Deep connections: divergence histories with gene flow in mesophotic *Agaricia* corals

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Abstract

Vastly understudied, mesophotic coral ecosystems lie below shallow reefs (> 30 m depth) and comprise ecologically distinct communities. Brooding reproductive modes appear to predominate among mesophotic-specialist species and may limit genetic connectivity among populations. Using reduced representation genomic sequencing, we assessed spatial population genetic structure (at 50 m depth) in an ecologically important mesophotic-specialist species, *Agaricia grahamae* among locations in the Southern Caribbean. We also tested for hybridisation with the closely related (but depth-generalist) species *Agaricia lamarcki*, within their sympatric depth zone (50 m). In contrast to our predictions, no spatial genetic structure was detected between the reefs of Curaçao and Bonaire (~ 40 km apart) within *A. grahamae*. However, cryptic taxa were discovered within both nominal species, with those in *A. lamarcki* (incompletely) partitioned by depth and those in *A. grahamae* occurring sympatrically (at the same depth). Hybrid analyses and demographic modelling identified contemporary and historical gene flow among cryptic taxa, both within and between *A. grahamae* and *A. lamarcki*. These results (1) indicate that spatial genetic connectivity in these ecologically important mesophotic species may be maintained over large geographic distances and (2) highlight that gene flow links taxa within this relativity diverse Caribbean genus.

Introduction

Mesophotic coral reef ecosystems lie below the well-studied shallow coral reefs (~ 30 - 150 m depth) (Lesser, Slattery & Leichter, 2009) and represent a substantial proportion of the world's potential coral reef habitat. These reefs have received considerable recent attention due their hypothesised role as ecological refuges (Bongaerts, Ridgway, Sampayo, & Hoegh-Guldberg, 2010a; Bongaerts & Smith, 2019; Glynn, 1996; Semmler, Hoot, & Reaka, 2017). Consequently, vertical genetic boundaries have been assessed between populations of scleractinian species (*i.e.* , hard corals) found in both shallow and mesophotic reefs, *i.e.* , "depth-generalist" species. In such studies, vertical genetic structure has been commonly observed, though often varying among species and location (Bongaerts et al., 2017; Brazeau, Lesser & Slattery, 2013; van Oppen, Bongaerts, Underwood, Peplow & Cooper, 2011; Serrano et al., 2014, 2016), discouraging the role of universal vertical replenishment (Bongaerts & Smith, 2019). This aside, coral communities at mesophotic depths are also threatened by thermal anomalies and tropical storms (Bongaerts & Smith, 2019). Despite many surveys of connectivity in depth-generalists, patterns of horizontal connectivity in "mesophotic-specialist" species

remain unexplored. If mesophotic-specialist species are horizontally well-connected, they should be more resilient to local disturbances than if populations are largely isolated.

Scleractinian corals have traditionally been classified into two major modes of reproduction, which differentially affect spatial genetic structuring (Bongaerts et al., 2017; Carlon, 1999). In brooders, maternal colonies brood and release developed larvae with the ability to settle within hours (Carlon, 1999). This results in low dispersal potential and potential philopatry of the larvae (Warner, Willis, van Oppen, & 2016). In contrast, larvae of broadcast spawners develop in the water column and are pelagic for longer (days to weeks) and thus have greater chances of dispersal (Carlon, 1999). Genetic surveys are often consistent with these expectations when examined over large distances ($>$ 20 km), where broadcast spawners exhibit low or negligible horizontal population structure (Baums, Johnson, Devlin-Durante, & Miller 2010; Huang et al., 2018; van Oppen, Lukoschek, Berkelmans, Peplow, & Jones, 2015; Nakajima, Nishikawa, Iguchi, Sakai, & Vollmer, 2010; Serrano et al., 2014; Severance & Karl, 2006; Studivan & Voss, 2018; Tay, Noreen, Suharsono, Chou, & Todd, 2015), whereas, brooding taxa typically have discernible population structure over similar distances (e.g., Carlon & Budd, 2002; Goffredo, Mezzomonao, & Zaccanti, 2004; Gorospe & Karl, 2015; Stoddart, 1984; Torda, Lundgren, Willis, & van Oppen, 2013; Underwood, Smith, van Oppen, & Gilmour, 2006; Zvuloni et al., 2008). At least in the Caribbean, most scleractinian coral species exclusive to mesophotic depths appear to be brooders due to their Symbiodiniaceae specificity patterns (Bongaerts et al., 2010a). This suggests that the populations of these depth-specialist species could be highly structured and thus more vulnerable to local disturbance.

Species boundaries in corals are poorly defined and are likely to be evolutionarily porous. Cryptic genetic groups are frequently described in corals (Arrigoni, Berumen, Storlarski, Terraneo, & Benzoni, 2019; Bongaerts et al., 2021; Gómez-Corrales & Prada, 2020; Ladner & Palumbi, 2012; Nakajima et al., 2017; Warner, van Oppen, & Willis., 2015) and both homoplasy and phenotypic plasticity can lead to the misidentification of genetically distinct taxa (Forsman, Barshis, Hunter, & Toonen, 2009; Kitahara, Fukami, Benzoni, & Huang, 2016). Incomplete reproductive barriers between closely related nominal species are common (reviewed in Willis, van Oppen, Miller, Vollmer, & Ayre 2006) as are the successful interspecific laboratory crosses (Willis, Babcock, Harrison, & Wallace, 1997). Regular hybridisation between species or, reticulate evolution, has long been suspected to be an important aspect of coral evolution (Veron, 1995). Multilocus genetic or genomic approaches are moreover uncovering evidence for historical introgression (Mao, Economo, & Satoh, 2018) and frequent observations of contemporary admixture are consistent with intermixing of semi-differentiated taxa (e.g., *Acropora* spp., Ladner & Palumbi, 2012; *Favia* spp., Carlon & Budd, 2002; *Madracis* spp., Frade et al., 2010; *Platygyra* spp., Miller & Benzie, 1997;*Pocillopora* spp., Combosch & Vollmer, 2015; *Porites* spp., Forsman et al., 2017; *Psammocora* spp., Stefani, Benzoni, Pichon, Cancelliere, & Galli 2008, *Seriatopora* spp., Bongaerts et al., 2010b; *Stylophora* spp., Arrigoni, Benzoni, Terraneo, Caragnano, & Berumen, 2016; octorals, Prada & Hellberg, 2013; and anthozoans, Quattrini et al., 2019). The examination of co-occurring closely related but genetically distinct groups can provide further insights into evolutionary dynamics of divergence with gene flow (Nosil, 2008; Bird, Fernandez-Sila, Skillings, & Toonen, 2012). For example, morphologically cryptic and sympatric coral taxa may represent incipient species where specific habitats delineate taxa (e.g., Carlon & Budd, 2002; Warner et al., 2015) or differences in reproductive timing (e.g., Rosser, 2015). Determining the extent to which scleractinians can exchange alleles intra- or interspecifically can provide insights into possible rates of adaptive evolution such as in response to anthropogenic stresses.

Here, we focus on the genus *Agaricia* (Order: Scleractinia), which is one of the most speciose genera in the Caribbean and perhaps the most dominant group at mesophotic depths. *Agaricia* species have predominately plating morphologies and have been described as both hermaphroditic (Fadlallah, 1983) and gonochoric (Kerr, Baird, & Hughes, 2011). A brooding reproductive mode has been observed (through larval experiments) for three out of the seven species (*A. humilis* ,*A. tenuifolia* and *A. agaricites* : Morse, Hooker, Morse, & Jensen, 1988) and has therefore been assumed for the genus.*Agaricia* species are also presumed to have maternal inheritance of symbionts due to their reproductive mode (Baird et al., 2009) resulting in host-endosymbiont specificity and with most species harbouring a distinct *Cladocopium* strain (Bongaerts et al., 2013). Within the Southern Caribbean, *Agaricia* species segregate by depth with some

habitat overlap, with three species occurring abundantly at mesophotic depths: depth-generalist, *Agaricia lamarcki* (most commonly found: ~ 15 – 50 m), and depth-specialists *A. grahamae* (~ 50 – 90 m) and *A. undata* (~ 60 – 90m) (Bongaerts et al., 2013, 2015a). Genetic structure has been assessed previously in *Agaricia* species, with horizontal spatial structure found over small distances in *A. agaricites* and *A. fragilis* (< 40 km) (Bongaerts et al., 2017; Brazeau, Sammarco, & Gleason, 2005) but not in *A. lamarcki* and *A. undata* (over similarly small distances: < 40 km) (Hammerman et al., 2018; Gonzalez-Zapata et al., 2018). However, the spatial genetic structure one of the most dominant mesophotic-specialist, *A. grahamae* , has not yet been determined. This species shares the same *Cladocopium*strain with *A. lamarcki* at their sympatric depth zone (50 m), with *A. lamarcki* predominantly hosting a different strain at shallower depths (Bongaerts et al., 2013, 2015b). Furthermore, mitochondrial markers (*atp6* , *nad5* and *cox1-1-rRNA*) have been unable to genetically differentiate *A. grahamae* and *A. lamarcki* (Bongaerts et al., 2013, 2015a), indicating their close-relatedness. Thus, there is potential for hybridisation between *A. grahamae* and *A. lamarcki* as well as host divergence of shallow and mesophotic populations within *A. lamarcki.*

In order to evaluate horizontal genetic structure and interspecific gene flow of these ecologically important mesophotic species, we used a reduced representation genome sequencing approach (nextRAD) to assess specimens collected using a manned submersible and deep technical diving. We tested the following three hypotheses: (1) there is horizontal genetic structure between populations of mesophotic depth-specialist scleractinian species, *Agaricia grahamae* between Curacao and Bonaire (> 40 km), (2) gene flow occurs or has occurred between *A. grahamae* and congener, *A. lamarcki*within the depth zone they share (50 m) and (3) depth-partitioning occurs within *A. lamarcki* between 15 and 50 m. After initial examination of the genetic data, we found two sympatrically occurring cryptic taxa each within both nominal species and thus post hoc decided to test the hypothesis that: (4) gene flow occurs between cryptic taxa or has occurred during their divergence. To examine spatial genetic structure and identify hybrids, we used individual-based assignment models and multivariate analyses. For testing whether and when gene flow occurred during the divergence of taxa, we used the Diffusion Approximations for Demographic Inference (dadi) (Gutenkunst, Hernandez, Williamson, & Bustamante, 2009) to model and compare various demographic scenarios.

Methods

Sample collection

Specimens of *Agaricia* were collected at eight different locations on the leeward side of the islands of Curacao and Bonaire in the Southern Caribbean, as part of the "XL Catlin Seaview Survey" carried out between March-April 2013 (Figure 1, S-T1). Samples were collected using technical SCUBA or the manned submersible "Curasub" operated by "Substation Curacao", under permits from the Curacao Government and the Bonaire Island Council. Specimens of the focal species *Agaricia grahamae* (Wells, 1973) were collected at a sampling depth of 50 m (+-2 m), with two additional populations sampled at 60 m (+-2 m) and 80 m (+-5 m), whereas specimens of *Agaricia lamarcki*(Milne-Edwards & Haime, 1851) were collected at a subset of four locations within Curacao at a sampling depth of 15 m (+-2 m) or 50 m (+-2 m). Morphological classification of the two species followed the taxonomic features specified by Wells (1973), Veron (2000) and Humann & DeLoach (2002). An additional 12 *A. grahamae* samples from San Andres, Colombia (SA) were collected under permits by the National Environmental Licensing Authority (ANLA), and added as outgroup samples: three were collected from the upper mesophotic zone (60 - 65 m) and nine from the lower mesophotic zone (85 m). Small fragments of colonies were stored in salt-saturated buffer solution containing 20 % DMSO and 0.5 M EDTA, and for a subset of specimens a skeletal voucher was bleached, rinsed in freshwater and dried.

DNA isolation, library preparation and sequencing

Isolation of genomic DNA from the coral host was carried out as reported in Bongaerts et al. (2017), using centrifugation steps to reduce endosymbiont contamination. Symbiodiniaceae were then isolated from two *A. grahamae* specimens (to sequence separately as a subtraction reference), using fluorescence-activated cell sorting (BD FACSAria Cell Sorter) at the Queensland Brain Institute. Quality and yield of gDNA were assessed using gel electrophoresis and a Qubit fluorometer, with a subset of samples (*A. grahamae* n = 176; *A. lamarcki* n = 51; Symbiodiniaceae n = 2) selected for downstream sequencing. For *A. lamarcki* , the Symbiodiniaceae ITS2 profile was determined for several of these samples in a previous study (n = 6; Bongaerts et al., 2015), and we screened the profiles of an additional 41 samples using the same ITS2-DGGE method against reference samples from that study. Library preparation was carried out using the nextRAD method (SNPsaurus, LLC), using a 9bp selective sequence ("GTGTAGAGG") to amplify loci consistently between samples. Genomic DNA was fragmented and ligated with adapter sequences using Nextera reagent (Illumina, Inc), and sequenced across a total of six HiSeq 2500 (Illumina, Inc) lanes using 100bp single-end chemistry and following the manufacturer's recommended protocol. Samples that failed in the initial run (three lanes), were purified using AMPure XP beads to remove potential inhibitors and sequenced again on the additional HiSeq lanes.

Sequence clustering and variant calling

TRIMGALORE v.0.4.5 (https://github.com/FelixKrueger/TrimGalore) was used to remove adapters and low-quality ends (Phred below 20) and discarding reads that were less than 30bp. Read clustering was conducted using the IPYRAD pipeline v.0.7.22 (Eaton & Overcast, 2017) using default settings, excepting: minimum depth statistical/majority = 10, filter for adapters = 1, maximum uncalled bases = 5, maximum heterozygotes = 8, and maximum number of SNPs per locus = 20. Initial filtering, symbiont contamination removal and defining clonal lineages followed Bongaerts et al. (2017) (available through: https://github.com/pimbongaerts/radseq), unless otherwise indicated. We used BLASTN to identify and remove any matches to three Symbiodiniaceae databases (RAD isolates from Bongaerts et al. (2017), *Breviolum minutum* (ITS2 type B1) genome (Shoguchi, Tanaka, Shinzato, Kawashima, & Satoh, 2013) and *Cladocopium* (ITS2 type C1) genome (Liu et al., 2018). Other potential microbial contamination was removed through a BLASTN search against the NCBI non-redundant nucleotide database, extracting positive matches (max. e-value of 10^{-4}) that were classified as non-Cnidarian taxa (using the NCBI Taxonomy Database). RAD loci were truncated to 100bp prior to downstream analysis. Two sequencing duplicates (but from the same library preparation) of each species were included in the dataset to assess genotyping error and as a comparison to identify natural clones. The occurrence of any genetically identical individuals (clones) were then evaluated through assessing the distribution of allelic similarities between all pairs of individuals. Pairs of individuals that had 96% similar reads and above were deemed as clonal groups and one representative of each pair was retained. This threshold was chosen due to a combination of the genetic similarity of sequencing replicates (at similarities of 99%), a break in the distribution of pairwise allele similarities, and the maximum similarity (95%) that was observed for individuals occurring at different sites. Two datasets were retained: one removing putative clonal individuals and a second with all individuals.

The VCF file containing SNP data was filtered using VCFTOOLS v.0.1.16 (Danecek et al., 2011) to have a minor allele count of three due to many singletons and doubletons likely being sequencing or PCR errors and thus have consequences on downstream population genetic analyses (Andrews 2016, Linck & Battey, 2019). To remove sites that were not represented across most individuals, we removed sites that had $> 50\%$ missing data across individuals and used a minimum depth of five per site. Certain individuals with low coverage across sites ($< 50\%$ of sites genotyped) were removed. The removal of individuals with high missing data was conducted before more stringent filtering as these individuals will bias which sites are retained. Lastly, as different missing data filtering thresholds can change observed genetic patterns substantially, we applied four different thresholds for sites: (1) 50% maximum missing data of sites across individuals, (2) 20%, (3) 10% and (4) 5% and these datasets were compared for congruence across analyses. Results from the 20%

missing data dataset are presented here unless reported otherwise due to congruence of results across the four thresholds.

Statistical analyses

Population Structure

To assess population structure of both species and initial evidence for hybridisation and introgression between species, methods that do not use*a priori* population assumptions were used. Models employed include: model-based multilocus population assignment methods based on maximum likelihood, (ADMIXTURE, v.1.3.0 Alexander, Novembre, & Lange, 2009) and Bayesian, (STRUCTURE, v.2.3.4 Pritchard, Stephands, & Donnelly, 2000) optimisation criteria as well as Principal Component Analysis (PCA) and likelihood-based genetic clustering (using functions 'glPCA', 'snap.clust' and 'find.clusters' in the package, ADEGENET v.2.1.3 Jombart, 2008 in R v.3.6.3 R core team, 2020). The consensus of all four methods was used to identify the number of genetic clusters (K) within the datasets and to assign individuals to these clusters. The datasets including clones and without clones were compared for differences. Both putatively "neutral" and "all loci" datasets were created by removing outlier SNPs found using PCADAPT R package v.4.3.3 (Luu, Bazin, & Blum, 2017). The PCADAPT method identifies SNPs that exhibit significantly large correlations with certain PC axes relative to the genomic background, based on Mahalanobis distance and corrections using a genomic inflation factor. The calculation of q -values was used to determine which loci to retain with a false discovery rate $< 10\%$ calculated by the QVALUE package v.2.18.0 (Storey, Bass, Dabney, & Robinson, 2019) in R. Genetic clustering patterns were then compared between both the neutral and all loci datasets to assess for any differences in structure.

For ADMIXTURE and STRUCTURE analyses, the datasets were randomly trimmed to one SNP per contig in order to reduce correlations caused by physical linkage. Replicate datasets (10 replicates) with one random SNP per contig were created for comparison. In ADMIXTURE we ran each dataset with a cross-validation of 100 for K = 1 - 7. In STRUCTURE we ran each dataset with a Burn-in of 100,000 and 50,000 MCMC repeats for K = 1 - 7. Cross-validation error between runs, log-likelihood ratios and Evanno's Best K (Evanno, Regnaut, & Goudet, 2005) were evaluated to find the most likely number of clusters for each dataset in both analyses. For the Principal Component Analysis, the number of PC axes were deemed appropriate by assessing the steepness of the slope between eigenvalues (where the slope becomes less steep as the cut off) as well as qualitatively assessing any structure on each axis iteratively until structure dissipates. For likelihood-based genetic clustering using the 'snap.clust' function, we chose the number of genetic groups (K) with lowest value for the Akaike Information Criterion (AIC) and the Bayesian Information Criterion (BIC) between K = 1 – 10 for each dataset. We found two cryptic and sympatric genetic groups within each species (referred to as AG1 and AG2 within *A. grahamae* and AL1 and AL2 within *A. lamarcki* hereafter), these were treated as separate groups in subsequent analyses.

We calculated deviations from the Hardy-Weinberg Equilibrium for genetic groups within each nominal species using the 'summary' function in ADEGENET, then used Bartlett's test for homoscedasticity and a t-test for differences in means between the expected and observed heterozygosity in the package STATS v.3.6.3 (R core Team). We calculated population genetic statistics for each species treating each genetic group (e.g., AG1 and AG2) as populations, in the HIERFSTAT package v.0.0.4 (Goudet, 2005) in R for F_{IS} and Weir and Cockerham's F_{ST}. We tested for significance using Goudet's G-statistic with 1,000 permutations. A chi^{2}test was used to detect correlations between the frequency of the genetic group in each depth profile for *A. lamarcki* using STATS.

Hybridisation and Introgression

Potential hybrids and individuals with various levels of mixed ancestry were found within in the assignment methods results. We investigated putative hybridisation using the software, NEWHYBRIDS v.1.1 (Anderson & Thompson, 2002). NEWHYBRIDS incorporates the predictable patterns of inheritance seen in mating events rather than using only allele frequencies. We assessed whether individuals had genotypes consistent

with any of eight hybrid classes: (1 and 2) pure parental, P1 or P2, (3) first- F1 or (4) second-generation, F2 hybrids (F1 hybrid offspring), (5 and 6) first generation backcross from F1 into each parent group, b-1 or b-2, or (7 and 8) second-generation backcross into each parent group, b-1-1 or b-2-2. The analysis was run for [?]10,000 steps and [?]10,000 MCMC with both Jeffery's and Uniform distributions testing for the eight possible genotype scenarios and each run was repeated five times. The number of steps the analyses was run for was determined by convergence of the parameters. We show results from the 5% missing datasets with neutral and unlinked SNPs due to inability to estimate hybrid classes with higher missing data thresholds.

Spatial Genetic Structure

We assessed the spatial genetic structure of the genetic groups within both *A. grahamae* and *A. lamarcki* to look for potential spatial and or environmental barriers to gene flow. We applied Redundancy Analysis (RDA) to assess the relative exploratory power of geographic distance and depth environment to SNP genotype data. RDA performs a multiple linear regression between matrices (Legendre & Legendre, 2012) and is a commonly used technique for assessing the relative contribution of multiple predictors. It is effective for uncovering predictors of population genetic structure (e.g., Forester, Lasky, Wagner, & Urban, 2018; Legendre & Fortin, 2010). We utilised the partial RDA model for each nominal species: SNPs ~ latitude + longitude + depth environment (categorical) + condition (genetic group). Because cryptic genetic groups within each species were found, conditioning was used to evaluate the relative contribution of depth and geographic location to SNP variance taking into account the variance between genetic groups. Missing genetic data was imputed with the most common SNP following Forester et al. (2018). For *A. grahamae* , we calculated the over-water distance matrix between locations using the function 'lc.dist' in the package MARMAP v.1.0.4 (Pante & Simon-Bouhet, 2013) in R. Here, we calculated the least-cost path between our locations which avoids land masses. These distances were then transformed into PCoA coordinate scores for input as exploratory factors into the RDA model. For *A. lamarcki* , which was only sampled in sites in Curacao, we used the raw latitudes and longitudes as input into the RDA model because the over-water distance was similar. We used the 'rda' function in the package VEGAN v.2.5 (Oksanen et al., 2018) in R. We began with the full models and used permutation tests (1,000 permutations) to permute the genotypes randomly and assess the global model, RDA axes and marginal significance using PERMANOVA ('anova.cca' function) (Legendre, Oksanen, & ter Braak, 2011).

Demographic Inference

In order to explore the possibility of gene flow occurring during the divergence of our taxa, we used the Diffusion Approximation of Demographic Inference (DADI) v.2.1.1 (Gutenkunst, et al., 2009) in PYTHON v.3.6. We treated the two clusters found previously within each species as separate populations (within *A. grahamae* : AG1 and AG2 and within *A. lamarcki* : AL1 and AL2). The Joint Allele Frequency Spectrum (JAFS) was used to examine the likelihood of various demographic scenarios by modelling forward-in-time changes to the JAFS using solutions to the Chapman-Kolmogrov Forward equation (*i.e.* , the Diffusion Approximation). We tested five different divergence scenarios for our 2-population comparisons: (1) divergence with no migration (no mig), (2) divergence with continuous symmetrical migration (sym mig), (3) divergence with continuous asymmetrical migration (asym mig), (4) divergence with ancient symmetrical migration followed by isolation (anc mig) and (5) divergence in isolation followed by symmetrical migration (sec cont) (see S1 for schematics of models). For each model, we incorporated inbreeding due to finding a statistically significant positive F_{IS} within each taxon (Blischak, Barker, & Gutenkunst 2020). Parameters for each of these models were fit for the JAFS of each pairwise population comparison, within (*i.e.* , AG1 and AG2) and between the known species (*i.e* ., AG1 and AL1), thus we assessed divergence patterns within six paired groups. The folded JAFS was used for representative individuals from each population, which had >0.95 admixture assignment using neutral, unlinked (one SNP per contig) and 20% missing loci datasets. The 'subsample' function in DADI was used to randomly select a subset of haplotypes for analysis in order to maximise the number of SNPs due to missing data issues and to avoid difficulties with modelling inbreeding when projecting SNP frequencies to smaller sizes. In each paired population comparison, singletons and doubletons were masked because these entries were unreliable due high error rates in sequencing. Model

parameters were optimised by simulating a model JAFS and calculating the likelihood of each model fit to our real JAFS. using the Nelder-Mead simplex as the optimising algorithm. We assured convergence by running optimisations until independent runs with the same parameter scores ([?]1% difference) and the lowest AIC occurred [?]2-3 times. We then compared AIC and log-likelihoods (using the likelihood ratio test when models were nested) for the most likely replicate of each demographic scenario as well as qualitatively assessing the residual plots between the simulated JAFS and the real JAFS. The residual plots were assessed for random distributions and residuals forming a normal distribution at zero. To assess Goodness-of-fit we used non-parametric bootstrapping, then used the distribution of likelihoods from the bootstraps for comparison to the real data likelihood. We applied the Godambe Information Matrix (GIM) (Coffman, Hsieh, Gravel, & Gutenkunst, 2016) using bootstraps to calculate the confidence intervals of the parameter estimates.

Results

Sequence Clustering and Variant Calling

Reduced representation sequencing was performed on 227 individuals to obtain 686,608 SNPs and 130,890 loci. We identified 41 individuals with high genetic similarity (putative clones), representing 20 clonal groups and one individual of each clonal group was kept for subsequent analyses (ST-1 and 2). Filtering measures and genetic assignment of species groups obtained four datasets of neutral loci with a maximum 20% missing data per locus threshold (see S-T2 for specific filtering results): 1. All individuals dataset including both species (161 individuals, 4,306 SNPs), 2a. *A. grahamae* with San Andres outgroup (118 individuals, 2,983 SNPs), 2b. *A. grahamae* with no outgroup (106 individuals, 2,725 SNPs) and 3. *A. lamarcki* (41 individuals 2,515 SNPs). The congruent results from ADMIXTURE and STRUCTURE (only ADMIXTURE results are reported here), PCA and clustering analyses agreed with our morphological taxonomic classification of the two species: *A. grahamae* and *A. lamarcki* and further analyses were performed on these groups separately. Congruent results also found two distinct genetic clusters within both species that were found sympatrically across sites and depths within each species (named: AG1, AG2, AL1 and AL2).

Population Structure

Morphologically identified *A. grahamae* and *A. lamarcki*formed separate genetic clusters and one individual which was morphologically classified as *A. grahamae* had 0.5 mixed ancestry at K = 2 in ADMIXTURE and had intermediate PC1 scores between the two species clusters (Figure 2). This individual was treated as a provisional F1 hybrid. At K = 3, two cryptic clusters within *A. grahamae* (AG1 and AG2) occurred sympatrically at sites within Curacao, Bonaire and outgroup San Andres, Colombia. At K = 4, *A. lamarcki*also spilt into two clusters (AL1 and AL2). Across all methods (ADMIXTURE, STRUCTURE and 'snapclust'), K = 4 was deemed most likely for this dataset. The same two clusters were found in the subset *A. grahamae* dataset at K = 2 (Figure 3). At K=3, three individuals formed a separated cluster and appear as outliers separated from both *A. grahamae* groups on PC1. AG2 was more commonly found in Bonaire compared to Curacao sites (10 individuals found in Bonaire compared to 4 found in Curacao) and more closely related to most individuals collected from San Andres (SA) (7/8 assigned to AG2 at K=2). The AG2 individuals from San Andres formed a separate cluster at K = 4. Across all population structure methods, K = 3 was deemed most likely. We removed the *A. grahamae* /*A. lamarcki* putative hybrid, three outlier individuals and outgroups samples from San Andres from the *A. grahamae*dataset to assess these individuals in isolation for spatial and hybrid analyses. *A. lamarcki* also had the same two clusters found in the "all individuals" dataset which occurred sympatrically at all sites and within both depths. AL1 was more commonly found at 50 m (12/19) and AL2 at 15 m (22/24) (Figure 4, $\chi^2 = 10.96$, df = 1, p<0.01). Across all methods for the *A. lamarcki*dataset, K = 2 was deemed most likely. After having subset each of AG1, AG2, AL1 and AL2, into separate datasets, we found no further genetic structure (increasing K did not reveal any more clusters

and did not improve likelihood greatly) across all population structure analyses.

Hardy-Weinberg Equilibrium estimates were calculated for the cryptic taxa and F-statistics were calculated for each species with cryptic taxa treated as populations. Cryptic taxa within each nominal species were not in HWE (AG1: H_{obs} = 0.12, H_{exp} = 0.15, t = 30.17, df = 2589 p<0.01, AG2: H_{obs} = 0.30, H_{exp} = 0.34, t = 10.70, df = 973, p<0.01, AL1: H_{obs} = 0.27, H_{exp}= 0.32, t = 19.62, df = 1718, p<0.01 and AL2: H_{obs} = 0.23, H_{exp} = 0.27, t = 21.90, df = 2093, p<0.01) with an excess of homozygosity. Inbreeding within populations for each species was high (AG: F_{IS} = 0.18 and AL: F_{IS} = 0.19) accompanied by substantial population differentiation between cryptic taxa (AG: F_{ST}= 0.17, p<0.01, AL: F_{ST} = 0.18, p<0.01).

In terms of the Symbiodiniaceae associated with *A. lamarcki* , the corals predominately associated with the two ITS2 profiles (C3/C3d/C3.N6/C3.N7 and C3/C11/C11.N4/C3.N5) reported in Bongaerts et al. (2013, 2015; although sometimes with an extra unidentified band) and were partitioned between 15 m and 50 m depth. However, there was no association observed with the AL1 and AL2 lineages (S2), with both profiles occurring in both lineages.

Hybridisation

Between A. grahamae and A. lamarcki

From the ADMIXTURE results for the dataset including both species, 115 individuals assigned to *A. grahamae* with >0.98 assignment and 42 individuals assigned to *A. lamarcki* with >0.99 assignment at K = 2. Of the admixed individuals, three were the outlier individuals identified previously within the *A. grahamae* dataset and one putative hybrid (also identified in the PCA results) had 0.5 admixture (Figure 2). The three outlier individuals and outgroup samples from San Andres were removed to create another dataset for input into NEWHYBRIDS (n = 149, 5% missing, SNPs = 555). In NEWHYBRIDS, all individuals assigned as pure species with 0.99 probability (P1 or P2) apart from the putative F1 hybrid which assigned as a F1 hybrid with a 0.99 probability.

Between cryptic groups within A. grahamae

We also assessed the patterns of admixture between the two *A. grahamae* lineages (AG1 and AG2). ADMIXTURE results presented 55 individuals assigned to AG1 >0.99 assignment and 14 individuals for AG2 at K = 2. The remaining 37 individuals predominately assigned to AG1 (0.8 – 0.98). Due to finding population structure between the outgroup samples from San Andres, we used a dataset comprised of only AG1 and AG2 individuals from Curacao and Bonaire (*A. grahamae* outliers and hybrid were also removed) for input into NEWHYBRIDS (n = 106, 5% missing, SNPs = 514). NEWHYBRIDS assigned 86 individuals with predominately P1 assignment (0.62 – 0.99) (pure parental AG1) and 12 individuals with predominately P2 assignment. The remaining individuals: 6 individuals (predominately assigned to AG1) and 2 individuals (predominately assigned to AG2) had higher assignments to hybrid categories (S-T3). Most notably, the highest probabilities for these admixed individuals were second generation back-crosses into each parental. Due to the limitations of the NEWHYBRIDS analysis, we were not able to estimate genotype classes of more advanced backcrosses which these individuals may more accurately represent.

Between cryptic groups within A. lamarcki

Within the *A. lamarcki* dataset, ADMIXTURE found 12 individuals assigned to AL1 >0.99 and 26 assigned to AL2 >0.99 and three individuals were admixed. Two of these admixed individuals were assigned to AL1 with ~0.7 and 0.78 assignment and one with 0.98 to AL2. A more stringent filtering dataset was used for input to NEWHYBRIDS (n = 41, 5% missing, SNPs = 622). In NEWHYBRIDS, two individuals presented higher assignment to hybrid classes than pure parentals: one *A. lamarcki* individual collected from 50 m at East Point, Curacao had a 0.99 probability of being a F2 (offspring of two F1s), and another from 50 m, CARMABI Buoy 0 had mixed assignments, 0.34 for pure parental AL1, 0.41 for a first generation back-cross into AL1 and 0.25 for second generation back-cross into AL1. The second individual, potentially representing a further back cross into AL1.

Spatial Genetic Structure

No strong correlation between genotype or depth, latitude and longitude for either species was uncovered with redundancy analyses. For *A. grahamae* , although the global model was significant (R^2 = 0.04, R^2_{adj} = 0.002, F = 1.05, P = 0.005) it only explained 4% of the variance. None of the canonical axes were significant in explaining variation in SNPs (*i.e.* , RDA1 – 4: P [?]0.1) and PC1 explained more variation than RDA1 (0.015 > 0.011). This was further substantiated through removal of each term, apart from Condition(Clusters), improving the AIC of the model. For *A. lamarcki* , the full model was globally non-significant (R^2 = 0.07, R^2_{adj} = 0.0002, F = 1.00, P = 0.483) as was each reduced model. Thus, neither horizontal (by space) nor vertical (by depth) locations were substantial predictors of genetic variation within cryptic taxa in both nominal species.

Demographic Inference

The demographic modelling results from dadi consistently found that models including migration (gene flow) had higher likelihoods than those with no migration (Tables 1, 2, Figure 5 and S3). In the "no migration" models, divergence time approached the lower bound parameter limit suggesting that between all pairwise comparisons divergence was extremely recent which is an unlikely scenario. This suggests that gene flow occurred during the divergence of the two species (*Agaricia grahamae* and *Agaricia lamarcki*) as well as during the divergence of the two cryptic taxa found within each species (AG1, AG2, AL1 and AL2). For all pairwise comparisons the symmetrical and asymmetrical continuous migration models showed similar results, with the asymmetrical migration models having only minimal differences in migration rates. Thus, only the continuous symmetrical migration models are reported here. In the ancient migration model optimisations between all population-pairs, T2 (the second epoch where populations diverged in isolation) approached the lower the parameter limit (~ 0) and thus equating this model (ancient migration) to the continuous symmetrical migration scenario. The continuous symmetrical migration and secondary contact models had equal likelihood (<2 AIC) for within nominal species comparisons (AG1 vs. AG2 and AL1 vs. AL2, Table 1). For both AG groups vs. AL1, secondary contact had higher likelihood >2 AIC than continuous migration model (Table 2). But for AG groups vs. AL2, the secondary contact model had equal likelihood with continuous migration. Migration rates estimated from dadi were larger between more closely related pairs than the more distant pairs, suggesting that more divergent taxa are likely to experience less gene flow (Tables 1 and 2). Parameter uncertainties were often larger than 0.5 of the parameters and thus are not shown. These were also not converted into real time units because of the unreliability of parameter estimates due to a low number of SNPs used as well as having unreliable mutation rate and generation time estimates. The main purpose of this analysis was to detect where gene flow occurred over the divergence history between all taxa, and thus conversion into real time units was not necessary for the aims of this study.

Discussion

Mesophotic coral ecosystems are known to harbour unique depth-specialist species, yet the ecology and evolution of these species remain almost completely unstudied. Given the assumed brooding reproductive mode within the *Agaricia* genus, we expected populations of the mesophotic-specialist species *A. grahamae* to be genetically structured over short spatial scales. However, no horizontal spatial structuring was detected between reefs within Curacao and Bonaire nor between the two islands (~40 km apart; Figures 2, 3 and RDA results). Similarly, no horizontal spatial structure was found within Curacao for the depth-generalist congener, *A. lamarcki*(Figure 4). Instead, we uncovered two sympatrically occurring and yet distinct cryptic taxa within each nominal species (Figures 2, 3 and 4) that were incompletely depth-partitioned in *A. lamarcki* but with no detectable depth or geographic segregation in *A. grahamae* . These cryptic taxa appear to be connected by historical and contemporary gene flow as indicated by the presence of backcrosses and through demographic analyses (Table 1, Figure 5, S2 and ST-3). The divergence history of *A. grahamae* and *A.*

lamarcki was also characterised by interspecific gene flow (Table 2, Figure 5 and S2), suggesting past semi-permeable boundaries between these species.

Lack of genetic structuring between reefs and islands

Contrary to our expectations of spatial genetic structure over small distances, genetic homogeneity was found for *A. grahamae* between Curacao and Bonaire (< 40 km) as evidenced by RDA (see Results) and genetic structure results (Figure 3). Both cryptic taxa found within *A. grahamae* also occurred at San Andres (> 1,000 km away) and thus, it is unlikely that the two cryptic groups within *A. grahamae* were recently allopatrically formed. The congener, *A. lamarcki* was assayed only in Curacao but also showed no genetic differentiation between the sampled reefs (RDA results, Figure 4). Genetic homogeneity within either island (Curacao and Bonaire) may not be too surprising because reef communities are fairly continuous along leeward sides of the islands which could facilitate stepping-stone gene flow and occasional long-distance dispersal. However, Curacao and Bonaire are separated by deep oceanic water with a north-west bound surface current and a west-east sub-surface counter current (Andrade, 2003), presenting a physical dispersal barrier. In contrast to our results (and consistent with limited dispersal), *Agaricia agaricites* and *A. fragilis*were found to have localised structure (Brazeau et al., 2005; Bongaerts et al., 2017). Our results do, however, match to those described for*A. lamarcki* and *A. undata* (Gonzalez-Zapata et al., 2018; Hammerman et al., 2018) where populations did not exhibit local genetic structure (over similarly short distances: < 40 km). It is conceivable that reproductive modes within *Agaricia* species are more variable than assumed and that the dispersal abilities within*A. lamarcki* , *A. grahamae* and *A. undata* are potentially greater than that of *A. agaricites* and *A. fragilis* . Taken together these findings across studies highlight variability in spatial genetic structuring that can occur even among congeners.

Distinct depth distributions of A. lamarcki but not A. grahamae taxa

Depth constitutes a strong environmental gradient for scleractinian corals, as it modulates light and other environmental conditions upon which corals depend (Bongaerts et al., 2015b). Although no depth-partitioning was observed for *A. grahamae* taxa in Curacao between the upper (50 m) and lower (85 m) mesophotic zone (Figure 3), we did find a difference in the relative abundance of the cryptic taxa by depth in *A. lamarcki* (15 vs 50 m, Figure 4, $\chi^2 = 10.96$, df = 1, p<0.01). Given the exponential decay of irradiance with depth, the most extreme differences appear at shallow depths, whereas differences become smaller within the mesophotic zones (e.g., between 50 and 85 m depth). The observed depth-differentiation within*A. lamarcki* but not *A. grahamae* follows these light transitions, although environmental factors such as nutrient availability, salinity, flow environment and temperature also vary between shallow and mesophotic depth zones (Dollar, 1982; Lesser et al., 2009; Bongaerts et al., 2015a) and could be contributing factors. Similar to the present study, a survey of *A. lamarcki* using ddRAD (Hammerman et al., 2018) also found two sympatric cryptic genetic groups but within Puerto Rico (sampled mostly between 10 – 20 m depth). At the population level, depth differentiation has been observed in Bermuda for the congener *A. fragilis* , where populations at 12 and 40 m were strongly differentiated (Bongaerts et al., 2017). Future surveys that can measure differences in microhabitats within the same depth profile may be informative for determining more precise environmental niches distinguishing cryptic taxa rather than depth alone.

In contrast to cnidarian host genotypes, we found almost complete depth partitioning of the symbiont profile within *A. lamarcki* (S2) which further supports the potential for depth-associated divergence. However, the symbiont profiles did not correspond directly to the different host taxa. The symbiont profile found in individuals of*A. lamarcki* at mesophotic depths was the same profile shared by*A. grahamae* (S2, Bongaerts et al., 2013, 2015b). Thus, this could indicate an ancestral association with this symbiont, more recent acquisition through host hybridisation, or potentially horizontal symbiont acquisition of this depth-specific endosymbiont (Quigley, Warner, Bay, & Willis, 2018). Another explanation for this disparity may be incomplete host-symbiont lineage sorting. Host divergence (between *A. lamarcki* taxa) could predate symbiont sorting due to retention in the maternal line. Further experimental work should look into symbiont inheritance patterns and use modern methods of symbiont genotyping (Amplicon sequencing) in order to decipher this inconsistency in symbiont profile and host genotype as multiple hypotheses are possible.

Gene flow between cryptic taxa and species

Cryptic lineages are prolifically found within genetic studies of scleractinians, yet rarely has their divergence history been examined in detail (but see Prada & Hellberg, 2020). These cryptic taxa are often closely related and sympatrically occurring and thus have the potential to interbreed. Here, we find evidence of two genetically distinct taxa within both species (Figures 2, 3 and 4) and evidence of backcrosses between the taxa within species (see Results, S-T3). An F1 hybrid was also found between *A. grahamae* and the "deep" *A. lamarcki* (Figure 3) which could suggest a continued low rate of recent interbreeding between species. Demographic models that included gene flow during divergence (*i.e.* , continuous migration, ancient migration and secondary contact) consistently had higher likelihoods than the null models of no migration for both between cryptic taxa within and between species (Figure 5, S2, Tables 1 and 2).

Although results from dadi gave the greatest support to the two-epoch models of divergence in isolation followed by secondary contacts (Tables 1 and 2), if population expansions or bottlenecks have occurred, divergence time can be over-estimated and results can favour the secondary contact model (Momigliano, Florin, & Merila, 2021). As RAD datasets with *de novo* assemblies are prone to high error rates in low frequency SNP calling (Andrews, Good, Miller, Luikart, & Hohenlohe, 2016), we did not include singletons and doubletons in the analyses and thus were unable to accurately model population size changes and differentiate between the different migration scenarios (*i.e* ., ancient migration vs. continuous migration vs. secondary contact). Thus, our inferences about timing and relative model support (among models including migration) should be interpreted cautiously. Nonetheless, models with no migration were consistently rejected and therefore we can confidently conclude that limited migration between distinct taxa has occurred between both cryptic taxa within and between species. Additionally, the relative amount of estimated gene flow scaled with divergence time, where migration was less between *A. lamarcki* and*A. grahamae* as compared to migration between less diverged taxa within each species. These results are consistent with hypothesis that genetic permeability scales with divergence time (Roux et al., 2016).

Our inability to confidently resolve whether the very early stages of divergence occurred with or without gene flow hampers inferences regarding the geography of speciation, *i.e.* , in sympatry or allopatry. Our results and those of other studies (e.g., *Madracis*spp., Frade et al., 2010; *Eunica felxuosa* and *Pocillopora damincornis* , Prada & Hellberg, 2020; and *Agaricia fragilis* , Bongaerts et al., 2017; Prada & Hellberg, 2020) confirm that low levels of gene flow connect such closely related taxa, but yet gene flow is insufficient to homogenise them. Without physical barriers between cryptic taxa, exogenous and/or endogenous barriers must maintain divergence. The occurrence of exogenous selection has been shown in many famous examples to maintain species barriers through disruptive selection in face of homogenising gene flow (e.g., sticklebacks, Dean et al., 2019; Darwin's finches, Han et al., 2017; *Heliconious*butterflies, Merot, Salazar, Merrill, Jiggins, & Joron, 2017; and cichlids, Poelstra, Richards, & Martin, 2018). Among scleractinians there is considerable circumstantial evidence for depth-associated environmental attributes (including light, nutrient availability, temperature, water flow, etc.) providing strong exogenous selection that could contribute to maintaining divergence despite gene flow (Bongaerts et al., 2011, 2017; Carlon & Budd, 2002; Gorospe & Karl, 2015; van Oppen et al., 2011; Prada & Hellberg, 2013; Serrano et al., 2014). Consistently, depth partitioning is observed throughout the*Agaricia* genus, with each nominal species inhabiting a distinct depth profile yet each remaining sympatric at the edge of their depth range (Bongaerts et al., 2013). Depth-associated factors appear to play a role in divergence-with-gene flow within *A. lamarcki* taxa, between *A. grahmae* and *A. lamarcki* but not within *A. grahamae* taxa.

Endogenous barriers may also be maintaining the cohesiveness of cryptic taxa and indeed the replicated pattern of genome-wide divergence (not just divergence at selected outlier loci) implicates isolating mechanisms may not be solely limited to environmental factors. Pre-zygotic isolation is most likely to occur through either gametic incompatibilities or temporal and spatial isolation in spawning in organisms where one or both gametes spawn, such as in corals and other marine invertebrates. In the *Orbicella* genus, more closely related species experienced temporal differences in spawning time yet with gametic compatibilities (in crossed experiments) and more distantly related species had overlapping times with gametic incompat-

ibilities (Knowlton, Mate, Guzman, Rowan, & Jara, 1997; Levitan et al., 2004). Thus, demonstrating the interactions and development of reproductive barriers in corals. On the other hand, in Indo-Pacific closely-related*Acropora* species spawning times often overlap and interspecific gamete compatibility can be high, though in the presence of conspecific sperm the number of hybrid offspring produced is low (Willis et al., 2006). Post-zygotic isolation studies through experimental work in crosses of *Acropora* species have found surprisingly equal or higher fitness F1 hybrids (compared to parentals) in parental habitats as well as greater fitness in hybrids than parentals in higher temperature or environmentally variable habitats (Willis et al., 2006; Chan, Peplow, & van Oppen, 2019). This apparent lack of post-zygotic isolation mechanisms highlights the potential adaptive role of hybridisation in *Acropora* corals and requires the examination of fitness in F2s and backcrosses. However, due to practical difficulties there is limited spawning and larval crossing experiments in many coral species (including all brooders) and thus most endogenous pre- or post-zygotic barries have not been tested. So, there is much scope for future experimental work to tease apart the diverse patterns of reproductive isolation mechanisms or lack thereof in corals. The common occurrence of sympatric yet incompletely reproductively isolated genetic taxa within scleractinians is perplexing and suggests that common features contribute to this widespread phenomenon.

Conclusions

The Caribbean region has offered several important examples to study species diversification with scleractinian genera like *Orbicella* ,*Eunicea* , *Madracis* and *Agaricia* (Knowlton et al., 1997; Medina, Well, & Szmant, 1999; Fukami et al., 2004; Frade et al., 2010; Bongaerts et al., 2013, 2017; Gonzalez-Zapata, Prada, Avila, & Medina 2018). Here, we show that beyond the niche partitioning between nominal *Agaricia* species, there is undescribed cryptic taxonomic diversity with taxa linked by low levels of gene flow. Although,*A. lamarcki* follows the pattern of depth partitioning characteristic of the genus, the nature of cryptic diversity in *A. grahamae* remains unexplained and requires further investigation. This discovery of pervasive inter-taxon gene flow stresses the importance of considering multiple closely related taxa in population genomic assessments; since erroneous conclusions could be drawn regarding assignment to spatial population structure, cryptic taxa, or by purely relying on morphology to group individuals into taxa. Importantly introgression is likely to be common in scleractinian corals (Mao et al., 2018) and single species studies ignore this important source of genetic diversity.

The lack of genetic structuring of mesophotic coral populations among reefs and islands indicates that mesophotic-specialist species may be more horizontally connected than we anticipated, which has important implications for their ability to recover from localised disturbances. The spatial genetic structure disparity between members of the genus may be reflective of undescribed differences in reproductive mode, which warrant further investigation to better understand the dispersal capabilities of mesophotic-specialist corals. This study draws attention to the lack of knowledge in the ecology of mesophotic corals. In light of recent reports of disturbances to mesophotic ecosystems, understanding mesophotic coral connectivity should be a priority in future studies.

Author Contributions

P.B designed and planned study. P.B, K.B.H and N.E conducted field work in Curacao and Bonaire. J.A.S provided samples from San Andres (Colombia). K.R.W.L conducted all laboratory work. K.E.P analysed data and wrote the manuscript. P.B and C.R wrote manuscript and provided guidance on all analyses. R.N.G provided advice on demographic analyses. All authors contributed manuscript edits.

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Data accessibility

Raw NextRAD sequences are stored on NCBI BioProject Accession XXXXXXXXXXX. Metadata with sequences are stored on Genomic Observatories MetaDatabase (GEOME) XXXXXXX. Scripts from the demographic modelling using dadi are stored on https://github.com/kepra3/kp_dadi as an electronic notebook.

References

Alexander, D. H., Novembre, J., & Lange, K. (2009). Fast model-based estimation of ancestry in unrelated individuals. *Genome Research* ,*19* (9), 1655–1664. https://doi.org/10.1101/gr.094052.109

Anderson, E. C., & Thompson, E. A. (2002). A model-based method for identifying species hybrids using multilocus genetic data.*Genetics* , *160* (3), 1217–1229.

Andrade, C. A. (2003). Evidence for an eastward flow along the Central and South American Caribbean Coast. *Journal of Geophysical Research* , *108* (C6), 3185. https://doi.org/10.1029/2002JC001549

Andrews, K. R., Good, J. M., Miller, M. R., Luikart, G., & Hohenlohe, P. A. (2016). Harnessing the power of RADseq for ecological and evolutionary genomics. *Nature Reviews Genetics* , *17* (2), 81–92. https://doi.org/10.1038/nrg.2015.28

Arrigoni, R., Benzoni, F., Terraneo, T. I., Caragnano, A., & Berumen, M. L. (2016). Recent origin and semi-permeable species boundaries in the scleractinian coral genus *Stylophora* from the Red Sea.*Scientific Reports* , *6* (1), 34612. https://doi.org/10.1038/srep34612

Arrigoni, R., Berumen, M. L., Stolarski, J., Terraneo, T. I., & Benzoni, F. (2019). Uncovering hidden coral diversity: A new cryptic lobophylliid scleractinian from the Indian Ocean. *Cladistics* ,*35* (3), 301–328. https://doi.org/10.1111/cla.12346

Ayre, D. J., & Hughes, T. P. (2000). Genotypic diversity and gene flow in brooding and spawning corals along the Great Barrier Reef, Australia.*Evolution* , *54* (5), 1590–1605. https://doi.org/10.1111/j.0014-3820.2000.tb00704.x

Baird, A. H., Guest, J. R., & Willis, B. L. (2009). Systematic and biogeographical patterns in the reproductive biology of scleractinian corals. *Annual Review of Ecology, Evolution, and Systematics* ,*40* (1), 551–571. https://doi.org/10.1146/annurev.ecolsys.110308.120220

Baums, I. B., Johnson, M. E., Devlin-Durante, M. K., & Miller, M. W. (2010). Host population genetic structure and zooxanthellae diversity of two reef-building coral species along the Florida Reef Tract and wider Caribbean. *Coral Reefs* , *29* (4), 835–842. https://doi.org/10.1007/s00338-010-0645-y

Bird, C. E., Fernandez-Silva, I., Skillings, D. J., & Toonen, R. J. (2012). Sympatric speciation in the post "Modern Synthesis" era of evolutionary biology. *Evolutionary Biology* , *39* (2), 158–180. https://doi.org/10.1007/s11692-012-9183-6

Blischak, P. D., Barker, M. S., & Gutenkunst, R. N. (2020). Inferring the Demographic History of Inbred Species from Genome-Wide SNP Frequency Data. *Molecular Biology and Evolution* , *37* (7), 2124–2136.

Bongaerts, P., Carmichael, M., Hay, K. B., Tonk, L., Frade, P. R., & Hoegh-Guldberg, O. (2015b). Prevalent endosymbiont zonation shapes the depth distributions of scleractinian coral species. *Royal Society Open Science* , *2* (2), 140297–140297. https://doi.org/10.1098/rsos.140297

Bongaerts, P., Ridgway, T., Sampayo, E. M., & Hoegh-Guldberg, O. (2010a). Assessing the 'deep reef refugia' hypothesis: Focus on Caribbean reefs. *Coral Reefs* , *29* (2), 309–327. https://doi.org/10.1007/s00338-009-0581-x

Bongaerts, P., Cooke, I. R., Ying, H., Wels, D., den Haan, S., Hernandez-Agreda, A., Brunner, C. A., Dove, S., Englebert, N., Eyal, G., Foret, S., Grinblat, M., Hay, K. B., Harii, S., Hayward, D. C., Lin, Y., Mihaljević, M., Moya, A., Muir, P., … Hoegh-Guldberg, O. (2021). Morphological stasis masks ecologically divergent coral species on tropical reefs. *Current Biology* , S0960982221003675. https://doi.org/10.1016/j.cub.2021.03.028

Bongaerts, P., Frade, P. R., Hay, K. B., Englebert, N., Latijnhouwers, K. R. W., Bak, R. P. M., Vermeij, M. J. A., & Hoegh-Guldberg, O. (2015a). Deep down on a Caribbean reef: Lower mesophotic depths harbor a specialized coral-endosymbiont community. *Scientific Reports* ,*5* (1). https://doi.org/10.1038/srep07652

Bongaerts, P., Frade, P. R., Ogier, J. J., Hay, K. B., van Bleijswijk, J., Englebert, N., Vermeij, M. J., Bak, R. P., Visser, P. M., & Hoegh-Guldberg, O. (2013). Sharing the slope: Depth partitioning of agariciid corals and associated Symbiodinium across shallow and mesophotic habitats (2-60 m) on a Caribbean reef. *BMC Evolutionary Biology* , *13* (1), 205. https://doi.org/10.1186/1471-2148-13-205

Bongaerts, P., Riginos, C., Brunner, R., Englebert, N., Smith, S. R., & Hoegh-Guldberg, O. (2017). Deep reefs are not universal refuges: Reseeding potential varies among coral species. *Science Advances* ,*3* (2), e1602373. https://doi.org/10.1126/sciadv.1602373

Bongaerts, P., Riginos, C., Hay, K. B., van Oppen, M. J., Hoegh-Guldberg, O., & Dove, S. (2011). Adaptive divergence in a scleractinian coral: Physiological adaptation of Seriatopora hystrix to shallow and deep reef habitats. *BMC Evolutionary Biology* ,*11* (1), 303. https://doi.org/10.1186/1471-2148-11-303

Bongaerts, P., Riginos, C., Ridgway, T., Sampayo, E. M., van Oppen, M. J. H., Englebert, N., Vermeulen, F., & Hoegh-Guldberg, O. (2010b). Genetic Divergence across Habitats in the Widespread Coral Seriatopora hystrix and Its Associated Symbiodinium. *PLoS ONE* , *5* (5), e10871. https://doi.org/10.1371/journal.pone.0010871

Bongaerts, P., & Smith, T. B. (2019). Beyond the "Deep Reef Refuge" Hypothesis: A Conceptual Framework. In *Mesophotic Coral Ecosystems* (pp. 881–895). Springer, New York.

Brazeau, D. A., Lesser, M. P., & Slattery, M. (2013). Genetic structure in the coral, *Montastraea cavernosa* : Assessing genetic differentiation among and within mesophotic reefs. *PLoS ONE* ,*8* (5), e65845. https://doi.org/10.1371/journal.pone.0065845

Brazeau, D. A., Sammarco, P. W., & Gleason, D. F. (2005). A multi-locus genetic assignment technique to assess sources of *Agaricia agaricites* larvae on coral reefs. *Marine Biology* , *147* (5), 1141–1148. https://doi.org/10.1007/s00227-005-0022-5

Carlon, D. B. (1999). The evolution of mating systems in tropical reef corals. *Trends in Ecology & Evolution* , *14* (12), 491–495. https://doi.org/10.1016/S0169-5347(99)01709-7

Carlon, D. B., & Budd, A. F. (2002). Incipient speciation across a depth gradient in a scleractinian coral? *Evolution* ,*56* (11), 2227–2242. https://doi.org/10.1111/j.0014-3820.2002.tb00147.x

Chan, W. Y., Peplow, L. M., & van Oppen, M. J. H. (2019). Interspecific gamete compatibility and hybrid larval fitness in reef-building corals: Implications for coral reef restoration. *Scientific Reports* ,*9* (1), 4757.

https://doi.org/10.1038/s41598-019-41190-5

Coffman, A. J., Hsieh, P. H., Gravel, S., & Gutenkunst, R. N. (2016). Computationally efficient composite likelihood statistics for demographic inference. *Molecular Biology and Evolution* ,*33* (2), 591–593. https://doi.org/10.1093/molbev/msv255

Combosch, D. J., & Vollmer, S. V. (2015). Trans-Pacific RAD-Seq population genomics confirms introgressive hybridization in Eastern Pacific *Pocillopora* corals. *Molecular Phylogenetics and Evolution* , *88* , 154–162. https://doi.org/10.1016/j.ympev.2015.03.022

Danecek, P., Auton, A., Abecasis, G., Albers, C. A., Banks, E., DePristo, M. A., Handsaker, R. E., Lunter, G., Marth, G. T., Sherry, S. T., McVean, G., Durbin, R., & 1000 Genomes Project Analysis Group. (2011). The variant call format and VCFtools. *Bioinformatics* ,*27* (15), 2156–2158. https://doi.org/10.1093/bioinformatics/btr330

Dean, L. L., Magalhaes, I. S., Foote, A., D'Agostino, D., McGowan, S., & MacColl, A. D. C. (2019). Admixture between ancient lineages, selection, and the formation of sympatric stickleback species-pairs.*Molecular Biology and Evolution* , *36* (11), 2481–2497. https://doi.org/10.1093/molbev/msz161

Dollar, S. J. (1982). Wave stress and coral community structure in Hawaii. *Coral Reefs* , *1* (2), 71–81. https://doi.org/10.1007/BF00301688

Eaton, D., & Overcast, I. (2017). *ipyrad: Interactive assembly and analysis of RADseq* .

Evanno, G., Regnaut, S., & Goudet, J. (2005). Detecting the number of clusters of individuals using the software structure: A simulation study. *Molecular Ecology* , *14* (8), 2611–2620. https://doi.org/10.1111/j.1365-294X.2005.02553.x

Fadlallah, Y. H. (1983). Sexual reproduction, development and larval biology in scleractinian corals: A review. *Coral Reefs* ,*2* (3), 129–150. https://doi.org/10.1007/BF00336720

Forester, B. R., Lasky, J. R., Wagner, H. H., & Urban, D. L. (2018). Comparing methods for detecting multilocus adaptation with multivariate genotype-environment associations. *Molecular Ecology* ,*27* (9), 2215–2233. https://doi.org/10.1111/mec.14584

Forsman, Z. H., Barshis, D. J., Hunter, C. L., & Toonen, R. J. (2009). Shape-shifting corals: Molecular markers show morphology is evolutionarily plastic in Porites. *BMC Evolutionary Biology* ,*9* (1), 45. https://doi.org/10.1186/1471-2148-9-45

Forsman, Z. H., Knapp, I. S. S., Tisthammer, K., Eaton, D. A. R., Belcaid, M., & Toonen, R. J. (2017). Coral hybridization or phenotypic variation? Genomic data reveal gene flow between Porites lobata and P. Compressa. *Molecular Phylogenetics and Evolution* , *111* , 132–148. https://doi.org/10.1016/j.ympev.2017.03.023

Frade, P. R., Reyes-Nivia, M. C., Faria, J., Kaandorp, J. A., Luttikhuizen, P. C., & Bak, R. P. M. (2010). Semi-permeable species boundaries in the coral genus *Madracis* : Introgression in a brooding coral system. *Molecular Phylogenetics and Evolution* ,*57* (3), 1072–1090. https://doi.org/10.1016/j.ympev.2010.09.010

Fukami, H., Budd, A. F., Levitan, D. R., Jara, J., Kersanach, R., & Knowlton, N. (2004). Geographic differences in species boundaries among members of the *Montastraea annularis* complex based on molecular and morphological markers. *Evolution* , *58* (2), 324–337. https://doi.org/10.1111/j.0014-3820.2004.tb01648.x

Glynn, P. W. (1996). Coral reef bleaching: Facts, hypotheses and implications. *Global Change Biology* , *2* (6), 495–509. https://doi.org/10.1111/j.1365-2486.1996.tb00063.x

Goffredo, S., Mezzomonaco, L., & Zaccanti, F. (2004). Genetic differentiation among populations of the Mediterranean hermaphroditic brooding coral *Balanophyllia europaea* (Scleractinia: Dendrophylliidae). *Marine Biology* , *145* (6), 1075–1083. https://doi.org/10.1007/s00227-004-1403-x

Gómez-Corrales, M., & Prada, C. (2020). Cryptic lineages respond differently to coral bleaching. *Molecular Ecology* , mec.15631. https://doi.org/10.1111/mec.15631

Gonzalez-Zapata, F. L., Bongaerts, P., Ramirez-Portilla, C., Adu-Oppong, B., Walljasper, G., Reyes, A., & Sanchez, J. A. (2018). Holobiont diversity in a reef-building coral over its entire depth range in the mesophotic zone. *Frontiers in Marine Science* , *5* . https://doi.org/10.3389/fmars.2018.00029

Gorospe, K. D., & Karl, S. A. (2015). Depth as an organizing force in*Pocillopora damicornis* : Intra-reef genetic architecture.*PLOS ONE* , *10* (3), e0122127. https://doi.org/10.1371/journal.pone.0122127

Goudet, J. (2005). Hierfstat, a package for r to compute and test hierarchical F-statistics. *Molecular Ecology Notes* , *5* (1), 184–186. https://doi.org/10.1111/j.1471-8286.2004.00828.x

Gutenkunst, R. N., Hernandez, R. D., Williamson, S. H., & Bustamante, C. D. (2009). Inferring the joint demographic history of multiple populations from multidimensional SNP frequency data. *PLoS Genetics* , *5* (10), e1000695. https://doi.org/10.1371/journal.pgen.1000695

Hammerman, N. M., Rivera-Vicens, R. E., Galaska, M. P., Weil, E., Appledoorn, R. S., Alfaro, M., & Schizas, N. V. (2018). Population connectivity of the plating coral *Agaricia lamarcki* from southwest Puerto Rico. *Coral Reefs* , *37* (1), 183–191. https://doi.org/10.1007/s00338-017-1646-x

Han, F., Lamichhaney, S., Grant, B. R., Grant, P. R., Andersson, L., & Webster, M. T. (2017). Gene flow, ancient polymorphism, and ecological adaptation shape the genomic landscape of divergence among Darwin's finches. *Genome Research* , *27* (6), 1004–1015. https://doi.org/10.1101/gr.212522.116

Huang, W., Li, M., Yu, K., Wang, Y., Li, J., Liang, J., Luo, Y., Huang, X., Qin, Z., Wang, G., Su, H., & Wei, F. (2018). Genetic diversity and large-scale connectivity of the scleractinian coral *Porites lutea*in the South China Sea. *Coral Reefs* , *37* (4), 1259–1271. https://doi.org/10.1007/s00338-018-1724-8

Humann, P., & DeLoach, N. (2002). *Reef Coral Identification. Second. Jacksonville* .

Jombart, T. (2008). adegenet: A R package for the multivariate analysis of genetic markers. *Bioinformatics* , *24* (11), 1403–1405. https://doi.org/10.1093/bioinformatics/btn129

Kerr, A. M., Baird, A. H., & Hughes, T. P. (2011). Correlated evolution of sex and reproductive mode in corals (Anthozoa: Scleractinia).*Proceedings of the Royal Society B: Biological Sciences* ,*278* (1702), 75–81. https://doi.org/10.1098/rspb.2010.1196

Kitahara, M. V., Fukami, H., Benzoni, F., & Huang, D. (2016). The new systematics of Scleractinia: Integrating molecular and morphological evidence. In Stefano Goffredo & Z. Dubinsky (Eds.), *The Cnidaria, Past, Present and Future* (pp. 41–59). Springer International Publishing. https://doi.org/10.1007/978-3-319-31305-4_4

Knowlton, N., Mate, J. L., Guzman, H. M., Rowan, R., & Jara, J. (1997). Direct evidence for reproductive isolation among the three species of the *Montastraea annularis* complex in Central America (Panama and Honduras). *Marine Biology* , *127* (4), 705–711. https://doi.org/10.1007/s002270050061

Ladner, J. T., & Palumbi, S. R. (2012). Extensive sympatry, cryptic diversity and introgression throughout the geographic distribution of two coral species complexes: Geographic patterns of diversity and introgression. *Molecular Ecology* , *21* (9), 2224–2238. https://doi.org/10.1111/j.1365-294X.2012.05528.x

Legendre, P., & Fortin, M.-J. (2010). Comparison of the Mantel test and alternative approaches for detecting complex multivariate relationships in the spatial analysis of genetic data. *Molecular Ecology Resources* , *10* (5), 831–844. https://doi.org/10.1111/j.1755-0998.2010.02866.x

Legendre, P., & Legendre, L. (2012). Canonical analysis. In*Developments in Environmental Modelling* (Vol. 24, pp. 625–710). Elsevier. https://doi.org/10.1016/B978-0-444-53868-0.50011-3

Legendre, P., Oksanen, J., & ter Braak, C. J. F. (2011). Testing the significance of canonical axes in redundancy analysis: Test of canonical axes in RDA. *Methods in Ecology and Evolution* , *2* (3), 269–277. https://doi.org/10.1111/j.2041-210X.2010.00078.x

Lesser, M. P., Slattery, M., & Leichter, J. J. (2009). Ecology of mesophotic coral reefs. *Journal of Experimental Marine Biology and Ecology* , *375* (1–2), 1–8. https://doi.org/10.1016/j.jembe.2009.05.009

Levitan, D. R., Fukami, H., Jara, J., Kline, D., McGovern, T. M., McGhee, K. E., Swanson, C. A., & Knowlton, N. (2004). Mechanisms of reproductive isolation among sympatric broadcast-spawning corals of the*Montastraea annularis* species complex. *Evolution* ,*58* (2), 308–323. https://doi.org/10.1111/j.0014-3820.2004.tb01647.x

Linck, E., & Battey, C. J. (2019). Minor allele frequency thresholds strongly affect population structure inference with genomic data sets.*Molecular Ecology Resources* , *19* (3), 639–647. https://doi.org/10.1111/1755-0998.12995

Liu, H., Stephens, T. G., Gonzalez-Pech, R. A., Beltran, V. H., Lapeyre, B., Bongaerts, P., Cooke, I., Aranda, M., Bourne, D. G., Foret, S., Miller, D. J., van Oppen, M. J. H., Voolstra, C. R., Ragan, M. A., & Chan, C. X. (2018). *Symbiodinium* genomes reveal adaptive evolution of functions related to coral-dinoflagellate symbiosis.*Communications Biology* , *1* (1), 95. https://doi.org/10.1038/s42003-018-0098-3

Luu, K., Bazin, E., & Blum, M. G. B. (2017). pcadapt: An R package to perform genome scans for selection based on principal component analysis. *Molecular Ecology Resources* , *17* (1), 67–77. https://doi.org/10.1111/1755-0998.12592

Mao, Y., Economo, E. P., & Satoh, N. (2018). The roles of introgression and climate change in the rise to dominance of *Acropora* corals.*Current Biology* , *28* (21), 3373-3382.e5. https://doi.org/10.1016/j.cub.2018.08.061

Medina, M., Weil, E., & Szmant, A. M. (1999). Examination of the*Montastraea annularis* species complex (Cnidaria: Scleractinia) using ITS and COI sequences. *Marine Biotechnology* , *1* (1), 89–97. https://doi.org/10.1007/PL00011756

Merot, C., Salazar, C., Merrill, R. M., Jiggins, C. D., & Joron, M. (2017). What shapes the continuum of reproductive isolation? Lessons from *Heliconius* butterflies. *Proceedings of the Royal Society B: Biological Sciences* , *284* (1856), 20170335.

Miller, K. J., & Benzie, J. A. H. (1997). No clear genetic distinction between morphological species within the coral genus *Platygyra* .*Bulletin of Marine Science* , *61* (3), 907–917.

Milne-Edwards, H., & Haime, J. (1851). *A monograph of the British fossil corals. 2 (1851). Corals from the oolitic formations* . Palaeontograph. Soc.

Momigliano, P., Florin, A.-B., & Merila, J. (2021). Biases in demographic modelling affect our understanding of recent divergence.*Molecular Biology and Evolution* , *msab047* . https://doi.org/10.1093/molbev/msab047

Morse, D. E., Hooker, N., Morse, A. N. C., & Jensen, R. A. (1988). Control of larval metamorphosis and recruitment in sympatric agariciid corals. *Journal of Experimental Marine Biology and Ecology* ,*116* (3), 193–217. https://doi.org/10.1016/0022-0981(88)90027-5

Nakajima, Y., Nishikawa, A., Iguchi, A., Nagata, T., Uyeno, D., Sakai, K., & Mitarai, S. (2017). Elucidating the multiple genetic lineages and population genetic structure of the brooding coral *Seriatopora*(Scleractinia: Pocilloporidae) in the Ryukyu Archipelago. *Coral Reefs* , *36* (2), 415–426. https://doi.org/10.1007/s00338-017-1557-x

Nakajima, Y., Nishikawa, A., Iguchi, A., & Sakai, K. (2010). Gene flow and genetic diversity of a broadcast-spawning coral in northern peripheral populations. *PLoS ONE* , *5* (6), e11149. https://doi.org/10.1371/journal.pone.0011149

Nosil, P. (2008). Speciation with gene flow could be common: News and views. *Molecular Ecology* , *17* (9), 2103–2106. https://doi.org/10.1111/j.1365-294X.2008.03715.x

Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P., O'hara, R., Simpson, G., Solymos, P., Stevens, M. H. H., & Wagner, H. (2018). Package 'vegan' community ecology package. *See Https://Cran.r-Project.Org/Web/Packages/Vegan/Index.Html* .

Pante, E., & Simon-Bouhet, B. (2013). marmap: A package for importing, plotting and analyzing bathymetric and topographic data in R. *PLoS ONE* , *8* (9), e73051. https://doi.org/10.1371/journal.pone.0073051

Poelstra, J. W., Richards, E. J., & Martin, C. H. (2018). Speciation in sympatry with ongoing secondary gene flow and a potential olfactory trigger in a radiation of Cameroon cichlids. *Molecular Ecology* ,*27* (21), 4270–4288. https://doi.org/10.1111/mec.14784

Prada, C., & Hellberg, M. E. (2013). Long prereproductive selection and divergence by depth in a Caribbean candelabrum coral. *Proceedings of the National Academy of Sciences* , *110* (10), 3961–3966. https://doi.org/10.1073/pnas.1208931110

Prada, C., & Hellberg, M. E. (2020). Speciation-by-depth on coral reefs: Sympatric divergence with gene flow or cryptic transient isolation? *Journal of Evolutionary Biology* , jeb.13731. https://doi.org/10.1111/jeb.13731

Pritchard, J. K., Stephens, M., & Donnelly, P. (2000). Inference of population structure using multilocus genotype data. *Genetics* ,*155* (2), 945–959.

Quattrini, A. M., Wu, T., Soong, K., Jeng, M.-S., Benayahu, Y., & McFadden, C. S. (2019). A next generation approach to species delimitation reveals the role of hybridization in a cryptic species complex of corals. *BMC Evolutionary Biology* , *19* (1), 116. https://doi.org/10.1186/s12862-019-1427-y

Quigley, K. M., Warner, P. A., Bay, L. K., & Willis, B. L. (2018). Unexpected mixed-mode transmission and moderate genetic regulation of*Symbiodinium* communities in a brooding coral. *Heredity* ,*121* (6), 524–536. https://doi.org/10.1038/s41437-018-0059-0

Rosser, N. L. (2015). Asynchronous spawning in sympatric populations of a hard coral reveals cryptic species and ancient genetic lineages.*Molecular Ecology* , *24* (19), 5006–5019. https://doi.org/10.1111/mec.13372

Roux, C., Fraisse, C., Romiguier, J., Anciaux, Y., Galtier, N., & Bierne, N. (2016). Shedding light on the grey zone of speciation along a continuum of genomic divergence. *PLOS Biology* , *14* (12), e2000234. https://doi.org/10.1371/journal.pbio.2000234

Semmler, R. F., Hoot, W. C., & Reaka, M. L. (2017). Are mesophotic coral ecosystems distinct communities and can they serve as refugia for shallow reefs? *Coral Reefs* , *36* (2), 433–444. https://doi.org/10.1007/s00338-016-1530-0

Serrano, X., Baums, I. B., O'Reilly, K., Smith, T. B., Jones, R. J., Shearer, T. L., Nunes, F. L. D., & Baker, A. C. (2014). Geographic differences in vertical connectivity in the Caribbean coral*Montastraea cavernosa* despite high levels of horizontal connectivity at shallow depths. *Molecular Ecology* , *23* (17), 4226–4240. https://doi.org/10.1111/mec.12861

Serrano, X. M., Baums, I. B., Smith, T. B., Jones, R. J., Shearer, T. L., & Baker, A. C. (2016). Long distance dispersal and vertical gene flow in the Caribbean brooding coral *Porites astreoides* .*Scientific Reports* , *6* (1), 21619. https://doi.org/10.1038/srep21619

Severance, E. G., & Karl, S. A. (2006). Contrasting population genetic structures of sympatric, mass-spawning Caribbean corals. *Marine Biology* , *150* (1), 57–68. https://doi.org/10.1007/s00227-006-0332-2

Shoguchi, E., Tanaka, M., Shinzato, C., Kawashima, T., & Satoh, N. (2013). A genome-wide survey of photoreceptor and circadian genes in the coral, *Acropora digitifera* . *Gene* , *515* (2), 426–431. https://doi.org/10.1016/j.gene.2012.12.038

Stefani, F., Benzoni, F., Pichon, M., Cancelliere, C., & Galli, P. (2008). A multidisciplinary approach to the definition of species boundaries in branching species of the coral genus *Psammocora*(Cnidaria, Scleractinia). *Zoologica Scripta* , *37* (1), 71–91.

Stoddart, J. A. (1984). Genetic differentiation amongst populations of the coral *Pocillopora damicornis* off southwestern Australia.*Coral Reefs* , *3* (3), 149–156. https://doi.org/10.1007/BF00301959

Storey, J. D., Bass, A. J., Dabney, A., & Robinson, D. (2019).*qvalue: Q-value estimation for false discovery rate control.*(2.18.0) [R package]. http://github.com/jdstorey/qvalue

Studivan, M. S., & Voss, J. D. (2018). Population connectivity among shallow and mesophotic *Montastraea cavernosa* corals in the Gulf of Mexico identifies potential for refugia. *Coral Reefs* ,*37* (4), 1183–1196. https://doi.org/10.1007/s00338-018-1733-7

Tay, Y. C., Noreen, A. M. E., Suharsono, Chou, L. M., & Todd, P. A. (2015). Genetic connectivity of the broadcast spawning reef coral*Platygyra sinensis* on impacted reefs, and the description of new microsatellite markers. *Coral Reefs* , *34* (1), 301–311. https://doi.org/10.1007/s00338-014-1206-6

Torda, G., Lundgren, P., Willis, B. L., & van Oppen, M. J. H. (2013). Genetic assignment of recruits reveals short- and long-distance larval dispersal in *Pocillopora damicornis* on the Great Barrier Reef.*Molecular Ecology* , *22* (23), 5821–5834. https://doi.org/10.1111/mec.12539

Underwood, J. N., Smith, L. D., van Oppen, M. J. H., & Gilmour, J. P. (2006). Multiple scales of genetic connectivity in a brooding coral on isolated reefs following catastrophic bleaching: Genetic connectivity in a brooding coral. *Molecular Ecology* , *16* (4), 771–784. https://doi.org/10.1111/j.1365-294X.2006.03187.x

van Oppen, M. J. H., Bongaerts, P., Underwood, J. N., Peplow, L. M., & Cooper, T. F. (2011). The role of deep reefs in shallow reef recovery: An assessment of vertical connectivity in a brooding coral from west and east Australia: Vertical connectivity in a brooding coral.*Molecular Ecology* , *20* (8), 1647–1660. https://doi.org/10.1111/j.1365-294X.2011.05050.x

van Oppen, M. J. H., Lukoschek, V., Berkelmans, R., Peplow, L. M., & Jones, A. M. (2015). A population genetic assessment of coral recovery on highly disturbed reefs of the Keppel Island archipelago in the southern Great Barrier Reef. *PeerJ* , *3* , e1092. https://doi.org/10.7717/peerj.1092

Veron, J. E. N. (1995). *Corals in space and time: The biogeography and evolution of the Scleractinia* . Cornell University Press.

Veron, J. E. N. (2000). *Corals of the World* (Issue C/593.6 V4).

Warner, P. A., van Oppen, M. J. H., & Willis, B. L. (2015). Unexpected cryptic species diversity in the widespread coral *Seriatopora hystrix* masks spatial-genetic patterns of connectivity. *Molecular Ecology* , *24* (12), 2993–3008. https://doi.org/10.1111/mec.13225

Warner, P. A., Willis, B. L., & van Oppen, M. J. H. (2016). Sperm dispersal distances estimated by parentage analysis in a brooding scleractinian coral. *Molecular Ecology* , *25* (6), 1398–1415. https://doi.org/10.1111/mec.13553

Wells, J. W. (1973). New and old scleractinian corals from Jamaica.*Bulletin of Marine Science* , 43.

Willis, B. L., Babcock, R. C., Harrison, P. L., & Wallace, C. C. (1997). Experimental hybridization and breeding incompatibilities within the mating systems of mass spawning reef corals. *Coral Reefs* ,*16* (0), S53–S65. https://doi.org/10.1007/s003380050242

Willis, Bette L., van Oppen, M. J. H., Miller, D. J., Vollmer, S. V., & Ayre, D. J. (2006). The Role of Hybridization in the Evolution of Reef Corals. *Annual Review of Ecology, Evolution, and Systematics* ,*37* (1), 489–517. https://doi.org/10.1146/annurev.ecolsys.37.091305.110136

Zvuloni, A., Mokady, O., Al-Zibdah, M., Bernardi, G., Gaines, S. D., & Abelson, A. (2008). Local scale genetic structure in coral populations: A signature of selection. *Marine Pollution Bulletin ,56* (3), 430–438. https://doi.org/10.1016/j.marpolbul.2007.11.002

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