Coral Reefs (2025) 44:353–358
https://doi.org/10.1007/s00338-024-02598-2

NOTE

Species-specific patterns of population genetic structure differ on a microgeographic scale

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Received: 24 April 2024 / Accepted: 18 November 2024 / Published online: 8 December 2024

Abstract Coral exhibits substantial variation in pelagic larval duration, dispersal range, and population connectivity. In this study, we used reduced representation genotyping to compare the genetic structure of Caribbean reef-building species along the southeastern Dominican Republic coastline to assess connectivity within the likely dispersal kernel. Despite relatively small geographic distance between reefs, species-specific differences in genetic structure were observed. The broadcasting coral *Orbicella faveolata* had high levels of genetic connectivity. Between the two brooding species, *Agaricia agaricites* showed strong genetic subdivision, while *Porites astreoides* exhibited high levels of gene flow. These results suggest that multiple factors outside of life history characteristics influence genetic differentiation among populations, with species-level variability underscoring the importance of restoration and management strategies tailored to individual species, considering regional genetic and environmental variability.

Spanish Los corales presentan una notable variación en la duración de su etapa larval pelágica, el rango de dispersión y la conectividad entre sus poblaciones. En este estudio, utilizamos técnicas de genotipificación de representación reducida para comparar la estructura genética de especies constructoras de arrecifes del Caribe a lo largo de la costa sureste de la República Dominicana y evaluar la conectividad dentro del núcleo probable de dispersión. A pesar de las distancias geográficas relativamente cortas entre los arrecifes, se observaron diferencias específicas por especie en la estructura genética. El coral desovante Orbicella faveolata mostró altos niveles de conectividad genética. Entre las dos especies incubadoras, Agaricia agaricites presentó una marcada subdivisión genética, mientras que Porites astreoides mostró altos niveles de flujo génico. Estos resultados sugieren que múltiples factores, además de las características de su ciclo de vida, influyen en la diferenciación genética entre poblaciones, destacando la importancia de diseñar estrategias de restauración y manejo adaptadas a cada especie, teniendo en cuenta la variabilidad genética y ambiental de la región.

Keywords Population connectivity · Dominican Republic · Dispersal patterns

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00338-024-02598-2.

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Introduction

An extended pelagic larval duration (PLD) can extend a sessile marine organism's range, increasing genetic connectivity among distant populations (Nishikawa et al. 2003; Hoffman et al. 2011; Thomas et al. 2020). Life history traits such as reproductive mode can influence PLD, impacting individual fitness, population persistence, and species evolution (Fadlallah 1983; Nishikawa et al. 2003; Hoffman et al. 2011). Corals can sexually reproduce by either releasing unfertilized gametes (termed broadcasting) or releasing developed planula larvae (brooding). Reproductive mode, due to differing developmental stages of broadcasted and brooded offspring, is hypothesized to create differences in PLD, and subsequently the potential for dispersal between populations (Fadlallah 1983; Nishikawa et al. 2003).

The influence of reproductive mode on PLD and population connectivity has been studied in Indo-Pacific coral species, with broadcasters displaying a higher dispersal potential and genetic connectivity across a range of geographic scales compared to brooders (Nishikawa et al. 2003; Thomas et al. 2020). Conversely, studies have demonstrated that larvae from brooding corals can also have high dispersal, potentially supporting high gene flow observed among even distant populations (Ayre and Hughes 2000). These mixed findings indicate that along with reproduction mode and PLD, additional life history traits influence species' population connectivity.

For regions such as the Caribbean basin, characterized by a blend of restored, degraded and relatively healthy reefs, genomic tools can aid in pinpointing vulnerable areas and suitable outplanting locations to facilitate genetic exchange among populations (Mumby et al. 2007; Rippe et al. 2017). Work to date in the Caribbean indicates low to moderate genetic structure across a range of distances and species (Baums et al. 2005; Porto-Hannes et al. 2015; Serrano et al. 2016; Hammerman et al. 2018). The most prevalent boundary to gene flow is between the eastern and western Caribbean (Baums et al. 2005; Devlin-Durante and Baums 2017; Rippe et al. 2017) though multiple Caribbean species have demonstrated potential to disperse large distances and maintain high genetic connectivity (Porto-Hannes et al. 2015; Serrano et al. 2016). However, the majority of studies to date have focused on single species, leaving a gap in our understanding of species-level variability in population structure across shared reef sites (Porto-Hannes et al. 2015). Additionally, previous work in the Caribbean has primarily focused on reefs across large physical or ecological distances (Baums et al. 2005; Serrano et al. 2016), with little knowledge as to whether the structure of Caribbean species observed across large geographic scales persists on a microgeographic scale (Brazeau et al. 2005).

Here, we sampled and sequenced two regionally abundant brooding species (*Porites astreoides* and *Agaricia agaricites*) and one broadcasting species (*Orbicella faveolata*) from five Dominican Republic reef sites within a ~ 100 km^2 area to assess the local scale genetic connectivity of corals. While our results reinforce the general Caribbean trend of low to moderate population structure, there was discrete variability in population structure by species, with *O. faveolata* and *P. astreoides* exhibiting higher gene flow across sites compared to *A. agaricites*.

Methods

Sample collection

Tissue samples approximately 2 cm^2 were collected from twenty individuals of each species at five reef sites along the southeastern coast of the Dominican Republic and exported under CITES permit #DO-01328 (Fig. 1a, Supplementary Methods).

DNA extraction and library preparation

Genomic DNA was extracted, and reduced representation 2b-RAD libraries were prepared following a pooled adaptor ligation scheme (https://github.com/z0on/2bRAD_denovo) (Wang et al. 2012). Bioinformatic analysis was performed on the USC CARC HPC system following the 2b-RAD de novo pipeline (https://github.com/z0on/2bRAD_denovo). Samples were separated by species for bioinformatic analysis.

Mapping to reference and symbiont genomes

Reads for all species were mapped to their respective host and symbiont reference genomes (Supplementary Methods). Reads mapping to symbiont genomes were extracted to quantify symbiont genera of samples (Figure S1). Only reads mapping exclusively to host contigs were retained for subsequent analyses.

Population structure and clonal removal

Coverage was first evaluated to remove samples with < 10% of sites at a minimum of 5 × coverage (Table S1). Genotype likelihoods were generated in ANGSD 0.932 (Korneliussen et al. 2014) and filtered to retain high confidence SNPs (Supplementary Methods). High confidence sites were used to generate an Identity by State (IBS) matrix and hierarchical clustering was performed using hclust in R v4.3.0 (R Core Team 2023). When available, technical replicates were used to set clonal identification thresholds following Manzello et al. (2019). For species with evidence of high clonality

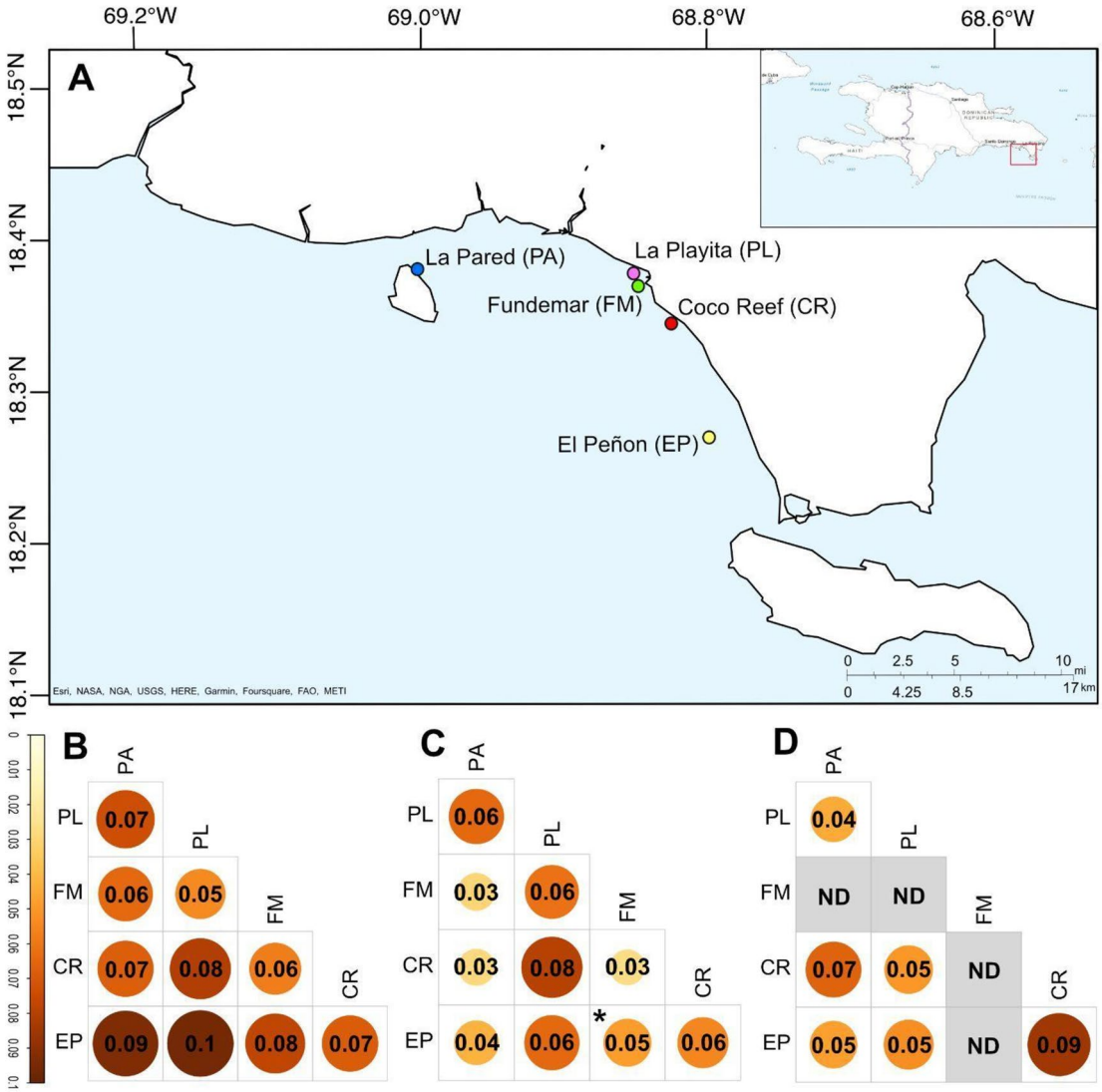

Fig. 1 Map of sampling reefs along the southeastern Dominican Republic (**a**). Pairwise Fst values between sites for *A. agaricites* (**b**), *P. astreoides* (**c**), and *O. faveolata* (**d**). Fst values across all plots are shaded following the same color scale from light yellow (Fst = 0.03) to dark red (Fst = 0.1). ND indicates no pairwise Fst data due to low remaining sample size at FM. *Asterisk denotes a value outside of calculated 95% confidence intervals

(*P. astreoides*) or a lack of technical replicates (*A. agaricites*), serial hierarchical clustering was performed (Table S2, Supplementary Methods). One individual from each clonal cluster was retained as a representative of that genotype, and remaining samples were defined as unique genotypes.

A deep split in the initial *O. faveolata* dendrogram indicated the presence of cryptic species (Figure S2). Additional *Orbicella* spp. samples from the Florida Keys (Manzello et al. 2019) aided in distinguishing lineages. Among our samples, 23 clustered with *O. annularis* and *O.franksi*, while the remaining 23 clustered with *O. faveolata*. Putative *O. annularis* and *O.franksi* samples were removed, and ANGSD was rerun on the remaining *O. faveolata* samples, producing a new IBS matrix (Table S2).

Host population genomics without clones

A multidimensional scaling (MDS) analysis was performed on pairwise IBS distances for unique genets using the R-package vegan (Oksanen et al. 2022). Admixture was evaluated from genotype likelihoods for 1–10 genetic clusters (K) using ADMIXTURE (Alexander et al. 2009).

Global pairwise fixation index (Fst) values were calculated in ANGSD with 95% confidence intervals (Korneliussen et al. 2014) (Supplementary Methods, Table S3). One site, FM, had only 3 *O. faveolata* samples remaining following filtering for clones and cryptics and was thus excluded from Fst calculations. To test for a correlation

between genetic and geographic distance of sites, a simple Mantel test was performed in R.

Results and discussion

We observed differences in the local population structure among species along the southeastern Dominican Republic coastline. High levels of genetic connectivity across sites for *O. faveolata* indicate extensive gene flow consistent with expected broadcast spawning dispersal patterns (Figs. 1d, 2c). Within the brooding species, *P. astreoides* exhibited high genetic connectivity, while *A. agaricites* was characterized by reduced genetic overlap across reef sites (Figs. 1bc, 2a).

Agaricia agaricites had the greatest overall amount of genetic subdivision (Fst 0.05–0.1) with two genetic clusters ($K=2$, Figure S3) receiving the highest statistical support following methods from Alexander and Lange (2011) (Figs. 1b, 2a). The closest geographic sites, FM and PL (< 1 km), exhibited the greatest gene flow (Fst 0.05), while the second highest fixation index was calculated between EP and PA, the two furthest sites (25 km, Fst 0.09). However, Mantel test results for geographic distance and genetic differentiation were insignificant ($r=0.58$, $p=0.13$). Previous studies have also found subpopulation structure in *A. agaricites* on a microgeographic scale, with populations as close as 12 km displaying significant genetic variance (Brazeau et al. 2005).

The *P. astreoides* dataset supported only one genetic cluster ($K=1$), with high gene flow evident across sites (Fig. 1c), and the relationship of distance and Fst was not significant ($r=-0.34$, $p=0.68$). Our finding of minimal population structure across sites (Fst 0.03–0.08) is consistent with larger-scale studies, which demonstrated high gene flow across geographic distances in *P. astreoides* (Serrano et al. 2016; Shilling et al. 2023). Interestingly, one site (PL) had the highest Fst values across all pairwise combinations despite close geographical proximity to neighboring sites (Fig. 1ac). These findings, along with previous studies demonstrating that *P. astreoides* populations can exhibit fine-scale genetic differentiation (Riquet et al. 2022), indicate that despite large-scale homogeneity, factors such as larval duration plasticity, environmental selection, and mixed reproductive strategy may also influence *P. astreoides* population structure (Zhang et al. 2019; Riquet et al. 2022).

ADMIXTURE modeling reported a single genetic cluster for *O. faveolata* ($K=1$), which is further supported by the multi-layered overlap of ellipses in the MDS plot (Fig. 2c). Low pairwise Fst values (Fst ≤ 0.05) between the majority of sites also indicated low levels of genetic subdivision, with no significant Mantel test results ($r=0.01$, $p=0.50$) (Fig. 1d). Previous genomic work on *O. faveolata* populations has demonstrated high genetic mixing across the Caribbean basin (Porto-Hannes et al. 2015; Rippe et al. 2017), aligning with our findings on a microgeographic scale.

The relative abundance of *Durusdinium* within *O. faveolata* and the cryptic *Orbicella* spp. varied by site (ANOVA, $p=0.0237$) and species (ANOVA, $p=0.0225$) (Supplementary Methods, Table S4). For these two lineages, all four analyzed symbiont genera were found at each reef site, but composition varied. Coco Reef, El Peñon and Fundemar had high relative abundance of *Durusdinium* and *Cladocopium*, while no La Playita samples had high *Cladocopium* levels (Figure S1). Additionally, La Pared was the only site with individual samples dominated by *Breviolum* (Figure S1). Variation in symbiont communities across reef sites, despite high host gene flow, has been observed in other coral species in the Pacific (Davies et al. 2020). The previously established relationship between symbiont type and environmental conditions (Finney et al. 2010; Davies et al. 2020), as well as the symbiont's influence on coral holobiont

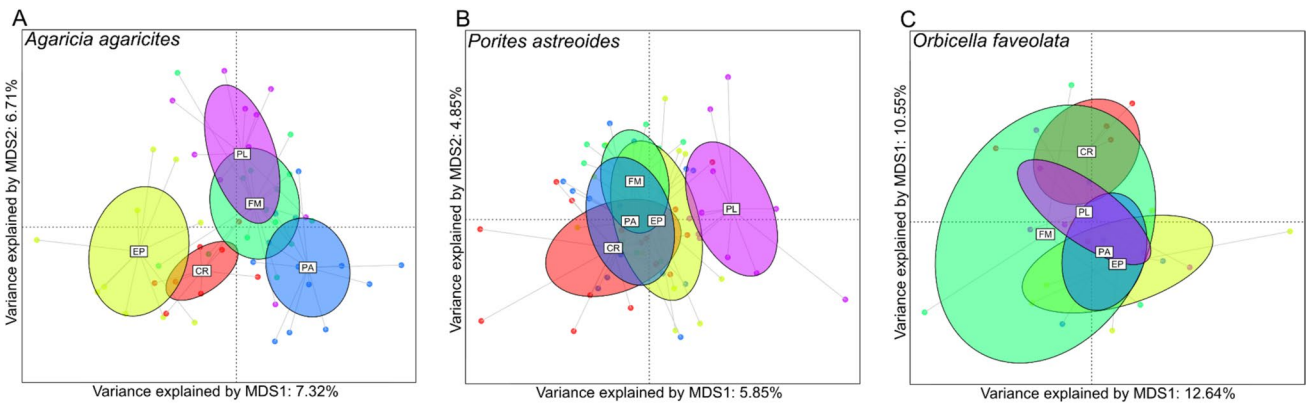

Fig. 2 Scaled MDS Plots for *A. agaricites* (**a**) *P. astreoides* (**b**) and *O. faveolata* (**c**). Ellipses and point colors correspond to the reef site samples were taken from

resilience (Manzello et al. 2019), hints at potential variation in environmental parameters of focal reef sites, local adaptation, or population vulnerability to disturbance. Here, site-specific symbiont community composition in *O. faveolata* might reflect variation in Symbiodiniaceae availability or acquisition among nearby reefs. Future work characterizing the environmental and biological landscape in this region may help clarify potential drivers.

The identification of cryptic *Orbicella* species underscores the disparity between morphological and genomic diversity and emphasizes the role of population genomics in understanding local biodiversity (Grupstra et al. 2024). Relying on morphological identification alone can lead to an overestimation of population size. Smaller populations can heighten a local population's vulnerability to environmental disturbances and reduce the genetic diversity available for spawning events (Gómez-Corrales and Prada 2020). In addition, co-occurring cryptic *Orbicella* species in the Caribbean can display different bleaching responses, indicating some populations are more fit to withstand warmer ocean conditions (Gómez-Corrales and Prada 2020). The ecological niche cryptic corals fill may also differ despite morphological similarity, changing the function of a reef depending on cryptic lineages present (Johnston et al. 2022). Here, demographic shifts and functional changes on reefs targeted for conservation may otherwise go undocumented if the contribution of cryptic *Orbicella* species is not carefully considered.

Taken together, our results indicate that factors beyond life history characteristics drive observed variability in population structure between species. Differences in responses to environmental selection and/or demographic histories, such as recent expansion, may be driving observed patterns, and further work is needed to test for these effects. We also confirm that differences in population structure seen on larger scales for *O. faveolata*, *A. agaricites* and *P. astreoides* (Nishikawa et al. 2003; Thomas et al. 2020) are evident at microgeographic scales in the Caribbean. Continued investigation of coral population genomic structure in the Caribbean on both a local and basin-wide scale, performed in tandem with extensive environmental data collection, will contribute to a greater understanding of factors driving variation in population structure across species, dispersal ranges, and cryptic lineages.

Acknowledgements This study was conducted with funding support from Iberostar's Wave of Change Coral Restoration program to WCM and start-up funding from the University of Southern California to CDK. SO was partially funded by a USC Provost's Undergraduate Fellowship.

Author contributions WCM, CDK, MBP, and MM conceived and designed the study. MBP, BAF, JC-T, EH, and WCM conducted fieldwork. SO, MR, HKC, WCM prepared 2b-RAD libraries. SO, MR, and CDK completed the analysis. SO led manuscript writing, and all co-authors contributed to revisions.

Funding Open access funding provided by SCELC, Statewide California Electronic Library Consortium.Funding Open access funding provided by SCELC, Statewide California Electronic Library Consortium.

Declaration

Conflict of interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

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