# Studying the genomics of natural and restored populations of Acropora palmata is crucial for understanding their genetic diversity and the impact of conservation efforts

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# Abstract

Coral reef ecosystems in the Caribbean are on the brink of ecological collapse, largely due to the significant decline in once-abundant populations of *Acropora* species. For this reason, *Acropora palmata* is now classified as critically endangered by the IUCN. In response, restoration programs are in place, but assessment of the genomic diversity of colonies used for restoration has lagged. We studied the genome-wide variation of *A. palmata* using a low-coverage whole genome approach in Quintana Roo, Mexico. We collected over a hundred colonies across reefs spanning over 150 km, including one reef under active restoration efforts. Our analysis based on thousands of genome-wide markers, revealed high levels of genomic diversity with low levels of clonality. Remarkably, the reef under restoration showed genetic diversity comparable to the natural populations, while just one reef presented decreased genetic variability. Our results indicate gene flow among populations with subtle patterns of genetic differentiation, suggesting limiting geographic isolation. We demonstrate that coral restoration from naturally occurring fragments and sexual recruits encompasses sufficient genetic variation on par with that of natural populations. Therefore, we ascertain that current restoration efforts in Quintana Roo include enough genetic diversity to maintain nurseries and provide a viable long-term approach to restoring natural populations of decimated Acroporids in Mesoamerican reefs.


# Introduction

The unprecedented decline of Elkorn coral (*Acropora palmata*) populations in the Caribbean Sea in the last decades is one of the primary causes of stony coral loss in the region[59,80,2]. Being on the brink of becoming ecologically extinct, with less than 10% of its original coverage remaining, led to the classification of *A. palmata* as critically endangered by the International Union for Conservation of Nature (IUCN). Under this bleak outlook, the government of Mexico conferred it a special conservation status [67]. Restoration programs are currently undertaking across the Mexican Caribbean to respond to this dramatic decline. However, the assessment of the genomic diversity of Acroporids used in restoration has lagged, despite being essential to ensure the success of restoration efforts.

Successfully restoring coral populations requires knowing the restored populations' genetic diversity and its distribution across the seascape. High genetic diversity provides the evolutionary potential of species to adapt to unknown environmental changes. Therefore, it can be a proxy for the population's potential to withstand local extinctions[62,76,77,58,63,7]. Therefore, accounting for the levels of genetic diversity in the remaining coral populations is crucial to improve resource management and enhance the effectiveness of restoration efforts, which is vital for the future sustainability of coral populations[25,70].

Studies on the genetic diversity of Scleractinian corals have revealed the existence of subdivided populations, with significant restrictions in gene flow, leading to genetic differentiation among populations[7]. The analysis of population subdivision (*i.e.*, structure) and genetic differentiation relies on identifying genetic variants, such as single nucleotide polymorphisms (SNPs) or microsatellite markers.

Although microsatellites can easily detect marked patterns of population structure (low to no gene flow), genome-wide studies based on SNPs provide higher resolution to detect subtle genetic discontinuities[64].

To make conservation and management strategies for *A. palmata* and other threatened corals more effective, a comprehensive understanding of genetic variation within and among populations is imperative[78,36]. Patterns of genetic structure observed among populations reflect the degree of isolation, historical divergence timelines, and fluctuations in population sizes[64]. Hence, to assess this variation accurately is crucial to elucidate population connectivity first to reinforce conservation strategies[4]. This helps establish guidelines for selecting genetic sources in restoration efforts and insights into the distribution of variation within and among populations across different degrees of gene flow and spatial connectivity. Ideally, this information will allow reef practitioners to preserve historical gene flow and local adaptation, thereby minimizing further losses of genetic diversity[53,54].

For critically endangered species like *A. palmata*, adding metrics of genetic diversity of current restoration methods is crucial. Proactive restoration activities should promote the natural recovery of reefs by facilitating the movement of sexual recruits through connected populations characterized by high genetic and genotypic diversity[47]. Such metrics can now be easily acquired through new sequencing techniques such as low coverage Whole Genome Sequencing (lc-WGS), which allows finer-resolution genetic analyses. This technique employs a depth of coverage between 0.5 and 6x and has become a powerful and cost-effective tool for population genomics studies in both model and non-model species[17,49]. Lc-WGS enhances the detection of genome-wide single nucleotide polymorphisms (SNPs) compared to sequencing a smaller number of individuals but with greater depth of coverage[19]. This technique has been successfully implemented for well-studied species such as *Acropora millepora*[29] and *Acropora nana*[48].

Here, we analyze the genomic diversity and its distribution in *A. palmata* from natural and restored populations, encompassing colonies generated through clonal propagation and sexual reproduction, located in northern Quintana Roo, Mexico (Caribbean). We used high-throughput sequencing to score Single Nucleotide Polymorphism (SNP) variants from a lc-WGS sequencing. Our objective was to analyze genetic diversity and structure through SNP markers of *A. palmata* in six natural populations and one restored reef (Cuevones Reef). This study aims to enhance the effectiveness of restoration programs and contribute to the conservation of Acroporids in the Mesoamerican Reef System and the Caribbean Sea.

## Materials and methods

# Study site

The study was conducted in the northern region of the state of Quintana Roo, Mexico (Fig. 1., 21°26'7.08" N, 86°46'54.26" W, and 20°19'42.66" N, 87°20'29.45" W) (Fig. 1). This location is part of the Mesoamerican Barrier Reef System (MBRS)[42] and falls within the Mexican Caribbean Biosphere Reserve (CONANP, 2018). The region covers an approximate area of 150 km, extending from Ixlache to Akumal (Table S 1 ).

Particularly, Limones Reef, spanning an area of approximately 1.5 km$^{31}$, holds a significant *A. palmata* cover, ranging from 34.7 to 35%[66,15]. Additionally, coral cover as high as 50% has been reported for this reef[55].

The restored Cuevones Reef is in the bay of Isla Mujeres, north of Cancun. This reef was damaged by the impact of a cruise ship in 1997, affecting a total area of 480 m$^2$. In response to the incident, the Cuevones Reef has been inaccessible to the public since 1998 to facilitate its natural recovery. However, in 2011, the coral cover had only increased by 1.3–4.5%[68]. As a result, in 2012, active coral reef restorations were started in an area of 350 m$^{2\ 56}$.

# Sample collection

Sampling was conducted in August 2019, during the rainy season from May to October (permit number SGPA/DGVS/009198/18). A total of 128 samples of *A. palmata* were collected from six natural populations (Ixlache, Farito, Cadenita, Bajito Nizuc, Limones, and Akumal) and one restored reef (Cuevones Reef), consisting of fragments produced by clonal propagation (fragmentation) and sexual recruits. At each sampling site, 18 to 35 fragments were randomly collected from different colonies of *A. palmata*, except in Farito, where *A. palmata* is now very rare and only three colonies were found. To compare the genetic diversity of a restored reef with that of natural populations, we collected nine wild colonies, 14 colonies produced through sexual reproduction (sexual recruits), and 12 colonies produced by clonal propagation at Cuevones Reef. To reduce the chance of sampling clones, colonies chosen for the study were separated by a minimum distance of five meters[9,28]. We also included six donor colonies from Ixlache and two from Akumal, as part of the CRIAP- INAPESCA Restoration Program. Samples for genomic studies were obtained by clipping a ~ 2 cm apical tip from each coral colony. These samples were then preserved in 95% ethanol at 4°C and transferred to -20°C for short-term storage.

# DNA Extraction and Sequencing

To generate genomic libraries, we first isolated total genomic DNA from coral fragments using the DNeasy Blood & Tissue Kit (QIAGEN, Hilden, Germany). The quantification of DNA concentrations in each coral sample was conducted using a Qubit fluorometer (Thermo Fisher Scientfic). Agarose gel (1%) electrophoresis was employed to assess the integrity of coral genomic DNA. Genomic libraries were constructed using the Nextera XT kit, according to the lc-WGS Library Preparation Protocol as per the specifications outlined by Baym et al., 2015. Each genomic library's lc-WGS was performed on an Illumina NovaSeq PE100 at The Oklahoma Medical Center. The coverage depths of the sequenced samples ranged from 1.69x to 6.45x, with an average of 3.47x.

# Assembly and Single Nucleotide Variant calls

The quality of the raw sequence reads was assessed using FastP v 0.23.0[18] (Chen et al., 2018). The alignment of *A. palmata* sequences to the reference genome of *Acropora millepora* (v1.1)[81] was performed with the BWA v.0.7.17 [14,46]. After alignment, the paired-end sequencing BAM files were assembled with SAMtools v.1.14[46] to generate VCF v.4.2 format files. Quality filtering on the VCF files

was performed using dDocent's SNP filtering workflow[60] (Table S 2). Thirteen individuals were excluded from the analysis due to the sequence quality filters, as they had more than 50% missing data.

# Population Genomics Analysis

# Genotypic diversity

Multilocus genotypes (MLGs) and genotypic diversity analysis were conducted using the *mlg.filter* function of the poppr v. 2.9.3 package[43], employing the "contracted" method (Collapsing MLGs by genetic distance). Additionally, the *bruvo.dist* distance[13] and the Nearest Neighbor algorithm were applied with a threshold of 0.012, defining the minimum distance to consider two genotypes as unique (Fig. S 1). This method allows each GLM to be represented by a single individual for subsequent analysis, thus allowing for detection of naturally occurring clones within our samples. Genetic diversity was assessed through Stoddart and Taylor's (1988) G, Shannon-Wiener's (1949) H, observed heterozygosity (Ho) and expected heterozygosity (He). Genetic diversity values were calculated using the *basic.stats* function of the hierfstat v. 0.5-7 package[33]. Standard deviation and 95% confidence intervals were determined using the *diversity_stats* and *diversity_ci* functions from the poppr v.2.9.3 package[44].

Genetic structure was evaluated using the $F_{ST}$ fixation index, computed through the *stamppFst* function and the Weir and Cockerham (1984) method within the StAMPP v. 1.6.3 package[57]. We performed a Minimum Spanning Networks (MSN) to calculate the genetic distances between each multilocus genotype (MLG), which groups multilocus genotypes (MLGs) according to the genetic distances between them. Each MLG is a node, and the edges (lines connecting the nodes) represent the genetic distance. Nodes are connected by the minimum distance between individuals, so a set of nodes with identical genetic distances is obtained based on a dissimilarity index[44]. The analysis was performed using the *bitwise.dist* function from poppr v. 2.9.3 package[44]. A Principal Component Analysis (PCA) was performed using the *glPca* function in the adegenet package[39]. The ggplot2 package[79] was utilized to create a graphical representation of the PCA and generate ellipses encompassing 95% of the variance for each PCA population. The population assignments observed in the PCA results were further explored using a Discrimination Analysis of Principal Components (DAPC)[38]. Execution of the DAPC analysis was accomplished with the *dapc* function from the adegenet v.2.0.0 package[37] (Jombart and Collins, 2015). Employing the k-means clustering analysis[34], we determined the optimal number of clusters (k) by identifying the lowest Bayesian Information Criterion (BIC) value among ten cluster replicates. Molecular variance (AMOVA)[27] was analysed with the *poppr.amova* function of the poppr v. 2.9.3 package[44]. To examine the correlation between genetic distance matrices [$F_{ST}/(1-F_{ST})$] and geographic distances, the Mantel Test[71] was performed using the *mantel.rtest* function within the ade4 v.1.6-2 package[24]. The significance level of the AMOVA and Mantel Test were evaluated by randomized Monte Carlo simulations with 999 permutations with the *randtest* and *mantel.rtest* function respectively of the ade4 v.1.6-2 package[24].

# Results

## Genotypic diversity

Our sequencing effort and SNP-filter pipeline produced a final dataset of 6,580 SNPs across 128 individuals of *A. palmata* (Table S 3). After implementing quality filters, 13 individuals were eliminated from the analysis as each exhibited over 50% missing data (Table 1).

We also eliminated nine clonal individuals belonging to a single genotype (Table 2), which led us to 107 unique MLGs for downstream analysis (Table 1).

Table 1
Number of individuals sequenced included in the population genetics analysis (MLGs)

| Number of individuals | | | |
|---|---|---|---|
| **Secuenced** | **Missing data** | **Clonal** | **Population analyses (MLGs)** |
| 128 | 13 | 9 | 107 |

Table 2
Clonal individuals of genotype MLG.21 that were not included in the population genetics analysis.

| Nearest neighbor – 0.012 | |
|---|---|
| **Individual tag** | **Site** |
| 131 | Cadenita |
| 141 | Cadenita |
| 182 | Limones |
| 183 | Limones |
| 184 | Limones |
| 18 | Limones |
| 9 | Limones |
| 186 | Cuevones |
| 187 | Cuevones |

## Genetic diversity

The restored Cuevones reef displayed the highest genetic diversity (H = 3.43), which was on par with that of natural populations in the Limones reef (H = 3.25), and Bajito Nizuc reef (H = 3.29) (Table 3 and Fig. 2).

Ixlache recorded the highest expected heterozygosity (He = 0.167), followed by the restored Cuevones reef (He = 0.149), with Akumal exhibiting the lowest value (He = 0.082). The He values suggest that the probability of encountering a randomly selected heterozygous individual at the sampling sites is less than 17% (< 0.167). In addition, we observed that Ho exceed He at all sites, indicating a predominance of heterozygotes within the population (Table 3 and Fig. 2).

Table 3
Statistic of the population of Acropora palmata including standard deviation and 95% confidence intervals.

| Sitio | MLGs | H | H.est | H.ci | Ho | Ho dst | Ho ci | He | He dst | He ci |
|---|---|---|---|---|---|---|---|---|---|---|
| **Cuevones** | 31 | 3.434 | 2.876 | 3.247, 3.621 | 0.162 | 0.110 | 0.160, 0.165 | 0.149 | 0.087 | 0.144, 0.148 |
| **Limones** | 26 | 3.258 | 2.699 | 3.042, 3.475 | 0.156 | 0.118 | 0.154 ,0.159 | 0.140 | 0.093 | 0.138, 0.142 |
| **Farito** | 2 | 0.693 | 0.319 | 0.013, 1.374 | 0.182 | 0.333 | 0.173, 0.191 | 0.145 | 0.228 | 0.141, 0.156 |
| **Cadenita** | 13 | 2.565 | 2.025 | 2.251, 2.879 | 0.144 | 0.168 | 0.140, 0.148 | 0.125 | 0.124 | 0.122, 0.128 |
| **Akumal** | 2 | 0.693 | 0.305 | 0.015, 1.371 | 0.104 | 0.260 | 0.098, 0.110 | 0.082 | 0.185 | 0.076, 0.088 |
| **Bajito Nizuc** | 27 | 3.296 | 2.748 | 3.065, 3.527 | 0.173 | 0.121 | 0.170, 0.176 | 0.153 | 0.094 | 0.151, 0.156 |
| **Ixlache** | 6 | 1.792 | 1.267 | 1.333, 2.25 | 0.191 | 0.230 | 0.186, 0.196 | 0.167 | 0.150 | 0.163, 0.170 |

H - Shannon-Wiener Index of MLG diversity (Shannon, 1948); Ho - Observed heterozygosity; He - Expected heterozygosity (Nei, 1978). est – standard deviation; ci – confidence intervals.

# Genetic Structure

# Fixation Index – $F_{ST}$

The low $F_{ST}$ values suggest high gene flow among populations ($F_{ST}$ = 0.003–0.076). The highest $F_{ST}$ values were observed between Cadenita and Farito ($F_{ST}$ = 0.076) and between Farito and Akumal ($F_{ST}$ = 0.06) (Fig. 3). AMOVA analysis indicates that 98.86% of the variation occurs within populations, while 1.14% is observed among populations ($\phi$ = 0.011, p = 0.02, Table 4). This suggests a subtle genetic differentiation among *A. palmata* populations in the study area despite evidence of widespread gene flow.

Table 4
Analysis of Molecular Variance (AMOVA) among and within sampling sites.

| | Df | Sum of squares | Variance % | Phi (φ) | p-value |
|---|---|---|---|---|---|
| Between samples | 6 | 173.7393 | 1.1379 | 0.0114 | 0.023 |
| Within samples | 100 | 2498.3454 | 98.8621 | | |
| Total | 106 | 2672.0847 | 100 | | |

# Minimum Spanning Networks

The MSN genetic distance analysis found a connection between immediate nodes with a genetic distance from 0.02 to 0.08. Genotypes or central nodes, nine from Limones Reef and 147 from Cuevones Reef had the highest number of connections to other genotypes within the population (Fig. 4). Two significant groups are discernible. The upper group of the network predominantly comprises individuals from the Limones Reef (61.53% of collected individuals). In contrast, the lower group consists mainly of individuals from the Ixlache, Cadenita, and Bajito Nizuc reefs (83%, 69%, and 59% of collected individuals from each respective reef). Additionally, a smaller distinct cluster is observed in the lower-left quadrant, primarily represented by individuals from the Ixlache and Limones reefs (17% and 15% of collected individuals from each respective reef) (Table 3S). Genetically close individuals from different reefs form these groups, providing evidence of genetic exchange between populations of *A. palmata* in northern Quintana Roo. However, these groups mainly comprise MLGs from Cuevones and the other group of MLGs from Limones.

# Discriminant Principal Component Analysis (DPCA)

The DPCA analysis shows no clear division between the reefs studied, although, Cadenita (on the left) does separate from the main cluster (Fig. 5). There is an overlap between Akumal, Bajito Nizuc, Ixlache, and Limones. This pattern is consistent with the $F_{ST}$ pairwise comparisons.

Using k-means clustering analysis and BIC value (Figure S 2 and Figure S 3), we discerned two distinct genetic groups (k = 2) in the present study (Fig. 6). Individuals from Farito and Ixlache exhibit a heightened probability of falling within genetic group 1, consistent with $F_{ST}$ comparisons Individuals originating from the Akumal reef are more likely to be affiliated with genetic group 2, while the remaining population exhibits a more even distribution across both genetic groups. Overall, the graph indicates genetic exchange among reefs in northern Quintana Roo, except the more remote Ixlache and Akumal reefs, which are 143 km apart. This analysis confirms the pattern of genetic differentiation between Cadenita and Farito. Nevertheless, it should be noted that only two individuals were analyzed at both Farito and Akumal, which may influence the observed genetic variability.

# Mantel test

We observed a weak and non-significant correlation between geographic and genetic distance (Rxy = 0.071, p = 0.299). Since the most significant differentiation ($F_{ST}$ = 0.076) was found between the sites of Cadenita and Farito, separated by only approximately 1.68 km, our findings lack substantial evidence to support the assertion that geographical distance significantly contributes to the genetic differentiation among the reefs in Northern Quintana Roo (Fig. 7).

## Discussion

# Genetic diversity

Our results indicate that integrating both asexual and sexual to |restore the Cuevones Reef has proven successful in retaining levels of genetic diversity comparable to those found in natural reefs. This is highly significant for restoration programs as it enables the preservation of genetic diversity and increases resilience, consequently, improving conservation efforts of coral reefs in the region in the face of local disturbances and global threats. Particularly, after the massive bleaching event caused by the Niño 2023 event[16,20,32].

Previous studies have documented that utilizing local populations in restoration efforts maintains a pre-existing genetic identity and reinstates historical patterns of genetic diversity[7]. Furthermore, introducing diverse genotypes from various locations in the Mexican Caribbean reef is expected to expedite its recovery and enhance its resilience. Introducing genotypes from different locations can help maintain or even improve the genetic variability of coral populations. According to DeFilippo et al. (2022), with sufficient natural genetic variation, corals are more likely to adapt to warming temperatures and other stressors. Therefore, restoration programs should prioritize maintaining and enhancing the genetic variation of populations, which may be more effective in the long term than strategies based solely on introducing heat-tolerant genotypes.

Although the diversity of the Cuevones reef is comparatively high within the scope of this study, our observed heterozygosity (He) values for *A. palmata* (He = 0.125–0.167) are relatively lower than those reported in other regional studies in the eastern and western Caribbean and the Mexican Caribbean. Specifically, studies using SNP markers in the region reported He values ranging from 0.195 to 0.216[22]. In microsatellite studies, Gómez-Campo (2015) reported He values between 0.763 and 0.812 for *A. palmata* at seven locations in the Mexican Caribbean; Baums et al. (2008) reported an average He of 0.76 for the Caribbean region. Meanwhile, Domínguez-Maldonado et al. (2022) reported an average He of 0.315 for the Mexican Caribbean and the Gulf of Mexico. Hence, our findings on diversity in natural populations may reflect the ongoing population bottlenecks this species faces within the Caribbean region. These populations persist under continued threat, experiencing significant and repeated mortality events. Thus, there is an urgent need to standardize restoration techniques to ensure the recovery efforts for these populations[23,50].

Recognized as one of the Mesoamerican Reef System's best-preserved reefs, Limones Reef displays notable diversity values (H = 3.25 and He = 0.14). This could be attributed to the protective measures implemented by government and academic institutions, including the Autonomous University of Mexico (UNAM), the National Fisheries Institute (INAPESCA), and the National Commission for Protected Natural Areas (CONANP). For instance, shortly after hurricanes Emily and Wilma in 2005, the Puerto Morelos Reef National Park (PMRNP) initiated rehabilitation efforts, relocating 221 coral fragments between the reef lagoon and the Limones reef crest[66]. This intervention likely contributed to the preservation of coral cover at the site. Unfortunately, there was no subsequent monitoring of this initiative, so how many fragments initially survived and how many are still alive to date, is unknown.

In mid-2012, the *A. palmata* coverage on this reef exceeded 30%, closely resembling the reported figures for reefs in the northeastern Yucatan Peninsula during the late 1970s[40,41]. In 2019, Drury et al. found a positive correlation between genetic diversity and coral cover, hinting at potential associations with complementarity, influencing cover through niche partitioning, and/or interactions among genets. The high genetic diversity observed at Limones Reef may be attributed to local oceanographic conditions conducive to forming eddies[52], potentially facilitating larval retention and accumulation[73]. These conditions likely contributed to the natural recovery of *A. palmata* at the site, as indicated by Rodríguez-Martínez et al. (2014), who documented a high proportion of small colonies and minimal partial mortality of this species. This is the first genetic study carried out on this reef, and the results will allow us to better inform the necessary actions to preserve the condition of the Limones Reef.

Also, our study's observed diversity among individuals is noteworthy; among the 128 *A. palmata* colonies analyzed, only 7% were identified as clonal. Previous genetic analyses of *A. palmata* have shown that reefs can often be monoclonal or consist of a limited number of genotypes (genets) [6,11]. In addition, in high-throughput sequencing studies with high marker density, each sample is usually composed of a single genotype[74]. Gómez-Campo (2015) identified 130 (44%) genotypes from 297 samples over an area of 324 km in a microsatellite study conducted in Quintana Roo (Cancún-Xcalak). The sampling, including the collection of clones was carried out using the polar plot method.

# Genetic Structure

We identified subtle genetic differentiation among populations of *A. palmata* ($F_{ST}$ = 0.012, p = 0.02) in northern Quintana Roo. We found genetic differentiation between the Cadenita and Akumal reefs, which are approximately 143 km apart. This result is consistent with the findings of Drury et al. (2017), where utilizing SNPs from a reduced-representation sequencing approach in the threatened coral *A. cervicornis* revealed the population structure within the Florida Reef Tract, even at the level of individual reefs, likely attributed to the presence of unique alleles. However, Cadenita and Farito, separated by only about 1.68 km showed the greatest genetic differentiation ($F_{ST}$ = 0.076). In Farito, only three colonies of *A. palmata* were found during sampling. This is probably due to the population decline and consequent loss of genetic variability at this touristic site.

Previous genetic studies on Acroporids have shown variable results, suggesting the influence of spatial scale on patterns of genetic structure. Nonetheless, it is worth mentioning that SNP markers detect subtle genetic differences at local scales in populations where other markers, such as microsatellites had not identified them. For example, Gómez-Campo (2015) found no genetic structure in *A. palmata* populations in the Mexican Caribbean, suggesting that it is a panmictic population ($F_{ST}$ = 0.000, p = 0.474). In contrast, other studies have found a significant regional structure for populations separated by more than 500 km in nuclear and mitochondrial genes[3,51]. In the Florida Reef Tract, analysis of *A. cervicornis* using microsatellites showed little population differentiation and no significant population structure[10]. These results were confirmed with mitochondrial control region sequences that showed no significant population structure for *A. cervicornis* at the same site (Hemond & Vollmer, 2010). However, significant genetic differentiation was evident when the analysis was extended to broader scales at the Caribbean level[10]. Drury et al. (2016) showed population structure in the Florida Reef Tract and high diversity within A. *cervicornis* populations for the first time through SNP markers scored by Genotyping by Sequencing (GBS).

The results of the AMOVA in this study reveal that the predominant variation exists within populations (98.86%). This variation can be attributed to the subtle genetic structure within the population, where individuals from different subpopulations (reefs) show minimal genetic distance. This suggests ongoing sexual reproduction and a potential lack of barriers between the studied reefs[45]. High intra-population genetic variation may confer resilience to stressors and climate change factors, including temperature anomalies and acidification[25]. In the scenario where populations are interconnected, restoring a deteriorated reef becomes achievable solely through recruiting larvae from distant and well-preserved reefs, exemplified by the Limones and Bajito Nizuc reefs. Therefore, these two reefs could be functioning as source reefs, playing a crucial role in sustaining the *A. palmata* populations in the northern Mexican Caribbean. This genetic exchange could accelerate the adaptation process by introducing favorable alleles from one population to another, although there is also the probability of contributing non-adaptive alleles[1]. This information is essential for formulating effective policies and managing resources efficiently. Understanding genetic connectivity provides essential insights into how populations are maintained and replenished after environmental disturbances. It also serves as a valuable indicator of population resilience[75].

Environmental factors such as ocean currents and the life cycle of *Acropora* species must also be taken into consideration in explaining their genetic connectivity. There is a notable correlation between ocean surface currents and larval dispersal routes, suggesting that species with planktonic larvae inhabiting regions connected by currents tend to show high genetic similarity[65]. In the case of *A. palmata*, after fertilization, larvae undergo a developmental period of 78 hours before displaying the first signs of motility[6]. Pelagic larvae become competent to settle within 5 days but can remain planktonic for up to 20 days[5], supplying a chance for dispersal and gene flow between reefs. This extended planktonic phase not only allows for the colonization of distant reefs but also eases gene flow between populations,

contributing to the observed connectivity and genetic exchange between reefs in the northern Quintana Roo region.

DNA sequencing studies reveal a considerable amount of diversity yet to be described, and their evolutionary and ecological implications[35,12]. Our understanding of the potential impacts of genotypic diversity or genet-genet interactions on community function in marine ecosystems is yet limited[72]. Therefore, further exploration of persisting coral populations at the genomic level is imperative to unravel the intricate relationships between genetic diversity and the ecological dynamics of coral reef ecosystems.

## Conclusion

Our study indicates that combining sexual and asexual reproduction for reef restoration is effective in both preserving and potentially augmenting the genetic diversity of *A. palmata* populations in the northern Mexican Caribbean. The natural reefs of Bajito Nizuc and Limones were the most diverse in the area, both characterized by extensive coral coverage. Therefore, they can be recognized as "source" reefs, and may play a crucial role in coral restoration and the recovery of populations in the region. Due to the loss of nearly 95% of the Acroporid populations in the Caribbean, it becomes crucial to preserve the genotypes identified in this study, as they may facilitate the adaptation of these populations to climate change. We emphasize that the most effective strategy for managing and conservating coral reefs is maintaining population genetic variability. This approach also indicates resilience in the face of the ongoing threats posed by a changing climate. We also show the effectiveness of lc-WGS for genotype identification and its application in assessing the diversity and genetic connectivity of Scleractinia corals. Thus, providing relevant information to achieve conservation objectives with evolutionary implications.

## Declarations

# 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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# Author Contribution

V.A.C. and M.G.C. Conceptualization, Investigation, Methodology, Data Curation, Formal Analysis, Visualization, Software and Writing – Original Draft. G.L.P. Conceptualization, Writing - Review and Editing. R.R.M. and A.C.P.S. Methodology and Resources. V.A.C. and A.C.P.S. Funding acquisition. C.P. and J.E.A.G. Project administration, Supervision, Review and Editing.

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# Data Availability

The data will be provided upon request to Arias-González (arias@cinvestav.mx).

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# Figures

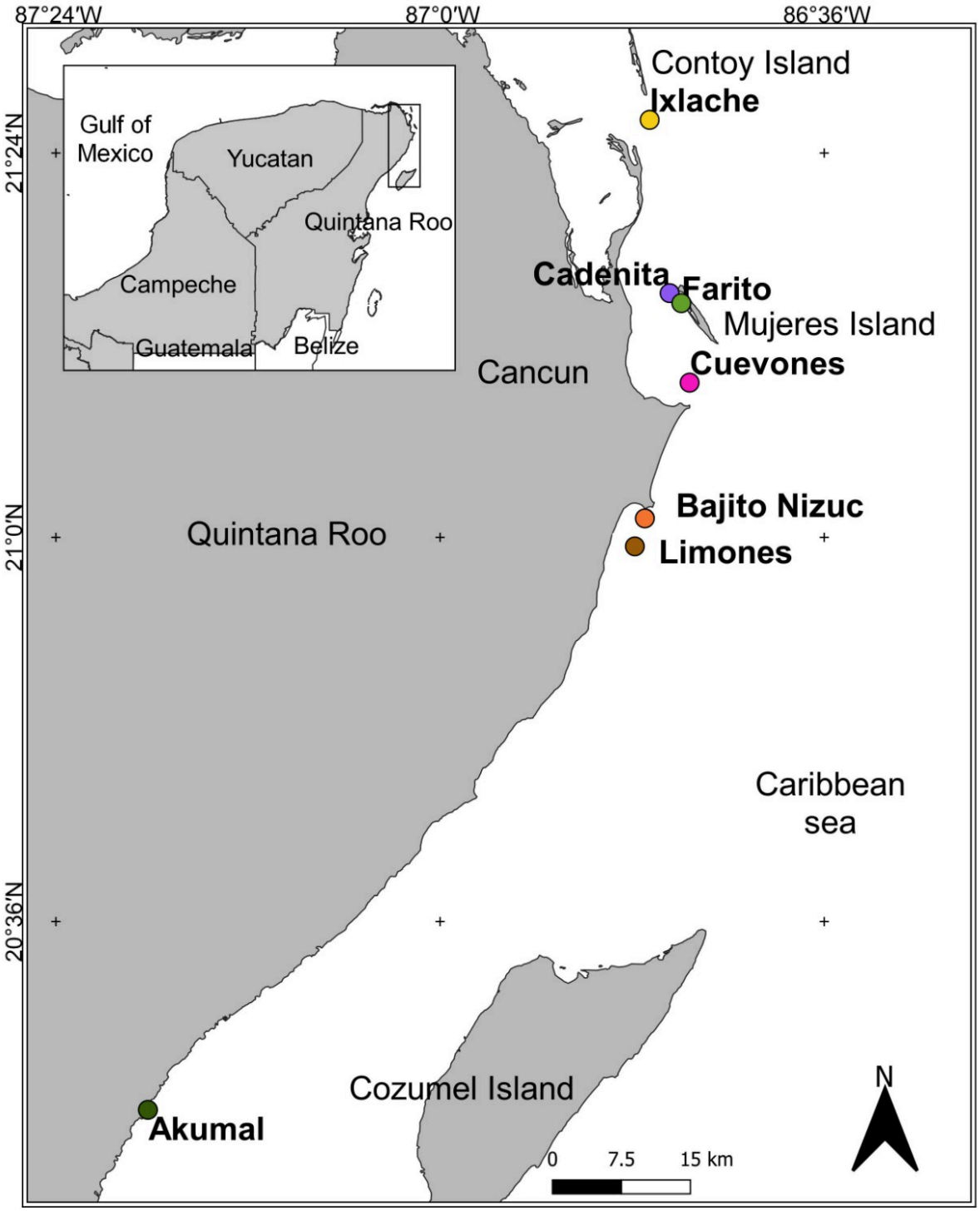
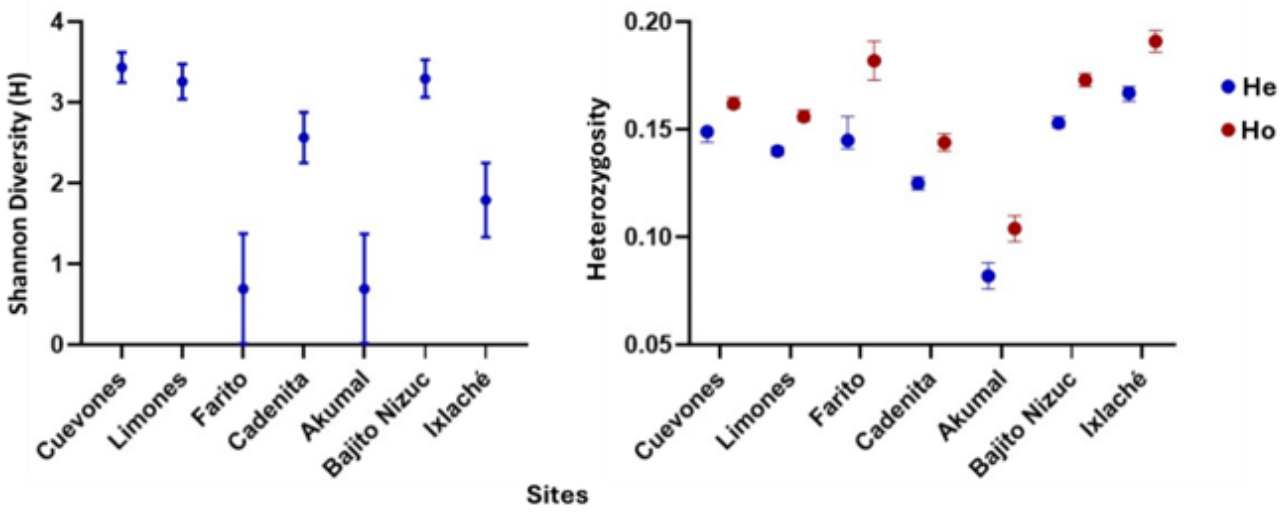


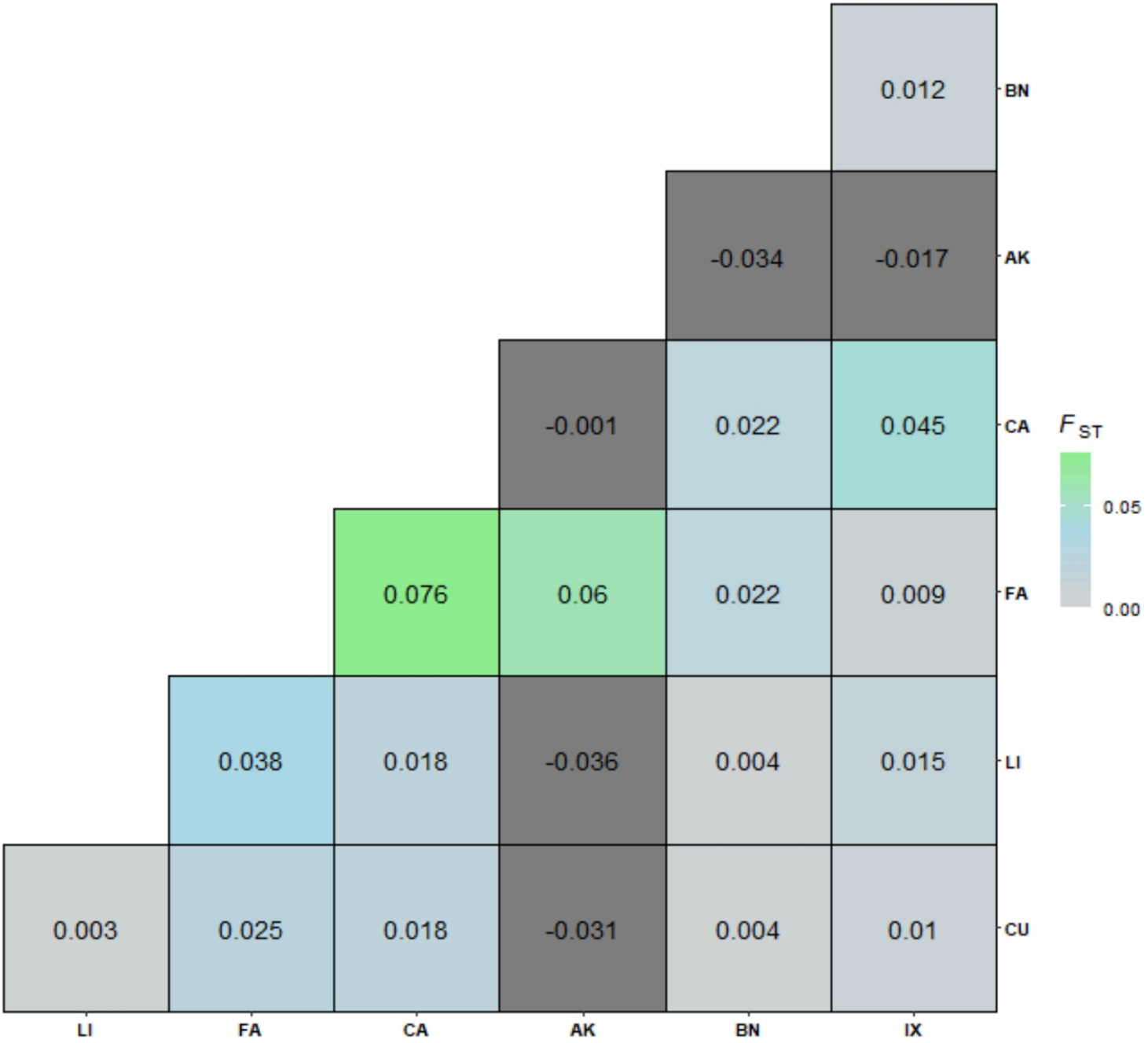

Figure 1

The study area is north of Quintana Roo, which is part of the Mesoamerican Barrier Reef System and the Caribbean Sea.



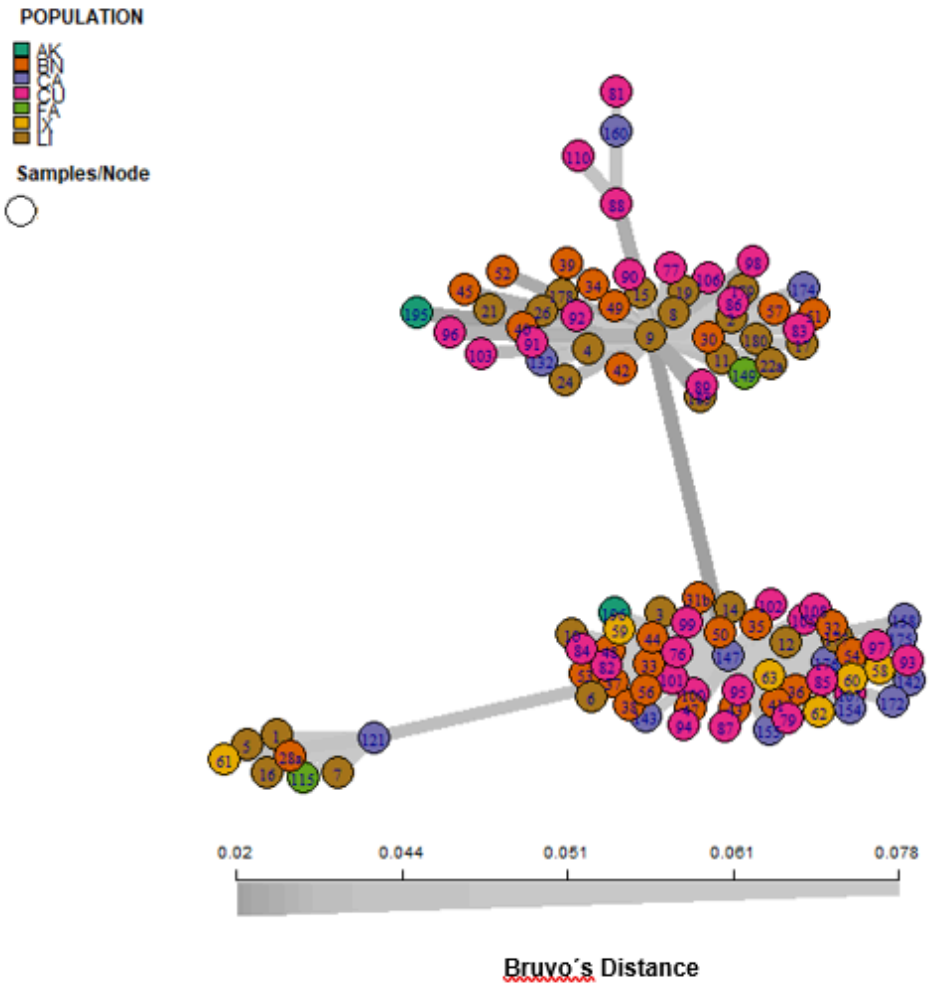

## Figure 2

The genetic diversity index is expressed as Shannon Diversity (H) (a). Expected heterozygosity (He) and observed heterozygosity (Ho) (b). The graphs show the mean ± SD and 95% confidence intervals



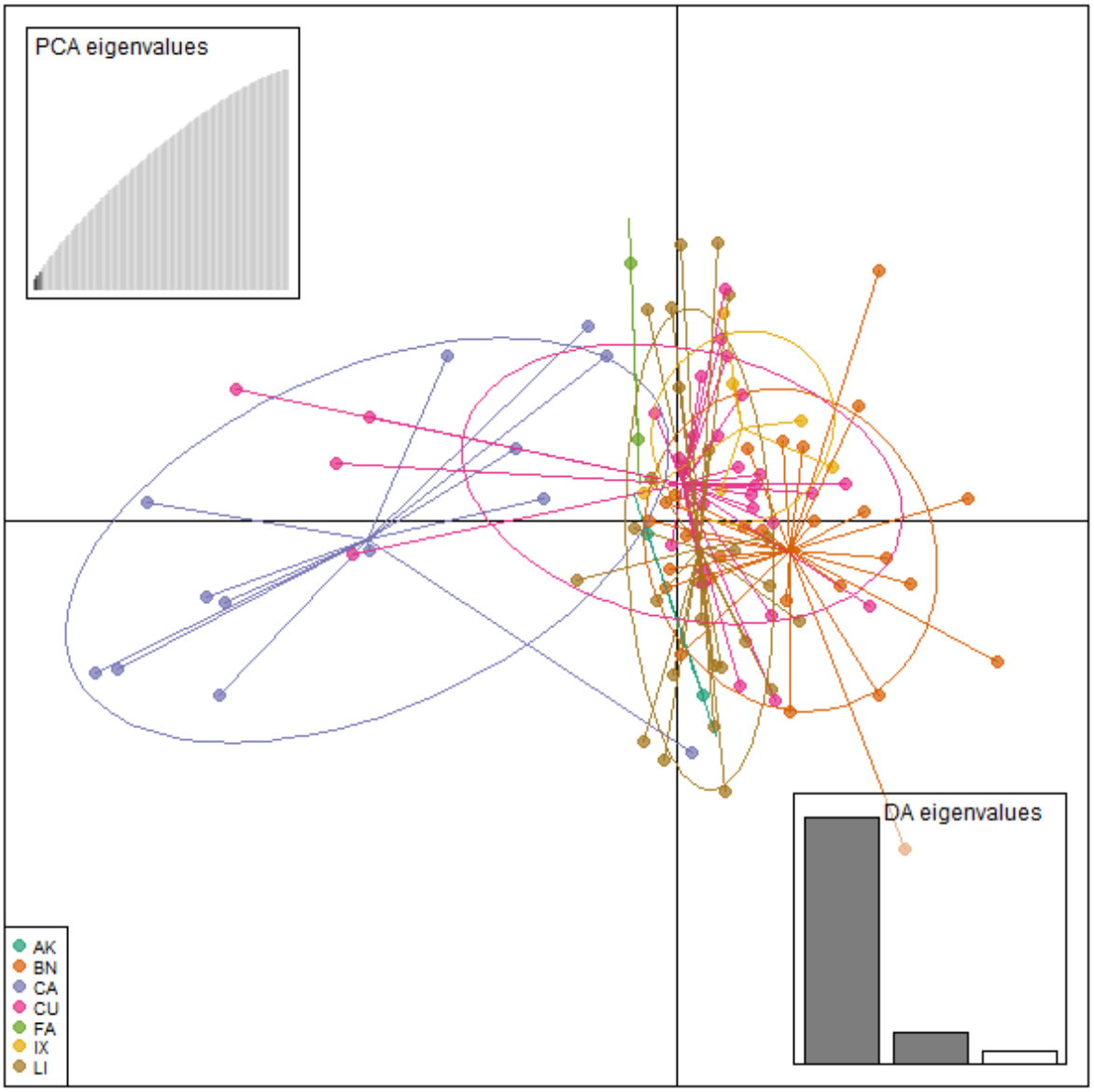

## Figure 3

Heat map showing pairwise population differentiation, estimated by fixation index ($F_{ST}$), for SNP markers in A. palmata. The color scale ranges from light gray to green, representing rising $F_{ST}$ values, and indicates significant differences between populations ($p < 0.05$).



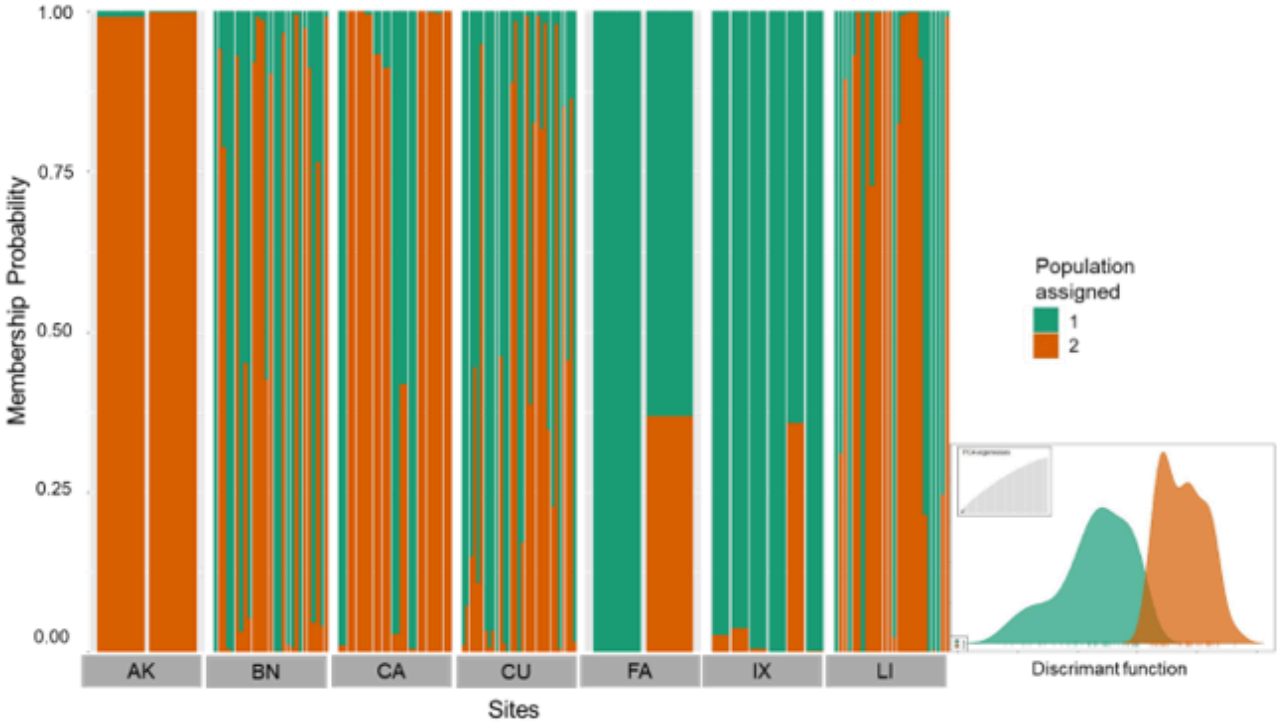

## Figure 4

Minimum spanning networks based on Bruvo's genetic distance for SNPs markers for *A. palmata* populations. Each circle represents an MLG (genotype), and each color represents a reef. The length and thickness of the lines connecting MLGs represent their genetic distance, calculated as the number of different alleles. Akumal (AK), Bajito Nizuc (BN), Cadenita (CA), Farito (FA), Ixlache (IX), Limones (LI).




## Figure 5

DPCA, based on SNP markers, defines the similarities and differences among seven reefs in northern Quintana Roo. The results depict a less differentiated population of A. palmata. Each reef, along with inertia ellipses, is displayed in distinct colors, while data points stand for individuals: Akumal (AK), Bajito Nizuc (BN), Cadenita (CA), Farito (FA), Ixlaché (IX), and Limones (LI).




## Figure 6

The DPCA composite barplot presents individual samples of A. palmata (x-axis), with the y-axis denoting the probability of membership linked to an assigned genetic group (k=2). The graph employs distinct colors (green for group 1 and orange for group 2). The graph on the right represents the discriminant function 1.

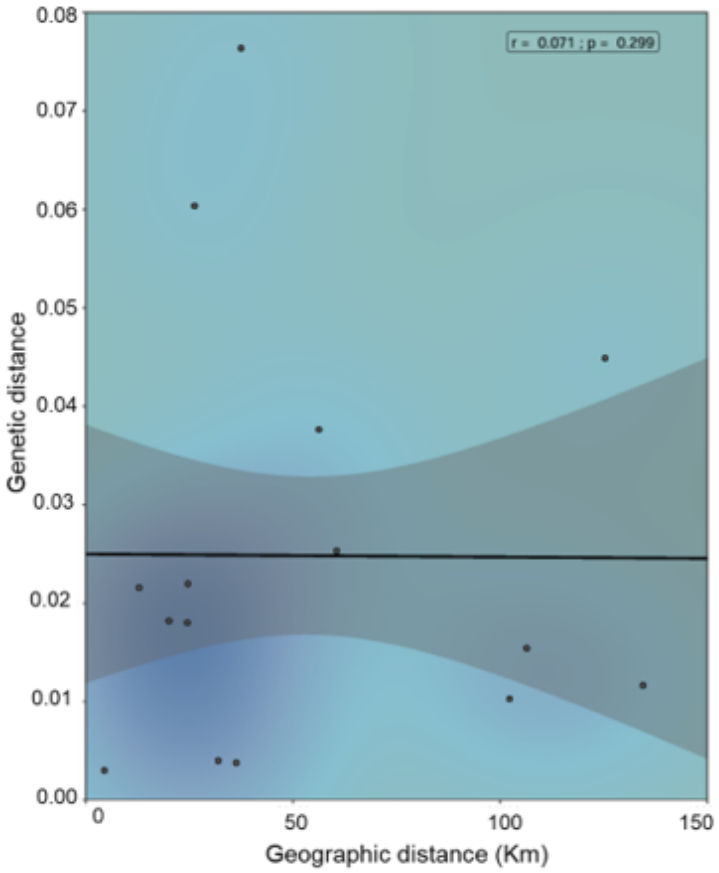



**Figure 7**

Mantel test graph showing the correlation between genetic and geographical distances for SNPs of A. palmata in Northern Quintana Roo. Darker colors indicate higher densities of pairwise genetic and geographic distance comparisons. The plot includes a linear regression line with a 95% confidence interval and shows significant correlation coefficients ($p < 0.05$).

# Supplementary Files

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- SupplementaryInformationAlvaradoCernetal..pdf