time period may have muted the signal of a recent expansion (reviewed in Peischl et al., 2016). This potential diminution is corroborated by a previous study by Nakabayashi et al. of *A. hyacinthus* population genetics in this region using microsatellites, which detected a further decrease in genetic diversity in sites that expanded more recently than Amakusa (Nakabayashi et al., 2019). Alternatively, lack of separation between Amakusa and Kushimoto/Shirahama could point to a lasting signature of range expansion for Kushimoto/Shirahama and additional bottlenecks driving further reductions of genetic diversity in the more recently expanded sites from Nakabayashi et al. (2019).

The observed genetic clustering between Amakusa and Shirahama/Kushimoto, despite long oceanographic distance between these regions and high migration rates from core sites predicted by larval dispersal models (Nakabayashi et al., 2019), could be driven by neutral or selective processes. We pose discrete thermal environments as a possible mechanism for environmental selection given that winter temperature lows can drive bleaching patterns in this species across this region (Suzuki et al., 2013) and SST showed a stronger correlation with genetic structure compared to our proxies for nutrient availability (chlorophyl *a*) and light exposure. We acknowledge the limitations of satellite captured data and that many other environmental parameters were not measured here, however these data serve as a hypothesis generating tool. For the neutral force hypothesis, edge sites could be experiencing higher drift, given the evidence for asymmetrical gene flow and lower effective population sizes at these sites. However, with drift's inherent randomness it seems unlikely that drift alone could produce such similar genetic signatures across sites on opposite sides of mainland Japan. As the three edge sites experience different thermal regimes than the two core sites, it is also possible that discrete environmental selection pressures could be driving this clustering. Indeed, Mantel tests showed greater positive correlations between genetic distance and minimum SST metrics compared to oceanographic distance. However, we cannot rule out genetic differentiation driven by neutral processes nor selective pressures from non-temperature related environmental conditions and future physiological work is needed to disentangle these hypotheses.

The presence of higher purifying selection detected at edge sites was counter-intuitive given that theoretical (Klopfstein et al., 2006a) and empirical studies (Zhao et al., 2020) predict the opposite pattern. This prediction is based on the positive correlation between purifying selection and effective population size (largely due to lower inbreeding in larger populations (Perrier et al., 2017)) and the observation that deleterious allele surfing along an expansion front should lead to higher mutational load at edge populations (Klopfstein et al., 2006). However, there are circumstances where edge populations can demonstrate higher purifying selection. Firstly, bottlenecked populations can also show higher purifying selection if bottlenecks are followed by N_e increases (Beissinger et al., 2016). Second, bottlenecks tend to purge highly deleterious mutations (Grossen et al., 2020). Lastly, if edge and core populations occupy different environments, diverse selective constraints against de novo mutations could alter this signal (Barrett, 2010). We find the third hypothesis to be the most compelling here. Given that a large proportion of the coral genome is responsive to environmental stress, and genes that underlie critical thermal maximum (CT_{max}) or minimum (CT_{min}) can undergo selection to remove large-effect alleles from the population by purifying selection (Baums et al., 2006), this could manifest itself as stronger purifying selection genome-wide. If a deleterious allele is more consequential in colder environments, this could explain higher purifying selection in edge populations with exposure to suboptimal temperatures leading to increased selection efficacy (Peischl et al., 2016). Future experiments elucidating thermal performance of corals in this region will help elucidate the role of purifying selection in these populations.

To begin to explore whether selective or neutral processes are important for distinguishing these genetic clusters within the temperate lineage, we performed outlier loci analyses. When investigating the outlier loci between the edge population and the core population, three ESR outlier genes were detected only one of which was annotated. This gene was protocadherin, which is a cell-adhesion protein previously implicated in pH tolerance in temperate corals relative to subtropical corals (Suzuki et al., 2013). Two of the three non-ESR outlier genes were glutamate receptors, which are well-known for their importance in circadian rhythm and day/night cycles in coral (Zhao et al., 2020). These gene functions fit well into the types of environmental differences that exist across latitudes and suggest that these core and edge populations within the temperate region might be uniquely adapted to their respective environments.

5. Conclusions

Our genomic analyses provide insight into the evolution and ecology of cryptic *A. hyacinthus* lineages in Japan and the mechanisms that might underly the observed population structure between edge and core populations at this species' range edge. We uncovered discrete demographic histories between lineages and evidence supporting the maintenance of genetic separation between sympatrically occurring species through DM incompatibilities. Within the temperate lineage we show evidence for historical occupation of marginal sites and population structure that corresponds to degrees of habitat marginalization, potentially demonstrating this lineage's unique ability to continually expand north. Future work characterizing the physiological differences between lineages and populations will be necessary to ground truth inferences of temperature adaptation detected here. Overall, this work helps build on the growing research in this region that will be critical for evaluating the resilience of Japan's reefs and predicting future range expansion.

Data availability

Raw read data can be found on the sequence read archive (SRA BioProject accession number: PRJNA735187).

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CRediT authorship contribution statement

SWD conceived of the project and oversaw project development. NY completed all collections including permits. JEF prepared all sequencing libraries and conducted all analyses. TY and CBB provided temperature data. JEF wrote the manuscript with contributions from SWD. All authors edited and approved the final version.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2021.152423.

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